T.R. New
Editor

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Cover illustration: The cover illustration shows several examples of spectacular weta (Orthoptera) from New Zealand, where their conservation has depended largely on offshore islands as refuges and introduction sites, as discussed in papers in this publication. The insects can be fitted with harmonic radar transponders or micro-transmitters for individual tracking. Shown are a Cook Strait Giant Weta, and two Mercury Island Tusked Weta (photograph courtesy of Danny Thornburrow, Corinne Watts and Ian Stringer).

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EDITORIAL

A special issue on insect conservation and islands

T. R. New

'Island environments' have long had special significance in conservation, because they imply isolation and, often linked with this, vulnerability of the species present. In this special issue, a number of themes relevant to the wellbeing of insects on islands are discussed, and examples from many parts of the world displayed to attest to the continuing relevance and interest of this area of documenting and conserving insects. Conservation integrates with biogeography in elucidating the unusual taxonomic features of many island insects, and the amount of basic information available on island insect faunas throughout the world is extremely patchy.

Following a general introductory essay to help 'set the scene', the first group of papers deals with insects on some of the best-documented islands, those of Europe. Studies on selected insect groups on Mediterranean and Baltic islands illustrate the relatively confident interpretations of faunal affinity and conservation need that can be made in such well-studied cases. Each island and island group has individual peculiarities and a review of the insects of southern Atlantic Ocean islands demonstrates the more restricted and characteristic faunas at those more extreme latitudes. With the major exception of the Hawai'ian archipelago, many of the islands of the Pacific region are much less fully documented, and a series of papers on islands within the Australian region demonstrate both the difficulty of determining which insects may be important conservation targets, and some of the pernicious threats that face them. Understanding the ecology of island insects and the peculiarities of island faunas is demonstrated by several further papers dealing with Indonesia, and with the Indian Ocean islands.

Conservation concerns focusing on individual island species are exemplified by papers on a spectacular Jamaican butterfly and a possibly alien grasshopper in Hawai'i. Practical conservation of insects involves novel and intensive approaches, such as the use of islands as predator-free translocation sites for New Zealand weta, and an innovative conservation breeding exercise on a notable island endemic stick insect. A concluding paper discusses some of the wider conceptual and philosophical issues on recognition and values of island insect conservation.

I am very grateful to all participating authors for their enthusiastic support of this special issue, and to the numerous colleagues who have reviewed manuscripts, some at very short notice but always professionally and perceptively. I hope the outcome will be a worthwhile window on some of the problems faced by island insects and how at least some of those problems are gradually coming to be better understood. Our Publishing Editor at Springer, Zuzana Bernhart, has continued to support this enterprise enthusiastically, and much of the work of preparing the papers for publication has fallen to Pauline Lichtveld, whose exemplary professionalism has ensured the high production standard of this special issue.

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ORIGINAL PAPER

Insect conservation on islands: setting the scene and defining the needs

T. R. New

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Abstract The putative peculiarities of island insects and the factors important in their conservation are noted. Endemism and speciation lessons from island insects have contributed significantly to wider understanding of aspects of insect diversification. The twin complexes of threats to island insects involve (1) internal processes, essentially habitat changes by human activity, and their consequences and (2) externally-imposed effects from alien invasive species, both of these operating in environments that may lack much of the buffer capability present in larger continental areas or in richer communities. Many island insects now persist only in small inaccessible remnant habitats, and protecting these is a key theme in planning insect conservation on islands. The possible effects of climate change may be severe, particularly on 'low islands' such as many coral cays.

Keywords Endemism · Habitat loss · Invasive species · Isolation · Taxonomic radiation

Introduction

Insect faunas on islands have long held a particular fascination for entomologists, biogeographers and evolutionary biologists, in part because of the 'romanticism' of remote isolated environments but also because of the biological and evolutionary consequences of that isolation and, in turn, the vulnerability of many of the environments involved. The taxonomic novelties arising from single island or other narrow range endemism and of explosive radiations of species in isolated environments, the patterns of invasion and faunal development, and development of features such as flightlessness and unusual feeding habits (such as the predatory habit of *Eupithecia* caterpillars in Hawai'i: Montgomery 1983) have been important components of illuminating understanding of the natural world. However, many island environments have also proven to be highly vulnerable to anthropogenic changes and despoliation, invasion by alien (exotic) organisms (many of them transported by people—even by scientists: Whinam et al. 2005, noted the roles of expeditioners as vectors of exotic organisms to the remote subantarctic Macquarie Island), and wider exploitation. Patterns of insect distribution and speciation, and the taxa that have evolved on islands continue to be changed, and species and communities to be lost. In this introduction, some of the major concerns about insect conservation on islands are exemplified and discussed. Much additional information on insect evolution on islands is included in the comprehensive review by Gillespie and Roderick (2002).

Islands

The very term 'island' implies isolation and, over the last half century or so, ecologists have drawn many parallels between true islands in the oceans and fresh water, and habitats and resources distributed patchily in the wider environment. Heterogeneity on all continents includes an enormous mosaic array of different biotopes and resources that are separated spatially and, in functional terms, may be just as isolated as more obviously defined islands. Thus, Beaver (1967) referred to the isolated dead snails sought by specialised carrion-feeding flies as 'island habitats', and

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Carlquist (1965) drew attention to the parallels between isolated mountain tops and true islands. The many similar contexts include rarer isolated host plants of insect herbivores as islands within multi species vegetation stands. Patterns of insect endemism on continents tend to reflect 'island distributions' on this scale of biotope or resource patchiness, and the vast majority of insect species that attract individual conservation attention are restricted in such ways—to some non-uniformly distributed specialised resource or environment. Island biogeography theory (particularly the seminal book by MacArthur and Wilson 1967) has been central to promoting understanding of such systems, at any level of definition. As such, islands may support isolated populations of species or constitute parts of a geographical or functional archipelago subject to cyclic or more irregular colonisations and extinctions by supporting metapopulations of insects transcending more than one island (Hanski and Gilpin 1997). Very similar conservation principles apply to island habitats within continents and to the 'true islands' that are the major focus here, and many of the examples noted do indeed have continental counterparts and parallels. As Gillespie and Roderick (2002, p. 597) put it ' … the perception of an isolated habitat as an island depends on the organism in question'.

This special issue deals predominantly with 'proper islands'—with oceanic or continental land entities and the insects they harbour in their terrestrial and freshwater environments. Continental islands are typically dominated by insects representative of those on nearby larger land masses, often as a 'subset' of those but, depending on the extent of isolation, speciation to varying extents from remnant resident taxa (palaeoendemics) is common. If repeated or continued colonisations are needed to replenish the island fauna, conservation considerations must then extend also to the continental source areas. Continental island insect diversity tends to decrease over time from that of the parental environment, but this depends also on distance from sources. Many islands might, conversely, show increases—such as in response to build up of fauna on source areas due to range changes. Oceanic island insect assemblages reflect the processes emanating from insect arrivals and subsequent events, with (commonly) their high levels of isolation and initial low diversity environments sometimes fostering high levels of endemism (such as in the Galápagos and Hawai'i) to produce diverse arrays of island or archipelago endemics of global evolutionary significance. These categories are broadly paralleled in Gillespie and Roderick's distinction between 'fragment islands' (any habitat that has broken off from larger habitat and become separated by an expanse of unlike matrix) and 'Darwinian islands' (any newly created habitat that appears within an unlike matrix). A very few cases reveal the initial stages of the complex ecological processes of developing insect assemblages, Surtsey (Iceland) being by far the most completely documented case (Fridriksson 1975) and making for informative comparison with the Krakatau archipelago (Indonesia) (Thornton 1996, 2007).

Many islands are far older. The Galápagos, for example, have been colonised over some 3–4 million years, and their vegetational and altitudinal complexity has facilitated complex patterns of colonisation and speciation. Broad patterns of insect colonisation of oceanic islands have been discussed by numerous authors. Thornton (2007) summarised many of the attendant themes, and the difficulties of interpreting colonisation processes and their consequences. In some cases, important island neoendemic radiations have arisen from single colonisation events in the past. One of the better understood endemic radiations on the Hawaiian archipelago, for example, is the dipteran family Drosophilidae. It is estimated to contain around 1000 Hawaiian species, of which about half have been described formally. Molecular (De Salle 2001), behavioural and morphological data (Kaneshiro et al. 2001) collectively help to elucidate their evolutionary relationships, to demonstrate their monophyly and the restricted distributions of most species, and to illustrate the pattern of subsequent colonisations along the island chain from older to younger islands. As Funk and Wagner (2001) noted, this archipelago presents evolutionary biologists with a 'conveyor belt' as islands drift progressively away from the hotspot from which they are formed, with a common picture of the most ancestral species on old islands and most derived species on the younger ones.

However, rates of insect introductions to islands are difficult to assess, not least because of lack of long term documentation and the difficulties of recording their initial presence. The pattern of winged insect introductions and establishment on the remote Gough Island (South Atlantic) was discussed by Gaston et al. (2003). Of 99 species then recorded on the island, 71 are established introductions, and 28 indigenous. The introduced species represent a putative establishment rate of around one in every three or four landings by people, suggesting substantial compatibility of the receiving environment and low 'biotic resistance'. If the number of founders is small, some form of genetic bottleneck may be an important influence on the evolutionary future of the ensuing population (Carson 1992, on Krakatau).

Insects on islands

Much of the concern for conservation of insects (and other biota) on islands flows directly from their isolation and individual peculiarity and irreplaceability. Loss of endemic species per se is clearly important, but the wider implication is that their loss disrupts or destroys the patterns needed to interpret the evolution of complex island faunas.

On oceanic archipelagoes, many insect species are restricted to single islands, so that taxonomic isolation manifests at the twin scales of island and archipelago. Where the age relationships between different islands is understood, as in Hawai'i, with different islands in the chain ranging from about 0.5 million years (Hawai'i) to around 30 million years old (Kure Atoll, some 2500 km to the west) (Howarth and Ramsay 1991), the patterns of transition between taxa may be evident from recent faunas. Thus, drawing from Zimmerman (1948), Gagné (1997) noted that there are probably more than 1000 species of endemic Hemiptera in Hawai'i, with many exhibiting 'a high degree of host or ecosystem specificity', but also (Gagné 1997, p. 6) that 'Many Hawaiian Heteroptera now occur in unstable environments that are threatened with extinction' with many of their host plants now virtually extinct. Using the 50 species of *Nesiomiris* (Miridae) as an example, Gagné noted that only 6 occurred on more than one island, and only two species occurred on three islands. Forty four of the species are also monophagous on either a single host plant species (41) or on species within the same section or genus (3).

Another Hawaiian endemic mirid genus, *Savona*, includes 40 species (Asquith 2001), many of them separated most easily by details of male genitalia. *Savona* has radiated to exploit 17 genera of host plants in 14 families, and also demonstrates progressive colonisation from older to younger islands, accompanied by host-mediated speciation in areas of colonisation. All but one species of *Savona* are single island endemics, many of them restricted to particular high volcanoes on an island. The general pattern of single island endemism is common among many insect groups in Hawai'i.

For radiations of phytophagous insects such as the above, the twin levels of isolation on single islands and on particular host plants (as 'evolutionary islands in time': see Opler 1974, on *Quercus* foliage-mining Lepidoptera in California) help to indicate the reasons for their vulnerability, as reflecting limited place of occurrence and extent of ecological specialisation. As elsewhere, insect conservation involves plant conservation, with widespread loss of indigenous vegetation of major concern on numerous islands and island groups. Many island plants rely on specific insect pollinators, which may have declined from human interference, particularly that related to agriculture, with consequent cascade effects.

Radiations of species, such as those noted above, may mask a degree of higher level faunal imbalance, in that many island insect faunas are depauperate at order level. Thus, only about half the orders of insects are represented in Hawaii, together with around 15% of extant families. The 10,000 or so endemic insect species on the archipelago (references in Howarth and Ramsay1991) represent radiations from a very limited subset of potential colonists. Clearly, the precise spectrum of successful colonists on any island reflects considerable chance but, for example, aeolian insect communities in widely separated parts of the world may exhibit considerable common elements (Thornton 2007), with early assemblages on bare lava in Hawai'i, Indonesia and the Canary Islands broadly rather similar in composition.

Conservation need

Habitat isolation and fragmentation in many terrestrial ecosystems (processes equivalent to the creation of continental islands) have many parallels with indicating conservation needs on true islands, and conservation needs and priorities may be very similar. The greater inhospitability to many insects of ocean over land, however changed that land may be, may act as a further filter to successful colonisation. As emphasised by MacArthur and Wilson (1967), and restated many times since, both the size of an island and its degree of isolation (measured most conventionally as distance from sources for recolonisation) are important considerations in colonisation or replenishment of island biotas, and of the richness that any particular island may sustain. On small habitat patches, as small islands, extinction of a population may be equivalent to extinction of the species (see Levins 1970).

The development of insect conservation includes many examples of the former, small habitat patches, approach applied to continental taxa. However, some putative species extinctions on islands have also caused concern.

One, the Lord Howe Island stick insect (*Dryococelus australis*), was believed to have been exterminated by rats but has recently been re-discovered in small numbers on the remote Balls Pyramid (Priddel et al. 2003; Honan this volume). Another, the St Helena earwig (*Labidura herculeana*, notable as the world's largest earwig), appears to be truly extinct. It was endemic to St Helena, and was collected there by a Belgian expedition in 1965–1967, but more recent searches have not found it. However, as is common with insects, confirming extinction is in itself difficult. Several Hawaiian earwigs, likewise, are known only from old museum specimens. Again, however, many continental extinctions involve such narrow range endemics and many current insect conservation concerns involve such species

Howarth and Ramsay (1991) opened their comprehensive essay on island insect conservation with the statement 'To assess the status of island insects and their habitats is a daunting task'. However, there is wide agreement that substantial numbers of insect extinctions have indeed occurred on oceanic islands, in particular. Awareness that numerous other insects there are threatened (and are declining in range and abundance) is also widespread, and continues to lead to a variety of conservation concerns and measures to evaluate and counter threats and protect critical habitats. Many such measures are necessarily rather broad. Knowledge (or inference) that invasive insect species, such as putative biological control agents, may pose threats to native species, for example, may lead to increased efforts to screen these effectively, and to improved quarantine measures. Quantifying the need for this occurs often against very incomplete faunal knowledge. Again from Howarth and Ramsay (1991): 'In many island groups, biological surveys of the islets need to be completed and conservation plans implemented'. The extent of invasion by exotic species is commonly unclear. They may come to predominate, sometimes very conspicuously, as in the case of some social Hymenoptera, but are more often less easily detected or sought. Thus, Asquith and Miramontes (2001) surveyed the ichneumonid and braconid parasitoid wasps in a native montane forest on Kauai (Hawai'i). Fewer than 10% of the 2017 individuals captured represented native species, with two species introduced as biocontrol agents comprising half the catch.

Causton et al. (2006) reported 463 alien insect species from the Galápagos Islands, some 23% of the total insect fauna, with 186 of these recorded only since a previous inventory study in 1998. They comprise members of 16 orders and 137 families, and Peck (2006) regarded continued effective surveillance for exotic species as a key conservation need on the archipelago. The criteria for predicting invasiveness of insects discussed by Causton et al. (2006) have very high relevance in other isolated environments.

The twin complexes of threat to native insects on islands may be categorised as 'internal' and 'externally imposed'. Internal threat reflects the changes made to island biotas by human needs and development on such small land masses, as a microcosm of the similar changes occurring widely on continental areas. Broadly, these are the alterations to natural habitats involving loss of natural vegetation and water bodies for agricultural conversion, urban development (including catering for the expanding tourist industry through recreation resorts and sporting facilities such as golf courses), and other needs. Externally imposed threats are the impacts of alien invasive species, be they deliberately or accidentally introduced. Factors such as endemism augment the global significance of the taxa threatened, and endorse the importance of island insect assemblages as entities worthy of strenuous conservation, as largely irreplaceable facets of our biotic inheritance. Both categories are multifaceted, in both impact and scale. Their impacts may be even more severe than on larger land masses, on which more effective 'buffering' may be possible, simply because of the greater areas involved. In short, many island biota are supposed commonly to have high vulnerability, with consequent and corresponding high conservation need.

Many ecologists have claimed that island ecosystems are 'fragile' in lacking the ability to counter changes (such as those from introductions of exotic species) that could be buffered adequately in larger areas. Factors contributing to this may include the severity of disturbance, small populations of native species with highly localised distributions, the small number and/or extent of refuges, and the intricate relationships between native species leading to cascade effects (see Gagné 1988). The threats noted above are predominantly of rather recent occurrence, or have intensified in recent times. Clearly, the two categories form a continuum—much internal disturbance is associated with deliberate introduction of alien species (such as for agricultural or forestry crops), and clearing of indigenous vegetation may be a planned precursor to this. Howarth and Ramsay (1991), however, disputed whether island ecosystems are indeed especially 'fragile', as implied above, in that once perturbations are mitigated or removed and appropriate management introduced such systems may recover. Long term monitoring studies on such trajectories are rare, but the viewpoint that the history of human impacts on any island, rather than any inherent fragility, may be a better reflector of the amount of injury caused is clearly admissible. Thus, the Galápagos are one of few notable Pacific Island groups not settled before European discovery, with localised settlement only since the 1930s.

Scale of disturbance is highly relevant, but habitat losses can scarcely be doubted as a major threat to insects on many islands, and the effects of invasive species may also be more severe than on large and more diverse landmasses. Debate will assuredly continue over the relative importance and long term effects of all the processes involved, but conservation can not await the outcome. It must be prosecuted to safeguard and proactively manage 'what is left' against the compelling backdrop of the more obvious and inferred threats to island species and ecosystems.

Islands have important additional roles in insect conservation, as refuges for species and as sites for translocation of species or populations more severely threatened on mainland areas. The pioneering programmes on this theme have been on the flagship weta of New Zealand (Watts et al. this volume). Several species of these spectacular Orthoptera are known only from particular small offshore islands of New Zealand, and some have been lost from the mainland from predation by rodents. The larger species are especially vulnerable because of the difficulty of hiding (Meads 1990). Rodents have been eradicated from some islands, rendering them safe for release of captured or captive-bred weta, or allowing small naturally-occurring populations chance for enhanced survival. The first case of weta translocation was of the Stephens Island giant weta (now, Cook Strait giant weta), *Deinacrida rugosa*, of 43 individuals from Mana Island to Maud Island in 1976 (Meads and Moller 1978). This species is now confined to islands, and occurs on five rodent-free islands and two islets in the Cook Strait area (Sherley 1998).

The premises for this strategy, that alien species (in the above case, rodents) may be easier to eradicate from small islands than from larger continental landmasses and that their re-entry might be more easily prevented, have wider interest and relevance in developing conservation practice at all levels—from single species through site conservation to ecosystem conservation for invertebrates. However, gaining the ability to base such programmes on even reasonably comprehensive biological understanding remains a formidable task. Only for Hawaii, amongst the major oceanic island groups, has concerted effort for conservation been progressed substantially. This has been done largely from the background discussed by authors in Stone and Scott (1985), with both internal and external threats (these mainly by invasive species) posing serious concerns for native insects.

Internal threats: habitat loss and change

Gagné (1988) remarked that more than 75% of the land area of Hawai'i had been converted to human use, with loss not only of native vegetation and ecosystems but also of traditional (cultural) low intensity agricultural practices.

Similar comments could be made for numerous other islands which now support resident human populations, with much of that change occurring rapidly within the twentieth century. It is thus largely inevitable that highly specialised endemic organisms will suffer loss of habitat or have their critical resources diminished and/or degraded, and be 'forced' progressively into smaller and more isolated habitat remnants less accessible to human influences, and that many may be lost. Thus, whereas the status of Hawai'i's invertebrates cannot be assessed fully, numerous species are candidates for federal listing as Endangered Species, and their plight may be reflected by that of a better-documented animal group, birds. More than half of Hawai'i's original bird species are extinct, and most of the remainder endangered or threatened in some way, as another manifestation of the archipelago's extinction crisis.

For many islands, any form of natural habitat protection, such as by national parks or other reserves is relatively recent and necessarily focused on areas that are no longer pristine. Many such reserve areas are small in relation to expanses of highly altered land, and it is rare for the majority of an island area to be included in a managed national park, as on the Galápagos. Intrusions may be extremely difficult to monitor and control, not least because 'ecotourism' is often an important component of conservation, as on the Galapagos, with attendant problems of visitor pressures and risks of further exotic species being introduced. Hawaii Volcanoes National Park (founded in 1916, and the largest protected area in the archipelago), for example, supports numerous invasive insect species including the ants *Pheidole megacephala*, *Anoplolepis longipes* and *Linepithima humile*, and wasps such as *Vespula pennsylvanica*. Control of the last was noted by Stone and Pratt (2002) as a need to conserve 'certain unique and rare native invertebrates' in the park.

Clearing of indigenous vegetation on islands has been the most widespread and severe initial perturbation and threat to numerous insects, but is commonly augmented by other changed island management, such as changed fire regimes for purposes far removed from conservation. The variety of land tenures and ownerships render any concerted or larger scale management difficult to achieve, and land changes (as well as those to waterbodies—such as impoundment, drainage, diversion, pollution, and others) may be accompanied by some form of incentive motivated by economic gain. Such measures are not in any way confined to islands but, again reflecting isolation, may have particularly devastating effects. The spectrum of habitat changes and related threats to insects on islands is limited only by human ingenuity and need, and most island biologists have their personal fund of 'horror stories' involving such internal changes and their consequences, sometimes involving influences of overseas trade interests. Isolation and inaccessibility have been the key influences, often fortuitous, in conserving at least partially representative natural habitats of many native insects on many islands. Strenuous efforts to conserve as many of these remnants as possible, and to protect them from further despoliation, are a central theme in island insect conservation.

Invasive species—a key theme in island insect conservation

Invasive species on islands fall into two major categories, which intergrade: species introduced long ago (for example, by Polynesians to many Pacific region islands) and species introduced in recent decades and up to the present. Effects of the former can largely be only inferred by comparison with areas from which the key species are absent, when such places exist. With adequate monitoring—which, almost invariably, is not present—the effects of some recent introductions can be evaluated in greater detail. Much inference may, of course, persist. The effects of classical biological control agents (mostly predatory insects and parasitoids) on islands are often controversial, but with serious and continuing concerns over their possible effects on native non-target species. These effects are often difficult to evaluate, rather then infer: for example, the purported extinction of the moth *Levuana iridescens* on Fiji by the introduced tachinid *Bessa remota* is now doubted (Sands 1997, Kuris 2003). However, there is widespread belief that such polyphagous agents have potential to be harmful: exotic parasitoid wasps introduced to Hawai'i may have contributed to the declines of endemic Lepidoptera, for example (Howarth 1991, 2001, for discussion). At the least, such suggestions have led to improved protocols for screening potential classical biological control agents, and broadened awareness of the possible wider consequences of their introduction and use in island environments. Some studies have suggested that some introduced insects, such as the Argentine ant (*Linepithima humile*) in Hawai'i, may have greater adverse effect on specialised native species than on other introduced species (Liebherr and Kruschelnycky 2007). The adventive carabid *Trechus obtusus* (originally from Europe) was associated with decline of cooccurring native *Mecyclothorax* beetles in forests on Maui, but abundance of *Trechus* was not affected significantly by presence of the ants. In contrast, *Linepithima* may be linked with substantially reduced abundance of some of the brachypterous and locally endemic species of *Mecyclothorax*. However, invasive social Hymenoptera are amongst the species causing greatest and most widespread concerns (see references in Ward et al. 2006, for summary), and can be extremely difficult to eradicate. As O'Dowd et al. (2003) demonstrated for the crazy ant (*Anoplolepis gracilipes*) on Christmas Island, their persistence may sometimes result in widespread 'invasional meltdown' (see commentary on this term by Simberloff 2006). Local eradication or, at least, local suppression may be feasible. More commonly, eradication may be attempted or succeed only in local more accessible areas of an island (such as for species impinging on human health issues or affecting crops), and remote highland or forested areas are not given high priority for such attention.

The conservation need

The threats to island insects noted above are by no means confined to island environments, of course, and some are amongst the paramount concerns for insect conservation globally. They are emphasised here as 'tangible' in island contexts, commonly demonstrably associated with losses of endemic species and also as possibly amenable to management. Threat abatement or management may be particularly practicable in the very small areas of many islands, and with the realisation that their effects may be both greater and more conspicuous there than on larger continental areas. Studies on such threats on islands have done much to illuminate the nature of their effects and the ways in which they increase insect vulnerability. Some other influences are much more difficult to appraise.

Most of the islands mentioned above are 'high islands': mountainous volcanic lands projecting several hundred metres or more above the sea and which allow for considerable diversification and heterogeneity in biotopes and resources, facilitating insect diversity (Peck et al. 1999). In contrast, many islands in the western Pacific and elsewhere are very different in appearance. They are 'low islands' founded on coral cays, some only a few metres high at their highest point. Thus, One Tree Island (a research station operated by the University of Sydney on Australia's Great Barrier Reef, and some 98 km from the coast) is a coral rubble cay only some four hectares in extent. It supports at least 396 species of invertebrates (89% of them insects), with Hymenoptera and Diptera especially rich in species, and allowing Heatwole (1981) to comment 'The invertebrate fauna of One Tree is very rich'. In general, high islands are likely to support more insects than low islands in similar climatic zones—essentially they provide a 'three-dimensional environment' rather than a more limited 'two-dimensional' one. Varied topography may be far more important than area alone in fostering insect diversity. The division into high and low islands is itself overly simple, as each is a very broad category. In the Pacific, for example, Thomas (1965) delimited four broad categories of islands as (1) low islands of carbonate rock, usually small and connected by reef to form atolls, and widespread in the tropical Pacific; (2) islands of elevated reef rock, slightly larger than the above and exemplified by Christmas Island (Indian Ocean), parts of Fiji, Nauru and others; (3) volcanic islands; and (4) islands containing ancient continental rocks, these including most of the larger Pacific islands, and including Indonesia and the Philippines.

Low islands may be very vulnerable to sea level rises anticipated to occur within the next few decades as climate changes. Projections imply that some islands will be submerged completely, and human transmigration to other, less vulnerable, islands in the region may impose additional pressures on those.

On many islands, the most suitable balance between exploitation and protection is a very delicate one, but the possible effects of climate change on island biotas are largely impracticable for insect conservation biologists to address. However, addressing even the most tangible threats is often problematical. Many of the islands of greatest interest for insect conservation are remote, and many have few (if any) concerned resident entomologists. Knowledge of the insect fauna of many such islands has been acquired serendipitously, or through the zeal of individual workers, and is sometimes founded predominantly in the results of scientific expeditions decades or more ago. There are, of course, exceptions, in which particular insect orders or wider faunas have been surveyed in considerable detail to provide excellent baseline inventories of the taxa present, with these then available as a foundation for future monitoring. For Lepidoptera, for example, Gerlach and Matyot (2006) enumerated 552 species, 275 of them endemic, from the Seychelles. Earlier, Holloway (1977) surveyed the Lepidoptera of Norfolk Island, Australia, and discussed their distribution patterns and ecology. Insects of some relatively low richness Subantarctic islands have also been surveyed in detail (Greenslade 2006, on Macquarie Island), and it may be feasible to select a series of such documented islands in different parts of the world, from which to found a long-term monitoring program for assessing some effects of climate change.

Remoteness has not necessarily conferred security. Zimmerman (1965) responded to a question asking how many islands in the Pacific are still 'sufficiently virgin to enable a study of the primitive conditions on islands' by saying (abbreviated here) 'very few, almost no such islands as a matter of fact'. He noted also that 'the faunas are largely lost forever', with the effects of vegetation stripping by goats and repeated burning cited specifically as contributors to this (Zimmerman 1965). Most such changes have not been monitored whilst they occurred, and so have passed undocumented. Likewise, exploitation such as international razing of forests on islands for the pulpwood industry (a process noted by Howarth and Ramsay 1991, for New Zealand as 'difficult to prevent as much of the forest is privately owned') has been extensive in some parts of the western Pacific.

Such scenarios contrast markedly with those on many continental islands in more densely attended parts of the world, where conservation needs are more straightforward to define, through confident and informed comparison with nearby continental areas revealing the existence of taxonomic and ecological novelties, and the threats to them. Thus, the insects of many islands off the United Kingdom and throughout the Mediterranean region are, in broad terms, well documented and within major spheres of conservation interest and attention. Their faunas commonly depend on continued colonisation from mainland source populations as a counter to demographic stochasticity leading to extinctions. Thus, the incidence of the grayling butterfly (*Hipparchia semele*) on British and Irish islands reflects island area, extent of isolation and size of nearest source populations (Dennis et al. 1998). The migration capacity of the individual species is also important (Dennis 2000). However, islands may also be significant refuges for insects more threatened on mainland areas. As one example, the compilation by Thomas (2007) includes a note on the recovery plan for butterflies and burnet moths of the Argyll Islands, Scotland, where these islands are a recognised stronghold for several notable Lepidoptera in the United Kingdom.

This level of detail, and capability for practical attention, is not available for islands over much of the rest of the world, notwithstanding the great intrinsic interest and importance of island insect faunas. However, that interest has clear potential to foster wider interest in the conservation of island insects and the environments in which they can thrive, as important elements of our natural world.

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ORIGINAL PAPER

Butterflies of European islands: the implications of the geography and ecology of rarity and endemicity for conservation

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Abstract Depending on their faunal content islands can function as important 'vehicles' for conservation. In this study, we examine data on 440 butterfly species over 564 European islands in 10 island groups. To determine the status of the butterfly fauna, we have adopted two approaches, island-focused and species-focused, examined using principal components analysis and regression modelling. In the former, we relate species richness, rarity and endemicity to island geography (area, elevation, isolation and location in latitude and longitude); in the latter, species occurrence on islands is examined in relation to distribution, range, range boundaries, and altitudinal limits on the continent as well as species' ecology (number of"/> host plants) and morphology (wing expanse). Species on islands are also assessed for their status on the continental mainland, their distributional dynamics (extinctions, distribution changes) and conservation status (Red Data Book, European Habitat Directive, Species of European Conservation Concern and Bern Convention listing. Unexpectedly, we find that a large fraction of the European butterfly species is found on the islands (63.4%; 59% on small islands) comprising some 6.2% of the land area of Europe. Although species occurring on the islands tend, on the whole, to have lower conservation status and are not declining over Europe, 45 species are endemics restricted to the islands. Species richness shows only a weak locational pattern and is related as expected to isolation from the continental source and island area; but, both rarity and endemicity have distinctive geographical bias to southern Europe, on islands now under increasing pressure from climate change and increasingly intensive human exploitation. The vulnerability of species on

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islands is emphasised in the relationship of island occurrence (% occurrence and presence/absence of species on any island) with continental distributions. A large proportion of the variation (84%) is accounted by continental distribution, the southern range limit and lower altitudinal limit. Most species (69%) occur on very few islands (<5%). In view of ongoing species dynamics on islands, migrations and extinctions of species, island repositories of species depend in large part on conservation of butterflies at continental sources. The unique faunas and rare species on islands also depend on appropriate concern being given to the island faunas. Conservation of European islands is thus a two-way process, sustaining sources and conserving island refuges. Residuals from the regressions (islands with more or fewer species, rare and endemic species; species occurring more or less frequently than expected on islands) provide warning signals of regions and islands deserving immediate attention.

Keywords Endemicity · Europe · Lepidoptera · Rarity · Refuges · Species richness

Introduction

Island faunas and floras have always been of great concern to conservation. Islands provide two well established roles; first, as refuges for widespread taxa found on adjacent land masses; second, as evolutionary centres, thus living repositories of unique faunal elements, endemic species and higher taxa (Whittaker 1998). Just what each island contributes to this mix of ubiquity and endemicity is well known to depend on island geography—island area, isolation and variety in biotopes (MacArthur and Wilson 1967; Williamson 1981)—and geological history (New 2007a).

Islands may provide refuges for plants and animals from human pressures for the same reasons that distinct taxa accumulate on them. Although untested, it might be thought that economic development of islands would relate to their area and isolation, in turn measurements of potential and access, with more intensive development occurring on larger islands and those close to shores of political stakeholders. But, there are exceptions; for example, where small oceanic islands occupy strategic positions on a global stage and/or are intensively exploited (e.g. Frenot et al. 2001; Chown et al. 2005; Reaser et al. 2007). The European islands vary enormously in size from a few hectares (e.g. Hilbre, Cheshire, UK) to large land masses and unitary states in their own right (e.g. British mainland, Iceland). They also vary widely for degree of isolation, from islands connected temporarily to continental shores at low tide or by insubstantial sandy tombolos (e.g. M. Argentario off Tuscany) to those that have arisen from volcanic activity associated with hot spots and ocean ridges and never connected to the European or African continents (e.g. Azores, Iceland, Canary islands, Aeolian Archipelago).

Increasing numbers of studies on the island biogeography of European plants and animals have been carried out in recent years. For the most part, these have focused on specific island groups or archipelagos (e.g. Aegean, Greuter 1971; Fattorini 2002; Hausdorf and Hennig 2005). As far as we are aware none have undertaken a large scale overview of all European island groups. Two reasons for this are forthcoming. First, data are still accumulating on plants and animals of islands; mapping whole faunas is a relatively recent and labour intensive venture and requires enough well informed recorders to complete the task successfully as in the case of British birds (Gibbons 1993), plants (Preston et al. 2002) and butterflies (Asher et al. 2001). Second, there is the issue of access to many islands, a problem exacerbated by the sheer number of islands, over 80,000 in the Finnish territory of the Baltic Sea alone (Stanners and Bourdeau 1995; see Kotze 2008). Access to islands is nevertheless expanding at an increasing rate with growing wealth of Europeans and their penchant for travel. This has two linked consequences: increasing collection of data from islands is accompanied by their increasing exploitation.

In this article, we attempt a broad examination of the conservation potential for butterflies of islands around the European coastline. In doing so, we adopt two approaches, referred to as island-focused and species-focused (Dennis and Shreeve 1997; Lomolino 2000; Dapporto and Dennis 2008a). In an island-focused approach, emphasis is on island physical geography (i.e. latitude, longitude, area, altitudinal range, isolation) and its impact on island faunal characteristics, such as species richness, rarity and endemicity. In a species-focused approach, attention is on individual species—their presence or absence on islands, and their relative abundance on islands, in relation to their conservation status.

In the island-focused approach we examine the relative influences of island geographical position (longitude, latitude, archipelago or group membership, and isolation) and island dimensions (area, elevation) on species richness, rarity and endemicity. There are clear geographical patterns to these butterfly faunal characteristics over Europe (Dennis et al. 1991, 1995, 1998c). From this work, it is expected that endemicity will increase on islands towards lower latitudes and with increasing isolation. On the other hand, species' richness should correspond more closely to increased island dimensions and decreasing isolation. Previous work has not considered the pattern of European endemics or rarity across the islands, but it is expected that as southern regions of Europe formed glacial refuges both will increase in southern island groups.

A species-focused approach has two broad objectives. A first question is how important are European islands for individual species generally? Fundamentally, it is expected that the incidence of species on islands will closely correlate with their abundance (distribution records) and geographical ranges on the European continent. Which species are significantly more and less abundant on islands than expected from this relationship? Does morphology (wing expanse), habitat limitations (montane biotopes) or resource abundance (host plants) explain the occurrence of species failing to fit the broad geographical pattern? Second, to what extent do islands provide refuges for species with high conservation status? Islands are clearly of great significance for autochthonous endemics; but, are they also important for continent-wide endemics, species listed as of high status, and species whose distributions are declining? Is there a taxonomic pattern underlying associations of island occurrence with these species-specific variables?

Methods

Island groups, species and data sources

Records have been collated for 440 of 476 butterfly species on 564 European islands (Appendix 1). The longitudinal geographical limits for the study are 35° W to 35° E, though islands off Russia in the Barents Sea and White Sea (Bolotov 2006; Bolotov and Shutova 2006) are excluded from this survey; 36 European butterflies in the European Butterfly Atlas (Kudrna 2002) that fail to occur further west than 35° E are also excluded. The islands have been divided up into 10 basic groups (Aegean, Adriatic, West Mediterranean, Atlantic ocean, West Atlantic seaboard, British, Irish, Kattegat, Baltic and Norwegian/North Atlantic) particularly for purposes of standardising the number of island records for archipelagos and island groups that have been 'sampled' to different extents, but also to ascertain distinctions of island faunas for geographical variables. The sources for island records (Appendix 1) are derived from collations in previous studies of island biogeography (Owen and Smith 1993a; Dennis and Shreeve 1996, 1997; Dennis et al. 2000; Dapporto and Dennis 2008a) and numbers continue to be added with occasional visits by entomologists (e.g. Withrington and Verovnik 2008), but increasingly records are accumulating with dedicated survey (e.g. Asher et al. 2001; Saarinen et al. 2003; Fox et al. 2006), appearing in atlases (e.g. Stoltze 1996; Kolligs 2003) or being stored on web sites (http://www.toyen.uio.no/norlep). The species (Appendix 2) comprise those listed in the Distribution Atlas of European Butterflies (Kudrna 2002) with a number of corrections envisaged as of August 31, 2007 in preparation for the second edition of this atlas.

For the most part decisions made on species' status (i.e. species or subspecies) are unlikely to affect the findings for island biogeography. However, the status of island endemics is subject to constant revision (Brunton and Hurst 1998) or confirmation (Dapporto 2008); as species endemic to islands are few in number (Appendix 2; n = 45) changes in their classification will influence the proportion of endemics recorded for islands but are unlikely to change significantly the outcome of island-focused analyses on endemicity. Access to the full species/island datafile is obtained though the corresponding author.

Variables

The variables and their codes used in this study are listed in Table 1 with attributes for species followed by those for islands. In Table 1 variables for species are listed in order of geography, ecology, morphology and conservation status. A number of variables describe their occurrence on islands: their presence on any island (bIS), whether they are island endemics (Ei) and their abundance on islands (pISO). Further variables describe their geography on the European continent, whether European endemics (Ee), their distribution on the continent of Europe (cDI) and range bounds (Wlim, Elim, Nlim, Slim) and range extent (LATr, LONGr, BS, COUNTRIES) within continental Europe. A single variable describes their morphology (size in wing length, WE) and another variable their ecological bounds (number of larval host plants used, HP). Biotope limitations associated with altitude are described by upper and lower altitudinal limits (ALTuc, ALTlc respectively). Two variables describe species changing distribution status (EURTREND, CONEXT) and four variables describe species conservation status (Red Data Book listing RDB, European habitat Directive listing FHH, Species of European Conservation Concern ECC, and species listed under the Bern Convention BC).

Variables for islands break down into two groups describing island faunas and island geography. Seven faunal variables are described, one a measure of species richness (S), and two measures for rarity (Rd and Rc) and four for endemicity (nEi, pEi, nEe and pEe). Both measures of rarity are calculated as the inverse of the mean proportions for individual species distributions over Europe, with Rd based on DI (see below) and Rc on the proportion of countries occupied of 44 listed (see Dennis et al. 2000). Endemicity is simply the number and proportion of species on islands that are island endemics (Ei, pEi) and European endemics (Ee, pEe) respectively.

Table 1 Variables used in present study

Variable	Description
	Species variables
FAMILY	Family of a butterfly species with Satyridae treated as a distinct family
Ee	European endemic species (taken from BS, code 4; Kudrna 2002)
Ei	Island endemic species (including species likely to have originated on islands)
pcDI (Arcsine)	Corrected Distribution Index for a species (Kudrna 2002) following removal of island records from BRF; records as proportion of maximum possible (see text for explanation)
BRF	Basic Recording Fields occupied in European atlas (Kudrna 2002)
pISO (Arcsine)	Proportional occurrence of a species on European islands standardised over 10 island groups (see text for explanation)
bIS	Incidence (presence or absence) of a species on any island over Europe
COUNTRIES	Number of countries occupied by a species (Van Swaay and Warren 1999)
BS	Biogeographical status (Kudrna 2002); codes: 1. vagrants to Europe or headquarters outside Europe, 2. European-alicontinental (headquarters inside and outside Europe), 3. quasi European (concentrated in Europe, recorded also outside Europe), 4. European endemic species
HP (Ln)	Number of host plants for a species (Dapporto and Dennis 2008a)
WE (Ln)	Wing expanse (Higgins and Riley 1983; Lafranchis 2004)
CONEXT	Number of countries in which a butterfly species has become extinct (Van Swaay and Warren 1999)
EURTREND	Distribution trend in Europe over the past 25 years (Van Swaay and Warren 1999); coded: −3 decreasing 50–80%, −2 decreasing 20–50%, −1 decreasing 15–20%; 0 stable, +1 increasing 125–200%
RDB	Red Data Book Status (Van Swaay and Warren 1999); codes: L low risk, V vulnerable, E endangered, C critically endangered; coded 1 to 4 respectively with non registered butterfly species coded 0
ECC	Species of European Conservation Concern (Kudrna 2002). 1. species not classified; 2. [4a] global distribution restricted to Europe, but not threatened, and [4b] global distribution concentrated in Europe but not threatened; 3. [3] species threatened in Europe but with headquarters within and outside Europe; 4. [1] species restricted to Europe and globally threatened, and [2] species concentrated and threatened in Europe. [original coding]
FFH	Species protected by the EU Habitat Directive 92/43; codes: 2 species listed in Annex II, 4 species listed in Annex IV (Kudrna 2002); both coded 1, species not listed coded 0
BC	Species listed in Appendix II (strictly protected species) of Bern Convention; codes: + listed, * proposed. (Kudrna 2002). Both coded 1 with unlisted species coded 0
Wlim (Sqrt)	European continental western limit for a species (Kudrna 2002)
Elim (Square)	European continental eastern limit for a species (Kudrna 2002)
Nlim (Ln)	European continental northern limit for a species (Kudrna 2002)
Slim (Ln)	European continental southern limit for a species (Kudrna 2002)
LATr (Sqrt)	European continental latitudinal range for a species
LONGr (Ln)	European continental longitudinal range for a species
ALTuc	Common upper limit altitudinal distribution for a species (Higgins and Riley 1983; Lafranchis 2004)
ALTlc (Sqrt)	Common lower limit altitudinal distribution for a species (Higgins and Riley 1983; Lafranchis 2004)
	Island variables
S (Ln)	Species richness of islands (number of species including migrants)
Rd (Arcsine)	Rarity index for island based on cDI for species
Rc (Arcsine)	Rarity index for islands based on COUNTRIES for species
pEi (Arcsine)	Proportion of species that are island endemics
pEe (Arcsine)	Proportion of species that are European endemics
nEi	Number of island endemics on islands
nEe	Number of European endemics on islands
Lt (Ln)	Latitude of island (decimal score)
Lg (Ln)	Longitude of island (+minimum value; decimal score)
A (Log10)	Area of island (square km)
ELEV (Log10)	Maximum elevation above sea level (m)
Dm (Ln)	Isolation from nearest continental shore of Europe, Asia (Turkey) or Africa (km)

Table 1 continued

Variable	Description
Di (Log10)	Isolation from nearest larger source (landmass with more species or a larger area) (km)
IG	Island group; 10 island groups (see text for explanation)
REGION	Northern islands (coded 1) and southern islands (Mediterranean islands and ocean groups in Azores and Macaronesia; coded 2), the boundary at approximately 45° N

Sources and scores for most variables are evident in Table 1 but some need further explanation. The Distribution Index (DI) of Kudrna (2002) has been modified for island records to give a corrected Distribution Index (cDI); for this, island records were subtracted from the number of occupied basic recording Fields (BRF) tabulated in Kudrna (2002). The proportional occurrence (abundance) of species on islands (pISO) is not the proportional occurrence of a species on all islands but the mean proportion of occurrence for the 10 groups of islands; this correction has been made in view of the varying numbers of islands off different parts of Europe and the inevitable, different degrees of recording intensity on islands. Distance to the nearest larger source is typically taken to the nearest larger island, which usually has more species, or is the same as the continental source (Dm). But in some situations a nearby smaller island (e.g. Corsica for Sardinia) has more species recorded on it. In a few cases it has been necessary to take the distance to the mainland source as being the African coastline (i.e. Canary islands; Lampedusa) or Asian coastline (i.e. Dodecanese islands, Cyprus). An anomaly is that Turkey is included as part of Europe by some authorities (Van Swaay and Warren 1999) but not by others (Kudrna 2002). Distribution cover in Europe (BRF, DI), and the geographical range variables, do not include distributions within Turkey or North Africa. Analyses have been modified where appropriate (and described) to cater for this omission, but not all anomalies related to source of origin can be easily accounted, and in some cases (e.g. *Vanessa vulcania* may have its origin in a North American relative of *Vanessa indica*; Vane-Wright and Hughes 2007) founders may not have arrived from nearest-neighbouring continents.

Analyses

Different collections of islands were used for the island-focused and species-focused analyses. The islands (Fig. 1) selected for island-focused study were limited to those including at least four of five well-known, migrant species (*Pieris brassicae, P. rapae, Colias crocea, Vanessa atalanta* and *Vanessa cardui*). These species are highly visible, they occur throughout Europe during the summer season and records for them can be used to establish a minimal surveying standard for islands inasmuch as they are expected to be recorded with repeated visits to islands (see Dennis and Shreeve 1996, 1997; Dennis et al. 2000). An exception has been made for Scandinavian and North Atlantic islands where islands (e.g. Finnish Åland islands) having three of the migrants were included if they were known to have been surveyed ≥15 occasions. For the species-focused analyses, data from all islands have been included. In these analyses our interest is in the relative occurrence of species on islands compared with their abundance on the European continent. Inevitably, the number of records for species on islands will be influenced by their individual apparency to observers (Dennis et al. 2006); nevertheless, each species should be equally apparent to observers on islands and on mainland Europe. Therefore, there is no *prima facie* reason based on individual apparency or abundance for excluding records for any species from islands. We recognise that records for some species may however be affected by species' flight times and seasonal timing of visits by recorders to islands.

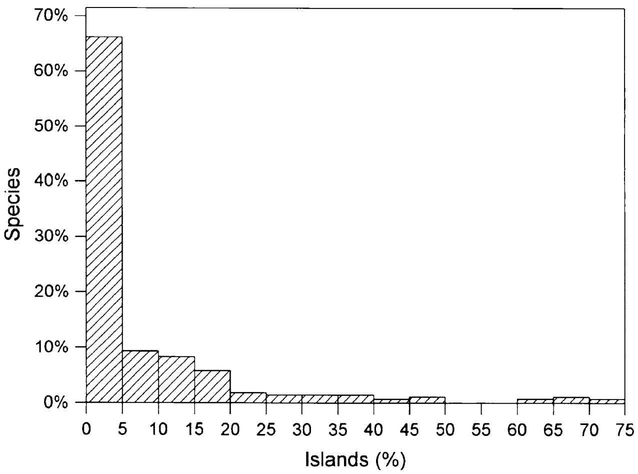

Fig. 1 The distribution of island occurrence ($N = 540$ islands) for European butterfly species ($N = 440$ species)

Island-focused analysis

The objective has been to identify key predictors for species richness (S), rarity (Rd and Rc) and endemicity (nEi, nEe, pEi and pEe) on 300 islands that are considered to have been adequately sampled. For this work, as only three islands (Tjome, Tromø, Faeroe islands) belong to the southernmost Norwegian/North Atlantic group, they have been allocated to the West Atlantic Seaboard group. Theoretical and empirical findings in island biogeography raise a number of well-known expectations (e.g. a close link between species richness and island area and isolation from continental sources). Interest is directed towards assessing the relative strength of geographical variables on faunal characteristics of islands. Key expectations are (i) that latitude influences endemicity and rarity more than species richness, and (ii) that distinct faunal clusters occur for northern islands and southern islands related to island geography.

An initial exploration of relationships in island-faunal characteristics has been sought by applying principal components analysis. In this, faunal characteristics have been entered as supplementary variables against island geography variables. The relative contribution of geographical variables in accounting for species' richness, rarity and endemicity have been examined using regression techniques (multiple stepwise regression analysis for species' richness and rarity; Poisson log-link regression for number of endemics; general regression modelling for the proportion of endemics on islands). As distributional relationships were found to be more complex, general regression modelling was used to seek out both polynomial relationships and interactions among variables for the proportion of endemics on islands. In plots observed from expected values for different faunal variables, different island groups have been distinguished including association with different regions (north and south) of Europe. Different outcomes are expected for northern and southern islands because of Pleistocene events (climatic and glaciation tabula rasa; Dennis et al. 1991), but also because of climatic differences which affect migration to islands (Dennis and Bardell 1996). Sunshine, warmth and calm conditions dominate southern Europe for longer periods in the summer months when adult butterflies are flying.

Species-focused analysis

Two objectives were established. (i) The first was to identify factors influencing the proportional abundance and occurrence (presence/absence) of species on islands. For island occurrence (bIS), species were divided into two groups, those present on any island (coded 1) and those absent from all islands (0); occurrence was examined against geographical predictors using stepwise logit regression (backwards removal). Abundance of species on islands (pISO) was explored using stepwise multiple regression and GRM (response regression catering for polynomial relationships and interactions among variables); both approaches used stepwise backwards removal. Because the relationship between proportional occurrence of species on islands (pISO) and (pcDI) is non linear even after transformation of variables, proportional occurrence was subjected to a rank transformation and entered into multiple stepwise regression against predictors. Significant variables from this analysis were then explored for polynomial influences and interactions among variables in a GRM (response regression) with proportional occurrence as a dependent variable. For all analyses, species occurring on islands but absent from continental Europe (occurring in Asia (Turkey) and Africa) were excluded from analyses. (ii) A second objective has been to test the association of island-species associations with measures of conservation status. A non parametric test of association was applied to ranked variables (Gamma).

Analyses were conducted in SPSS 9.05 (SPSS Inc.) and Statistica 7.0 (Statsoft Inc.) based on null hypotheses of no differences. Significance was taken as $P < 0.05$ unless multiple comparisons were used, when a Bonferroni correction was applied. Transformations used to scale variables and to normalise distributions for variables are noted in Table 1.

Results

The current data on 440 European butterfly species reveal that 279 of them (63.4% of whole) occur on 564 islands which comprise approximately 6.2% of European land area (629,263 km^2 of 10.2m km^2). Much of the total area for islands is taken up by eight very large islands (British mainland, Ireland, Iceland, Corsica, Sardinia, Sicily, Crete and Cyprus; 495,400 km^2) occupying 78.7% of whole island area; even so 259 (58.8%) species are found on the remaining smaller islands. Most species occupy proportionately very few islands (69% on <5% of islands; 67% corrected for island groups), though a number, mainly migrants, are found on over 50% of islands (Fig.1).

Island-focused analysis

In a principal components analysis only the first two eigenvalues >1; together they account for nearly 70% of the variance. Axis 1 (Table 2a, Fig. 2) reveals polarisation of latitude (Lt), with positive loadings, from elevation (ELEV), area (A) and isolation from nearest source (Di), all with negative loadings. Axis 2 distinguishes longitude (Lg, negative loadings) from isolation from continental sources (Dm, positive loadings). Faunal variables have been entered as supplementary to analysis. Rarity (both Rc and Rd) and island endemicity (pEi and nEi) load highly on axis 1, all with negative scores. Species richness (S) loads high

Table 2 Principal components analysis (PCA) loadings, communalities and Pearson correlations for island geography and faunal characteristics

Variable	Axis 1	Axis 2	Communality (2 axes)
(a) Loadings and communalities from PCA			
Latitude (Lt)	0.75	0.22	0.62
Longitude (Lg)	0.30	−0.84	0.80
Isolation (Dm)	−0.30	0.86	0.83
Isolation (Di)	−0.71	0.01	0.51
Elevation (ELEV)	−0.89	−0.10	0.80
Area (A)	−0.71	−0.37	0.64
Species richness (S)	0.07	−0.73	0.54
Rarity (Rc)	−0.70	−0.32	0.59
Rarity (Rd)	−0.68	−0.35	0.59
Endemicity (pEi)	−0.51	0.13	0.28
Endemicity (pEe)	−0.25	0.25	0.12
Endemicity (nEi)	−0.50	0.02	0.25
Endemicity (nEe)	−0.23	−0.09	0.06

	Lt	Lg	Dm	Di	ELEV	A
(b) Pearson correlations among island geography variables						
Latitude (Lt)	1.00	0.05	−0.01	−0.44	−0.66	−0.37
Longitude (Lg)	0.05	1.00	−0.65	−0.16	−0.16	0.02
Isolation (Dm)	−0.01	−0.65	1.00	0.19	0.22	−0.09
Isolation (DI)	−0.44	−0.16	0.19	1.00	0.44	0.40
Elevation (ELEV)	−0.66	−0.16	0.22	0.44	1.00	0.66
Area (A)	−0.37	0.02	−0.09	0.40	0.66	1.00

Faunal variables entered as supplementary to analysis, $N = 300$ islands

Pearson $r \geq \pm 0.16$, $P < 0.05$ (Bonferroni $r \geq \pm 0.18$)

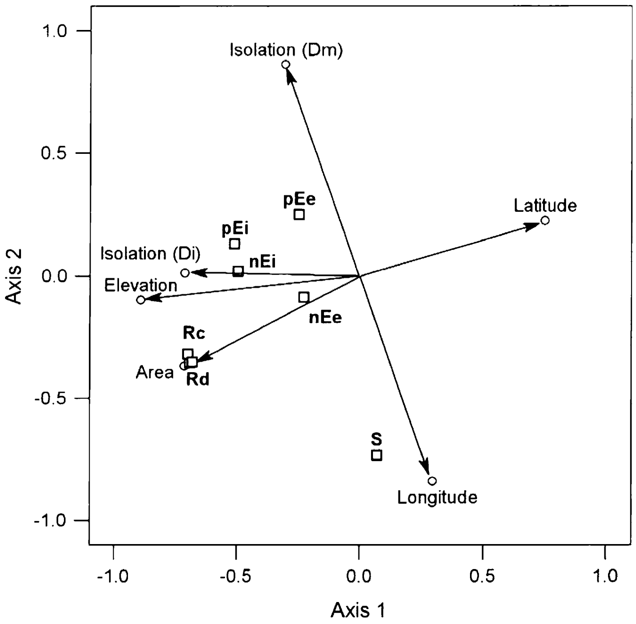

Fig. 2 Principal components plot of faunal variables within first two axes for geographical variables of European islands. Faunal variables entered as supplementary to analysis. S—Species richness, Rd and Rc—Rarity, nEi and nEe—Number of endemics, pEi and pEe—Proportion of species on islands that are endemics; see Table 1 for variable descriptions and transformations

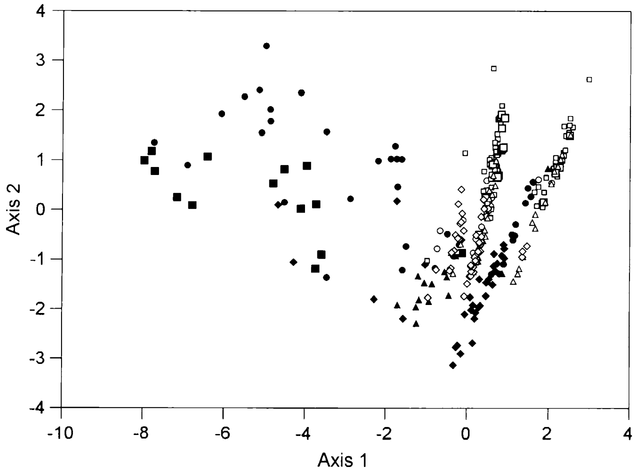

Fig. 3 Plot of islands within first two axes of a principal components analysis based on their faunistics (S—Species richness, Rd and Rc—Rarity, nEi and nEe—Number of endemics, pEi and pEe—Proportion of species on islands that are endemics) in Fig. 2. Island groups: Northern region north of 45° N open symbols, southern region black symbols; black diamond Aegean, black triangle Adriatic, black circle West Mediterranean, large black square Atlantic ocean, open circle West Atlantic seaboard, open small square British, open large square Irish, open triangle Kattegat, open diamond Baltic

(negative) on axis 2. Loadings for European endemicity (pEe and nEe) are low (~0.25) and not well resolved. From the PCA plot, there is a suggestion that rarity and endemicity (primarily nEi and pEi, to a lesser extent nEe and pEe) relate to latitude, island area, elevation, and isolation from nearest larger source, whereas species richness (S) is more closely aligned to island longitude and isolation from continental sources. In these relationships island elevation is closely correlated with island area ($r = 0.66$) and negatively with latitude ($r = -0.65$). Isolation from the continental source is negatively correlated with longitude ($r = 0.65$) (Table 2b). In the plot of islands in the same axes (Fig. 3), the island groups appear as distinct clusters; southern islands are distinguished clearly from northern islands and indicated to have higher rarity, endemicity and richness. Macaronesian islands, particularly, but also numerous islands in the west Mediterranean and Aegean are associated with higher rarity and endemicity.

Regression analysis identifies the factors linked most closely to island faunistics. A substantial portion of species richness (S) (65%) is accounted for by four variables (Table 3) in backwards stepwise multiple regression; these are isolation from continental source, followed by island area, with small contributions from latitude and longitude.

Table 3 Regression results of island faunistics on geographical variables

Dependent variable	Variable	Beta	*SE* beta	*B*	*SE B*	R^2	*P*
Richness (S)	Intercept			0.38	0.536		0.48
	Latitude	0.18	0.037	0.60	0.123	0.032	<0.0001
	Longitude	0.19	0.044	0.25	0.057	0.024	<0.0001
	Isolation (Dm)	−0.53	0.044	−0.17	0.014	0.478	<0.0001
	Area	0.41	0.037	0.22	0.020	0.114	<0.0001
Rarity (Rd)	Intercept			2.21	0.083		<0.0001
	Latitude	−0.58	0.042	−0.26	0.017	0.578	<0.0001
	Longitude	−0.28	0.036	−0.05	0.006	0.049	<0.0001
	Isolation (Dm)	−0.40	0.040	−0.02	0.002	0.037	<0.0001
	Isolation (Di)	0.09	0.034	0.01	0.005	0.005	0.01
	Area	0.23	0.043	0.02	0.003	0.087	<0.0001
Rarity (Rc)	Intercept			2.99	0.130		<0.0001
	Latitude	−0.65	0.034	−0.57	0.030	0.619	<0.0001
	Longitude	−0.22	0.037	−0.08	0.013	0.032	<0.0001
	Isolation (Dm)	−0.29	0.038	−0.03	0.003	0.019	<0.0001
	Isolation (Di)	0.08	0.035	0.02	0.010	0.005	0.02
	Area	0.24	0.033	0.03	0.005	0.072	<0.0001

	Variable	Estimate	*SE*	Wald	*P*
Endemicity (nEi)	Intercept	5.49	2.729	4.04	0.04
	Latitude	−5.28	0.673	61.52	<0.0001
	Longitude	1.14	0.255	20.03	<0.0001
	Isolation (Dm)	0.70	0.109	42.02	<0.0001
	Isolation (Di)	−1.09	0.212	26.19	<0.0001
	Elevation	2.64	0.329	64.46	<0.0001
Endemicity (nEe)	Intercept	2.35	1.026	5.26	0.02
	Latitude	−0.77	0.258	8.80	0.003
	Area	0.41	0.050	68.81	<0.0001

Variables not listed were not significant in the models and omitted from the table

Richness and rarity were analysed using multiple stepwise (backwards) regression and endemicity using Poisson log-link regression. Richness model (S): $R^2 = 64.7\%$, $F_{4,295} = 135.21$, $P < 0.0001$, *SE* estimate = 0.383; Rarity model (Rd): $R^2 = 75.7\%$, $F_{5,294} = 152.08$, $P < 0.0001$, *SE* estimate = 0.043; Rarity model (Rc): $R^2 = 74.7\%$, $F_{5,294} = 173.51$, $P < 0.0001$, *SE* estimate = 0.087; Endemicity model (nEi): $R^2 = 54.2\%$, Loglikelihood = −164.5, $DF = 294$, $P < 0.0001$; Endemicity model (nEe): $R^2 = 25.3\%$, Loglikelihood = −409.7, $DF = 297$

Richness (S) increases with proximity to the continent, island area and higher latitude and longitude. Thus, Macaronesian islands tend to have low species' richness. The plot of observed against predicted estimates for species richness (Fig. 4) reveals no overt island group influences in the residuals. Some 16 islands have large residuals (Table 4); most are negative. This approach identifies the same variables as being significant as a Poisson log-link regression on species richness and is used for the purposes of this article.

The equations for both rarity variables (Rd and Rc) are very similar and thus only observed versus predicted estimates are illustrated for rarity based on distribution records (Rd); a large amount of the variation (75–76%) is accounted for by five variables. The key contribution is from latitude (58–62%), followed by area (7–9%) and small contributions from longitude and the two isolation measures. Rarity increases with lower latitudes and greater island area but also westwards, with shorter distances to continental shores and, apparently, with greater isolation from neighbouring larger sources. Thus the plot of rarity (Rd; Fig 5) reveals a distinct geographical pattern with northern islands having low rarity and southern islands, especially Macaronesian islands, having high rarity. Eleven islands are substantial residuals, seven having much higher rarity than expected (Table 4).

Applying Poisson log-link regression, a substantial portion of the variation (54%) of island endemicity (nEi) is

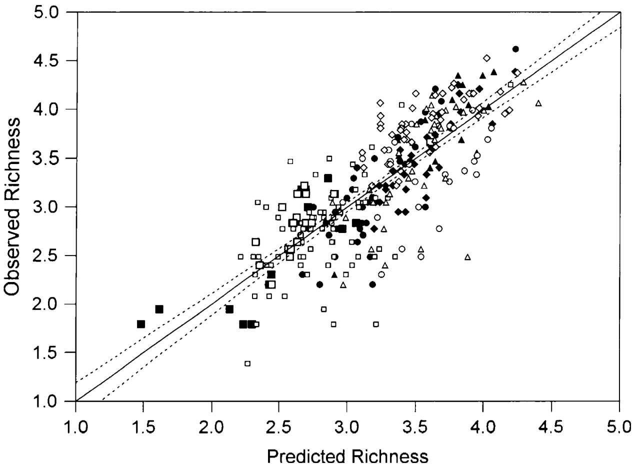

Fig. 4 Observed versus species richness (S, Ln transformed) from the regression of species richness against geographical variables (latitude, longitude, isolation (Dm) and area of islands). See Table 3 for regression parameters

accounted for by five variables, the most important being latitude, elevation and isolation from continental shores (Dm). Island area does not contribute to island endemicity. Numbers of island endemic species increase with lower latitude, higher elevation and increasing distance from continental shores; they also increase with increasing longitude and less isolation from neighbouring sources. The two large Mediterranean islands of Corsica and Sardinia have far greater endemicity than predicted, as do seven satellite islands within the Tyrrhenian Sea (Fig. 6, Table 4); two Greek islands have much lower unique endemicity (nEi) than expected. Only a modest portion of variation is accounted for the number of European endemics on islands (nEe) using Poisson log-link regression (~25%); they increase with island area and decreasing latitude; island area is the most important variable. Corsica and Sardinia are again two outstanding positive residuals, as is Sicily which is relatively deficient in unique island endemics (Fig. 7). Only three of the 13 islands with large residuals have many fewer European endemics than expected, all are Greek Dodecanese islands close to the Turkish coastline.

A complex of geographical factors accounts for the proportion of endemics on islands, 17 variables or variable combinations for island endemicity (pEi, R^2 = 67.5%, $F_{17,282}$ = 34.42, $P < 0.0001$) and 13 for European endemicity (pEe, R^2 = 44.5%, $F_{13,286}$ = 17.67, $P < 0.0001$) and are not investigated further in this article.

Species-focused analysis

Only species with occupied basic recording fields on the continent were included in this analysis. Therefore it

Table 4 Islands with extreme values (>|2.0| standardised residuals) for species richness, rarity and endemicity

Island	Standard residual
Species richness (S)	
Skokholm	2.30
Munkö	2.13
Sprogø	−2.01
Rottumeroog	−2.17
Shetland main	−2.25
North Ronaldsay	−2.29
Ragø	−2.29
Round	−2.30
Mandø	−2.34
Faeroe islands	−2.47
Lyø	−2.54
Montecristo	−2.58
Gröde-Appelland	−2.74
Foula	−2.88
Saltholm	−3.64
Yell	−3.70
Rarity (Rd)	
Madeira	2.98
Terceira	2.88
Porto Santo	2.46
Isola Tavolara	2.27
Munkö	2.20
Sâo Miguel	2.17
Foglö Överö-Ulversö	2.08
Belle Isle	−2.11
Lampedusa	−2.53
Saltholm	−2.65
Pantelleria	−2.87
Endemicity (Ei)	
Elba	4.81
Capraia	4.47
Corse	4.11
Sardegna	3.66
Isola S. Maria	3.61
Spargi	3.05
Giglio	2.89
Caprera	2.31
Gorgona	2.18
Tinos	−2.31
Paros	−2.44
Endemicity (Ee)	
Corse	4.29
Sardegna	3.80
Isola Tavolara	3.04
Spargi	2.53
La Gomera	2.49

Table 4 continued

Island	Standard residual
La Palma	2.29
Caprera	2.25
Capraia	2.25
Sicilia	2.20
Elba	2.19
Samos	−2.01
Lesvos	−2.20
Rodhos	−2.24

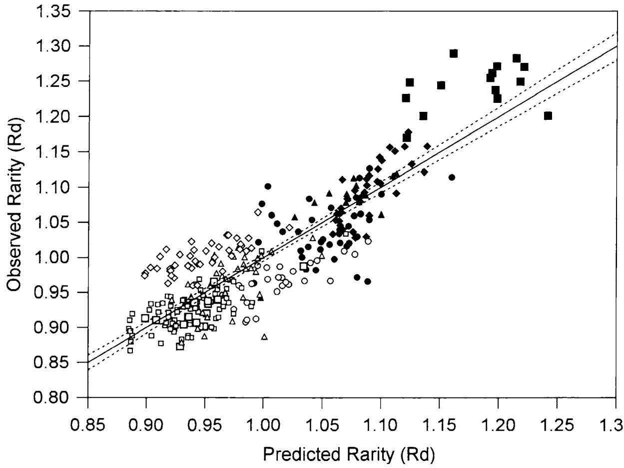

Fig. 5 Observed versus predicted rarity (Rd, Arcsine transformed) from the regression of species' rarity against geographical variables (latitude, longitude, isolation (Dm), isolation (Di) and area of islands). See Table 3 for regression parameters and Fig. 3 for island symbols

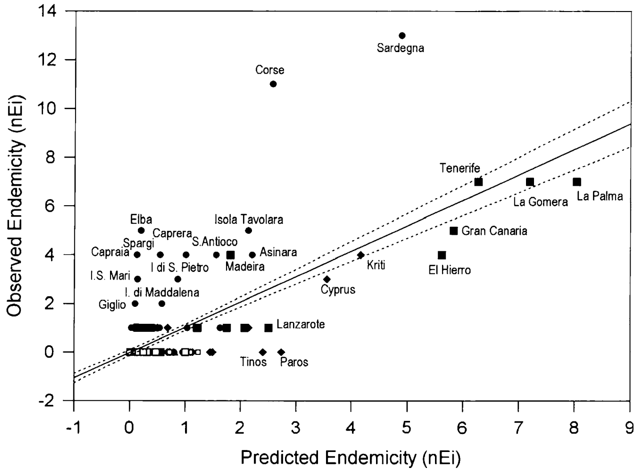

Fig. 6 Observed versus predicted endemicity (nEi) from the regression of island endemicity against geographical variables (latitude, longitude, isolation (Dm), isolation (Di) and elevation of islands). See Table 3 for regression parameters and Fig. 3 for island symbols

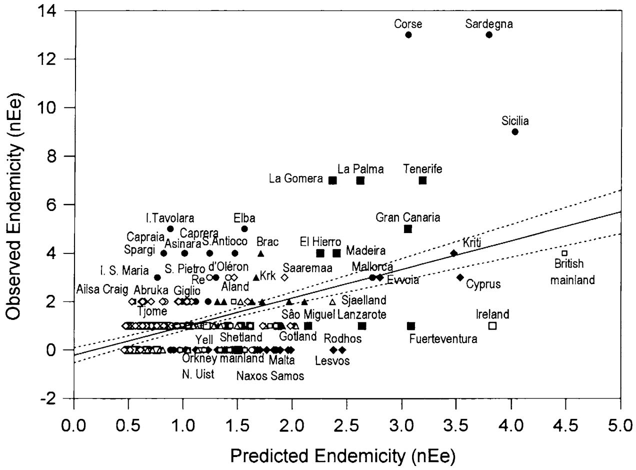

Fig. 7 Observed versus predicted endemicity (nEe) from the regression of European species' endemicity against geographical variables (latitude and area of islands). See Table 3 for regression parameters and Fig. 3 for island symbols

excludes island endemics. Multiple (backwards stepwise) rank regression significantly accounted for proportional occurrence of species on islands ($R^2 = 74.0\%$, $F_{3,341} = 322.9$, $P < 0.0001$); it identified three prominent variables: distribution index (pcDI) accounts for most variation (65%) and the remainder is explained by the lower altitudinal limit for species (ALTlc) and the southern range limit for species (Slim) (Table 5). This result was closely matched by the logit regression for occurrence of species on islands (Table 5). When these three variables were placed in a GRM the relationship was refined ($R^2 = 84.0\%$, $F_{7,\ 369} = 280.4$, $P < 0.0001$) and three polynomial relationships and two interactive variable associations identified (Table 5). The distribution of observed versus predicted distributions is illustrated in Fig. 8; species with substantial positive or negative residuals (>±1.95SE) are named on the plot and in Table 6.

A number of significant relationships were found linking conservation status variables and island faunal variables (Table 7). Proportional occurrence of species on islands (pISO) is associated with distribution trends in Europe (EURTREND); species that occur more frequently on European islands tend to have more positive distribution trends on the mainland of Europe than species less frequent on islands. Species which are European endemics (Ee) also seem to have distributions that have more positive trends compared with those that are not endemics, but this effect disappears when the relatively small number of European endemics (discounting island endemics) found on European islands is considered. Extinction rates over countries in Europe are associated with island occurrence (bIS) and European endemicity. Species which occur on any island over Europe have become extinct in more countries in Europe than those that are more restricted. Among

Table 5 Regression parameters for species' occurrence and proportional abundance on islands against geographical and ecological variables

Variable	Beta	*SE* beta	*B*	*SE B*	R^2 change	*P*
(a) Multiple (backwards stepwise) regression on ranked proportional occurrence of species on islands						
Intercept			579.95	82.107		<0.0001
pcDI	0.59	0.034	321.29	18.726	0.65	<0.0001
ALTlc	−0.26	0.034	−1.87	0.244	0.06	<0.0001
South	−0.20	0.029	−147.48	22.237	0.03	<0.0001

Variable	*SS*	*DF*	*MS*	*F*	*P*
(b) GRM on proportional occurrence of species on islands					
Intercept	0.349	1	0.349	49.81	<0.0001
pcDI		0			
pcDI^2	1.237	1	1.237	176.44	<0.0001
South	0.325	1	0.325	46.33	<0.0001
South^2	0.304	1	0.304	43.39	<0.0001
ALTlc	0.164	1	0.164	23.45	<0.0001
ALTlc^2	0.038	1	0.038	5.38	0.02
pcDI*South	0.165	1	0.165	23.56	<0.0001
pcDI*ALTlc		0			
South*ALTlc	0.136	1	0.136	19.34	<0.0001
Error	2.587	369	0.007		

Variable	Estimate	*SE*	Wald	*P*
(c) Logit regression of occurrence of species of any island				
Intercept	−18.07	5.033	12.89	0.0003
pcDI	9.80	1.593	37.83	<0.0001
South	−5.04	1.391	13.11	0.0003
ALTlc	−0.08	0.014	33.77	<0.0001

See Table 1 for variables. The distribution index (pcDI) correlated significantly with most other variables entered into regression (Pearson *r*: countries 0.96, northern range margin 0.84, latitudinal range 0.80, longitudinal range 0.85, number of host plants 0.75, eastern range margin 0.65, western range margin −0.53, upper altitudinal limit 0.56; all $P < 0.0001$). Species ranked proportional occurrence on islands: $R^2 = 74.0\%$, $F_{3,341} = 322.9$, $P < 0.0001$ *SE* of estimate: 50.86; proportional occurrence $R^2 = 84.0\%$, $F_{7,\,369} = 280.4$, $P < 0.0001$; species' occurrence: loglikelihood $= -126.77$, $P < 0.0001$. Only species with occupied recording fields were included in analyses

European endemics the pattern is reversed; they have become extinct in fewer European countries than non-European endemics, but this relationship disappears when European endemics limited to islands are considered. The four conservation status variables have a constant sign with proportional occurrence of species on islands (pISO) and their presence/absence (bIS) on any island; species which are incident on islands and have greater proportional occurrence are less vulnerable and have lower conservation status. The relationship is significant for species of European conservation concern (ECC), species of Red Data Book Status (RDB) and species listed in the Bern Convention (BC) for proportional occurrence of species on islands (pISO), but only for ECC and RDB for island incidence (bIS). European endemicity is associated with ECC (positive) and RBD (negative), a relationship maintained for European endemics found on islands but limited to Red Data Book species for all endemics (both European wide and unique island) (Table 7).

No significant associations link residual occurrence of species over islands (pISOres, residuals from the regression of proportional species' occurrence on geographical variables; see Table 5) with distribution trends, country extinctions or conservation status.

Discussion

Some valuable findings for conservation emerge in this pan-European island view of butterfly faunas. First, a large fraction of the European butterfly fauna is found to be distributed widely over the islands. Second, and as expected, area and isolation govern species richness on islands, but other aspects of island butterfly conservation

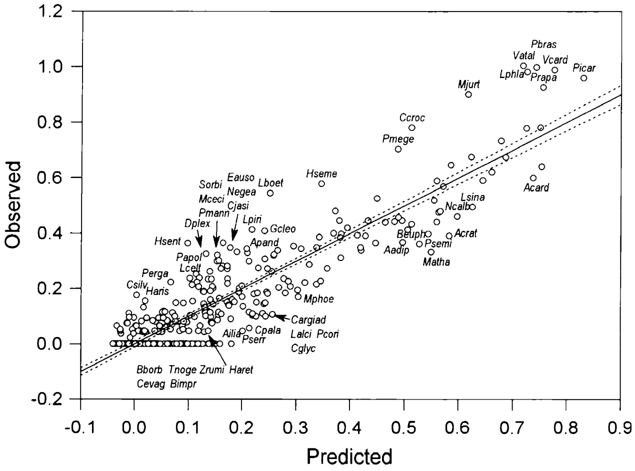

Fig. 8 Observed versus predicted proportional occurrence (pISO, Arcsine transformed) of European butterfly species on islands based on regression against distributional cover on the European continent (pcDI), lower altitudinal limit of continental distributions (ALTlc) and latitude of southern distributional margin on the European continent (South). See Table 5 for regression results

value, rarity and endemicity, have geographical bias, particularly to southern islands. Third, the occurrence and abundance of species over islands is shown to relate closely not only to geographical parameters for islands but also to the essential geography of species at the continental source, to abundance distribution and spatial extent over Europe. Fourth, the analyses allow focus on species dynamics over islands, indicative of whether this corresponds to contemporary geography or not. The results identify islands where more species and more rare or endemic species are expected to occur but have not yet been found. Those species found less frequently on islands than expected are likely subjects for particular concern. Finally, the study gives a view of contemporary conservation status for island species in Europe, based on data for the continental source for those island species. In essence, the survey provides the basis for assessing winners and losers among butterfly species in the modern, heavily industrialised and developed Europe and how islands can play their part in conserving organisms, in this case butterflies.

Europe's island butterfly species bank

Conservation status of organisms is typically measured in terms of rarity or loss (Warren et al. 1997; Van Swaay and Warren 1999). But, it should also have a view to opportunity and vulnerability, how vulnerable a fauna is likely to be to projected events (Fattorini 2005). If numbers of butterfly species on European islands failed to reflect the fraction of land the islands occupy in Europe, as might well be expected with their isolation by sea, then island butterfly

Table 6 Butterfly species occurring more frequently and less frequently than expected from continental distribution, lower altitudinal limit and limit to southern range margin (see Table 5)

Species	Standardised residual
Lampides boeticus	3.50
Vanessa atalanta	3.40
Maniola jurtina	3.36
Colias crocea	3.21
Hipparchia senthes	3.18
Lycaena phlaeas	3.04
Pieris brassicae	3.04
Hipparchia semele	2.78
Pararge megera	2.59
Vanessa cardui	2.53
Nymphalis egea	2.42
Leptotes pirithous	2.32
Danaus plexippus	2.32
Carterocephalus silvicolus	2.07
Charaxes jasius	2.04
Pieris rapae	2.03
Maniola cecilia	2.02
Gonepteryx cleopatra	1.99
Pieris ergane	1.87
Spialia orbifer	1.76
Pieris mannii	1.74
Euchloe ausonia	1.71
Parnassius apollo	1.66
Argynnis pandora	1.63
Libythea celtis	1.62
Hipparchia aristaeus	1.61
Polyommatus icarus	1.52
Boloria improba	−1.51
Tomares nogelii	−1.51
Coenonympha glycerion	−1.52
Cupido argiades	−1.53
Argynnis adippe	−1.54
Leptidea sinapis	−1.57
Melitaea phoebe	−1.60
Nymphalis c-album	−1.63
Zerynthia rumina	−1.63
Anthocharis cardamines	−1.64
Colotis evagore	−1.65
Polyommatus coridon	−1.73
Polyommatus semiargus	−1.74
Borbo borbonica	−1.79
Lycaena alciphron	−1.80
Pyrgus serratulae	−1.85
Carterocephalus palaemon	−1.87
Hipparchia arethusa	−1.90
Boloria euphrosyne	−1.97

Table 6 continued

Species	Standardised residual
Apatura ilia	−2.16
Aporia crataegi	−2.29
Melitaea athalia	−2.59

faunas might not be of particular conservation significance. To find the reverse is unexpected; some 63.4% of the 440 European butterfly species are found on islands, 59% on small islands excluding the big eight (British mainland, Ireland, Iceland, Corsica, Sardinia, Sicily, Crete and Cyprus), all on just 6.2% of the land mass. This in itself places a premium on conserving island faunas; it is underwritten by the further observation that 69% of these species each occur on < 5% of the 540 islands studied, though samples of islands have been taken around the entire shoreline apart from the Russian White and Barents Seas. These island patterns of species richness in butterflies should be seen in a wider context of global diversity. Europe is a very small part of the land area of the globe (7%). But, it is an incredibly varied landmass morphologically (four major physical zones) with immense geological, substrate (soil), climatic and plant (biome) variability (Stanners and Bourdeau 1995). It is an area of great faunal diversity, well illustrated by the extensive array of faunal units for butterflies (Dennis et al. 1991); many of the faunal units relate to glacial refuges south of the northern margin of the Alpine chain. It is of little surprise then that the region is a substantial and diverse source of species for southern islands. The key to island occupancy may be that the mainland is a long peninsula in the western part of which there are few locations >200 km from the sea.

Factors in species' richness, rarity and endemicity

Just how valuable the different islands are for conservation depends on the numbers of colonists, their status as rare species, their uniqueness as endemics. The island-focused analyses have been valuable in exposing the broad geographical parameters underlying species' richness, rarity and endemicity. As expected, richness is largely determined by isolation from the continent, the main potential source for them, and island area. Analyses of faunal structures have already been undertaken on European butterflies (Dennis et al. 1991, 1995, 1998c). From this work, it is expected that rarity and endemicity increase in southern European islands. The island-focused analyses confirm the expectation. The dimensions of islands also significantly influence rarity and endemicity. Larger islands tend to have more varied substrates and biotopes and therefore have a higher probability of housing resources for butterfly specialists. In the case of unique island endemics, island elevation is a key variable while area is not significant. Part of this conundrum is linked to the correlation between island area and elevation. But, an important part of

Table 7 Correlations (gamma) of five variables describing species' occupancy of, and endemicity on, European islands with conservation status variables

Variable pair	Gamma	*Z*	*P*
pISO & EURTREND	0.15	2.20	0.03
pISO & CONEXT	0.10	1.94	0.053
pISO & ECC	−0.50	−9.42	<0.0001*
pISO & FFH	−0.18	−1.59	0.11
pISO & RDB	−0.27	−4.10	<0.0001*
pISO & BC	−0.25	−2.62	0.009
bIS & EURTREND	0.05	0.56	0.57
bIS & CONEXT	0.38	5.17	<0.0001*
bIS & ECC	−0.52	−8.89	<0.0001*
bIS & FFH	−0.15	−1.10	0.27
bIS & RDB	−0.20	−2.58	0.01
bIS & BC	−0.19	−1.61	0.11
nEe & EURTREND	0.42	3.70	0.0002
nEe & CONEXT	−0.42	−4.69	<0.0001*
nEe & ECC	0.58	10.85	<0.0001*
nEe & FFH	−0.04	−0.27	0.78
nEe & RDB	−0.57	−5.42	<0.0001*
nEe & BC	0.05	0.41	0.68
nEe for islands & EURTREND	0.51	1.98	0.047
nEe for islands & CONEXT	−0.22	−1.38	0.17
nEe for islands & ECC	0.60	6.26	<0.0001*
nEe for islands & FFH	−0.11	−0.32	0.75
nEe for islands & RDB	−0.69	−2.63	0.008*
nEe for islands & BC	−0.30	−0.90	0.37
nEe + nEi for islands & FFH	−0.06	−0.25	0.80
nEe + nEi for islands & RDB	−0.39	−2.79	0.005*
nEe + nEi for islands & BC	0.20	1.26	0.21
pISOres & EURTREND	−0.09	−1.51	0.13
pISOres & CONEXT	−0.07	−1.40	0.16
pISOres & ECC	0.06	1.23	0.22
pISOres & FFH	0.01	0.10	0.92
pISOres & RDB	0.03	0.49	0.63
pISOres & BC	−0.02	−0.26	0.80

See Table 1 for variables. Analysis restricted to non-island endemics and species with records on the European mainland (non island endemics with Asian or African sources omitted). For pISO, bIS and nEe, $N = 376$; for nEe restricted to islands $N = 217$ and all endemics nEe and nEi $N = 279$. * Significance at $P < 0.05$ for Bonferroni adjustment applied to multiple tests. See Table 1 for variables; pISOres are residuals from regression of proportional occurrence of species on islands (pISO) with geographical variables (pcDI, Slim and ALTlc; see Table 5). nEe + nEi are endemics both European and island on islands and tested only against conservation status measures the association between island endemics and elevation of the islands is that greater elevation provides a wider range of potential refuges for shifting biotopes and their faunas as climate changes through glacial-interglacial cycles, as well as from increasing human impact. Patterns in rarity and island endemicity (nEi) also differ for longitude and isolation; rarity increases with proximity to continental source and isolation from more proximate (island) sources, whereas for island endemicity this relationship is reversed. Thus, the geographical agents producing rare and endemic species differ; the common thread, however, is that they are both biased to southern Europe.

The link between faunal elements and island butterfly rarity and endemicity

Both rarity and endemicity have strong island-group associations. In previous work, it was demonstrated that faunal units (elements, groups) and their dynamics (spatial shifting, mixing, reformation, erosion, taxon generation) are locked into climatic (glacial-interglacial) cycles (Dennis et al. 1991, 1995). These cycles have inevitably had a profound effect on island species associations and geographical status. A significant feature of this is that no autochthonous island endemic butterfly species occur north of the Devensian polar front (c.18 ka BP); only south of it have conditions been sufficiently stable (within tolerance limits for butterfly species) for the evolution of autochthonous endemics. In this way, large southern islands including archipelagos (i.e. Aegean), experiencing periods of isolation, have the capacity for generating new species. As southern shorelines drop during glacial stages and island isolation decreases (105–115 m eustatic fall during last glacial maximum in the Mediterranean; Lambeck and Bard 2000; Geraga et al. 2000; Lambeck et al. 2004; Rabineau et al. 2006), islands have the potential for acting as refuges with climate cooling. Subsequently, with deglaciation and warming, they become centres of dispersal for more widespread species. During this latter process, there is facility for endemics being transmitted to continental shores. The island-focused analysis emphasises once again the importance of sites, both on mainland and island, in southern Europe for the long term refuge and conservation of organisms over the whole of Europe (Dennis and Williams 1995). The Mediterranean basin (with Macaronesia) has been defined as a global hotspot on the basis of endemicity of plants and vertebrates and threat status (>70% of habitat destroyed) (http://www.biodiversityhotspots.org/xp/hotspots/mediterranean/Pages/default.aspx). Our work demonstrates that the islands of the Mediterranean basin and Macaronesia also serve as hotspots for butterfly endemicity, reinforcing the importance of this region in a global context.

Factors influencing the frequency of butterfly species over islands

The link between islands and their potential continental sources is supported by findings of the species-focused analysis. The largest predictor of both island occurrence (presence/absence on any island, bIS) and abundance over islands (pISO) is ubiquity on the continent, specifically measured by the abundance of records in the European atlas (pcDI, Kudrna 2002). This measure correlates highly and significantly with number of countries occupied, longitudinal and latitudinal range, all four basic compass direction range margins, and number of larval host plants (see Table 5 legend). It is therefore a sound measure of distributional extent and geographical range and reflects ecological potential for colonisation. The other variables contributing to island occurrence (bIS, pISO) also make for good geographical sense. Species with higher latitude southern range margins occupy fewer islands and so do species with more elevated lower altitudinal limits. To pick an obvious example of species so affected by southern range margins and higher altitudinal biotopes, *Erebia* species (Satyrinae) do not occur on any Mediterranean island regardless of some islands having mountain peaks that in elevation exceed many of these species' lower altitudinal limits.

Reflections from measurements of conservation status

As butterflies that occupy more islands are more ubiquitous over the European continent, it would be thought that they have relatively low conservation priority. Indeed, species that occupy more islands (pISO) are significantly less inclined to distributional loss as measured by European trends in distributions (EURTREND) than those that occupy fewer islands. Generally, too, with the exception of island endemics, species that are more abundant across islands are taxa of less conservation concern on three measures, species of European Conservation Concern (ECC), Red Data Book species (RDB), and species listed by the Bern Convention (BC). This, of course, does not mean that they are invulnerable to loss. As witnessed in the British islands, butterflies may still exist on islands (e.g. *Argynnis adippe, Boloria euphrosyne, Melitaea athalia*; Fox et al. 2006) but be in severe decline.

An important sub group of European butterflies, European endemics, have fared significantly better in trends (fewer declines) and extinctions (fewer country extinctions) than non-European endemics; they also have significantly lower Red Data Book Status. The pattern is similar for unique island endemics. This contrasts with the negative indications based on distributional features describing Species of European Conservation Concern (ECC), but then

Red Data Book classification specifically identifies vulnerability from rarity and loss whereas ECC is a measure founded more on distributional features. A further counter signal for well being of island species is the significant tendency for butterflies that occur on any island (excluding island endemics) to become extinct in European countries. This may arise simply as a statistical artefact that being ubiquitous species there are more countries in which to become extinct. Even so, it is a warning sign, established by firmer observations made of butterfly extinctions over Europe (Thomas and Clarke 2004; Thomas et al. 2004) and how this process can eventually affect island butterflies. There is, of course, firm evidence that just as butterflies can decline dramatically on very large islands, so too can they become extinct on them, even when the affected species once had substantial populations (e.g. *Maculinea arion; Aporia crataegi*; Warren et al. 2001; Fox et al. 2006).

Residual patterns in species' richness, rarity and endemicity

Known declines and losses from islands raise to prominence another aspect of the results from this study: residuals from the island-focused and species-focused analyses. In interactive systems of mainland-small islands and island archipelagos, there will always be losses, as there are gains; on the assumption of stable environmental conditions there is expected dynamic homeostasis in numbers of species on islands, but a turnover of taxa with losses and gains. Few European islands are surveyed frequently and intensively enough to monitor this process. The exception is the Åland islands, Finland, with the superlative research done on *Melitaea cinxia* metapopulations (Hanski et al. 1994; Nieminen et al. 2004). From this, and records for islands where resident entomologists engage in synoptic recording, it is clear that gains occur as do losses (e.g. *Nymphalis c-album* and *Pararge aegeria* on the Isle of Man; *Thymelicus lineola* in Ireland; *Pararge aegeria* on Colonsay; Jeffcoate 2008; Bowles and Fox 2007, http://www.wexfordnaturalists.com/gaggle.php). For most islands, data are obtained from occasional survey and sporadic visits. Analyses such as the current one provide indications where priorities and concerns should perhaps be based. The residuals indicate islands and species doing better or worse than expected. Assuming we have available, and have selected, suitable predictors these residuals establish a platform for future inquiry. They also confirm that for many islands, species dynamics is far from being in homeostasis, but then some biologists argue that non-equilibrium may be the norm (Rohde 2006). If it were, then the patterns and residuals for species' richness, rarity and endemicity would not differ for global geography (latitude, longitude). Contrasts for both levels of rarity and endemicity among an island's fauna indicate that turnover affects taxa differently, and among different island groups strongly suggests distinctions in environment and environmental history for those island groups. Although many endemics on islands would seem recent evolutionary products (*Maniola* species in Aegean; Thomson 1987), the origins of others undoubtedly date back millions of years (e.g. *Gonepteryx* and *Pararge* species in Macaronesia; Brunton and Hurst 1998; Weingarten et al. 2006). The geological history and human history of Europe's islands is one characterised by high magnitude environmental events (Martrat et al. 2004) in which a non-equilibrium state for many islands is not surprising. Since Devensian deglaciation, major systematic and stochastic environmental events have impinged on island ecosystems (i.e. climate change, volcanicity, vegetation succession, deforestation, fires, overgrazing, urbanisation with tourism; Dennis et al. 2000) that inevitably will have affected some species (specialists) more than others (generalists; long distance migrants). Refuges in such situations are often provided by dissected topography and high elevation (e.g. Crete, Corsica, Sardinia) limiting access to human exploitation.

The residual islands from island-focused analysis deserve attention. Islands with summed high positive residuals for richness, rarity and endemicity, represent important faunas to conserve whilst others with high negative residuals are possibly islands where more species, rare and endemic species may be sought. It is also possible that on islands with a dearth in expected endemics, losses may have occurred in old elements with Holocene intensive human land use (e.g. Aegean; Dennis et al. 2000). The residual species in the species-focused analysis fulfil much the same function. For those with high positive residuals (Table 7) there are indications of extensive migration capacity (e.g. *Vanessa cardui, V. atalanta*), great colonization potential (e.g. *Maniola jurtina, Polyommatus icarus*), species with distinctive Mediterranean margin ecology (e.g. *Charaxes jasius* which feeds on pan-Mediterranean *Arbutus unedo* L or *A. andrachne* L; Blondel and Aronson 1999; Makris 2003) and species which have coastal climatic affinities (*Hipparchia semele*; Dennis 1992). Species with large negative residuals are often already causes for concern, possibly resource specialists with low colonization capacity (e.g. *Argynnis adippe; Melitaea athalia*; Kemp et al. 2008) and poor migrants (e.g. *Leptidea sinapis*). There is again an issue of survey; some species may be missed because they appear at a time of the year when few entomologists visit islands (e.g. spring butterfly *Anthocharis cardamines*) or because of an inability of inexperienced recorders to separate similar species (e.g. *Pontia* spp., *Hipparchia* spp.). The key thing here is that the list of residuals provides a basis for understanding what makes for good immigrants and colonists. The data should soon attain a standard that allows accurate predictions of incidence for specific islands around the entire European fringe.

Island endemics and their taxonomic status

A special group is undoubtedly the unique island endemics (Appendix 2). It is highly probable from their restriction to islands that they are autochthonous—they have likely evolved on the islands. It is likely, too, that some species mostly restricted to islands, having attained small footholds on the neighbouring continental coastline, are also island autochthonous endemics that have migrated there under their own power or have spread to the coast with human traffic during historical times. Potential examples occur in the Aegean (*Hipparchia mersina, M. halicarnassus* and*Maniola megala*) and Tyrrhenian (*Coenonympha elbana*). Endemics, whatever their origin, also present special cause for concern, their uniqueness typically linked to small area of occupancy or geographical range; where their populations are also sparse and/or small and under pressure from environmental change, then their priority for concern increases (Gardiner 2003). Endemics are entirely on southern islands. Unfortunately, not only is the Mediterranean heating up and drying out with climate change (Xoplaki et al. 2003; Paeth and Hense 2005; Hoerling et al. 2006; Sarris et al. 2007; Beniston et al. 2007; Bianchi 2007), a process in which the switch to rapid warming has geological precedents (Martrat et al. 2004), but many islands are under pressure from developments for tourism (e.g. Tyrrhenian islands; Cyprus) (Haslam 1997; Pasqualini et al. 1999; Kent et al. 2002; USAID Biodiversity Analysis Cyprus 2006; Dapporto and Dennis 2008b) as well as from more traditional land use pressures (e.g. grazing; Hill et al. 1998). These pressures have had an impact on biogeographical relationships among islands (e.g. Balearic Islands, Palmer et al. 1999) as well as directly on Lepidoptera (Petanidou et al. 1991) and place a premium on considering the future for island endemics.

One problem with small area island endemics is their taxonomic status. In some cases it is questionable whether they should be attributed species status; when in doubt we have excluded them (e.g. *Polyommatus villai* on Elba, Jutzeler et al. 2003; *Melitaea emipunica*; Russell et al. 2005). Following this work the species status of *Coenonympha elbana* has also been questioned (Wiemers 2007) and changes suggested for species within the *Agrodiaetus dolus* group (Lukhtanov et al. 2007). Nevertheless, increasing work on them shows that even those butterfly populations regarded as perhaps ‘strong’ subspecies, rather than as species, have distinctive features, and underlying this is genetic differentiation (e.g. *Pararge xiphioides*, Owen and Smith 1993b; *Gonepteryx* species, Brunton and Hurst 1998); the subspecies category indicates a degree of genetic distinction and is suggested to present an important basis for conservation (Samways 1998). Where these become of special focus for conservation, the genetic distinctions are often underlain by ecological differences that must necessarily be taken into account in their management. In this study some relatively small changes in decisions regarding taxa could have made substantial differences to their status. Indeed, different decisions have been made by different authorities. Thus, if *Hipparchia neapolitana* is separated from *H. blachieri* (Balletto et al. 2005), the headquarters for *H. blachieri* in Sicily would assume greater conservation status. It is clear that question marks hang over the taxonomic status of many current butterfly taxa in Europe and differences of opinion occur (cf. Kudrna 2002; Balletto et al. 2005). Inevitably, lowering the threshold for accepting species status subdivides distributions, emphasises evolutionary and genetic distinctions, increasing rarity and endemicity, and places greater pressure on conservation programmes (Dennis 1997). Descimon and Mallet (2008) discuss the features of *bona* and *mala* species and the consequences of over-enthusiastic splitting for species inflation; they argue that the distinction between ‘good’ and ‘bad’ species depends on concordance or discordance of four main types of evidence (i.e. morphological/genetic, phylogenetic, reproductive and geographic criteria). In the process of decision making about taxonomic status, it is clear that current developments in molecular biology do not provide a panacea; even when there are obvious ecological and morphological (genital) distinctions among closely related taxa, the genetic differences may be slight as in the case of some New World skippers (e.g. *Polyctor* species, *Cobalus* species) where long sequences of DNA reveal limited alternatives at very few nucleotides (Burns et al. 2007). Of course, differences of opinion over taxa must necessarily be conveyed through formal channels of the Code for Zoological Nomenclature (Anon 1985). The point being made here is that morphological differences among populations suggest underlying differences in selection pressures, in genetics; as consequently this implies distinctions in habitats and resources (see New 2007b), these differences must necessarily be considered for conservation and any site management must necessarily cater for them.

This work provides an assessment of the conservation significance of European island butterfly faunas and an identification of contributing variables to richness, rarity and endemicity. Relationships between European mainland and island faunas will undoubtedly be sharpened with ongoing mapping on the continent, dedicated surveys on island species, further taxonomic assessments of potential endemics and finer analyses of taxonomic associations. Progress is underway for the publication of the second edition of the European atlas (Kudrna 2002); this will allow a more precise determination of sources for islands than used in this preliminary survey. Even so, we can conclude that although, all in all, areally, islands are unspectacular fractions of Europe, in faunal terms, comparatively, their conservation potential is immense.

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Appendix 1: List of European islands with their locations (longitude and latitude) used in the survey, organised by island group[1]

Group 1. Aegean and east Mediterranean islands

East Mediterranean

Cyprus (Greece, Turkey) [5] 33.00E 35.00N
(Makris 2003; John 2007; John et al. 2006)

Aegean and Aegean arc (Greece and Turkey)

Amorgós [0] 25.54E 36.49N
Anáfi [0] 25.44E 36.23N
Andíparos [1] 25.02E 37.00N
Ándros [5] 24.54E 37.49N
Astipálea [3] 26.22E 36.32N
Áyios Efstrátios [2] 24.58E 39.34N
Évvia [5] 23.15E 38.30N
Éyina (Aegina) [5] 23.26E 37.45N
Folégandros [0] 24.53E 36.37N
Foúrni [3] 26.29E 37.36N
Gökçeada [3] 25.54E 40.12N
Híos (Chios) [5] 26.07E 38.23N
Ídhra [3] 23.28E 37.19N
Ikaría (Nikaria) [5] 25.40E 37.35N
Inoússa [3] 26.14E 38.33N
Íos [1] 25.16E 36.44N
Kálimnos [5] 26.59E 36.57N
Kárpathos (Scarpanto) [5] 27.12E 35.30N
Kássos [3] 26.58E 35.22N
Kéa [3] 24.20E 37.38N
Kíthira [5] 22.59E 36.10N
Kíthnos [0] 24.25E 37.25N
Kós (Cos) [5] 27.19E 36.53N
Kríti (Crete) [5] 25.00E 35.00N
Léros [5] 26.50E 37.10N
Lésvos (Lesbos) [5] 26.16E 39.16N
Límnos (Lemnos) [5] 25.19E 39.53N
Megísti (Kastellórizon) [4] 29.35E 36.08N
Míkonos [0] 25.22E 37.26N
Mílos [5] 24.25E 36.44N
Náxos [4] 25.24E 37.06N
Níssiros [5] 27.13E 36.35N
Páros [5] 25.06E 37.04N
Pátmos [5] 26.35E 37.20N
Políegos [0] 24.37E 36.46N
Psará [1] 27.09E 36.57N
Psérimos [1] 27.09E 36.57N
Ródhos (Rhodes) [5] 28.00E 36.15N
Sámos [5] 26.50E 37.41N
Samothráki [5] 25.32E 40.27N
Sífnos [5] 24.43E 36.59N
Síkinos [0] 25.05E 36.40N
Sími [5] 27.51E 36.36N
Síros [5] 24.55E 37.26N
Skiáthos [5] 23.30E 39.10N
Skíros [5] 24.34E 38.55N
Skópelos [0] 23.43E 39.07N
Spétse (Spetses) [5] 23.09E 37.16N
Thássos [5] 24.34E 40.39N
Thíra (Santorini) [5] 25.27E 36.24N
Tílos [5] 27.18E 36.49N
Tínos [5] 25.08E 37.33N

(Gaskin and Littler 1988; Dennis et al. 2000, 2001a, b; Coutsis pers. obs.; Gascoigne-Pees pers. comm.; http://www.butterfly-guide.co.uk/regions/greece/; http://thasos.users.btopenworld.com/butterflies.htm; http://www.chiosnet.gr/tourism/nature/chios_butterflies_moths.htm).

Group 2. Adriatic islands

Adriatic Sea (Croatia)

Brac [5] 16.30E 43.20N
Cres-Lošinj [5] 14.25E 44.50N
Dugi otok [5] 15.02E 44.00N
Hvar [5] 16.28E 43.11N
Korčula [5] 17.05E 42.56N

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[1] [n] = number of five indicator species (*Pieris brassicae, P. rapae, Colias crocea, Vanessa atalanta; V. cardui*) present on island. Islands surveyed at least 15 times

Kornat [0] 15.20E 43.50N
Krk [5] 14.34E 45.02N
Mljet [5] 17.30E 42.45N
Pag [5] 15.00E 44.50N
Rab [5] 14.50E 44.50N
Rava [2] 15.05E 44.02N
Šolta [2] 16.15E 43.20N
Sušak [2] 16.30E 42.45N
Unije [5] 14.15E 44.40N
Vis [5] 16.11E 43.03N

(Jakšić 1988; Withrington and Verovnik 2008)
Ionian Sea (Greece)

Itháki [0] 20.40E 38.25N
Kefallinia (Cephalonia) [5] 20.29E 38.13N
Kérkira (Corfu) [5] 19.55E 39.38N
Levkás [3] 20.30E 38.40N
Zákinthos (Zante) [5] 20.54E 37.47N

(Rebel 1910, 1932; Willemse 1980, 1981; Gaskin and Littler 1986; Gaskin 1995; Parker 1996, 2007; Whitehead 1998; Hall et al. 2003; Papapavlou and Katsouni 2008; Olivier pers. comm. [*Hipparchia volgensis*])
Tremiti Islands (Italy) Adriatic

Caprara [3] 15.33E 42.08N
San Domino [3] 15.30E 42.06N
San Nicola [4] 15.31E 42.07N

(Balletto et al. 2005)

Group 3. West Mediterranean islands

North central Mediterranean

Corse (Corsica) (France) [5] 9.00E 42.00N
Sardegna (Sardinia) (Italy) [5] 9.00E 40.00N

(Rungs 1988; Lafranchis 2001; Kudrna 2002; Shaw 2002; Jutzeler et al. 2003; Gallet 2003; Brusseaux and Nel 2004; Balletto et al. 2005; Leigheb et al. 2005–2006; Guyot pers. comm.)
Sardinian islands

Caprera [5] 9.30E 41.11N
Isola Asinara [5] 8.14E 41.05N
Isola dei Cavoli [3] 0.33E 39.05N
Isola di Maddalena [4] 9.25E 41.13N
Isola di Mal di Ventre [3] 8.18E 39.59N
Isola di S. Pietro/Panarea [4] 8.15E 39.08N
Isola di S. Antioco [5] 8.25E 39.04N
Isola la Vacca [3] 8.26E 38.56N
Isola S. Maria [5] 9.23E 41.17N
Isola Molara [2] 9.45E 40.53N
Isola Tavolara [4] 9.43E 40.55N
Serpentara [4] 9.38E 39.08N
Spargi [4] 9.22E 41.15N

Archipelago Toscano: Ligurian/Tyyrhenian sea (Italy)

Capraia [4] 9.54E 43.03N
Elba [5] 10.20E 42.49N
Gorgona [5] 9.54E 43.25N
Giglio [4] 10.54E 42.23N
I di Giannutri [3] 11.06E 42.15N
M. Angentario [5] 11.11E 42.23N
Montecristo [5] 10.18E 42.20N
Pianosa [5] 10.06E 42.35N

Golfo di Gaeta/Salerno: Tyrrhenian sea (Italy)

Capri [5] 14.13E 40.33N
Ischia [5] 13.57E 40.44N
Nisida [4] 14.09E 40.49N
Ponza [4] 12.58E 40.53N
Procida-Vivara [5] 14.01E 40.46N

Æolian Islands: Tyrrhenian Sea (Italy)

Lipari [4] 14.58E 38.27N
Salina [4] 14.52E 38.34N
Stromboli [5] 15.13E 38.47N
Ustica [4] 13.12E 38.43N
Vulcano [4] 14.58E 38.26N

South central Mediterranean (Italy)

Favignana [1] 12.22E 37.56N
Lampedusa [5] 12.37E 35.31N
Linosa [2] 12.52E 35.53N
Pantelleria [5] 11.57E 36.50N
Sicilia (Sicily) [5] 14.00E 37.30N

(Balletto et al. 2005; Russell et al. 2005; Dapporto and Cini 2007; Dapporto unpublished data; Dapporto and Dennis in prep., Parenzan and Porcelli 2006; Volpe and Palmieri 2006; Dapporto unpublished data)
Maltese Islands

Comino [4] 14.21E 36.01N
Gozo [5] 14.15E 36.03N
Malta [5] 14.30E 35.00N

(Valletta 1971; Sammut pers. comm.)
Balearic Islands (Spain)

Cabrera [2] 2.56E 39.08N
Formentera [5] 1.30E 38.41N
Ibiza [5] 1.26E 38.54N
Mallorca (Majorca) [5] 2.39E 39.35N
Menorca (Minorca) [5] 4.15E 39.54N

(Kudrna 2002; García-Barros et al. 2004; Carreras et al. 2004, Honey pers. comm.)

Group 4. South oceanic volcanic islands (Macaronesia)

Azores (Portugal) West

Corvo [4] 31.08W 39.41N
Flores [4] 31.13W 39.30N

Azores (Portugal) Mid

Faial [4] 28.42W 38.35N
Graciosa [3] 28.03W 39.03N
Pico [3] 28.25W 38.28N
Sâo Jorge [3] 28.03W 38.40N
Terceira [4] 27.13W 38.43N

Azores (Portugal) East

São Miguel [4] 25.27W 37.33N
Santa Maria [4] 25.07W 36.58N

(Owen and Smith 1993, Meyer 1993; Olivier and Coutsis 1997; Russell 2003; Vieira 2003; Tennent 2005)
Madeiras (Portugal)

Madeira [5] 16.53W 32.38N
Porto Santo [4] 16.20W 33.04N

Canary islands (Spain)

El Hierro [4] 17.55W 27.48N
Fuerteventura [4] 14.02W 28.20N
Gran Canaria [4] 15.34W 27.56N
La Gomera [5] 17.14W 28.07N
Lanzarote [4] 13.38W 29.01N
La Palma [5] 17.46W 28.41N
Tenerife [5] 16.39W 28.17N

(Owen and Smith 1993, Wiemers 1995; Baldwin 1995; Brunton and Hurst 1998; Meyer 1993; Foster 2000; Wakeham-Dawson et al. 2001, 2002; Gascoigne-Pees et al. 2002; Wakeham-Dawson and Franquinho Aguiar 2003, Fernandez 2004; Tennent 2005)

Group 5. West Atlantic coastal islands

French islands/Bay of Biscay

Belle Ile [5] 3.10W 47.19N
Ile de Noirmoutier [5] 2.15W 47.01N
Ile d'Oléron [5] 1.14W 45.59N
Ile de Ré [5] 1.28W 46.09N
Ile d'Yeu [5] 2.21W 46.44N

(Coombes pers. comm.; Luquet pers. comm.; Perrein and Guilloton pers. comm.; Lévesque 1994)
Channel Islands (UK)

Alderney [5] 2.12W 49.43N
Herm [5] 2.27W 49.28N
Guernsey [5] 2.35W 49.27N
Jersey [5] 2.07W 49.13N
Jethou [2] 2.26W 49.27N
Sark [5] 2.22W 49.26N

(Dennis and Shreeve 1996; Hull pers. comm.)
Wadden Sea (Netherlands)

Ameland [5] 5.46E 53.27N
Gried [4] 5.15E 53.15N
Rottumeroog and Rottumerplaat [4] 6.35E 53.55N
Schiermonnikoog [5] 6.10E 53.28N
Terschelling [5] 5.21E 53.24N
Texel [5] 4.49E 53.04N
Vlieland [5] 40.55E 53.15N

(Tax 1989; Hoentjen and Meijering 1994; Zumkehr 1994)
North Sea (Germany)

Amrum [5] 8.20E 54.38N
Föhr [1] 8.30E 54.43N
Gröde-Appelland [4] 8.38E 54.38N
Heligoland [2] 7.53E 54.10N
Pellworm [0] 8.39E 54.31N
Sylt [5] 8.19E 54.53N

(Kolligs 2003, http://www.oag-helgoland.de/beob/aktuell.html).
Off Jutland (Denmark)

Fanø [4] 8.20E 55.20N
Mandø [4] 8.30E 55.15N
Romø [4] 8.30E 55.05N

(Stoltze 1996)

Group 6. British (English, Welsh and Scottish) islands

British islands

British mainland [5] 2.20W 54.28N

England

Brownsea [5] 1.59W 50.40N
Brownsman [4] 1.36W 55.38N
Bryher [5] 6.21W 49.57N
Great Arthur [0] 6.26W 49.94 N
Great Ganilly [3] 6.16W 49.56N
Great Innisvouls [0] 6.14E 49.57N
Gugh [2] 6.20W 49.54N
Hayling [5] 0.59W 50.48N
Hilbre [5] 3.10W 53.22N
Inner Farne [4] 1.36W 55.38N
Lindisfarne [5] 1.48W 55.41N
Looe or St George's [3] 4.27W 50.20N
Longstone [1] 1.36W 55.38N
Lundy [5] 4.40W 51.11N
Menawethan [0] 6.14W 49.56N
North Hares [1] 1.36W 55.38N
North Wamses [1] 1.37W 55.38N
Round [4] 6.19W 49.58N
Samson [3] 6.21W 49.55N
Sheppey [5] 0.28W 51.25N
South Wamses [0] 1.37W 55.37N
St Agnes [5] 6.21W 49.54N
Staple [3] 1.37W 55.37N
St Helens [1] 6.19W 49.58N
St Martin's [5] 6.17W 49.58N
St Mary's Isles of Scilly [5] 6.18W 49.55N
St Michael's Mount [4] 5.29W 50.06N
Steepholm [5] 3.07W 51.21N

Tean [3] 6.19W 49.58N
Thorney island [1] 0.55W 50.49N
Tresco [5] 6.20W 49.57N
West Wideopens [1] 1.38W 55.36N
White Island [0] 6.18W 49.59N
Wight [5] 1.18W 52.42N

Wales

Anglesey [5] 4.18W 53.16N
Bardsey [5] 4.48W 52.46N
Caldey [4] 4.42W 51.38N
Flatholm [4] 3.07W 51.22N
Grassholm [4] 5.29W 51.43N
Cardigan Island [0] 4.42W 52.09N
Holy Island, off Anglesey [5] 4.39W 53.16N
Llanddwyn [5] 4.24W 53.08N
Penrhyn-Gwyr [4] 4.20W 51.34N
Puffin [5] 4.01W 53.19N
Ramsey [4] 5.20W 51.53N
Skokholm [5] 5.16W 51.42N
Skomer [5] 5.18W 51.45N
Walney [5] 3.15W 54.05N

Man

Calf of Man [5] 4.46W 54.02N
Chicken Rock [1] 4.48W 54.03N
Man [5] 4.34W 54.11N

Scotland

Ailsa Craig [4] 5.07W 55.16N
Arran [5] 5.15E 55.30N
Baleshare [2] 7.23W 57.32N
Barra [5] 7.30W 56.59N
Bass Rock [4] 2.38W 56.05N
Benbecula [4] 7.15W 57.26N
Berneray nf98 [4] 7.11W 57.43N
Berneray nl57 [1] 7.38W 56.47N
Bressay [3] 1.05W 60.09N
Burnt Islands [2] 5.10W 55.55N
Burray [2] 2.54W 58.51N
Bute [5] 5.03W 55.51N
Calavay [0] 7.15W 57.30N
Canna [5] 6.30W 57.03N
Cara [3] 5.45W 55.38N
Carn nan sgeir [1] 5.22W 57.58N
Coll [5] 6.31W 56.38N
Colonsay [4] 6.10W 56.05N
Crowlin Islands [0] 5.50W 57.20N
Cramond [5] 3.20W 55.59N
Davaar [3] 5.32W 55.25N
Easdale [4] 5.38W 56.18N
Eigg [5] 6.10W 56.55N
Eilean Furadh Mor [0] 5.42W 57.52N
Eilean nan Each [0] 6.15W 56.50N
Ensay [2] 7.05W 57.46N
Eriskay [4] 7.15W 57.05N
Fair Isle [5] 1.38W 59.32N
Fetlar[3] 0.52W 60.36N
Fiaray [0] 7.26W 57.04N
Fidra [3] 2.48W 56.40N
Fladday [1] 7.50W 58.10N
Flodday [0] 7.21W 56.60N
Foula [4] 2.05W 60.08N
Fuday [0] 7.23W 57.03N
Garvellachs [0] 5.46W 56.15N
Gigha [4] 5.45W 55.41
Gighay [0] 7.20W 57.01N
Glas Eilean [2] 6.38W 57.51N
Glunimore [1] 5.33W 55.17N
Graemsay [0] 3.17W 58.56N
Great Bernera [1] 6.51W 58.13N
Great Cumbrae [4] 4.55W 55.46N
Grimsay [2] 7.16W 57.30N
Gunna [4] 6.44W 56.34N
Handa [4] 5.11W 58.23N
Harris-Lewis [5] 6.36W 58.05N
Heisker [1] 7.40W 57.31N
Hellisay [0] 7.21W 57.01N
Holy Island, off Arran [3] 5.15W 55.32N
Horse [3] 5.20W 57.59N
Hoy [4] 3.12W 58.49N
Inchcolm [4] 3.18W 56.02N
Inchkeith [3] 3.08W 56.02N
Inchmarnock [3] 5.09W 55.47N
Inchmickery [2] 3.27W 56.01N
Iona [4] 6.25W 56.19N
Islay [5] 6.17W 55.45N
Jura [4] 5.50W 55.57N
Kerrera [4] 5.33W 56.24N
Killegray [1] 7.05W 57.45N
Lady Isle nr Arran [4] 4.44W 55.31N
Lismore [1] 5.30W 56.30N
Little Bernera [0] 6.52W 58.16N
Little Cumbrae [4] 4.57W 55.43N
Longa [0] 5.48W 57.44N
Longay [2] 5.53W 57.19N
Luing [0] 5.38W 56.14N
Lunga [1] 5.42W 56.12N
May [5] 2.33W 56.12N
Minard [2] 5.15W 56.06N
Mingulay [0] 7.38W 56.49N
Monach Islands [0] 7.38W 57.31N
Mousa [1] 1.10W 60.00N
Muck [2] 6.15W 56.50N
Muldoanich [0] 7.26W 56.55N

Mull [4] 6.05W 56.37N
Noss [3] 1.05W 60.09N
North Rona [1] 5.82W 59.12N
North Ronaldsay [4] 2.23W 59.23N
North Uist [4] 7.16W 57.37N
Orkney mainland [5] 2.58W 58.29N
Oronsay [1] 5.56W 56.40N
Outer Skerries [2] 0.46W 60.25N
Pabay [1] 5.52W 57.16N
Pabbay nf88 [0] 7.13W 57.46N
Pabbay nl68 [0] 7.34W 56.51N
Papa Stour [3] 1.23W 60.20N
Pladda [3] 5.06W 55.26N
Preist [0] 5.30W 57.58N
Raasay [4] 6.03W 57.24N
Ronay [0] 7.11W 57.29N
Rousay [2] 3.02W 59.10N
Rhum [4] 6.17W 57.01N
Sanda [3] 5.35W 55.17N
Sanday ng20 [3] 6.29W 57.02N
Sanday hy63 [3] 2.34W 59.15N
Sandray [1] 7.52W 56.89N
Scalpay [4] 5.57W 57.18N
Scarba [0] 5.42W 56.10N
Scarp [1] 7.08W 58.01N
Scotasay [0] 6.44W 57.52N
Seil [4] 5.37W 56.17N
Sgat Mor [1] 5.18W 55.50N
Shapinsay [2] 2.34W 59.02N
Shiant islands [0] 6.21W 57.54N
Sheep [1] 5.57W 55.29N
Shetland mainland [5] 1.09W 60.09N
Shillay [0] 7.15W 57.48N
Skye [4] 6.12W 57.24N
Soa [0] 6.76W 56.51N
Soay [1] 6.13W 57.08N
South Rona [3] 5.59W 57.33N
South Ronaldsay [4] 2.57W 58.44N
South Uist [4] 7.24W 57.17N
Staffa [0] 6.21W 56.26N
St Kilda [3] 8.35W 57.49N
Sule Skerry [2] 4.24W 59.05N
Summer Islands [0] 5.26W 58.00N
Tanera Beg [1] 5.26W 58.00N
Tanera Mor [1] 5.24W 58.00N
Taransay [0] 7.02W 57.54N
Tiree [4] 6.49W 56.30N
Treshnish Isles [1] 6.26W 56.29N
Uinessan [0] 7.29W 56.55N
Ulva [2] 6.13W 56.29N
Unst [3] 0.52W 60.46N
Uyea [1] 0.59W 60.40N
Vatersay [1] 7.32W 56.56N
West Burra [1] 1.20W 60.05N
Westray [2] 2.57W 59.18N
Whalsay [3] 0.59W 60.21N
Wiay ng23 [0] 6.30W 57.20N
Wiay nf84 [0] 7.12W 57.24N
Yell [4] 1.05W 60.36N

(Young and Harper 1986; Dean 1990; Dennis and Shreeve 1996, 1997, Pennington 1997; Hulme 1998; Spalding and Tremewan 1998; Dennis et al. 1998a, b; Masters 2000; Jeffcoate 2008; Bowles and Fox 2007; Archer pers. comm.; Beavis pers. comm.; Dennis pers. obs.; Gander pers. comm.; Greatorex-Davies pers. comm.; Jeffcoate pers. comm.; Sandison pers. comm.; Shreeve pers. obs.).

Group 7. Irish islands

Ireland [5] 7.56W 53.25N
Achill [4] 9.54W 53.56N
Aran [3] 9.42W 53.07N
Bartragh Island, Killala Bay [0] 9.09W 54.12N
Bear [0] 9.54W 51.38N
Clare [4]10.00W 53.49N
Clear [5] 6.30W 51.26N
Cruit near Gola [1] 8.25W 55.01N
Dursey [5] 10.12W 51.36N
Garinish [3] 9.32W 51.44N
Gola [0] 8.20W 55.04N
Gorumna [2] 9.40W 53.15N
Great Blasket [4] 10.32W 52.05N
Great Copeland Belfast [2] 5.31W 54.40N
Great Saltee [5] 6.36W 52.00N
Great Skellig [1] 10.32W 51.46N
Inishbofin [3] (Mayo) 10.12W 53.37N
Inishirrer, Gola [0] 8.20W 55.07N
Inishmaan [5] 9.35W 53.04N
Inishmeane, Gola [0] 8.20W 55.06N
Inishmore [5] 9.45W 53.07N
Inishshark [0] 10.17W 53.37N
Inishsheer [4] 9.31W 53.03N
Inishtrahull [4] 7.14W 55.27N
Inishturk [0] 10.06W 53.42N
Inishvickillane [2] 10.36W 52.20N
John’s Copeland [5] 5.32W 54.41N
Lambay [4] 6.01W 53.29N
Lesser Saltee [4] 6.36W 52.07N
Mutton [1] 9.31W 52.48N
Omey [1] 10.09W 53.32N
Owey Island Donegal [0] 8.26W 55.03N
Puffin [2] 10.24W 51.50N
Rathlin [5] 6.15W 55.17N
Scarrif [2] 10.14W 51.43N
Sherkin [5] 9.25W 51.28N
Tory [5] 8.13W 55.15N

Umfin, Gola [0] 8.21W 55.06N
Valencia [3] 10.21W 51.54N
Whiddy [3] 9.30W 51.41N

(Lavery 1993; Dennis and Shreeve 1996; Wedd 2004; Rippey pers. comm.; *Thymelicus lineola* in 2005/2006: http://www.butterflyireland.com/phenology_2006-2005htm#BR).

Group 8. Kattegat islands

Kattegat (Denmark)

Agersø [3] 11.15E 55.15N
Anholt [4] 11.34E 56.43N
Arø [2] 9.40E 55.15N
Askø [0] 11.30E 54.52N
Avernakø [2] 10.17E 55.02N
Bagø [2] 9.45E 55.20N
Bjornø [2] 10.15E 55.06N
Bogø [5] 12.05E 54.55N
Bornholm [5] 14.56E 55.07N
Christianso (Ertholmene) [4] 15.12E 55.19N
Drejø [3] 10.25E 54.55N
Endelave [4] 10.20E 55.40N
Falster [5] 12.00E 54.49N
Fejø [4] 11.27E 54.50N
Femø [4] 11.35E 54.55N
Fyn [5]10.20E 55.18N
Hesselo [4]11.45E 56.11N
Hirscholmene [1] 10.40E 57.30N
Hjelm [3] 10.50E 56.10N
Laeso [4] 11.01E 57.15N
Langeland [5] 10.46E 54.56N
Lolland [5] 11.30E 54.57N
Lyø [4] 10.10E 55.05N
Mon [5] 12.18E 54.59N
Nekselø [4] 11.20E 55.45N
Nyord [4] 12.10E 55.05N
Omø [3] 11.12E 55.10N
Ragø [4] 11.20E 54.55N
Romsø [3] 10.50E 55.30N
Saltholm [4] 12.45E 55.40N
Samso [4] 10.36E 55.50N
Sejerø [2] 11.10E 55.50N
Sjaelland [5] 11.48E 55.28N
Skalø [0] 11.25E 54.55N
Sprogø [4] 10.55E 55.25N
Strynø [1] 10.40E 54.50N
Tasinge [4] 10.40E 55.00N
Thurø [3] 10.45E 55.05N
Tunø [4] 10.30E 55.55N
Vejrø [1] 11.25E 55.05N
Vejrø1 [1] 10.45E 55.55N
Æbelo [2] 10.10E 55.35N
Æro [4] 10.20E 54.52N

(Klefbeck 1951; Stoltze 1996)
Kattegat (Sweden)

Bohus Malmön [5] 11.19E 58.20N
Burholmen [3] 10.59E 58.50N t
Hallands Väderö [4] 12.34E 56.25N
Nidingen [5] 11.54E 57.18N
Nordkoster [4] 11.00E 58.54N
Rörö [4] 11.36E 57.46N
Saltö [4] 15.34E 56.09N
Sydkoster [4] 11.01E 58.52N
Tjörn [4] 11.40E 58.05N
Ven [5] 12.45E 55.55N
Vinga [3] 11.36E 57.37N

(Ryrholm unpublished data)

Group 9. Baltic and Bothnian Sea islands

Gulf of Riga (Estonia)

Abruka [4] 22.30E 58.05N
Hiiumaa [4] 22.38E 58.40N
Kihnu [1] 24.00E 58.05N
Muhu [3] 22.40E 58.35N
Ruhnu [4] 23.00E 57.48N
Saaremaa [5] 22.30E 58.12N
Vormsi [3] 22.40E 58.42N

Ålands Islands and Gulf of Finland (Finland)

Åland [5] 19.55E 60.15N ✔
Brändö main island [3] 21.05E 60.25N ✔
Brändö Åva [2] 21.05E 60.26N
Brändö Torsholma [0] 21.05E 60.24N
Brändö Korsö [1] 21.04E 60.23N
Eckerö main island [4] 19.33E 60.13N ✔
Eckerö Signilskär [2] 19.36E 60.12N
Föglö main island [4] 20.28E 60.00N ✔
Föglö Överö/ Ulversö [3] 20.32E 60.05N ✔
Föglö Finnholma [2] 20.32E 60.04N
Föglö Jyddö [3] 20.32E 60.04N ✔
Föglö Nötö [4] 20.31E 60.04N ✔
Föglö Vargskär [1] 20.33E 60.05N
Föglö Bänö [0] 20.34E 60.04N
Houtskar [4] 21.05E 60.10N (c. 3-4km^2) ✔
Isosaari [4] 25.00E 60.08N (1km^2; 3km isolation) ✔
Kumlinge main island [3] 20.45E 60.15N ✔
Kumlinge Seglinge [1] 20.43E 60.13N
Kökar main island [4] 20.58E 59.56N ✔
Kökar Kyrkogårdsö [0] 20.56E 59.55N
Sottunga main island [3] 20.40E 60.06N✔
Sottunga Husö [3] 20.47E 60.03N✔
Sund Prästö [0] 20.18E 60.14N
Vårdö main island [3] 20.20E 60.15N✔

(Nordstrøm 1955; Marttila et al. 2001; Laasonen and Laasonen 1991, Bruun 1992; Kesküla 1992; Huldén pers. comm.; Saarinen unpublished data; ✔ used in island-focussed analysis as having been visited > 15 times)

Baltic Sea (Sweden)

Alnön [4] 17.30E 62.46N
Björn [4] 17.59E 60.38N
Bjuröklubb [2] 21.34E 64.28N
Blå Jungfrun [4] 16.46E 57.16N
Brämön [3] 17.42E 62.12 N
Brändön [3] 22.19E 65.41N
Eggegrund [4] 17.33E 60.44N
Fagerön [4] 18.27E 60.13N
Frevisören [3] 23.24E 65.45N
Gotland [5] 18.28E 57.32N
Gotska Sandon [4] 19.25E 58.25N
Gräsö [4] 18.30E 60.22N
Haparanda Sandskär [3] 23.44E 65.20N
Holmön [3] 20.52E 63. 47N
Hornslandet [4] 17.28E 61.40N
Iggön [4] 17.18E 60.53N
Inre Hamnskär [4] 19.19E 59.44N
Landsort [4] 17.52E 58.45N
Måssten [4] 18.51E 60.11N
Munkö [4] 18.43E 59.14N
Norra Finnö [4] 16.51E 58.19N
Obbolaön [3] 20.18E 63.42N
Öland [5] 16.40E 56.50N
Ornö [4] 18.24E 59.03N
Örskär [4]18.23E 60.19N
Raggarön [4] 18.35E 60.12N
Rävsön [3] 18.28E 62.55N
Revsudden [5] 16.27E 56.46N
Runmarö [4] 18.45E 59.16N
Seskarö [3] 23.44E 65.44N
Singö [4] 18.45E 60.10N
Sladö [4] 15.24E 56.08N
Sturkö [5] 15.42E 56.05N
Svartklubben [4] 18.49E 60.10N
Ulvön [3] 18.38E 63.01N
Utklippan [3] 15.47E 56.01N
Utlängan [4] 15.50E 56.02N
Utö [4] 18.20E 58.56N

(Gustafsson 1987; Ryrholm unpublished data)

Group 10. Norwegian and North Atlantic islands

Andørja (Andøy) [0] 17.15E 68.50N
Askøy [1] 5.01E 60.25N
Austvågøy (Vågøy) [1] 14.30E 68.20N
Bjarkøy [0] 16.30E 69.00N
Bømlo [0] 5.15E 59.45N
Boroy [3] 10.33E 59.52N
Bronnoya [1] 10.32E 59.51N
Dønna [0] 12.30E 66.10N
Finnøy [1] 5.50E 59.10N
Frøya [0] 8.30E 63.45N
Hadseløya (Hadsel) [0] 14.30E 68.30N
Håoya [0] 10.34E 59.41N
Hinnø (Lødingen) [1] 15.45E 68.30N
Hitra [1] 8.30E 63.30N
Holsnøy (Meland) [0] 5.05E 60.35N
Huftarøy (Austevoll) [0] 5.15E 60.03N
Huser [0] 10.55E 59.05N
Karlsøy [0] 20.00E 70.00N
Kirkeøy (Hvaler) [3] 11.02E 59.05N
Kristiansund [0] 7.45E 63.05N
Kvåløya (Hammerfest) [0] 24.00E 70.35N
Kvitsøy [1] 5.25E 59.05N
Langoya, Våle [2] 10.23E 59.29N
Lurøy [0] 12.45E 66.25N
Moskenesøya [0] 12.45E 68.00N
Øksnes [0] 14.55E 68.50N
Ostoya [3] 10.34E 59.52N
Rauer [0] 10.41E 59.13N
Rennesøy [0] 5.45E 59.07N
Rølla (Ibestad) [0] 17.00E 68.45N
Senja (Tranøy, Berg, Torsken) [0] 17.00E 69.20N
Smøla [0] 8.00E 63.02N
Sotra-Store (Sund, Fjell, Øygarden) [1] 5.05E 60.17N
Stord [0] 5.25E 59.52N
Sula (Solund) [0] 6.05E 62.25N
Sula [0] 4.55E 61.08N
Tjeldøya (Tjeldsund) [0] 16.10 68.30N
Tjøme [4] 10.25E 59.10N
Tofteholmen [2] 10.33E 59.30N
Træna [0] 12.02E 66.28N
Tromøy [5] 8.53E 58.28N
Tysnesøy [1] 5.35E 60.00N
Utsira [0] 4.50E 59.20N
Vega [0] 11.55E 65.35N
Vestvågøy [1] 13.45E 68.15N

Faeroes (Denmark)

Streymoy [5] 6.47W 62.02N

Iceland

Iceland [2] 18.00W 65.00N

(Williams 1958; Nagypal pers. comm.; http://www.toyen.uio.no/norlep/; Ryrholm unpublished data; http://www.faroenature.net/UserFiles/File/FFFFFF_1998.pdf (Jensen and Patursson A, pp 9–12)).

Appendix 2: List of butterfly species used in study of European islands*[2]

Hesperiidae
Pyrginae
Carcharodus alceae (*tripolinus*) (Esper, 1870)
Carcharodus baeticus (Rambur, 1840)
Carcharodus flocciferus (Zeller, 1847)
Carcharodus lavatherae (Esper, 1783)
Carcharodus orientalis (Reverdin, 1913)
Carcharodus stauderi (Reverdin, 1913)
Erynnis marloyi (Boisduval, 1834)
Erynnis tages (Linnaeus, 1758)
Pyrgus alveus (Hübner, 1803)
Pyrgus andromedae (Wallengren, 1853)
Pyrgus armoricanus (Oberthür, 1910)
Pyrgus bellieri (*foulquieri*) (Oberthür, 1910)
Pyrgus cacaliae (Rambur, 1840)
Pyrgus carlinae (Rambur, 1840)
Pyrgus cathami (*fritillarius*) (Hübner, 1813)
Pyrgus centaureae (Rambur, 1840)
Pyrgus cinarae (Rambur, 1840)
Pyrgus cirsii (Rambur, 1840)
Pyrgus malvae (Linnaeus, 1758)
Pyrgus onopordi (Rambur, 1840)
Pyrgus serratulae (Rambur, 1840)
Pyrgus sidae (Esper, 1782)
Pyrgus warrenensis (Verity, 1928)
Spialia orbifer (Hübner, 1823)
Spialia phlomidis (Herrich-Schäffer, 1845)
Spialia sertorius (Hoffmansegg, 1804)
Spialia therapne (Rambur, 1832)*
Syrichtus cribrellum (Eversmann, 1841)
Syrichtus proto (Ochsenheimer, 1808)
Syrichtus tessellum (Hübner, 1803)
Heteropterinae
Carterocephalus palaemon (Pallas, 1771)
Carterocephalus silvicolus (Meigen, 1829)
Heteropterus morpheus (Pallas, 1771)
Hesperiinae
Borbo borbonica (Boisduval, 1833)
Gegenes nostrodamus (Fabricius, 1793)
Gegenes pumilio (Hoffmansegg, 1804)
Hesperia comma (Linnaeus, 1758)
Ochlodes sylvanus (Esper, 1777)
Pelopidas thrax (Hübner, 1821)

continued

Thymelicus acteon (Rottemburg, 1775)
Thymelicus christi (Rebel, 1894)*
Thymelicus hyrax (Lederer, 1861)
Thymelicus lineola (Ochsenheimer, 1806)
Thymelicus sylvestris (Poda, 1761)
Papilionidae
Parnassiinae
Archon apollinus (Herbst, 1798)
Parnassius apollo (Linnaeus, 1758)
Parnassius mnemosyne (Linnaeus, 1758)
Parnassius sacerdos (*phoebus*) (Stichel, 1906)
Zerynthia cerisyi (Godart, 1822)
Zerynthia cretica (Rebel, 1904)*
Zerynthia polyxena (Schiffermüller, 1775)
Zerynthia rumina (Linnaeus, 1767)
Papilioninae
Iphiclides podalirius (Linnaeus, 1758)
Papilio alexanor Esper, 1799
Papilio hospiton Gene, 1839*
Papilio machaon Linnaeus, 1758
Pieridae
Dismorphiinae
Leptidea duponcheli (Staudinger, 1871)
Leptidea morsei (Fenton, 1881)
Leptidea sinapis (*reali*) (Linnaeus, 1758)
Pierinae
Anthocharis cardamines (Linnaeus, 1758)
Anthocharis damone (Boisduval, 1836)
Anthocharis euphenoides Staudinger, 1869
Anthocharis gruneri Herrich-Schäffer, 1851
Aporia crataegi (Linnaeus, 1758)
Colotis evagore (Klug, 1829)
Euchloe ausonia (Hübner, 1806)
Euchloe belemia (Esper, 1798)
Euchloe charlonia (*bazae*) (Donzel, 1842)
Euchloe crameri Butler, 1869
Euchloe insularis Staudinger, 1861*
Euchloe penia (Freyer, 1852)
Euchloe simplonia Freyer, 1829
Euchloe tagis (*bellezina*) (Hübner, 1804)
Pieris brassicae (Linnaeus, 1758)
Pieris bryoniae (Hübner, 1791)
Pieris callidice (Hübner, 1800)
Pieris cheiranthi (Hübner, 1808)*
Pieris chloridice (Hübner, 1813)
Pieris daplidice (*edusa*) (Linnaeus, 1758)
Pieris ergane (Geyer, 1828)
Pieris krueperi (Staudinger, 1860)
Pieris mannii (Mayer, 1851)
Pieris napi (balcana) (Linnaeus, 1758)

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[2] Owing to uncertainty of the records, various taxa have been amalgamated in the listing of species. For example *Aricia artaxerxes* (Fabricius, 1793) includes reported sightings of *A. allous* Geyer, 1837 and *Pieris daplidice* (Linnaeus, 1758) includes *P. edusa* (Fabricius, 1777).

continued
Pieris rapae (Linnaeus, 1758)
Zegris eupheme (Esper, 1805)
Coliadinae
Catopsilia florella (Fabricius, 1775)
Colias alfacariensis Ribbe, 1905
Colias aurorina (*libanotica*) (Herrich-Schäffer, 1850)
Colias balcanica (*caucasica*) Rebel, 1903
Colias chrysotheme (Esper, 1780)
Colias crocea (Geoffroy, 1785)
Colias erate (Esper, 1805)
Colias hecla Lefebvre, 1836
Colias hyale (Linnaeus, 1758)
Colias myrmidone (Esper, 1780)
Colias palaeno (Linnaeus, 1758)
Colias phicomone (Esper, 1780)
Colias werdandi (nastes, tyche) Zetterstedt, 1840
Gonepteryx cleobule (Hübner, 1825)*
Gonepteryx eversi (Rehnelt, 1974)*
Gonepteryx palmae (Stamm, 1963)*
Gonepteryx cleopatra (Linnaeus, 1767)
Gonepteryx farinosa Zeller, 1847
Gonepteryx maderensis Felder, 1862*
Gonepteryx rhamni (Linnaeus, 1758)
Lycaenidae
Riodinidae
Hamearis lucina (Linnaeus, 1758)
Lycaeninae
Aricia agestis (Schiffermüller, 1775)
Aricia anteros (Freyer, 1839)
Aricia artaxerxes (*allous*) (Fabricius, 1793)
Aricia cramera (Eschscholtz, 1821)
Aricia eumedon (Esper, 1780)
Aricia montensis (Verity, 1928)
Aricia morronensis (Ribbe, 1910)
Aricia nicias (Meigen, 1830)
Azanus ubaldus (Cramer, 1782)
Azanus jesous (Guérin-Méneville, 1849)
Cacyreus marshalli (Butler, 1898)
Callophrys avis Chapman, 1909
Callophrys rubi (Linnaeus, 1758)
Celastrina argiolus (Linnaeus, 1758)
Chilades galba (Lederer, 1855)
Chilades trochylus (Freyer, 1844)
Cigaritis acamas (Klug, 1834)
Cupido alcetas (Hoffmansegg, 1804)
Cupido argiades (Pallas, 1771)
Cupido carswelli Stempffer, 1927
Cupido decoloratus (Staudinger, 1886)
Cupido lorquinii (Herrich-Schäffer, 1847)
Cupido minimus (Fuessly, 1775)

continued
Cupido osiris (Meigen, 1829)
Deudorix livia (Klug, 1834)
Cyclirius webbianus (Brulle, 1840)*
Favonius quercus (Linnaeus, 1758)
Glaucopsyche alexis (Poda, 1761)
Glaucopsyche melanops (Boisduval, 1828)
Glaucopsyche paphos (Chapman, 1920)*
Iolana iolas (Ochsenheimer, 1816)
Laeosopis roboris (*evippus*) (Esper, 1793)
Lampides boeticus (Linnaeus, 1767)
Leptotes pirithous (Linnaeus, 1767)
Lycaena alciphron (Rottemburg, 1775)
Lycaena candens (Herrich-Schäffer, 1844)
Lycaena dispar (Haworth, 1803)
Lycaena helle (Schiffermüller, 1775)
Lycaena hippothoe (Linnaeus, 1761)
Lycaena ottomana (Lefebvre, 1830)
Lycaena phlaeas (Linnaeus, 1761)
Lycaena thersamon (Esper, 1784)
Lycaena thetis (Klug, 1834)
Lycaena tityrus (*bleusei*) (Poda, 1761)
Lycaena virgaureae (Linnaeus, 1758)
Maculinea alcon (Schiffermüller, 1775)
Maculinea arion (Linnaeus, 1758)
Maculinea nausithous (Bergsträsser, 1779)
Maculinea teleius (Bergsträsser, 1779)
Plebejus aquilo (Boisduval, 1832)
Plebejus argus (Linnaeus, 1758)
Plebejus argyrognomon (Bergsträsser, 1779)
Plebejus bellieri (*corsicus, villai*) (Oberthür, 1910)*
Plebejus dardanus (Freyer, 1832)
Plebejus eurypilus (Freyer, 1852)
Plebejus glandon (Prunner, 1798)
Plebejus hespericus (Rambur, 1839)
Plebejus idas (Linnaeus, 1761)
Plebejus loewii (Zeller, 1847)
Plebejus optilete (Knoch, 1781)
Plebejus orbitulus (Prunner, 1798)
Plebejus psyloritus (Freyer, 1845)*
Plebejus pylaon (*sephirus*) (Fischer, 1832)
Plebejus pyrenaicus (Boisduval, 1840)
Plebejus trappi (Verity, 1927)
Plebejus zuellichi (Hemming, 1933)
Polyommatus admetus (Esper, 1785)
Polyommatus ainsae (Forster, 1961)
Polyommatus albicans (Herrich-Schäffer, 1851)
Polyommatus amandus (Schneider, 1792)
Polyommatus aroaniensis (Brown, 1976)
Polyommatus bellargus (Rottemburg, 1775)
Polyommatus caelestissimus (Verity, 1921)

continued

Polyommatus coelestinus (Eversmann, 1848)
Polyommatus coridon (*asturiensis*) (Poda, 1761)
Polyommatus damon (Schiffermüller, 1775)
Polyommatus daphnis (Schiffermüller, 1775)
Polyommatus dolus (*virgilius, fulgens*) (Hübner, 1823)
Polyommatus dorylas (Schiffermüller, 1775)
Polyommatus eroides (Frivaldszky, 1835)
Polyommatus eros (Ochsenheimer, 1808)
Polyommatus escheri (Hübner, 1823)
Polyommatus exuberans (Verity, 1926)
Polyommatus fabressei (Oberthür, 1910)
Polyommatus galloi (Balletto & Toso, 1979)
Polyommatus gennargenti (Leigheb, 1987)*
Polyommatus golgus (Hübner, 1813)
Polyommatus hispanus (Herrich-Schäffer, 1851)
Polyommatus humedasae (Toso & Balletto, 1976)
Polyommatus icarus (Rottemburg, 1775)
Polyommatus iphigenius (Herrich-Schäffer, 1847)
Polyommatus menalcas (Freyer, 1837)
Polyommatus nephohiptamenos (Brown & Coutsis, 1978)
Polyommatus nivescens (Keferstein, 1851)
Polyommatus ripartii (Freyer, 1830)
Polyommatus semiargus (*helena*) (Rottemburg, 1775)
Polyommatus thersites (Cantener, 1834)
Satyrium acaciae (Fabricius, 1787)
Satyrium esculi (Hübner, 1804)
Satyrium ilicis (Esper, 1779)
Satyrium ledereri (Boisduval, 1848)
Satyrium pruni (Linnaeus, 1758)
Satyrium spini (Schiffermüller, 1775)
Satyrium w-album (Knoch, 1782)
Scolitantides abencerragus (Pierret, 1837)
Scolitantides barbagiae (Prins & Poorten, 1982)*
Scolitantides baton (Bergsträsser, 1779)
Scolitantides bavius (Eversmann, 1832)
Scolitantides orion (Pallas, 1771)
Scolitantides panoptes (Hübner, 1813)
Scolitantides vicrama (*schiffermulleri*) (Moore, 1865)
Tarucus balcanicus (Freyer, 1845)
Tarucus theophrastus (Fabricius, 1793)
Thecla betulae (Linnaeus, 1758)
Tomares ballus (Fabricius, 1787)
Tomares nogelii (Herrich-Schäffer, 1852)
Turanana endymion (*panagea*) (Herrich-Schäffer, 1852)
Zizeeria knysna (Trimen, 1862)
Nymphalidae
Libytheinae
Libythea celtis (Laicharting, 1782)
Heliconiinae
Argynnis adippe (Schiffermüller, 1775)

continued

Argynnis aglaja (Linnaeus, 1758)
Argynnis elisa (Godart, 1823)*
Argynnis niobe (Linnaeus, 1758)
Argynnis pandora (Schiffermüller, 1775)
Argynnis paphia (Linnaeus, 1758)
Argyronome laodice (Pallas, 1771)
Boloria aquilonaris (Stichel, 1908)
Boloria chariclea (Schneider, 1794)
Boloria dia (Linnaeus, 1767)
Boloria eunomia (Esper, 1799)
Boloria euphrosyne (Linnaeus, 1758)
Boloria freija (Becklin, 1791)
Boloria frigga (Becklin, 1791)
Boloria graeca (Staudinger, 1870)
Boloria improba (Butler, 1877)
Boloria napaea (Hoffmansegg, 1804)
Boloria pales (Schiffermüller, 1775)
Boloria polaris (Boisduval, 1829)
Boloria selene (Schiffermüller, 1775)
Boloria thore (Hübner, 1806)
Boloria titania (Esper, 1793)
Brenthis daphne (Bergsträsser, 1780)
Brenthis hecate (Schiffermüller, 1775)
Brenthis ino (Rottemburg, 1775)
Issoria lathonia (Linnaeus, 1758)
Nymphalinae
Araschnia levana (Linnaeus, 1758)
Euphydryas aurinia (Rottemburg, 1775)
Euphydryas cynthia (Schiffermüller, 1775)
Euphydryas desfontainii (Godart, 1819)
Euphydryas glaciegenita Verity, 1928
Euphydryas iduna (Dalman, 1816)
Euphydryas intermedia (Ménétriés, 1859)
Euphydryas maturna (Linnaeus, 1758)
Hypolimnas misippus (Linnaeus, 1764)
Melitaea aetherie (Hübner, 1826)
Melitaea arduinna (Esper, 1784)
Melitaea asteria (Freyer, 1828)
Melitaea athalia (Rottemburg, 1775)
Melitaea aurelia (Nickerl, 1850)
Melitaea britomartis (Assmann, 1847)
Melitaea cinxia (Linnaeus, 1758)
Melitaea deione (Geyer, 1832)
Melitaea diamina (Lang, 1789)
Melitaea didyma (Esper, 1779)
Melitaea nevadensis (Oberthür, 1904)
Melitaea parthenoides (Keferstein, 1851)
Melitaea phoebe (*emipunica*) (Schiffermüller, 1775)
Mellicta trivia (Schiffermüller, 1775)
Mellicta varia (Meyer-Dür, 1851)

continued

Nymphalis antiopa (Linnaeus, 1758)
Nymphalis c-album (Linnaeus, 1758)
Nymphalis egea (Cramer, 1775)
Nymphalis ichnusa (Bonelli, 1826)*
Nymphalis io (Linnaeus, 1758)
Nymphalis l-album (Esper, 1780)
Nymphalis polychloros (Linnaeus, 1758)
Nymphalis urticae (Linnaeus, 1758)
Nymphalis xanthomelas (Esper, 1781)
Vanessa atalanta (Linnaeus, 1758)
Vanessa cardui (Linnaeus, 1758)
Vanessa virginiensis (Drury, 1773)
Vanessa vulcania (*indica*) (Godart, 1819)*
Limenitinae
Limenitis camilla (Linnaeus, 1764)
Limenitis populi (Linnaeus, 1758)
Limenitis reducta (Staudinger, 1901)
Neptis rivularis (Scopoli, 1763)
Neptis sappho (Pallas, 1771)
Charaxinae
Charaxes jasius (Linnaeus, 1767)
Apaturinae
Apatura ilia (Schiffermüller, 1775)
Apatura iris (Linnaeus, 1758)
Apatura metis (Freyer, 1829)
Thaleropis ionia (Eversmann, 1851)
Satyrinae
Aphantopus hyperantus (Linnaeus, 1758)
Coenonympha arcania (Linnaeus, 1761)
Coenonympha corinna (Hübner, 1806)*
Coenonympha dorus (Esper, 1782)
Coenonympha elbana (Staudinger, 1901)*
Coenonympha gardetta (Prunner, 1798)
Coenonympha glycerion (Borkhausen, 1788)
Coenonympha hero (Linnaeus, 1761)
Coenonympha iphioides Staudinger, 1870
Coenonympha leander (Esper, 1784)
Coenonympha oedippus (Fabricius, 1787)
Coenonympha pamphilus (Linnaeus, 1758)
Coenonympha rhodopensis Elwes, 1900
Coenonympha thyrsis (Freyer, 1846)*
Coenonympha tullia (Müller, 1764)
Erebia aethiopella (Hoffmansegg, 1806)
Erebia aethiops (Esper, 1777)
Erebia alberganus (Prunner, 1798)
Erebia arvernensis (*carmenta*) Oberthür, 1908
Erebia calcaria Lorkovic, 1953
Erebia cassioides (Reiner & Hohenwarth, 1792)
Erebia christi Rätzer, 1890
Erebia claudina (Borkhausen, 1789)

continued

Erebia disa (Becklin, 1791)
Erebia embla (Becklin, 1791)
Erebia epiphron (Knoch, 1783)
Erebia epistygne (Hübner, 1819)
Erebia eriphyle (Freyer, 1836)
Erebia euryale (Esper, 1805)
Erebia flavofasciata Heyne, 1895
Erebia gorge (Esper, 1805)
Erebia gorgone Boisduval, 1833
Erebia hispania Buttler, 1868
Erebia lefebvrei Boisduval, 1828
Erebia ligea (Linnaeus, 1758)
Erebia manto (Schiffermüller, 1775)
Erebia medusa (Schiffermüller, 1775)
Erebia melampus (Fuessli, 1775)
Erebia melas (Herbst, 1796)
Erebia meolans (Prunner, 1798)
Erebia mnestra (Esper, 1805)
Erebia montana (Prunner, 1798)
Erebia neoridas (Boisduval, 1828)
Erebia nivalis Lorkovic & de Lesse, 1954
Erebia oeme (Esper, 1805)
Erebia orientalis Elwes, 1900
Erebia ottomana (Herrich-Schäffer, 1847)
Erebia palarica Chapman, 1905
Erebia pandrose (Borkhausen, 1788)
Erebia pharte (Hübner, 1804)
Erebia pluto (Prunner, 1798)
Erebia polaris Staudinger, 1861
Erebia pronoe (Esper, 1780)
Erebia rhodopensis Nicholl, 1900
Erebia scipio Boisduval, 1832
Erebia sthennyo Graslin, 1850
Erebia stiria (Godart, 1824)
Erebia styx (Freyer, 1834)
Erebia sudetica Staudinger, 1861
Erebia triaria (Prunner, 1798)
Erebia tyndarus (Esper, 1781)
Erebia zapateri Oberthür, 1875
Hipparchia actaea (Esper, 1780)
Hipparchia algirica (Oberthür, 1876)
Hipparchia anthelea (Lefebvre, 1831)
Hipparchia arethusa (Schiffermüller, 1775)
Hipparchia aristaeus (Bonelli, 1826)*
Hipparchia azorina (Strecker, 1899)*
Hipparchia bacchus Higgins, 1967*
Hipparchia blachieri (*balletoi, neapolitana*) (Frühstorfer, 1908)
Hipparchia briseis (Linnaeus, 1764)
Hipparchia christenseni Kudrna, 1977*
Hipparchia cingovskii (Gross, 1973)

continued

Hipparchia circe (Fabricius, 1775)
Hipparchia cretica (Rebel, 1916)*
Hipparchia cypriensis (Holik, 1949)*
Hipparchia dryas (Scopoli, 1763)
Hipparchia fagi (Scopoli, 1763)
Hipparchia fatua (Freyer, 1845)
Hipparchia ferula (Fabricius, 1793)
Hipparchia fidia (Linnaeus, 1767)
Hipparchia geyeri (Herrich-Schäffer, 1845)
Hipparchia gomera Higgins, 1967*
Hipparchia graeca (Staudinger, 1870)
Hipparchia hermione (*alcyone*) (Linnaeus, 1764)
Hipparchia leighebi Kudrna, 1976*
Hipparchia maderensis (Bethune-Baker, 1891)*
Hipparchia mersina (Staudinger, 1871)
Hipparchia miguelensis (Le Cerf, 1935)*
Hipparchia neomiris (Godart, 1823)*
Hipparchia orestes (Prins & Poorten, 1981)
Hipparchia pellucida (Stauder, 1923)
Hipparchia prieuri (Pierret, 1837)
Hipparchia sbordonii Kudrna, 1984*
Hipparchia semele (Linnaeus, 1758)
Hipparchia senthes (Frühstorfer, 1908)
Hipparchia statilinus (Hufnagel, 1766)
Hipparchia syriaca (Staudinger, 1871)
Hipparchia tamadabae Owen and Smith 1992*
Hipparchia tilosi (Manil, 1984)*
Hipparchia tisiphone (Brown, 1980)
Hipparchia volgensis (Mazochin-Porshnyakov, 1952)
Hipparchia williamsi (Romei, 1927)
Hipparchia wyssii (Christ, 1889)*
Maniola bathseba (Fabricius, 1793)
Maniola cecilia (Vallantin, 1894)
Maniola chia (Thomson, 1987)*
Maniola cypricola (Graves, 1928)*
Maniola halicarnassus (Thomson, 1990)*
Maniola jurtina (Linnaeus, 1758)
Maniola lupina (Costa, 1836)
Maniola lycaon (Kühn, 1774)
Maniola megala (Oberthür, 1909)
Maniola nurag (Ghiliani, 1852)*
Maniola telmessia (Zeller, 1847)
Maniola tithonus (Linnaeus, 1771)
Melanargia arge (Sulzer, 1776)
Melanargia galathea (Linnaeus, 1758)

continued

Melanargia ines (Hoffmansegg, 1804)
Melanargia lachesis (Hübner, 1790)
Melanargia larissa (Esper, 1784)
Melanargia occitanica (Esper, 1793)
Melanargia pherusa (Boisduval, 1833)*
Melanargia russiae (Esper, 1784)
Oeneis bore (Schneider, 1792)
Oeneis glacialis (Moll, 1785)
Oeneis jutta (Hübner, 1806)
Oeneis norna (Becklin, 1791)
Pararge achine (Linnaeus, 1763)
Pararge aegeria (Linnaeus, 1758)
Pararge climene (Esper, 1784)
Pararge maera (Linnaeus, 1758)
Pararge megera (Linnaeus, 1767)
Pararge paramegaera (Hübner, 1824)*
Pararge petropolitana (Fabricius, 1787)
Pararge roxelana (Cramer, 1777)
Pararge xiphia (Fabricius, 1775)*
Pararge xiphioides (Staudinger, 1871)*
Proterebia afra (Fabricius, 1787)
Ypthima asterope (Klug, 1832)
Danainae
Danaus chrysippus (Linnaeus, 1758)
Danaus plexippus (Linnaeus, 1758)

* Island endemic species. Nomenclature from Kudrna (2002)

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ORIGINAL PAPER

Island size is not the only consideration. Ranking priorities for the conservation of butterflies on Italian offshore islands

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Abstract Ecological and historical factors virtually create a unique faunal assemblage on each island. From this perspective every island deserves protection. However, economic limitations usually restrict conservation efforts to particularly important areas. As part of the SLOSS issue (the relative importance of single large or several small areas), there is the long debated question of whether it is better to protect few large areas (islands) or several small areas (islands). Here, we assess the butterfly faunas of the Italian offshore islands, using several biodiversity measures, in order to highlight priorities for conserving butterfly richness, rarity and endemicity. First, the nested pattern of butterfly fauna was investigated to determine the relative importance of large and small islands. Then, residuals were assessed for the species-area relationship and for multiple regressions of richness, rarity and endemicity against geographic variables. Subsequently, two other indices were calculated: Biodiversity Conservation Concern and an index scoring islands in the order that maximizes the cumulative percentage of total, endemic, and rare species. The results clearly indicate that although greatest concern is for the island having the largest butterfly fauna in the sample (Elba), the importance of several small islands should not be ignored. This is primarily due to the substantial impact of source areas and consequently the occurrence of several rare and endemic species occurring on small islands as well as on large islands.

Keywords Butterflies · Endemicity · Italian islands · Nestedness · Rarity · SLOSS question · Species area relationship

Introduction

Faunal assemblages on islands are the result of a number of factors underlying island geography (area, latitude, altitude, isolation) and island ecology (geology, biotope availability, land use, management), but also to the biological characteristics of the organisms being considered (mobility, colonization capability) and their occurrence at island sources. Historical factors may also play important roles in determining which species occur on islands, generating diversity with long term-isolation (MacArthur and Wilson 1967; Simberloff 1974; Williamson 1981; Whittaker 1998; Lomolino 2000; Heaney 2007). In effect, island faunas can be considered as "individuals" carrying unique information belonging to a complex interaction of concurrent factors. The individuality of island faunas is evident from the morphological, ecological and genomic differences among closely related taxa inhabiting different islands (Brock and Adsersen 2007; Ryan et al. 2007; Dapporto in press). These differences retain, in depth, information on island biogeography: ecological differentiation and speciation mechanisms (e.g. Darwin's finches; Ryan et al. 2007). From this perspective the composite biotic characteristics of islands deserve protection. However, economic limitations (conservation load, broad and

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local scale economic strategies) often press for a selection of islands where conservation effort can be focused. Such conservation priorities should be identified so that financial resources when available can be allocated in the most effective way to preserve the largest fraction of biodiversity.

Island conservation often contrasts with local economic strategies, particularly in the Mediterranean area, where island economy is mainly driven by income from tourism. Accordingly, conservation measures are frequently focused on small and isolated islands where economic pressures are low. This directive is encouraged and motivated by the observation of spectacular radiation observed on small and remote oceanic islands. However, as Whittaker (1998) has pointed out, processes operating on islands are scale and location dependent. Specifically, he predicted that speciation may occur only on very isolated islands (the oceanic ones) but in less isolated areas (such as those of Mediterranean Sea) other processes are involved (Dennis et al. 1991). Indeed, here the faunal characteristics of flying insects are mainly determined by contemporary factors, and isolated and small islands often tend to be inhabited only by few, widespread species (Dennis et al. 2000; Fattorini 2006; Dapporto and Cini 2007; Dapporto et al. 2007; Dapporto and Dennis 2008). This is probably owing to the fact that distances separating islands and mainland in the Mediterranean basin are generally small compared to the flying capabilities of insects (Dennis et al. 2000). By comparison, large and less isolated islands often hold more interest for insect conservation (Dennis et al. 2000; Fattorini 2006; Dapporto and Cini 2007).

These considerations evoke the SLOSS issue (i.e. is it better to preserve a single large or several small islands? Wilson and Willis 1975; Rosenzweig 2004). There is one situation only in which, apparently, the answer is unequivocal and that is, when the insular populations are so perfectly nested that small island faunas form exact subsets of larger ones. In this situation, protecting the largest fauna will protect all the species in the sample with the benefit of larger population size within a larger area (Fischer and Lindenmayer 2005). As perfect nestedness is unlikely, the SLOSS issue deserves individual attention so that specific factors can be investigated. Lomolino (1994) and Rosenzweig (2004) have reviewed this topic for a large number of taxa and archipelagos; they discovered no common agent(s), each case suggesting a different strategy to be pursued. Thus, it is possible to answer the SLOSS question for a specific taxon and specific area but only by investigating several aspects of island biogeography including characteristics of species' assemblages.

The conservation value of areas and islands is often assessed on the basis of species' richness (Mittermeier et al. 1999). However, it is well known that the simple species-area relationship does not necessarily, entirely characterise conservation interest. Recent studies have focused on residuals of the species-area relationship (SAR) to find particularly rich areas and islands (Ulrich and Buszko 2005; Fattorini 2007). However, this approach is also probably simplistic, at least for Mediterranean butterflies. Indeed, island area is not the only predictor, and often not the most important, for butterfly richness in the Mediterranean region (Dennis et al. 2000; Dapporto and Dennis 2008). Thus, the residuals from SAR should probably be related to other determinants (isolation, island altitude, source richness) underlying island biogeography and influencing their faunas.

An island's species are not just a stochastic subset of source species; species differ for migration and colonisation capacity and this reflected in their ecological traits (Dapporto and Dennis 2008). Some species that are common at sources are absent or rare on islands and vice versa; consequently, rarity on islands may not correspond to rarity at neighbouring mainland sources. The usual way of viewing this considers that island faunas depend on mainland sources. But, this process can be reversed, as predicted by metapopulation models, and a two-way exchange occurs (Heaney 2007). Comparison of species' incidences on islands and mainland is a useful measure of the island-mainland relationship. Isolation has produced endemic species or subspecies on several islands and island groups that, owing to their uniqueness, should play a decisive role in determining conservation efforts. Thus, from the perspective of island-source comparisons, richness is not the only parameter that should drive conservation decisions.

Herein, we present practical guidelines, based on several measures, for the promotion of priorities in conserving butterfly diversity (richness, rarity and endemicity) on Italian offshore islands. In particular, we examine the notion that protection of the larger islands is to be preferred over the protection of smaller ones. We do this by studying nestedness among islands, using the approach of Rosenzweig (2004), and by scoring the Italian offshore islands for five different indices of conservation value. In determining priorities for conservation we establish which index is able to protect the larger part of biodiversity over the smallest total area. Finally, we investigate whether the present conservation efforts in these islands are directed towards the most important areas for preserving the insular faunas of butterflies in the Tyrrhenian area.

Material and methods

Additions and revisions have been made to data for butterflies on Italian offshore islands published in Dapporto and Dennis (2008) from new collections and more recently published work (Volpe and Palmieri 2006). The islands selected for study include at least four of five well-known, migrant species (*Pieris brassicae* Linnaeus, *Pieris rapae* Linnaeus, *Colias crocea* Fourcroy, *Vanessa atalanta* Linnaeus and *Vanessa cardui* Linnaeus). These species are highly visible, they occur throughout Europe during the summer season and records for them can be used to establish a minimal surveying standard for islands inasmuch as they are expected to be recorded with repeated visits to islands (see Dennis and Shreeve 1996, 1997; Dennis et al. 2000). Endemic species were defined as those taxa (species) restricted to the Italian Peninsula, Sardinia-Corsica, Sicily, and/or to one or more of the smaller circum-Italian islands. Nomenclature for taxa is derived from Balletto et al. (2005). For each island the following geographical characteristics were considered: area (km^2, A), maximum altitude (m, A_L), the shortest over-water distance from the nearest larger source area (island or mainland, km, I), latitude (L_T), and longitude (L_G). We considered as "source faunas" the butterflies recorded in the 50x50 km UTM land squares nearest to each island (Dapporto and Dennis, 2008). Richness is simply the number of species on an island (S). Rarity of species on islands (R) was determined as:

$$R = 1 - \left[\left(\sum_{i=1,j} p_i\right) / S\right]$$

where S = island richness, $p_i = n_i/N$, for i … j species, and n (occupied islands) $\leq$N (number of studied islands), the value of R ranging from 0 to 1 (Dennis et al. 2000). In effect, this is an inverse measure of the mean for the proportions of islands occupied by species. Endemicity of island species (E) was scored for each island and mainland area (S_E) as the number of species defined as being endemic on islands or their sources. The equivalent measures of richness, rarity and endemicity for sources are labelled S_S, S_R and S_E respectively. Number of island species (S), island area (A), island isolation (I), island altitude (A_L), island latitude (L_T) and longitude (L_G), and number of source species (S_S) were log transformed, and the proportion measures for island rarity (R) and source rarity (S_R) were arcsine transformed. Data for all the islands are summarised in Appendix1.

Nestedness

Nestedness is the tendency of smaller faunas to represent a subset of the species in larger faunas. There are several indices of nestedness. The first and most popular is matrix temperature (NTC, Patterson and Atmar 1986). This index provides an entropy value ranging from 0° (perfectly nested matrix) to 100° (perfectly disordered matrix). The significance of matrix temperature is tested by a Monte Carlo model. Ulrich and Gotelli (2007) recently revised the nestedness computation and provided a program (Ulrich 2006) calculating eight different indices. Among the eight indices, the matrix temperature metric did not have good statistical properties. According to their suggestions we used the Brualdi and Sanderson discrepancy index (Brualdi and Sanderson 1999) tested with a fixed-fixed null model that provides a conservative test for nestedness. The null model algorithm based on Monte Carlo random generation of matrices results in a standardized size effect as a Z transformed score

$$Z = [BR - \mu] / \sigma$$

where BR = observed index value, μ = mean from the simulation matrices and σ = standard deviation of the simulation matrices ($Z > |2|$, $P < 0.05$). Since islands have been selected on the basis of the presence of four of five immigrants, all the selected islands include combinations of these species. This may create a false nestedness signal. To avoid such a problem we removed the five immigrants from the nestedness analysis. Nestedness assessment may also be biased if the sample contains groups of islands with different pools of potential species. This is likely to occur in the Italian islands as there are at least two distinct geographical groups, (i) the islands potentially sourced by Sardinia and Corsica and (ii) the islands sourced by the Italian Peninsula and Sicily. Thus, we additionally performed two separate nestedness analyses for the two different island groups.

The combined area approach

Rosenzweig (2004) devised a method to examine the SLOSS issue. He predicted that if SLOSS made no difference, then the overall species number of an island group would equal the number of species in a large virtual island whose area equalled that of all combined islands. Following Rosenzweig (2004) we have investigated the log(S)–log(A) Species-Area Relationship (SAR) for the Italian islands and have calculated species' richness for the virtual, combined island based on this relationship. Rosenzweig (2004) argued that if the actual number of species present in the sample exceeds the number of species predicted in the virtual island, then several small islands would perform better than one large island and vice versa.

Analyses of regression residuals

Residuals from SAR in butterfly data were recently reviewed by Fattorini (2007). He suggested that regressions from the curvilinear power function $S = CA^Z$ give the best fit compared to other functions. This algorithm has been used to calculate the residuals for each island.

Additionally, we have obtained the residuals from island richness, rarity, and endemicity from multiple regression analyses. Source richness (S_S), source rarity (S_R), and number of endemics at source (S_E) respectively and the five geographical variables (island area A, altitude A_L, isolation I, latitude L_T, longitude L_G) were entered as independent variables (Dapporto and Dennis 2008). Then, for each island in each analysis (richness, rarity, and endemicity) we have calculated the differences between the regression residual and the upper value for the 95% confidence interval. Subsequently, only islands having positive values are regarded as having high residual values. Following Ulrich and Buszko (2005) we have constructed graphs in which residual values for richness, rarity, and endemicity are plotted in a two dimensional space. This uses a zero index marker (the upper 95% of confidence value) to divide the graphs into four groups (classes); important areas for conservation can then be highlighted. We also calculated the standardized residuals for richness, rarity and endemicity by treating their sum as a residual index (MRRes).

Biodiversity Conservation Concern (BCC)

Fattorini (2006) introduced this index to rank areas according to their conservation value. This index combines the conservation value of each species belonging to a given species' assemblage with total species richness. Fattorini (2006) argued that species are not equally threatened and the contribution of imperilled species cannot be regarded as their simple number or percentage, but it should be evaluated by increasingly weighting species according to their different risk of extinction.

The BCC can be calculated as

$$\mathrm{BCC} = \frac{\sum_{i=1}^{k} \frac{\alpha_i A_i}{N} - 1}{\alpha_{\max} - 1}$$

where α_i is the weight assigned to the ith category of endangerment, and A_i the number of species in the category αi. N is the total island richness.

This formulation ensures the index ranges from 0 (all species belonging to the lower conservation categories, $\alpha_i = 1$; i.e. Least Concern in the IUCN system) to 1 (all species belonging to the highest endangerment category, $\alpha_{\max}$). Fattorini scored species on the basis of the IUCN categories reported in van Swaay and Warren (1999) for Europe and on the basis of local red lists. However, van Swaay and Warren (1999) class very few species present in Italian offshore islands to IUCN categories and local red lists are not based on objective criteria (see Sforzi and Bartolozzi, 2001 for Tuscany mainland and islets). Therefore, we have decided to categorize species on the basis of their endemic status and their predictability for islets. Island endemics clearly rank as the most important species in island conservation and are given the highest values ($\alpha = 5$). Some species are endemic to some islets and limited parts of mainland areas; these were given the score $\alpha = 4$. Dapporto and Dennis (2008) demonstrated that occurrence for butterflies on Italian islets can be predicted on the basis of ecological traits (mostly related to species' colonization capability). However, a number of species present on islands were not predicted to occur there, suggesting that these species are less likely to re-colonize islands when extinct. From this may be inferred their conservation status and we scored them as $\alpha = 3$. Additionally islets are inhabited by several species that are endemic to wider source areas. As islands may represent valuable refuges for species endemic to wider regions when mainland areas are under anthropic pressure we scored these species as $\alpha = 2$. All other species are scored as $\alpha = 1$.

Assessing the performance of the indices in capturing biodiversity and the species accumulation approach

As suggested by Fischer and Lindenmayer (2005) the performance of a conservation index can be visualised by inserting the islands in decreasing order of the index value and calculating at each step the cumulative percentage of the total, endemic, and rare species (considered as those species occurring on one or two islands only) included in the islands; this is done for residuals from SAR, sum of standardized residuals and BCC index. The product is a set of cumulative percentage graphs for the islands.

These graphs include a further comparison. We searched for the island order that, at each step, maximizes the cumulative percentage of total, endemic, and rare species. The order of entering has been scored from 31 (the first inserted island) to 1. When islands shared a rank we selected for that step the smallest island.

Finally, tests of association among the three indexes were carried out using Pearson Correlation. Multiple stepwise regression analyses were used to determine which log-transformed island characteristics (area, isolation altitude, longitude, latitude, source richness) are most related to the four conservation indexes.

Assessment of current conservation measures for the Italian islets

We scored the current conservation measures for each island as follows (CL, Table 1):

Level 1: Islands completely (or mostly) protected; number of visitors per year curtailed.
Level 2: Islands with extensive protected areas; no curtailment of visitors.

Level 3: Islands largely unprotected; no curtailment of visitors.

The values for each conservation index were ranked from 1 (the lowest value in the sample) to 31 (the highest one) and combined. Relationships between current conservation ranking and the conservation indices were tested using the Kruskal–Wallis test and differences sought between islands associated with three areas (Italian Peninsula, Sardinia and Sicily). For this, Malta (a separate country) was included with Sicily and Montecristo and Capraia (being administratively part of Tuscany) with the Italian mainland sample.

Results

Nestedness

The frequency distribution for the 86 species found on Circum-Italian islands shows that a large proportion (30, 34.9%) of them occur on only one or two islands (Fig. 1). The Brualdi and Sanderson index, verified with a fixed-fixed null model, revealed a significant nested pattern (BR = 174, $\mu = 162.06$, $\sigma = 4.48$, Z = 2.67). However, the matrix temperature for all the 31 islands was rather high (T = 11.28°) because of numerous unexpected presences and absences. In particular, very high individual temperature values were scored by species endemic to or restricted to only one source (eight of the ten species having highest individual temperatures). Sub samples of Italian-Sicilian (BR = 96, $\mu = 99.49$, $\sigma = 3.74$, Z = −0.93) and Sardo-Corsican islands (BR = 32, $\mu = 30.02$, $\sigma = 1.84$, Z = 1.08) did not show significantly nested patterns. The Italian-Sicilian islands have a much lower temperature (10.82°) than the Sardo-Corsican islands (23.49°).

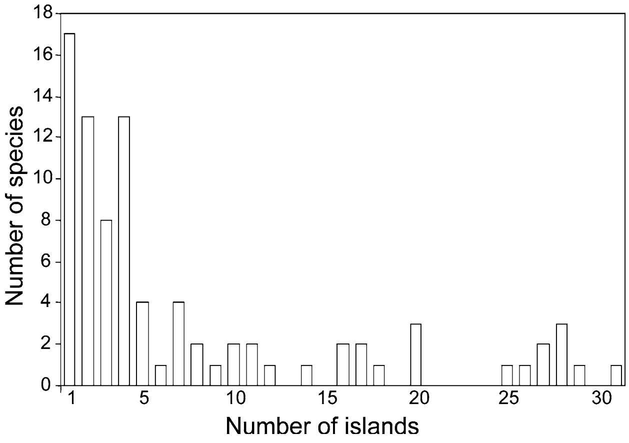

Fig. 1 Occurrence of the 86 butterfly species on the 31 Italian offshore islands studied

The combined virtual island approach

Regression analysis revealed a significant relationship between LogA and LogS ($\beta = 0.545$, $R^2 = 0.30$, $P = 0.001$). The number of species predicted for the virtual large island having an area of 1238 km^2 is 44 (Fig. 2), that is, about half of the actual number of species known for the whole island group (86). The contribution of several small islands is double that of a single island of the same area.

Analyses of residuals from multiple regressions

Nonlinear regression based on the power function revealed the following relationship:

$$S = 13.79A^{0.148}$$

Six islands have particularly rich faunas (Elba, Giglio, M. Argentario, Vivara, Ischia, Capri, Fig. 3, Table 1). These islands are nearest to the richest source area (the Italian mainland). The R^2 value (0.14) is quite low, thus suggesting that the largest part of variance is probably explained by other island characteristics. Multiple regression revealed similar results to those reported in Dapporto and Dennis (2008) based on a similar dataset. Richness was positively correlated with source richness (S_S) ($\beta = 0.528$; $R^2 = 0.19$, $P < 0.001$) and island area (A) ($\beta = 0.537$; $R^2 = 0.16$, $P < 0.001$), and negatively correlated with distance from the nearest source (I) ($\beta = -0.515$; $R^2 = 0.25$, $P < 0.001$) (model $F = 13.05$, $P < 0.001$ Fig. 4a, Table 1). Multiple regression disclosed a similar result for rarity which is negatively correlated with distance to the nearest source (I) ($\beta = -0.545$; $R^2 = 0.15$, $P < 0.001$) and positively with area (A) ($\beta = 0.421$; $R^2 = 0.17$, $P = 0.004$) and source

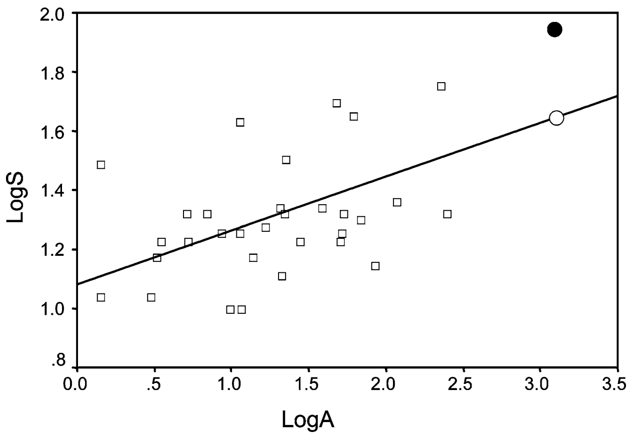

Fig. 2 Regression of log transformed richness (LogS) on area (LogA). The open circle represents the predicted richness value for a virtual island having an area corresponding to the sum of all the islands in the sample. The black circle represents the richness value (86) for which the choice of a single large or several small islands makes no difference

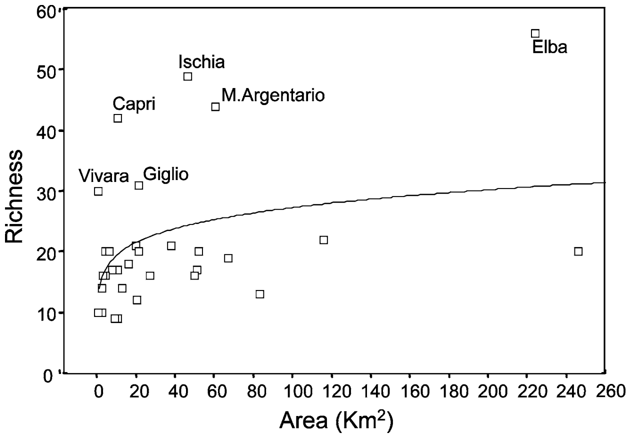

Fig. 3 Non-linear regression between island area and richness. Islands having high positive residuals are indicated

rarity (S_R) ($\beta = 0.525$; $R^2 = 0.21$, $P = 0.001$) (model $F = 13.51$, $P < 0.001$ Fig. 4b, Table 1). The number of endemic species correlated only with number of endemic species at source ($\beta = 0.657$; $R^2 = 0.43$, $P = 0.001$, model $F = 22.00$, $P < 0.001$ Fig. 4c, Table 1).

Some islands have positive residuals higher than the upper 95% confidence interval in all the three analyses (Fig. 4 a–c, Table 1). Observed values higher than the 95% confidence limits were plotted for pairs of characteristics; in the plots, residuals for richness and rarity were found to be strongly correlated (Fig. 4d). This may be only partially due to the weak nested pattern (underlying that, the richest islands also contain more rare species) but more probably to the tendency of dimensionless ratio measures to be correlated with their original variables (Nee et al. 2005). Six islands have positive residuals for richness and rarity (Tavolara from the Sardinian group, Ischia, Capri, Capraia, Giglio and Elba from Italian mainland). Some Sardinian islands and Elba and Giglio among the Italian mainland islands have higher endemicity than predicted (Fig. 4c). Endemicity-richness and endemicity-rarity have a similar trend indicating Tavolara, Capraia, Giglio and Elba to be the most important group for both endemicity-richness and endemicity-rarity (Fig. 4d, e).

By summing the standardized residuals of richness, rarity and endemicity (variable MRRes) a single value for each island was obtained. Among the top ten islands for MRRes, three were from the Sardinian group (Tavolara, Capraia, Spargi), six from the Italian mainland group (Ischia, Giglio, Elba, Capri, M. Argentario, Vivara), and one from the Sicilian group (Malta) (Table 1).

Biodiversity Conservation Concern (BCC)

The BCC index revealed a similar trend in scoring the conservation importance of islands as the pattern of residuals (above). Indeed, the most highly ranked islands from the previous analysis have high conservation priority on this index. Among the first ten islands four belong to the Sardinian group (Tavolara, S. Maria, Spargi, Caprera), four to Italian mainland group (Elba, Ponza, M. Argentario, Ischia) and two to the Sicilian group (Stromboli and Salina).

Assessing the performance of the indices in capturing biodiversity and the species accumulation approach

When cumulative curves of total, rare, and endemic species are obtained for islands in order of richness, there is a rapid increase in the number of species and rare species but not endemic species (Fig. 5a). The whole set of species is captured with the first 18 islands; 80% of richness, rarity and endemicity is captured by 3, 5 and 9 islands, respectively. The pattern was similar, but the gradient weaker for SAR residuals (Fig. 5b); 100% of species is captured by 25 islands and 80% of richness, rarity and endemicity in 4, 6, 14 islands respectively. The BCC (Fig. 5c) index revealed an opposite pattern, rapidly accumulating endemic species (more than richness) compared to rare ones; 100% of species is captured by 27 islands and the 80% of richness, rarity and endemicity in 9, 7, 10 islands respectively. Residuals from multiple regressions showed a similar trend for the three characteristics and the results are similar to those of previous indices; 100% of species is captured by 21 islands while the 80% of richness, rarity and endemicity in 3, 9, 12 islands respectively (Fig. 5d). The most rapid accumulation is obtained by inserting the islands in the order that at each step maximises the total percentage of all, rare and endemic species (Fig. 5e). Using this approach all species are contained within 10 islands (Elba, Ischia, Tavolara, Argentario, Vulcano, Ponza, S. Maria, Giglio, Lampedusa and Nisida), 80% of richness, rarity and endemicity is captured by 3, 5, 5 islands respectively. Moreover this index is particularly efficient in minimising the island area required to protect butterfly biodiversity. The area required to protect all species on the islands is only 33.3% of the cumulative virtual area compared to the 77.9, 66.3, 85.1 and 76.6% of richness, SAR residuals, BCC and multiple regression residuals, respectively (Fig. 5).

Correlation analyses revealed that the residuals from multiple regressions (MRRes) are significantly correlated with the other three indexes (Table 2). BCC is unrelated to the remainder and SAR residuals and accumulation approach (based on island rank in species) are strongly related (Table 2). Among the various indices only BCC is independent of island geography. SAR residuals are related to source richness ($\beta = 0.559$, $R^2 = 0.26$, $P < 0.001$) and isolation ($\beta = -0.479$, $R^2 = 0.23$, $P = 0.001$) (model

Table 1 Island indices (Residuals from SAR, SARRes; Residuals from multiple regression on richness, SRes, rarity, RRes and endemicity, ERes; Residuals from multiple regressions MRRes, Biodiversity Conservation Concern, BCC; percentage of biodiversity accumulation PercAcc), their rank scoring: SSAR, SMRRes, SBCC (PercAcc is already scored) and the sum of ranked scores (SRS)

Island	Tag	Area	CL	S	SARRes	SRes	RRes	ERes	MRRes	BCC	PercAcc	SSAR	SMRRes	SBCC	SRS
Gorgona	Go	2.2	1	14	−1.53	−0.07	−0.06	−0.39	0.59	0.018	19.0	20	20	7	66.0
Capraia	Ca	19.5	2	21	−0.39	0.12	0.03	0.96	3.67	0.048	10.0	22	27	18.5	77.5
Elba	El	223.5	2	56	25.33	0.03	0.01	2.61	4.95	0.067	31.0	31	31	29	122.0
Pianosa	Pi	10.3	1	17	−2.45	−0.17	−0.23	−1.39	−3.01	0.000	15.0	16	5	4	40.0
Giglio	Gi	21.2	2	31	9.34	0.11	0.12	0.61	3.83	0.048	24.0	26	28	20	98.0
Montecristo	Mo	10.4	1	9	−10.49	−0.16	−0.11	−3.04	−2.85	0.000	13.0	3	6	4	26.0
M. Argentario	Ar	60.3	3	44	18.73	−0.07	0.01	−0.39	1.38	0.051	28.0	28	23	23	102.0
Lipari	Li	37.6	2	21	−2.57	−0.12	−0.09	−0.64	−0.75	0.048	8.0	15	12	18.5	53.5
Vulcano	Vu	21	2	20	−1.63	−0.3	−0.24	−0.64	−3.34	0.050	27.0	18	4	21	70.0
Salina	Sa	26.8	2	16	−6.42	−0.3	−0.21	−0.64	−3.44	0.063	9.0	9	2	27	47.0
Stromboli	St	12.6	2	14	−6.05	−0.17	−0.1	−0.64	−1.2	0.071	12.0	10	10	30	62.0
Lampedusa	La	20.2	2	12	−9.50	−0.09	−0.05	−1.39	−0.07	0.042	23.0	5	17	14.5	59.5
Pantelleria	Pa	83	2	13	−13.50	−0.19	−0.17	−1.64	−2.49	0.000	3.0	1	8	4	16.0
Ustica	Us	8.7	2	9	−9.97	−0.3	−0.17	−1.64	−3.51	0.000	16.0	4	1	4	25.0
Ponza	Po	7.5	3	17	−1.57	−0.16	−0.1	−0.39	−0.9	0.059	26.0	19	11	25	81.0
Ischia	Is	46.3	3	49	24.69	0.16	0.15	−0.16	4.2	0.051	30.0	30	30	22	112.0
Capri	Cp	10.4	3	42	22.52	0.08	0	−0.93	1.91	0.042	14.0	29	25	14.5	82.5
Vivara	Vi	0.4	3	30	17.96	0.04	−0.03	−0.16	2.27	0.025	20.0	27	26	9	82.0
Nisida	Ni	4.1	3	20	3.01	−0.13	−0.01	−1.16	−0.24	0.025	22.0	25	15	9	71.0
Tavolara	Ta	5.9	1	20	2.07	0.05	0.09	1.1	4.08	0.063	29.0	24	29	27	109.0
San Pietro	SP	51	2	17	−7.66	−0.12	−0.07	−0.47	−0.11	0.044	6.0	7	16	16	45.0
Asinara	As	52	1	20	−4.73	−0.08	−0.05	−0.04	0.69	0.038	5.0	13	21	13	52.0
Maddalena	Ma	49.4	2	16	−8.54	−0.2	−0.14	−1.9	−2.64	0.031	7.0	6	7	12	32.0
Caprera	Cr	15.7	2	18	−2.72	−0.12	−0.11	0.1	0	0.056	11.0	14	18	24	67.0
S. Antioco	SA	115.6	3	22	−5.83	−0.21	−0.18	0.53	−0.48	0.045	2.0	11	14	17	44.0
S. Maria	SM	2	1	10	−5.28	−0.18	−0.06	−0.9	−0.48	0.075	25.0	12	13	31	81.0
Spargi	Sp	4.2	1	16	−1.05	−0.04	−0.02	0.1	1.51	0.063	17.0	21	24	27	89.0
Serpentara	Se	0.4	1	10	−2.04	−0.14	−0.14	−3.9	−3.34	0.000	21.0	17	3	4	45.0
Malta	Ml	246	3	20	−11.11	−0.04	−0.05	−0.94	1.1	0.025	1.0	2	22	9	34.0
Gozo	Go	67	3	19	−6.67	−0.14	−0.17	−0.94	−1.62	0.000	4.0	8	9	4	25.0
Comino	Co	2.5	3	16	0.21	−0.01	−0.09	−0.94	0.29	0.000	18.0	23	19	4	64.0

Islands area and conservation level (CL) are also provided

$F = 13.52$, $P < 0.001$). MMRes is significantly dependent on island latitude (higher latitude islands have larger MMRes values; $\beta = 0.362$; $R^2 = 0.13$, $P = 0.045$; model $F = 4.37$, $P = 0.045$). Percentage accumulation is positively associated with source richness ($\beta = 0.417$; $R^2 = 0.21$, $P = 0.013$) and negatively with island area ($\beta = -0.341$; $R^2 = 0.11$, $P = 0.048$; model $F = 6.69$, $P = 0.004$).

Assessment of conservation measures for the Italian islets

The values of the combined ranked scores of the four indices do not differ significantly among islands having different levels of protection (Kruskal–Wallis test, $n_1 = 8$, $n_2 = 13$, $n_3 = 10$, $\chi^2 = 1.0$, $P = 0.61$, Fig. 6a). However, when the islands are separated into three groups (on the basis of both geographical source and administrative domain) different trends are highlighted. Though not significant, the most valuable Sardinian islands tend to be in the best protection category that comprises most of islands (Kruskal–Wallis, $n_1 = 5$, $n_2 = 2$, $n_3 = 1$, $\chi^2 = 4.42$, $P = 0.11$, Fig. 6b). The trend for Italian mainland islands is the reverse and there is a significantly higher conservation importance for islands having lower protection (Kruskal–Wallis, $n_1 = 3$, $n_2 = 3$, $n_3 = 6$, $\chi^2 = 6.39$, $P = 0.04$, Fig. 6c). For the Sicilian and Maltese area none of the islands are in the best conservation category, and the

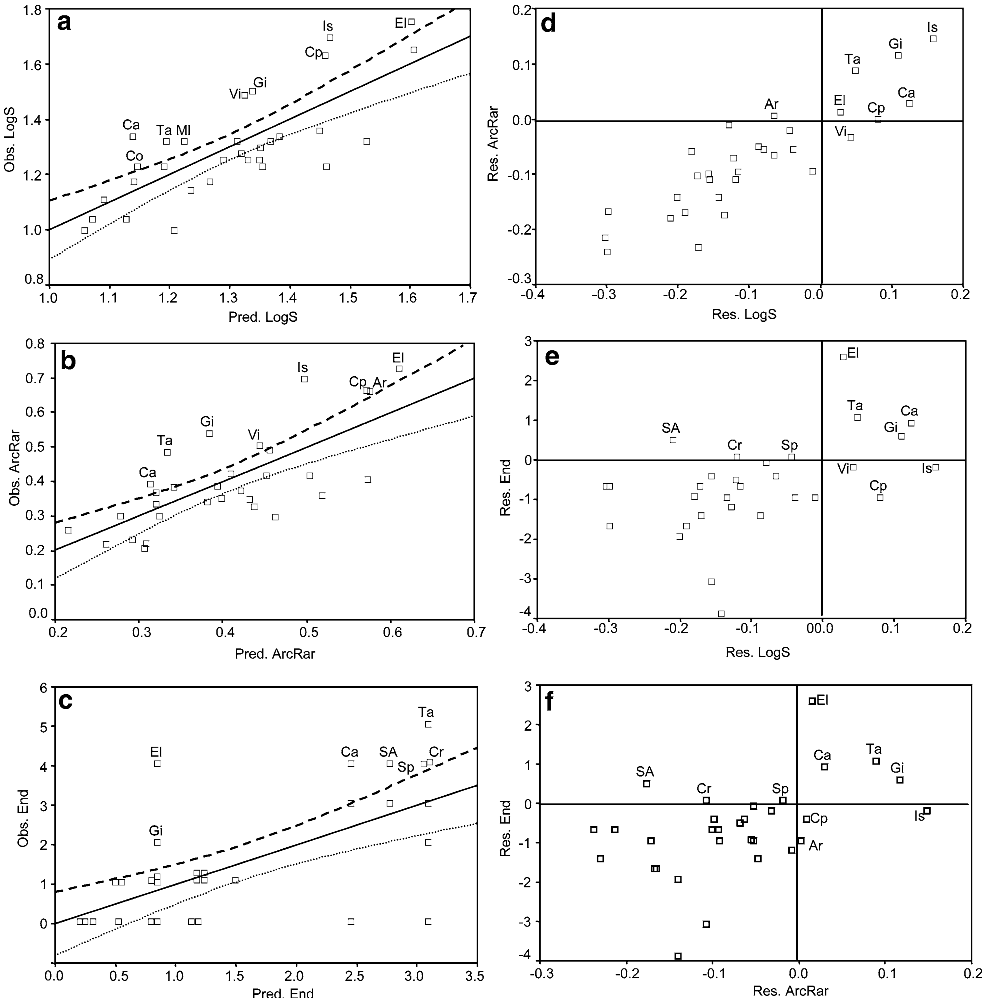

Fig. 4 Predicted vs observed values of richness (LogS, **a**), rarity (ArcRar, **b**) and endemicity (End, **c**) from stepwise multiple regressions. Visualization of residuals from the three regressions in Ulrich and Buskzo (2005) graphs. The 0 values indicate observed richness is equal to the upper 95% level of confidence

two remnant classes of islands have similar conservation values (Mann-Whitney $n1 = 8$, $n2 = 3$, $U = 9.5$ $P = 0.63$, Fig. 6c).

Discussion

Conserving faunas only becomes necessary when their persistence is threatened. From both the standpoint of projected climate changes in the Mediterranean region (Beniston et al. 2007) and increasing land exploitation (Debussche et al. 1999) there is both reality and prospect of threat for increasingly large fractions of Italian plants and animals, on the islands as well as on the peninsula (Penuelas et al. 2002; Samways et al. 2006). Faced with these changes, it is inevitable that with funding invariably limited for conservation priorities will be set, incorporating the islands as well as the mainland. Priorities are best established on the basis of threat, but in absence of suitable data on threat, appropriate surrogates exist in faunal components including richness, rarity and particularly endemicity, as in this survey. Below, we first consider the extent to which island butterfly faunas can be conserved on the largest islands. This is followed by an examination of criteria which best incorporate the key butterfly faunal components. Finally, we question the extent to which island butterfly faunas are currently protected.

Does island size matter?

There is a clear advantage to conserving faunas on larger islands. Species are more numerous, populations are spread out over more, heterogeneous biotopes and are usually larger and more numerous; conservation effort can be concentrated. However, there is the often quoted disadvantage, that of putting ‘all one’s eggs (conservation

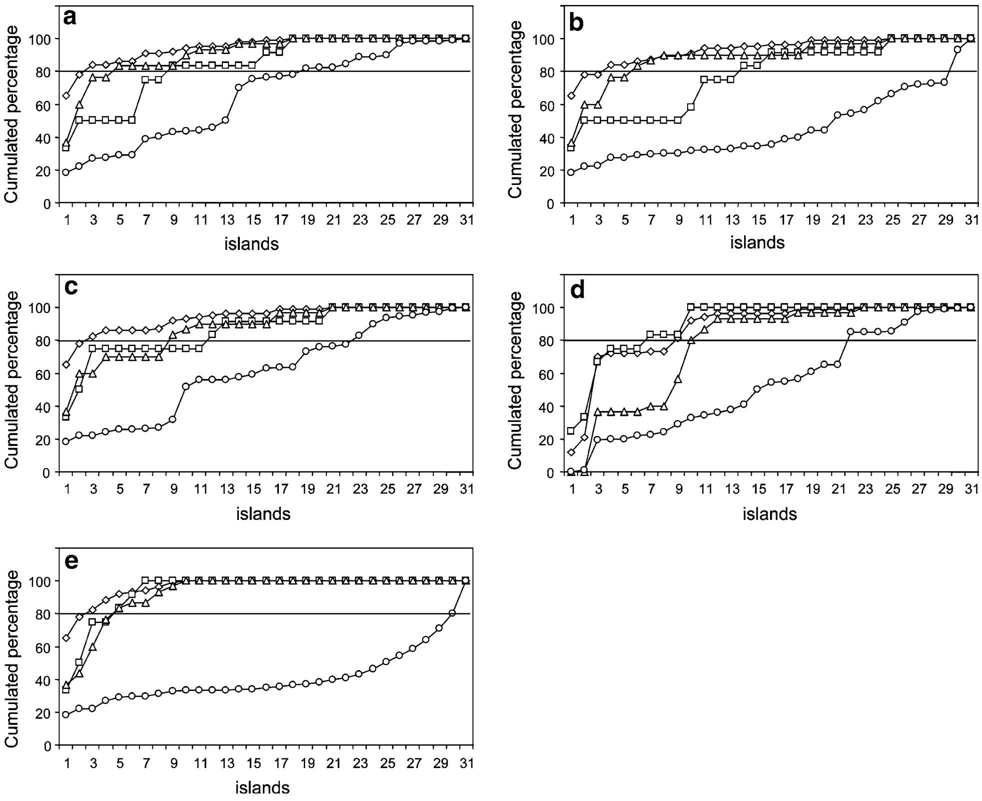

Fig. 5 Cumulative percentage of overall richness (rhombus), rare species (triangles), endemics (squares) and island area (circles) from ordinating the islands on richness (**a**), SAR residuals (**b**), multiple regression residuals (**c**), BCC index (**d**) and on percentage accumulation (**e**)

Table 2 Pearson correlations (*r*) and *P* values among the four biodiversity indices (abbreviations as in Table 1)

	PercAcc	SARRes	MRRes
SARRes	$r = 0.604$		
	$P < 0.001$		
MRRes	$r = 0.380$	$r = 0.688$	
	$P = 0.035$	$P < 0.001$	
BCC	$r = 0.316$	$r = 0.299$	$r = 0.450$
	$P = 0.083$	$P = 0.102$	$P = 0.011$

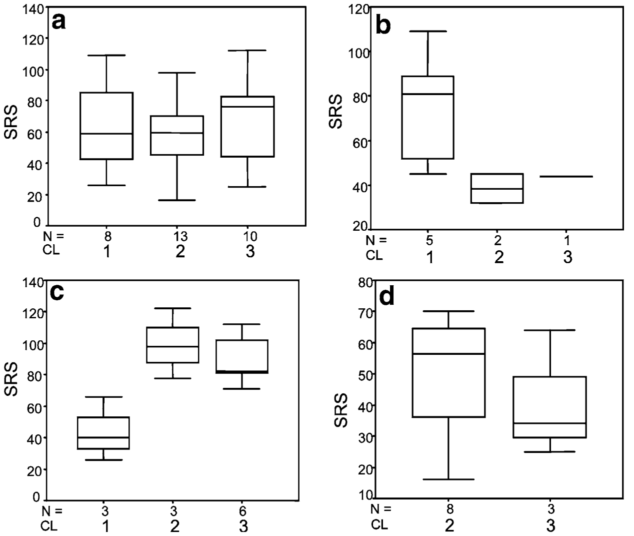

Fig. 6 Median scored rank sum (SRS) of indices according to the three different levels of conservation measures (CL) in the whole island sample (**a**), in Sardinian islands (**b**), in Italian Peninsula islands (**c**) and in Sicilian and Maltese islands (**d**)

resources) in one basket'. In the current analyses, one of the largest islands clearly emerges as a highly important faunal centre (i.e. Elba). On the other hand, the weight of evidence is against choosing islands is order of size for conservation resources. First, the islands are far from being perfectly nested (as detected by the rather high matrix temperatures for the MT index, and by the number of discrepancies for the BR index) (Fischer and Lindenmayer 2005). In particular the two sub samples of Italian-Sicilian and Sardo-Corsican islands did not reveal a significantly nested pattern. In fact, most species (30 of 86) are found on just one or two islands, classifying them as rare. Most of these species are present in richer islands but this is not the rule; many of the most important species (island endemics) conveying high temperature signals for nestedness would be omitted. Second, the comparison based on a virtual larger island (Rosenzweig 2004) revealed that half of the biodiversity would be lost in protecting a virtual single area as large as the sum of all the islands studied. It clearly demonstrates that small islands contain 'information' (species) that would be omitted from a virtual mass matching the combined size of all the islands. Moreover, several of the most important species for conservation would be omitted. A study of species endemic to the islands indicates that historical factors are responsible for different faunas (as for *Plebejus* spp., *Lasiommata* spp., *Hipparchia* spp., *Coenonympha* spp.) and that, arising from vicariance, cannot all be included in one island. In other words, the large virtual island should have a location and, consequently, a source; this, inevitably, will lead to the loss of many species endemic to other sources.

Third, although the species-area (SAR) approach indicates a significant influence of island area on island species' richness, the explained variation (14.4%) is very low. This finding is confirmed by the multiple regression approach. For island species' richness, isolation is more important than island area; for island rarity, area is only just slightly more important than isolation. For endemicity, there is no significant geographical parameter; it is not explained by area per se. Fourth, although some islands in the joint extreme residual plots (>95% upper confidence limits) isolate some large islands as key units for conservation, only Elba is identified among the largest islands and for the combined residual index (MRRes), six of the 10 most important islands are small ones. Fifth, the BCC index, which emphasises species' status, shows no relationship with island area or other geographical variable; island area is clearly not a key factor which is not surprising as the BCC index closely allies with island endemicity. Finally, species' accumulation – the most successful approach in terms of setting priorities for conservation as it captures all the faunal components in the smallest number of islands – isolates 10 islands, only one of which is large (i.e. Elba) and only a further two which are of modest size (i.e. Vulcano and Lampedusa). In fact, once faunal source influences have been removed in regressions, the influence of island area on species' accumulation is found to be negative. From these observations, it is evident that one single island is highly important faunistically, but that initial observations suggest the value in retaining some of the smaller islands together with the largest ones for preserving butterfly biodiversity.

Priorities for conserving islands?

Just what conservation entails for the islands depends on (i) the need for conservation and (ii) available resources allocated to it. It should be pointed out that even when resources are extremely limited and when there is no apparent threat, there is wisdom in monitoring key faunal elements (rare and endemic species) and important areas. Butterflies are useful indicators of such general pressures on landscapes (Thomas 2005) and if they are not monitored appropriately, then threats and losses may well escape attention (New 2007). For the strict protocol of conserving butterfly faunal resources with limited human resources, the most efficient solution emerging from the current analyses, percentage accumulation, identifies 10 key islands which house all elements in island diversity: Elba, Ischia, Tavolara, M. Argentario, Vulcano, Ponza, S. Maria, Giglio, Lampedusa and Nisida.

Although it is possible to neatly contain faunal elements in this way, the solution is largely abstracted of other considerations. Such are: (i) evenness of threat, (ii) relative costs in conserving different landscapes, (iii) relative importance of species for regional diversity, (iv) potential of islands for long-term conservation and (v) island biogeography dynamics, that is, interactions among islands and between islands and their primary sources, underlying persistence of species on islands. For instance, the biotopes on relatively, small isolated actively volcanic islands may be under less threat, with renewed kipukas (vegetation refuges) amid lava flows, than those on larger islands or others close to mainland sources and under considerable pressures from development. Moreover, costs will be related to land prices and degree of difficulty in restoring biotopes. It will also be affected by scale of perspective: species differ in terms of genetic resources and islands contrast in their significance for long term conservation potential. Larger islands tend to have greater elevation and such islands (e.g. Elba) provide better insurance against landscape and climate changes; species can move uphill or downhill as well across the island.

There is a more general practical consideration; an algorithm which aims to 'capture' maximum diversity for the smallest number of land units is potentially flawed. The approach may be appealing from an economic vantage when faced with broadcast threats over all islands and when resources are sparse, but it can fall foul of several basic biogeographical tenets. Selecting too small an area to contain maximum biodiversity may result in low persistence of small and isolated populations (the Noah's Ark effect, Pimm and Lawton 1998); such islands depend on neighbours and in this respect metapopulation dynamics are probably highly important for species' persistence on the Italian islands particularly for archipelagos (e.g. dependency of Comino and Gozo on Malta; interactions among islands in the Tuscan archipelago, Dapporto and Cini 2007). The main population sources for species seem to be the nearest larger neighbouring source areas (Italian Peninsula, Sardinia-Corsica, Sicily, North Africa, Dapporto and Dennis 2008); therefore, it seems that attempting to preserve butterfly biodiversity on islands independently of maintaining their continental source areas is a poor strategy. The combined protection on islands and mainland may to be the only realistic way forward. The primacy of neighbouring sources has been well demonstrated beforehand (Dapporto and Dennis 2008) and in the current analyses; sources richness, rarity and endemicity are key variables in regression analyses for the respective island variables.

From these observations some suggestions can be advanced for protecting butterflies on Italian islands. There is conflicting evidence for the importance of island area in our sample; although it is now clear that islands should not be picked purely on the basis of size, large islands generally make for larger sources and source is a dominant influence of island faunal characteristics. On this basis, and the comparative results, Elba is a pre-eminent candidate for conservation. Elba's fauna (the largest in the sample) has the highest overall concern. This island is located between the Italian mainland and Corsica and thus comprises a number of endemic species belonging to both areas (Dapporto and Cini 2007). Moreover owing to its large area and high altitude (the highest in the sample) Elba is very rich in biotopes and thus provides resources for several species absent elsewhere in Italian islands (e.g. *Aglais urticae* is confined to mountain areas in the Mediterranean region). A number of other islands that emerge as significant in various indices also deserve attention from the standpoint of actual threat to biotopes. On this basis, there is great concern for the faunas on Ischia, Capri and Giglio, islands sourced by the Italian mainland, thus with potential for persistence, but under immense pressure from tourism and development. Finally, faunas of some large islands are shown to have relatively low priority (e.g. Malta and S. Antioco) and some very small islands to have high priority. Among Sardo-Corsican islands, Tavolara, S. Maria and Spargi have as important a role as Vivara and Ponza among the Italian mainland group, owing to the proportion of endemics on them. Among Sicilian islands, the Aeolian Archipelago as a whole seems to play a fundamental role.

Conservation measures in the Italian islands

There are sound reasons for attending to the conservation of the Italian island insect faunas including butterflies. The Italian islands form part of the wider Mediterranean region which has been shown to act as the refuge, on a geological time scale, for plants (Huntley 1988) and butterflies (Dennis et al. 1991, this issue; Dennis and Williams 1995; Schmitt 2007). Island endemic species of butterfly only occur south of the Devensian polar front (45° N) at 18 ka BP, and islands have their share of these species as well as rare species also found on the mainland. The fact that most species have so few island 'refuges' now is reason to monitor changes in populations on islands and to have in place basic conservation strategies.

Despite good cause for conservation on the islands, conservation policy does not match priorities revealed by the conservation indices. Some islands, clearly important for butterflies, have low levels of protection. Elba and Giglio belong to the National Park of the Tuscan Archipelago so most of its area has protected status. However, no area on these islands is protected at the same high level as areas of the Tuscan Archipelago National Park (e.g. Montecristo, Gorgona and Pianosa) and several human activities are permitted. Moreover, large areas of these islands are often burned (e.g. human fires), a serious problem for many Mediterranean islands as for other regions (Dennis et al. 2000; Swengel and Swengel 2007). One obvious area of Elba that should have higher protection comprises the highest peak in the Italian islets (Monte Capanne, 1014 m). Worst situations are found for islands off Latium and Campania: Ischia, Ponza, Capri, Nisida and Vivara are important centres for butterfly biodiversity, but are not protected by any important measure. Some of these islands are experiencing rapid development; in recent legal submissions it was disclosed that these islands receive an exceptional level of planning applications. A similar pattern occurs for Sicilian and Maltese islands. The opposite only appears to be the case for Sardinian islands, where conservation measures are higher. Most of the islands identified in the current analysis as having high priority (i.e. Tavolara, S. Maria, Spargi) are completely (or mostly) protected and the number of visitors per year is curtailed.

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Appendix 1 Data for islands

Island	Area (km^2)	Isolation (km)	Altitude (m)	Latitude	Longitude	Richness	Rarity	Endemics	Source richness	Source rarity	Source endemics
Gorgona	2.2	33.3	255	43.25	9.53	14	0.33	1	73	0.39	2
Capraia	19.5	25.6	447	43.02	9.48	21	0.39	4	43	0.31	7
Elba	223.5	8.9	1019	42.46	10.17	56	0.67	4	86	0.42	2
Pianosa	10.3	13	27	42.35	10.04	17	0.30	0	86	0.42	2
M. Argentario	60.3	0	635	42.24	11.08	44	0.62	1	71	0.34	2
Giglio	21.2	14.4	498	42.21	10.53	31	0.52	2	71	0.34	2
Montecristo	10.4	43	645	42.19	10.18	9	0.22	0	43	0.31	7
S. Maria	2	2.5	49	41.18	9.21	10	0.30	3	42	0.26	9
Spargii	4.2	1.6	155	41.14	9.20	16	0.38	4	42	0.28	9
Maddalena	49.4	2	212	41.13	9.24	16	0.34	2	42	0.28	9
Caprera	15.7	0.5	212	41.12	9.27	18	0.37	4	42	0.28	9
Asinara	52	2	408	41.02	8.15	20	0.41	3	36	0.26	7
Ponza	7.5	13	280	40.54	12.57	17	0.35	1	87	0.38	2
Tavolara	5.9	2	565	40.54	9.42	20	0.47	5	41	0.27	9
Vivara	0.4	0.1	110	40.47	13.59	30	0.48	1	75	0.37	1
Nisida	4.1	1.5	109	40.44	14.17	20	0.49	0	75	0.37	1
Ischia	46.3	6	788	40.43	13.54	49	0.64	1	75	0.37	1
Capri	10.4	4	142	40.32	14.13	42	0.62	1	97	0.46	4
S. Pietro	51	3	211	39.08	8.16	17	0.38	3	36	0.26	8
Serpentara	0.4	3.5	54	39.08	9.36	10	0.23	0	45	0.31	9
S. Antioco	115.6	0	271	39.02	8.24	22	0.41	4	36	0.26	8
Stromboli	12.6	34.8	920	38.47	15.12	14	0.37	1	78	0.39	3
Ustica	8.7	51	244	38.42	13.10	9	0.21	0	76	0.36	3
Salina	26.8	4	962	38.33	14.50	16	0.35	1	78	0.39	3
Lipari	37.6	21	675	38.28	14.56	21	0.41	1	78	0.39	3
Vulcano	21	0.5	500	38.22	14.58	20	0.40	1	78	0.39	3
Pantelleria	83	70	836	36.47	11.59	13	0.22	0	52	0.30	3
Malta	246	85	253	36.03	14.26	20	0.36	0	40	0.28	2
Comino	2.5	1.6	135	36.02	14.20	16	0.30	0	40	0.28	2
Gozo	67	2.5	233	36.02	14.15	19	0.32	0	40	0.28	2
Lampedusa	20.2	125	133	35.30	12.34	12	0.26	0	52	0.30	2

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ORIGINAL PAPER

A multidimensional characterization of rarity applied to the Aegean tenebrionid beetles (Coleoptera Tenebrionidae)

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Abstract This paper attempts to use museum collection data to estimate measures of species rarity and then to relate these measures to extinction risk. For this purpose, 170 taxa (138 species and 32 subspecies) of tenebrionid beetles from 32 Aegean Islands (Greece) were considered. For each taxon, rarity was evaluated as geographic distribution (mean incidence on islands in the archipelago), potential habitat exploitation (total area of the islands occupied on the total area of the study system) and contactability (number of decades of taxon's records on the total number of decades of assumed persistence from 1870 to 2000). All of these indices were correlated to each other. Whether expressed in terms of range size or habitat exploitation rarity was a major determinant of a species' risk of extinction (evaluated as extinction decade). Thus, the designation of rarity provides a good basis for identifying species that are most in need of conservation at a particular scale.

Keywords Geographic distribution · Habitat specialization · Population size · Vulnerability · Extinction · Island biogeography · Greece

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Introduction

A multidimensional characterization of rarity, widely used for vertebrates (e.g. Kattan 1992; Dobson and You 1993; Manne and Pimm 2001), is generally considered difficult to apply to most insects because of several reasons, such as lack of detailed information on species biology, and difficulty in censusing and monitoring populations over long periods of time (e.g. Maes and van Swaay 1997; Grootaert et al. 2001; Kati et al. 2003). In her seminal papers on plant rarity, Rabinowitz (1981) and Rabinowitz et al. (1986) suggested three aspects of species be examined to assess the degree of rarity: (1) the area of the species range (wide/narrow distribution), (2) the number of different kinds of biotopes that species occupy (broad/restricted habitat specificity) and (3) local population size (large/small population). Such as multidimensional characterization of species rarity has been successfully applied to vertebrates (e.g. Manne and Pimm 2001), while it seems difficult to transfer to insects. In fact, for most insect species, only information from museum specimens is usually available. The objective here is to provide a practical way to make use of the valuable data, like collection localities and dates, hidden in museum collections. In particular, this paper attempts to estimate three measures of rarity based on museum collection data and then to relate these measures to extinction risk.

For this purpose I chose the tenebrionid beetles of the Aegean Islands (Greece). Tenebrionid beetles (Coleoptera Tenebrionidae) are an important group in the structure and functioning of Mediterranean insular biotas (Cartagena and Galante 2002). The importance of the tenebrionid beetles of the Aegean Islands from a conservation standpoint is enhanced by the high conservation concern of the East Mediterranean area (e.g. Médail and Quézel 1999;

Troumbis and Dimitrakopoulos 1998; Sfenthourakis and Legakis 2001; Fattorini 2006a). Furthermore, biodiversity hotspots already tend to be located preferentially in areas where species overlap in their range margins between neighbouring assemblages (Araújo 2002; Spector 2002) and the Aegean Islands are an important biogeographic crossroad between the Balkan and the Anatolian faunas (Dennis et al. 2000; Fattorini 2002a; Fattorini and Fowles 2005).

Materials and methods

Study area

In total, 32 islands were included in this study (Table 1). The study area is adequately described by Heller (1976), Sfenthourakis (1996), Dennis et al. (2000) and Fattorini (2002a). Phrygana is the dominant vegetation type throughout the islands, while oak forests and maquis habitats occur only in scattered patches on some of the largest islands. Fire and changing grazing pressures create irregular cycles of vegetational change in maquis, so that at one extreme, cover may be less than in most phrygana, while at the other it becomes scrub woodland with a closed canopy. Phrygana is more stable but can be destroyed by burning (Arianoutsou 1998; Cameron et al. 2000). Pre-Minoan Crete had significantly more woodland than it does today, but remains of plants typical of phrygana and maquis are found in interstadials of the last glaciation (Cameron et al. 2000). Thus, most of changes in faunal composition on the islands after the Pleistocene probably owe more to human activities than to natural variation in habitat structure and climate.

Data sources

The tenebrionid fauna of most of the Aegean Islands is well known as a result of intensive surveys from the beginning of the past century to the present (cf. Fattorini and Fowles 2005). Taxonomic treatment and data concerning species distribution are taken from Fattorini (2002a) and Fattorini and Fowles (2005). On the Aegean Islands, several tenebrionid species are represented by different subspecies endemic to individual islands or groups of islands. These populations can thus be recognized as ‘evolutionarily significant units’ (Samways 1998) and I have counted them as different taxa (cf. Fattorini 2002a, 2006b, c). The term ‘species’ will be used in reference to tenebrionid taxa for simplicity.

As a whole, 170 taxa (138 species and 32 subspecies) were initially considered in this study. Some records may reflect the preferences of the original collectors in terms of collection localities, habitats and species, but they are the best available data. To reduce such biases, eight species were omitted because of insufficient data. Data are available as Microsoft Excel files on request.

Species rarity and vulnerability

In this study, I defined three dimensions of rarity as: geographic distribution, potential habitat exploitation and species contactability.

Table 1 Island area and species richness

Island	Island area (km^2)	Species richness	Island	Island area (km^2)	Species richness
Amorgos	121.1	7	Mikonos	85.5	10
Anafi	38.4	12	Milos	150.6	19
Andros	380	13	Naxos	428	36
Castellorizon	7.3	8	Pano Koufonissi	3.8	12
Chios	842	10	Paros	194.5	8
Euboea	3658	42	Rhodos	1400	43
Folegandros	32.1	7	Samos	476.2	14
Ios	107.8	9	Santorin	75.8	26
Karpathos	301	15	Serifos	73.2	8
Kea	130.6	6	Sifnos	73.2	9
Kimolos	35.7	3	Sikinos	41	8
Kithnos	99.3	4	Siros	83.6	23
Kos	290.3	26	Skiros	209	11
Kriti	8260	71	Skopelos	96	7
Lemnos	460	10	Thasos	379	23
Lesvos	1630	17	Tinos	194.3	13

Geographic distribution. As in other studies (e.g. Dennis et al. 2000), I estimated the geographic range as the proportion of islands from which the species is known on the total number of islands. This index (termed ψ after Dennis et al. 2000) could theoretically vary for the study islands from 0.03125 (for species restricted to a single island) to 1 (a species occurring on all 32 islands). The more widely a species is distributed, the higher the index. This procedure leads to an estimation of rarity on the basis of the geographic distribution within the study area. Changes in species incidence on different islands over time was not addressed in this study. For species that are widely distributed outside of the Aegean area, the estimate of their range size refers to their relative distribution, and thus to their rarity, in the study area only. However, the study area clearly encompasses the entire geographic range of the tenebrionid species endemic to single islands or to certain groups of islands (subendemic species), or most of the range of species that have their distribution centered in the Aegean area. Also, there is evidence that the area occupied by individual species at one spatial scale is strongly correlated with that occupied at a larger scale (Gaston 1990). Thus, the estimate of species rarity obtained for the study system can be considered a rough estimate of general species rarity. Another possible bias in this procedure, is that some species may occur on islands different from those considered in the study, being more widely distributed than resulting from the analysis. For instance, a species quoted from only one of the 32 islands analyzed could actually occur on other islands, outside of the 32 considered here. However, this bias can be considered negligible, because of the high number of islands represented in the study (most of the islands from which faunistic information is available). Species occurring on one island (singletones) received a score of 0.03125, without regard to whether or not they are endemic to this island or if they occur on a single island but are also distributed in mainland areas. This is correct in a conservation perspective focused on the study area. It should be noticed that the single island endemics are only 33 taxa, most of which (20 taxa) endemic to Kriti, where the same species can be represented by different endemic subspecies. Weighting these endemics (associated to a large island) more than other singletones (associated to small islands) could lead to an inflated estimation of the conservation interest of Cretan populations. Endemics were not analyzed separately because they were specifically studied by Fattorini (2006d).

Potential habitat exploitation. Islands' areas were used to derive a measure of potential habitat exploitation. For this purpose, I summed the areas of the islands from which the species was known. Each species thus received a value of the 'area of occupancy', which is the sum of the areas of the individual islands inhabited within the archipelago. This value was then divided by the total area of the archipelago (the sum of the individual areas of the islands considered in the study). This final value has been used as an index of species potential habitat exploitation (ε). For the studied archipelago it could theoretically vary from 1.871×10^{-4} (for species occurring only on the smallest island) to 1 (a species occurring on all islands). The larger the total area of distribution, the higher the index.

The extent of the area occupied by a species may be related to habitat specialization (cf. Hanski et al. 1993). Thus, for some species this index could reflect their habitat specialization. However for very specialized species, this index could be a kind of inverse measure of a species' habitat specialization, because it is likely that the most specialized species will tend to be found within limited biotopes on very large islands. Weighting the species associated with rare habitats by the entire island area is an overestimation of their actual habitat specialization. For example, species mostly associated with wetland trees (e.g. *Bolithophagus reticulatus*, *Diaclina fagi* and *Nalassus plebejus*) tend to occur only on larger islands, because only the major islands possess wetlands, but they occupy only a small fraction of these large islands. However, the Aegean Islands are rather homogeneous in terms of their habitats, and species restricted to rare habitats occurring on certain islands only represent a negligible fraction. Phrygana and maquis are the most represented vegetation types throughout all islands. True forest habitats (mainly represented by *Quercus coccifera*, *Pinus halepensis* and *P. nigra* woods) occur only in scattered patches on some of the largest islands. However, xylophilous species represent a minor component of the tenebrionid fauna considered here (about 16 out of 162 species). Thus it is unlikely the localization of their habitats on some islands may substantially influence the general pattern. As a matter of fact, the aforementioned three species associated with wetland trees received low or very low scores of ε, thus resulting to be actually rare for habitat exploitation. To explore if this measure area of occupancy is related to habitat specialization, I compared the results obtained with this method with a classification into categories of habitat specialization. On the basis of ecological information reported by Dajoz (1976) and Schawaller (1996) and personal observations made in mainland Greece, Crete, Santorini and Anafi, I assessed the ecological tolerance of 37 species, which were classified as stenotopic or eurytopic. Out of a total of 16 species identified as stenotopic, 12 species (75%) were classified as 'rare' according to the method proposed here (habitat exploitation score < 0.185; see below); out of 21 eurytopic species, 4 (19%) were classified as 'rare' by habitat exploitation. Thus, there is evidence that this index mirrors habitat specialization.

Another possible measure of potential habitat exploitation could be an index that describes how strongly a species is associated with large islands. The most direct and easy to interpret measure of this type may be the mean area size of the islands occupied by a species. This method produced scores which are correlated to those obtained with method described above ($r = 0.491$, $P < 0.0001$). Using the median value (1689.6559) to dichotomize species (see below), 81 species should be classified as rare for the habitat with this last method. Out of these 81 species, well 62 (76.54%) were considered rare with the other method. Thus, the two methods produced similar results. However, out of the 16 species identified as stenotopic, 10 (62.50%) were classified as 'rare' according to this second method. Therefore, I preferred to use the index of potential habitat exploitation discussed above.

Although it is likely that for most species the 'index of potential habitat exploitation' discussed here is a possible proxy for habitat specialization, it can be considered, more cautiously, an index of potential habitat exploitation. Available data on tenebrionids living in Mediterranean coastal areas show that most species are not exclusively associated to specific vegetational associations, but to different stages of a given vegetational sere, although with different population density (Carpaneto and Fattorini 2001, 2003; Fattorini and Carpaneto 2001). For example, sand-dwelling species are usually distributed from the sea-shore to lower and high maquis, and sometimes even in very inland (also relatively high-altitude) areas, provided that open areas with sandy soils occur (Fattorini and Maltzeff 2001; Fattorini 2002b, 2005; personal observations in Santorin and mainland Greece). Thus it can be assumed that, for areas, which share similar climate and vegetation, tenebrionids can exploit a wider range of ecological conditions at increasing areas. Obviously, species with greater potential habitat exploitation should be less prone to extinction.

Contactability. Contactability was based on collection dates gathered by Fattorini (2006d) updated with additional material preserved at the Hungarian Museum of Natural History (Budapest). As a whole collection dates ranged from 1870 to 2000. To assess species contactability, I subdivided species records into decades, from 1870 to 2000. Species collected in the last 10 years were regarded as still present. Species contactability (δ) was estimated as the number of decades from which records of a given species were available on the total number of decades until extinction is assumed (last decade with records). This value could theoretically vary from 0.07 (for a species assumed to be present in 13 decades, but recorded from one decade only) to 1 (a species recorded in all decades until extinction is assumed). It is difficult to estimate how consistent was the collecting effort in each decade. However, there is indication that variations by years, as well as by islands, likely did not affect the overall pattern. Although there might be a tendency for some particular island to be studied by a specialist in one year and then to receive few, if any, visits subsequently, there is evidence that most islands were sampled repeatedly (see history of researches reported in Fattorini and Fowles 2005 and data reported by Fattorini 2006f). Also, about 51% of 86 species recorded from one island only was sampled in more than one decade (mean number of decades (±SD): 3.116(±1.300), range: 2–7). Thus, a substantial proportion of species restricted to a single island were repeatedly collected.

A species could be rarely encountered not only because it is numerically scarce, but also because it is restricted to certain biotopes, which are rarely searched or because it is secretive by nature. Species like sand-dwelling, fossorial tenebrionds, such as *Ammobius rufus*, *Trachyscelis aphodiodes*, *Phaleria* spp., may be rarely encountered because of their behaviour. Myrmecophilous species (like *Dichillus* spp.), mycetophagous species (e.g. *Bolitophagus reticulatus*, *Diaperis boleti*, etc.), or arboreal species living under bark (e.g. *Platydema europaeum*, *Hypophloeus* spp. *Menephylus cylindricus*, some Helopini) are secretive because the habitats where they live are difficult to sample. Thus, these species are usually represented in museum collections as few specimens collected by entomologists who found them while sampling these habitats to collect other insect groups. However, the very large sampling efforts (thousands of records) made through the decades by hundreds of collectors interested in different groups ensure that secretive species are detected (at least occasionally). Also the use of species occurrence (without reference to individual numbers) into decades, which are relatively large periods, reduces biases due to over- or underestimation of species frequencies due to occasional large samplings. As a matter of fact, in spite of their association with habitats rarely searched or their secretiveness, several of the aforementioned species have a rather large value of contactability. Finally, from a theoretical point of view, species contactability may be considered a proxy for population size (or density), because encounter rates should be proportional to population density (Strayer 1999).

Vulnerability index. Species with smaller ranges, lower abundances and narrower habitat tend to experience higher levels of threat (e.g. Manne and Pimm 2001). Thus, the different measures of rarity can be combined to obtain an index of vulnerability, increasing with the increase in such measures. Using ψ, δ and ε measures of rarity, I calculated an index of species vulnerability (v) applying the method proposed by Kattan (1992). The aforementioned three indices are really continuous variables. If species are dichotomized for each of these variables, an eight-celled model is created that reflects different types of rarity and commonness. Species that fall in the cell ‘wide range-large habitat exploitation-high contactability’ are ‘common’ in three dimensions, while those falling in the cell ‘narrow range-small habitat exploitation-low contactability’ are ‘rare’ in three dimensions and are the most vulnerable to extinction. The other six cells contain species rare in one or two dimensions. Kattan (1992) proposed assigning to each cell a number between 1 (species ‘rare’ in three dimensions) and 8 (species ‘common’ in three dimensions) to indicate susceptibility to extinction. The value 1 is assigned to species ‘rare’ in three dimensions, and 8 to species ‘common’ in three dimensions. Of the remaining six cells, three are rare in two dimensions and three are rare in one dimension (vulnerability index values 2–7). To rank these cells, Kattan used the following criteria. Species with narrow geographical distribution are more vulnerable at a global level, and species with restricted habitat specificity (here replaced by potential habitat exploitation) are more vulnerable regardless of their abundance (here replaced by contactability). As in other research (e.g. Dobson and Yu 1992), for each dimension (measure) I dichotomized species into two groups (common and rare) according to whether they were above or below the median and then I assigned each species to a cell as proposed by Kattan. The threshold median values to classify a species as ‘rare’ were: ≤ 0.0313 for geographic distribution, <0.185 for habitat exploitation, and <0.279 for contactability. Note that all these indices of rarity increase as species became less rare.

To study if vulnerability (measured by Kattan index) is biased for taxonomic or ecological characteristics, I focused on the two most speciose groups, with high number of taxa endemic to the study area, the genera *Dendarus* (20 species) and *Dailognatha* (13 species), and two ecologically clearly distinct categories, the psammophilous (10 species) and xylophilous (16 species) beetles. The observed frequency of Kattan index values in the two genera was compared with the distribution expected according to the general distribution in Fig. 1. Observed and expected distributions were compared using a chi-square test. Kattan index values 1–4 and 5–8 were pooled to obtain expected frequencies larger than or near to 5.

To study correlations among these indices, a Pearson coefficient of correlation was applied.

Temporal analyses

To determine if the aforementioned measures of rarity actually reflect species vulnerability to extinction, I correlated species loss to the measures of rarity by a Pearson coefficient. To study species loss through time, I divided the study period into decades. According to Fattorini (2002a, 2006b, e), the tenebrionid fauna of the Aegean Islands is relictual, thus discovery of new species through decades has to be regarded as a collection of species previously present but not sampled, not as additions to the local fauna by immigration. The latest decade in which a species has been found was considered as the decade in which the species disappeared from the study area, i.e. the decade in which the species was lost. Thus species were considered as continuously present in the study area from the first decade considered in this study to the decade of the most recent record(s), even if actually not recorded in some decades included in this range. Then, as a measure of species survival, I considered the last decade of occurrence (decade of loss). Rare species might appear to go extinct sooner than common species, simply because rare species are less often sampled. Thus, very rare species may not even be extinct in some cases, but only unsampled. It is difficult to account for this bias. However, this bias is likely reduced by the very large sampling efforts made through each decade and notably in recent years.

The aforementioned method led to the construction of a curve which can be used to estimate how sharply species were lost and to assess how realistic is the information obtained. The aim here was to obtain the best predictive function, which relates the number of species per decade to the progressive number of decades, without reference to any theoretical model. For this purpose I used polynomial

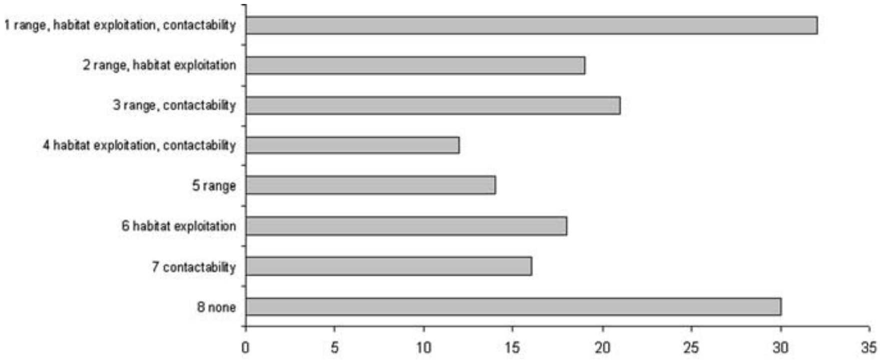

Fig. 1 Number of Aegean tenebrionids in each category of rarity. Number refer to Kattan’s index

approximations. When selecting a polynomial approximation, I started with the lower power of the independent variable (number of species present in a given decade). Degrees of the polynomial function were then increased until about 95% of variance was explained. To assess the realism of the curve I compared species loss to species discovery. For each decade, I recorded the number of species added by new records with respect to the previous decade (relative increase). Likewise, for each decade, I recorded the number of species, which disappeared with respect to the previous decade (relative loss). The difference, in each decade, between the species added and lost with respect to the previous decade was considered as a measure of species loss detrended by species accumulation. These detrended values were correlated with decade number (decades were numbered from the first to the last one), to search for possible temporal bias. The analysis obviously started with the number of species first recorded (or lost) in the second decade with respect to the first decade; thus, the correlation started with the second decade (1880–1890). I also calculated the mean of the detrended values, a negative mean suggesting an increasing number of species lost not compensated by species discovery. As an additional method, I also calculated, for each decade, the cumulative number of lost species through decades and I compared it with the cumulative number of known species through decades. After inspection of scatterplots and application of various fitting functions, the power function (fitted in Log-Log transformed space) was considered the most convenient model, because it fitted equally well the two curves, explaining the same proportion of variance (87% in both cases). The slope (z) of the power function was considered as a measure of the rate of species extinction and discovery. The z values were compared to establish the two rates.

In all aforementioned tests a minimum probability level of $P < 0.05$ was accepted (all tests were two-tailed). I made many tests on the same data set, thereby increasing risk of significant results occurring by chance. Although the sequential Bonferroni has become the standard method of dealing with multiple statistical tests, I believe that decreasing the significance level would have resulted in an even higher risk of ignoring real relationships. Moran (2003) showed that the sequential Bonferroni has several flaws ranging from mathematical (it ignores the number of statistical tests that are significant) to logical (there is no standard way to apply the test) to practical (e.g. the probability of finding a significant result declines in more detailed studies). Thus, in accordance with the suggestions of Moran (2003), I did not apply the Bonferroni correction, but focused on P-values and consistence of results.

Results

Species rarity and vulnerability

Values of species rarity for geographic distribution, habitat exploitation and contactability, are reported in Appendix. All of these indices were correlated to each other except for the correlation between contactability and potential habitat exploitation (Table 2). However, this is because of the presence of 8 species which were collected in all decades of assumed presence, but which disappeared very early (within the first one or two decades). If these 8 species are omitted, the correlation becomes significant ($P < 0.0001$). 32 species were rare for all 3 dimensions, 52 species were rare for 2 dimensions, 48 species were rare for 1 dimension, and 30 were no rare for any dimension. 86 species were geographically rare, 81 for habitat exploitation and 81 for contactability. The wide geographic range/restricted habitat exploitation/low contactability group was the least numerous (12 species), while the largest number of species (32) were classified as rare at all (i.e. for geographic range, habitat exploitation and contactability) (Fig. 1).

An analysis of the observed frequencies of Kattan index in the genera *Dendarus* and *Dailognatha* revealed that taxonomy did not influence Kattan values. For both genera, their observed distributions were not different from those expected from the general distribution ($\chi^2_{(1)} = 1.26$, $P = 0.262$ and $\chi^2_{(1)} = 0.01$, $P = 0.921$ for *Dendarus* and *Dailognatha*, respectively). An analogous procedure was adopted for the two ecological groups: psammophilous and xylophilous. Again, the observed distributions were not different from those expected from the general distribution ($\chi^2_{(1)} = 0.020$, $P = 0.889$ and $\chi^2_{(1)} = 0.144$, $P = 0.231$ for the psammophilous and xylophilous beetles respectively). Thus, belonging to a guild does not make species more vulnerable.

Table 2 Correlations (Pearson correlation coefficient) between rarity indices of Appendix

	Geographic distribution	Potential habitat exploitation	Contactability	Kattan index
Assumed decades of occurrence	0.311***	0.328***	–0.484***	0.299***
Geographic distribution		0.445***	0.307***	0.606***
Potential habitat exploitation			0.148 n.s.	0.631***
Contactability				0.272***

*** $P < 0.0001$, n.s = non significant.

Temporal analyses

Geographic range, habitat exploitation and Kattan's vulnerability indices were positively correlated to the number of decades preceding the last decade of occurrence (Table 2). Thus, species rarity actually affects species survival, the species with broader range and larger habitat exploitation surviving for longer times. The inverse relationship between the number of assumed decades of occurrence and contactability may be due to the large number of species collected only in recent decades, but which are assumed to be present in all previous decades. Species survival through decades (Fig. 2) shows a clear pattern of increasing extinction. Using the year 1960 as pivotal date (cf. Fattorini 2006d), out of 162 species, 43 (about 27%) have to be considered extinct.

A 3-degree polynomial function fitted the data very well, explaining a large amount of variance ($y = -0.1509x^3 + 2.771x^2 - 18.603x + 181.25$, $R^2 = 0.937$). Based on this function, an accelerated decline in species number can be evidenced during the last decades. A projection using this equation shows a virtual extinction of all species within the 18th decade, i.e. within the next 50 years. Species loss and discovery varied irregularly through time, with an increasing number of species lost not compensated by species discovery especially in the last decades (Fig. 3). The mean value (±SD) of species loss detrended by species discovery was –2.583 ± 17.635, suggesting great variations trough time. Species loss detrended by species discovery did not correlate with decades ($r_s = 0.441$, $P = 0.152$, $N = 12$, Spearman correlation), thus there is not a definite trend in temporal variation in detrended values. In other words, species discovery did not compensate for species loss through time.

The z value obtained for the power function interpolating the cumulative number of lost species through decades ($y = 0.677(\pm0.102) + 1.052(\pm0.129)x$, $r = 0.932$, $P < 0.0001$) was substantially greater then the z value for the accumulation curve ($y = 1.819(\pm0.031) + 0.330\ (\pm0.040)x$, $r = 0.935$, $P < 0.0001$) (errors refer to standard errors) (Fig. 4). Thus the rate of species discovery was greatly inferior to the rate of species loss: species disappeared more rapidly than discovered. Also, for the cumulative number of known species, z was less than 1, thus the curve is convex, as expected for an accumulation curve reaching a plateau. Although the power function is not bounded, the shape clearly conforms to the asymptotic patterns of accumulation curves used to estimate species richness (e.g. Thompson et al. 2003). By contrast, z was near to or greater than 1 for the cumulative number of lost species through decades. When $z > 1$, the power function is concave, and this indicates that species loss is increasing at a greater rate, without a plateau being reached.

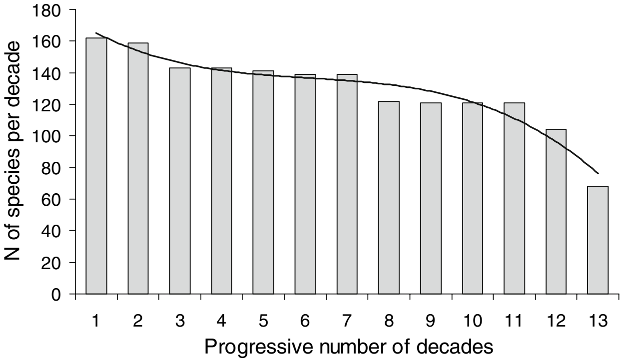

Fig. 2 Tenebrionid species numbers supposed to be present on the Aegean Islands from 1870 (decade 1) to 2000 (decade 13) fitted by a polynomial function (see text for details)

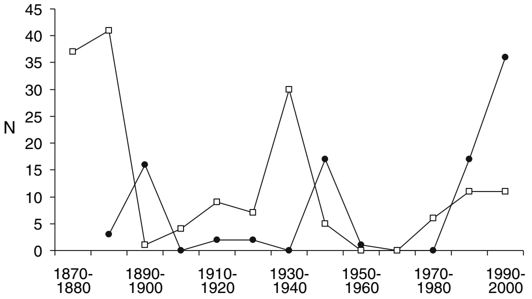

Fig. 3 Tenebrionid species discovered (empty squares) and lost (filled circles) on the Aegean Islands from 1870 to 2000

Discussion

Species rarity and vulnerability

Interrelations between species range size, abundance and ecological specialization have been found in several animal

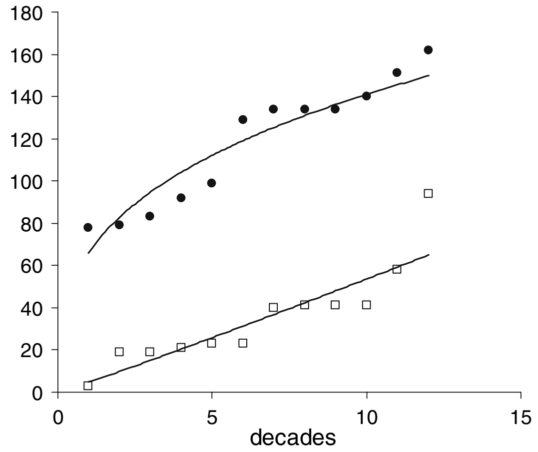

Fig. 4 Accumulation curves of tenebrionid species lost (filled circles) and discovered (empty squares) on the Aegean Islands from 1870 (decade 1) to 2000 (decade 13) fitted by the power function (see text for details)

taxa, but the underlying mechanism remains elusive and, in some circumstances, these relationships can be a consequence of the fact that the measures of these three dimensions are not truly independent (cf. Hanski et al. 1993). Apart from the problem if the measures used in this study are compelling proxies for habitat specialization and abundance, it is important to assess whether intercorrelations among the three measures of rarity used here are simply due to little independence between calculation methods. Geographic distribution and potential habitat exploitation could be interrelated simply because species occurring on more islands are necessarily distributed over larger areas. However, this is not the case, at least for the study system. There are species distributed on several small islands (with large geographic distribution but small potential habitat exploitation, such as *Dailogantha hellenica*, *D. quadricollis obtusangula*, *Eutagenia smyrnensis*) and species distributed on few but large islands (with small geographic distribution and large potential habitat exploitation, such as *Blaps cretensis*, *B. oertzeni*, *Cossyphus tauricus*, *Cylindronotus cretensis*). Thus the two measures are not necessarily redundant, although they can be statistically correlated. The two aforementioned measures could be intrinsically related to species contactability if the area occupied by each species is also going to determine its contactability. For example, a species distributed on several islands should be more easy to be collected. However, some species can be distributed in one or few islands, but they can be abundant (and hence easily contacted) here (e.g. *Asida fairmairei*, *Dendarus foraminosus*, *Pimelia minos*, *Probaticus euboeicus*, *Tentyria grossa grossa*), while others may be distributed on several islands but rarely sampled (e.g. *Akis elongata*, *Idastrandiella allardi*, *Nalassus plebejus*, *Probaticus tenebricosus*).

The strong link between conservation and rarity lies in the idea that rare species have a greater threat of extinction than common species do. Thus, conservation of rare species is driven by the view that the central goal of conservation is to prevent or limit the extinction of species. But, how good an indication of the risk of extinction of a species does the designation of being rare provide? In the Aegean tenebrionids, two indices of rarity strongly correlate with the number of decades of occurrence: the narrower, ecologically more specialized a species, lower the number of decades of its occurrence (i.e. faster it disappears). Thus, whether expressed in terms of range size or habitat exploitation, rarity is a major determinant of a species' risk of extinction at the particular scale at which the species was identified as rare. In this sense, the designation of rarity provides a good basis for identifying species that are most in need of conservation at a particular scale. In constructing a multidimensional representation of species rarity, in this study each species was scored with respect to small range size, habitat exploitation and contactability. These measures were adopted as the best available approach to take into account different measures of rarity, but other factors, like proximity to locations of high human density, certain life-history traits like low reproductive rate, large body size, geographic location, and high trophic level may predispose a species to high extinction risk (see Manne and Pimm, 2001) and, therefore, should be considered. Although this paper provides theoretical support and practical evidence that habitat exploitation and contactability may be closely related to habitat specialization and population density, this research did not attempt to assess if the measures of rarity used here are compelling proxies for these traditional measures.

Temporal analyses

A very large percentage of tenebrionid species loss during the last 50 years has occurred on the Aegean Islands. Although some species could be erroneously considered as being extinct because of lack of research, the emerging patterns clearly show an impressive decline, especially during recent years. This is a strong evidence of the actual decline in species numbers, because at least some islands have been thoroughly surveyed recently; thus, lack of records cannot be simply due to lack of research.

As expected, the most vulnerable (Kattan index) species are those with high rarity in terms of geographic distribution, habitat exploitation or contactability. Extinction did not affect species at random, but the species, which disappeared firstly were those with highest scores of rarity for geographic distribution and habitat exploitation.

Conclusions

This study represents a first attempt to apply a multidimensional characterization of rarity to a group of invertebrates. The methods described here were applied to a group of insects that are relatively well known in their distribution, but not in their ecology. Surely, most of the caveats discussed here would be less compelling for a group more thoroughly known from an ecological point of view, such as butterflies in northern Europe. For these reasons, butterflies have been widely proposed as a key indicator group of invertebrates and as a charismatic invertebrate counterpart to birds (e.g. Grill and Cleary 2003). However, since most insect groups are known as well as (or even less than) the Aegean tenebrionids, it is important to find that valuable results can be obtained also for imperfectly known taxa.

The methods used here are based on distributional records and dates of collection. These data are commonly available for insects. Thus the procedures derived here can be adopted for other insect groups in different geographic or temporal situations and may offer new practical tools in invertebrate conservation.

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Appendix Indices of species rarity for the Aegean Tenebrionids

Species	Assumed decades of occurrence	Geographic distribution	Potential habitat exploitation	Contactability	Kattan index
Akis elongata Brullé, 1832	12	0.156	0.430	0.167	7
Ammobius rufus Lucas, 1849	13	0.219	0.536	0.462	8
Anemia sardoa sardoa (Génè, 1839)	11	0.063	0.409	0.091	7
Apentanodes globosus globosus (Reiche, 1857)	12	0.063	0.420	0.250	7
Apentanodes globosus reductepleuralis Koch, 1935	7	0.031	0.069	0.143	1
Asida fairmairei fairmairei Boieldieu, 1865	13	0.063	0.185	0.385	6
Blaps abbreviata Mènètriès, 1836	2	0.031	0.180	0.500	2
Blaps cretensis Koch, 1948	12	0.031	0.406	0.250	3
Blaps oertzeni Seidlitz, 1839	12	0.031	0.406	0.167	3
Blaps taeniolata Ménétriés, 1832	7	0.094	0.084	0.286	6
Blaps tibialis Reiche, 1857	11	0.125	0.677	0.273	7
Bolitophagus reticulatus (Linné, 1767)	13	0.031	0.019	0.077	1
Cabirutus cribricollis (Baudi, 1875)	12	0.063	0.083	0.167	4
Calyptopsis caraboides (Brullé, 1832)	11	0.063	0.040	0.182	4
Cataphronetis reitteri Seidlitz, 1898	13	0.156	0.622	0.308	8
Catomus consentaneus (Küster, 1851)	13	0.156	0.464	0.385	8
Cephalostenus orbicollis (Ménétriés, 1836)	13	0.469	0.842	0.692	8
Cnemeplatia atropos atropos Costa, 1847	7	0.063	0.427	0.429	8
Colpotus byzantinicus (Waltl, 1838)	11	0.031	0.180	0.091	1
Colpotus pectoralis pectoralis Mulsant & Rey, 1853	13	0.031	0.180	0.308	2
Colpotus sulcatus (Ménétriés, 188)	13	0.344	0.680	0.538	8
Colpotus vogti Koch, 1948	12	0.031	0.023	0.167	1
Cossyphus tauricus Steven, 1882	11	0.031	0.406	0.182	3
Cylindronotus cretensis Seidlitz, 1898	13	0.031	0.406	0.231	3
Cylindronotus nigropiceus Küster, 1850	13	0.063	0.199	0.154	7
Cylindronotus tuberculiger Reiche, 1857	2	0.063	0.185	1.000	6
Dailognatha cylindritarsis cylindritarsis Koch, 1948	12	0.031	0.406	0.333	5
Dailognatha cylindritarsis probsti Picka, 1984	12	0.031	0.406	0.083	3
Dailognatha hellenica Reitter, 1898	13	0.375	0.072	0.308	6
Dailognatha quadricollis anaphiana Koch, 1948	12	0.031	0.002	0.250	1
Dailognatha quadricollis carceli Solier, 1835	13	0.125	0.163	0.538	6
Dailognatha quadricollis montana Koch, 1948	13	0.031	0.406	0.231	3
Dailognatha quadricollis obtusangola Reitter, 1896	13	0.375	0.084	0.462	6
Dailognatha quadricollis quadricollis Brullé, 1832	13	0.063	0.185	0.077	7
Dailognatha quadricollis rhodica Koch, 1948	13	0.063	0.084	0.231	4
Dailognatha quadricollis rugata Solier, 1835	13	0.031	0.406	0.462	5

Appendix continued

Species	Assumed decades of occurrence	Geographic distribution	Potential habitat exploitation	Contactability	Kattan index
Dailognatha quadricollis samosana Koch, 1948	2	0.031	0.023	0.500	2
Dailognatha quadricollis sporadica Koch, 1948	12	0.031	0.014	0.250	1
Dailognatha rugipleuris Reitter, 1896	7	0.031	0.000	0.143	1
Dendarus anaphianus Koch, 1948	13	0.031	0.002	0.154	1
Dendarus angulitibia Koch, 1948	2	0.031	0.010	0.500	2
Dendarus dentitibia Koch, 1948	7	0.031	0.019	0.286	2
Dendarus foraminosus Küster, 1851	13	0.031	0.406	0.538	5
Dendarus graecus Brullé, 1832	13	0.031	0.406	0.385	5
Dendarus messenius Brullé, 1832	13	0.344	0.284	0.462	8
Dendarus moesiacus (Mulsant & Rey, 1854)	13	0.156	0.107	0.385	6
Dendarus opacus Koch, 1948	13	0.031	0.406	0.385	5
Dendarus plicatulus paganettii Koch, 1948	7	0.031	0.010	0.143	1
Dendarus politus Reitter, 1917	13	0.031	0.406	0.385	5
Dendarus puncticollis Koch, 1948	12	0.031	0.406	0.250	3
Dendarus rhodius Baudi, 1876	12	0.094	0.098	0.333	6
Dendarus schatzmayri Koch, 1948	13	0.031	0.004	0.154	1
Dendarus sinuatus Mulsant, 1854	13	0.188	0.043	0.231	4
Dendarus stygius oertzeni Koch, 1948	2	0.031	0.180	0.500	2
Dendarus stygius stygius Waltl, 1838	2	0.031	0.023	1.000	2
Dendarus tenellus (Mulsant & Rey, 1854)	11	0.031	0.180	0.091	1
Dendarus werneri Koch, 1948	7	0.031	0.007	0.143	1
Dendarus wernerianus Koch, 1948	11	0.063	0.006	0.182	4
Dendarus wettsteini Koch, 1948	12	0.031	0.406	0.167	3
Diaclina fagi (Panzer, 1797)	13	0.031	0.019	0.077	1
Diaperis boleti (Linné, 1758)	2	0.031	0.180	0.500	2
Dichillus carinatus Küster, 1848	13	0.031	0.019	0.077	1
Dichillus obenbergeri Maran, 1935	13	0.031	0.406	0.308	5
Dichillus subsetulosus Reitter, 1886	7	0.031	0.069	0.143	1
Dichomma dardanum (Steven, 1829)	13	0.375	0.724	0.462	8
Doliema turcica Reitter, 1877	12	0.031	0.406	0.083	3
Eledona hellenica Reitter, 1885	2	0.031	0.180	0.500	2
Erodius orientalis boyeri Solier, 1834	8	0.031	0.406	0.375	5
Erodius orientalis brevicostatus Solier, 1834	13	0.188	0.441	0.538	8
Erodius orientalis oblongus Solier, 1834	13	0.188	0.569	0.462	8
Euboeus mimonti Boieldieu, 1865	11	0.031	0.180	0.182	1
Eutagenia minutissima Pic, 1903	12	0.094	0.489	0.250	7
Eutagenia smyrnensis (Solier, 1838)	13	0.250	0.054	0.385	6
Gonocephalum affine (Billberg, 1815)	12	0.094	0.489	0.083	7
Gonocephalum costatum costatum (Brullé, 1832)	12	0.125	0.510	0.333	8
Gonocephalum granulatum nigrum (Küster, 1843)	13	0.219	0.319	0.385	8
Gonocephalum rusticum (Olivier, 1811)	12	0.281	0.616	0.500	8
Gonocephalum setulosum setulosum (Faldermann, 1837)	12	0.125	0.499	0.333	8
Graecopachys quadricollis cretica (Koch, 1948)	13	0.031	0.406	0.385	5
Graecopachys quadricollis s.l. (Brullé, 1832)	13	0.625	0.345	0.462	8
Gunarus kaszabi Grimm, 1981	12	0.031	0.004	0.083	1
Helopelius aenipennis (Allard, 1876)	7	0.031	0.069	0.143	1
Helops coeruleus (Linné, 1758)	13	0.031	0.180	0.077	1

Appendix continued

Species	Assumed decades of occurrence	Geographic distribution	Potential habitat exploitation	Contactability	Kattan index
Helops glabriventris glabriventris Reitter, 1885	13	0.031	0.180	0.154	1
Helops glabriventris jelineki Picka, 1984	12	0.031	0.406	0.083	3
Helops rossii Germar, 1817	13	0.063	0.424	0.231	7
Hymatismus villosus Haag-Ruttenberg, 1870	7	0.031	0.406	0.143	3
Hypophloeus fasciatus Fabricius, 1790	2	0.063	0.586	0.500	8
Hypophloeus fraxini Kugel, 1794	7	0.063	0.025	0.286	6
Hypophloeus pini Panzer, 1799	4	0.063	0.084	0.500	6
Idastrandiella allardi (Reitter, 1884)	13	0.063	0.012	0.077	4
Idastrandiella graeca (Kraatz, 1877)	1	0.031	0.010	1.000	2
Idastrandiella mucorea (Waltl, 1838)	1	0.031	0.010	1.000	2
Iphthiminus italicus croaticus (Truqui, 1857)	12	0.063	0.586	0.167	7
Laena apfelbecki Schuster, 1915	1	0.031	0.180	1.000	2
Laena ferruginea Küster, 1846	11	0.031	0.406	0.182	3
Laena oertzeni Reitter, 1885	5	0.031	0.406	0.200	3
Menephilus cylindricus cylindricus (Herbst, 1784)	13	0.125	0.673	0.231	7
Micrositus orbicularis Mulsant & Rey, 1854	13	0.281	0.535	0.538	8
Microtelus asiaticus Solier, 1838	11	0.063	0.427	0.182	7
Nalassus plebejus (Küster, 1850)	13	0.063	0.199	0.077	7
Oochrotus glaber rhodicus Koch, 1935	11	0.031	0.069	0.182	1
Opatroides punctulatus Brullé, 1832	13	0.563	0.726	0.538	8
Opatrum geminatum s.l. Brullé, 1832	4	0.031	0.080	0.250	1
Opatrum obesum Olivier, 1811	13	0.375	0.808	0.615	8
Opatrum sabulosum sabulosum (Linné, 1758)	13	0.063	0.041	0.385	6
Opatrum verrucosum Germar, 1817	13	0.063	0.199	0.231	7
Pachychila frioli Solier, 1835	11	0.031	0.406	0.182	3
Pachyscelis villosa (Drapiez, 1820)	13	0.469	0.347	0.462	8
Palorus depressus (Fabricius, 1790)	2	0.031	0.406	0.500	5
Pedinus oblongus Mulsant & Rey, 1853	7	0.031	0.005	0.143	1
Pedinus olivieri Mulsant & Rey, 1853	12	0.031	0.406	0.417	5
Pedinus quadratus Brullé, 1832	13	0.438	0.620	0.462	8
Pedinus subdepressus Brullé, 1832	2	0.031	0.180	1.000	2
Pentaphyllus chrysomeloides (Rossi, 1792)	2	0.063	0.184	0.500	6
Phaleria acuminata s.l. Küster, 1852	12	0.031	0.406	0.083	3
Phaleria bimaculata s.l. (Linné, 1767)	13	0.250	0.614	0.538	8
Pimelia minos Lucas, 1853	12	0.031	0.406	0.417	5
Pimelia subglobosa (Pallas, 1781)	13	0.563	0.487	0.615	8
Platydema europaeum Laporte & Brullé, 1831	13	0.063	0.099	0.154	4
Platynosum paulinae Mulsant & Rey, 1859	7	0.031	0.069	0.143	1
Polycoelogastridium sexcostatum (Motschulsky, 1858)	11	0.063	0.475	0.273	7
Probaticus euboeicus (Reitter, 1885)	13	0.031	0.180	0.231	1
Probaticus graius (Allard, 1885)	2	0.031	0.021	0.500	2
Probaticus mori (Brullé, 1832)	13	0.094	0.655	0.308	8
Probaticus obesus (Frivaldski, 1832)	12	0.031	0.406	0.083	3
Probaticus tenebricosus (Brullé, 1832)	7	0.125	0.124	0.143	4
Probaticus tentyrioides (Küster, 1851)	2	0.031	0.180	1.000	2
Raiboscelis azureus obliteratus Allard, 1878	13	0.375	0.246	0.385	8
Raiboscelis coelestinus s.l. (Waltl, 1838)	13	0.250	0.264	0.308	8

Appendix continued

Species	Assumed decades of occurrence	Geographic distribution	Potential habitat exploitation	Contactability	Kattan index
Raiboscelis corvinus brodskyi Picka, 1984	13	0.031	0.406	0.154	3
Raiboscelis corvinus corvinus (Küster, 1850)	13	0.031	0.406	0.308	5
Raiboscelis corvinus slamai Picka, 1984	12	0.031	0.406	0.083	3
Scaurus aegyptiacus aegyptiacus Solier, 1838	11	0.063	0.004	0.182	4
Scleron multistriatum (Forskål, 1775)	12	0.156	0.449	0.333	8
Stenosis cretica Koch, 1940	13	0.031	0.406	0.154	3
Stenosis crivellari Koch, 1935	7	0.031	0.000	0.143	1
Stenosis esau Sahlberg, 1907	2	0.031	0.023	0.500	2
Stenosis intermedia dalmatina Reitter, 1916	2	0.031	0.180	1.000	2
Stenosis keosana Koch, 1948	2	0.031	0.006	0.500	2
Stenosis rhodica Koch, 1935	12	0.063	0.083	0.167	4
Stenosis silvestrii Koch, 1935	11	0.031	0.069	0.182	1
Stenosis syrensis naxica Koch, 1940	13	0.094	0.043	0.231	4
Stenosis syrensis syrensis Koch, 1936	2	0.063	0.008	0.500	6
Strongylium saracenum (Reiche & Saulci, 1857)	13	0.031	0.069	0.077	1
Tentyria grossa grossa Besser, 1832	12	0.031	0.406	0.250	3
Tentyria rotundata angulata Brullé, 1832	13	0.031	0.019	0.308	2
Tentyria rotundata mittrei Solier, 1835	13	0.125	0.148	0.462	6
Tentyria rotundata orbicollis Solier, 1835	13	0.344	0.090	0.308	6
Tentyria rotundata paganettii Schuster, 1915	12	0.031	0.406	0.250	3
Tentyria rotundata sulcatipennis Schuster, 1936	12	0.063	0.005	0.417	6
Tentyria sporadica sporadica Reitter, 1900	7	0.063	0.084	0.286	6
Trachyderma lima (Petagna, 1819)	12	0.156	0.490	0.333	8
Trachyderma philistina Reiche, 1857	7	0.031	0.069	0.143	1
Trachyscelis aphodioides Latreille, 1809	12	0.156	0.612	0.250	7
Uloma culinaris (Linné, 1758)	5	0.063	0.586	0.400	8
Uloma cypraea Kraatz, 1873	13	0.031	0.180	0.077	1
Xanthomus cyprius Grimm, 1991	13	0.031	0.069	0.077	1
Xanthomus graecus Dajoz, 1984	13	0.031	0.019	0.077	1
Xanthomus ovulus (Seidlitz, 1898)	12	0.031	0.406	0.333	5
Zophosis dilatata Deyrolle, 1867	12	0.094	0.098	0.250	4
Zophosis punctata punctata Brullé, 1832	13	0.719	0.945	0.769	8

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REVIEW PAPER

The occurrence and distribution of carabid beetles (Carabidae) on islands in the Baltic Sea: a review

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Abstract The distribution and occurrence of carabid beetles have been studied extensively in a number of archipelagoes in the Baltic Sea, a ca. 377,000 km^2, fairly shallow and young sea in northern Europe. This work has revealed some surprising results related to colonisation success and maintenance of populations. Dispersal from the mainland and between islands appears to be relatively easy because inter-island distances are small (tens or hundreds of metres) and the salinity of the Baltic is low, which allows survival during drift. This is reflected in the higher than expected proportion of brachypterous species on small islands. A lack of energetically expensive wings, flight muscles and flight fuel may give brachypterous species an advantage - in terms of resource allocation for survival and fecundity - over macropterous species in the colonisation of an island. Once an island is reached, successful colonisation mainly depends on the presence of suitable habitat. The most abundantly collected carabids on these islands are habitat generalists, but some degree of habitat association exists. Yet, the composition of carabid assemblages differs substantially among islands, possibly a result of chance effects. There is evidence that species on smaller islands occur in a wider variety of vegetation types than species on larger islands. Both habitat diversity and area *per se* are implicated in the positive species-area relationships found, but the small island effect has been identified as being significant in most of the archipelagoes investigated. *Pterostichus melanarius*, a eurytopic, wing-polymorphic species abundantly collected on the mainland is, unexpectedly, absent from small islands. Possible reasons for this include; (1) interspecific predation and competition for food by the closely related but slightly larger *P. niger*, which is dominant on small islands, (2) the apparent inability of *P. melanarius* to reproduce on small islands, (3) its reduced dispersal power as compared to *P. niger* and (4) the possible absence of some essential resources from small islands. In conclusion, the conservation value of highly threatened cultural landscapes on Baltic Sea islands, such as species rich wooded meadows, is discussed as well as the possible negative effects of climate change on carabid beetles.

Keywords Baltic Sea · Colonisation · Dispersal ability · Ground beetle · Habitat diversity · Island · Small island effect · Species-area relationship · Wing morphology

Introduction

Both the characteristics of islands in the Baltic Sea and of carabid beetles (Coleoptera, Carabidae) provide excellent opportunities for studying insular communities. Thousands of islands of varying sizes and levels of isolation are found in many archipelagoes in the Baltic Sea (Järvinen and Ranta 1987; Ås et al. 1997), and with continuous post-glacial land uplift, the number of islands is increasing, islands are increasing in area with a resultant increase in habitat diversity, thus the spatial configuration of islands is changing. Hypotheses related to isolation distance, area effects, age effects (higher islands are generally older than lower ones), and the effects of the spatial arrangements of islands (i.e. clustered vs. scattered) on communities can be

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studied relatively easily because of the magnitude of islands and the relative calmness of the Baltic Sea waters.

Carabid beetles, as a group, display a number of characteristics that make them ideal subjects for the study of insular environments (Rainio and Niemelä 2003). Different species possess different powers of dispersal, as was already appreciated by Darlington (1943), who studied the importance of carabid beetle wing morphs on mountains and islands. Species can be classified into full-winged (macropterous), reduced or wingless (brachypterous, apterous) and wing-polymorphic species (Den Boer 1970, Den Boer et al. 1980; Lindroth 1985, 1986), but dispersal ability is only appreciated when wing morphs are associated with wing muscle development (Den Boer et al. 1980; Den Boer 1990; Desender 2000; Matalin 2003), the willingness to fly and the environmental conditions suitable for flight. Most carabid beetles are generalist predators (Lövei and Sunderland 1996), yet species can be classified into specialisation, i.e., niche breadth (Dufrêne and Legendre 1997; Kotze and O'Hara 2003), and habitat association categories (Lindroth 1985, 1986). These autecological and other life history characteristics, such as breeding type (spring or autumn breeders) and fecundity are of considerable importance in explaining the distribution of carabid species on islands (Niemelä 1988a; Desender 2000; Zalewski 2004).

In this review I start with a brief history of the Baltic Sea and the current characteristics of the region. Then I evaluate research performed on carabid beetles on Baltic Sea islands, emphasising the role of species characteristics, such as flight capability and habitat affinity, on colonisation success and assemblage structure. The ecology of insular biota necessitates a discussion on island biogeography theory and metapopulation dynamics. These concepts will not be discussed in detail here; rather the importance of the small island effect, short inter-island distances, the low-salinity matrix and habitat heterogeneity on the occurrence and abundance of carabid species on Baltic islands will be addressed. I conclude with a look into anticipated future changes in the Baltic Sea, such as climate change, and discuss some conservation issues, in particular the value of cultural landscapes such as wooded meadows on these islands.

Baltic Sea history and current characteristics

Rapid glacio-isostatic rebound of the earth's crust following deglaciation during the late Weichselian and early Holocene has been a determining factor in the formation of the Baltic Sea (Eronen et al. 2001; Tikkanen and Oksanen 2002). Four main stages are recognised in the history of the Baltic basin since the last glaciation (but see Påsse and Andersson 2005 for an alternative view). Briefly, the Baltic Ice Lake (12600–10300 BP) formed when the ice margin retreated and freshwater began to accumulate in the Baltic basin. This period is characterised by at least three discharges of freshwater into the North Sea. The last discharge, around 10300 BP, coincided with a sharp warming of the global climate and a water level decrease of 25–28 m within a few years (Tikkanen and Oksanen 2002). This signalled the start of the Yoldia Sea stage (10300–9500 BP). During this period, saline water entered the Baltic basin through the lowlands of central Sweden, but had a minimal effect on the overall salinity of the Baltic, due to the large volumes of glacial melt water. Land uplift was still considerable during this stage, and was faster in central Sweden than the rise in ocean levels and the Baltic basin became isolated again to form a freshwater lake around 9500 BP, the last major limnetic phase of the basin (Schmölcke et al. 2006). This stage, called the Ancylus Lake (9500–8000 BP), was characterised by a transgression during which a rise in the water level caused extensive areas to be inundated once more (Tikkanen and Oksanen 2002). This transgression came to an end when the rising waters exceeded the Darss Sill, the Fehmarn Belt and the Great belt in the south-western part of the Baltic basin, and water began to flow again into the ocean via the Kattegat at around 9200 BP (Tikkanen and Oksanen 2002; Schmölcke et al. 2006). Around 9000 BP, the Ancylus Lake reached the level of the outside ocean, but it appears that saline water did not flow into the basin due to the narrowness of the connection to the ocean. Large expanses of dry land emerged and the Baltic Sea was characterised by many islands.

Ocean levels continue to rise, due to global warming that started around 9600 BC (Schmölcke et al. 2006), and saline water began to enter the Baltic Sea around 8400–8300 BP through the Straits of Denmark. By 7500 BP, most of the Baltic Sea was distinctly brackish (Eronen et al. 2001; Miettinen 2004), marking the onset of the next stage, the Littorina Sea (7500–4000 BP) (Tikkanen and Oksanen 2002). The ocean level rise led to a transgression at the beginning of the Littorina Sea stage (Eronen et al. 2001; Schmölcke et al. 2006), which ended around 6000–5000 BP when the rise in ocean levels came to an end. Land uplift continued but at a steadily declining rate. Furthermore, salinity started to decline slightly, as the Straits of Denmark became gradually narrower and shallower. The period since 4000 BP, when the level of salinity reached its present level, is referred to as the Limnea Sea (Eronen et al. 2001; Tikkanen and Oksanen 2002).

Today's Baltic Sea is characterised by a great number of islands. For example, the Stockholm archipelago alone consists of ca. 30,000 islands (Ås et al. 1997), the Åland archipelago of more than 6,000 islands (Hæggström 1988), the Finnish territory of the Baltic Sea of more than 80,000 islands larger than 100 m^2 in size (Raatikainen 1987), and the west Estonian archipelago of more than 1,000 islands (see Jüriado et al. 2006). Land uplift in Fennoscandia is continuing with a current rate from up to 9 mm yr^{-1} in the northern parts of the Gulf of Bothnia, to 4–5 mm yr^{-1} at the south-western coast of Finland and the Åland Islands, and to 1 mm yr^{-1} on the island of Gotland (see Fig. 1). The southern coastline of the Baltic Sea experiences a land fall rate of 1 mm yr^{-1} (Ekman and Mäkinen 1996; Eronen et al. 2001; Johansson et al. 2004; Påsse and Andersson 2005). Consequently, the number of islands is increasing, island area is increasing resulting in islands getting connected to one another and to the mainland, and the spatial configuration of islands is continually changing. Islands are often classified, based on a gradual change in appearance, into three zones. The inner zone, which is close to the mainland, is mostly characterised by older and larger islands, the middle zone by islands of different sizes, separated by larger distances from one another and from the mainland, and the outer zone by widely scattered groups of small islands (Ås et al. 1997), providing different colonisation opportunities for species.

Another unique characteristic of the Baltic Sea is its low but variable salinity. Ocean water enters the Baltic Sea from the North Sea via the Skagerrak and the Kattegat (see Fig. 1). The surface salinity at the Kattegat varies considerably around a mean of ca. 20‰. Surface salinity decreases from the south to the north of the Baltic Sea; in the Baltic proper it is ca. 8‰, in the Bothnia Sea it is ca. 5.5‰ and in the Bothnia Bay it is ca. 3.5‰ (Samuelsson 1996). These brackish levels are mainly maintained by river runoff (Matthäus and Schinke 1999) and by episodic inflows of large volumes of highly saline and oxygenated water (termed Major Baltic Inflows) via the Kattegat (Matthäus and Schinke 1999; Meier 2007). Ocean inflows are important to the deep waters of the Baltic, as they redress stagnant and anoxic conditions and improve the living conditions of the benthic community. From 1899 to 1993 there have been a total of 96 major inflows. Before the mid−1970's major inflows were observed more or less regularly, but since then only a few major inflow events have occurred, resulting in a significant decrease in salinity. The lack of recent major inflows seems to be correlated with higher river runoff during the latter part of the 20th century (Samuelsson 1996; Matthäus and Schinke 1999). Recent major Baltic inflows in January 1993, September 1997 and January 2003 terminated the exceptionally long stagnation period and renewed the deep water of the Baltic proper (Meier 2007).

Carabid beetles on Baltic Sea islands

The Carabidae of Northern Europe is a taxonomically and ecologically well-known group. Roughly 400 species inhabit Fennoscandia and Denmark (Lindroth 1985, 1986), ranging in size from 1.8 mm (*Tachys bistriatus* (Dft.)) to 34.6 mm (*Carabus coriaceus* (L.)), with nearly 80% of the species smaller than 10 mm. Furthermore, the group exhibits wing and wing-muscle polymorphism (see above).

In order for a population of a carabid species to establish on an island, individuals need to be able to disperse to the island, and once there, find suitable conditions for reproduction to build up sufficient numbers to avoid local extinction. In other words, the species' biological characteristics (such as dispersal ability, competitive ability, reproductive output and specialisation), its abundance and emigration rate in the source habitat, and island characteristics (such as island size, isolation and habitat composition) are influential in determining island occupancy. The observation that island carabid communities deviate significantly from the sampling hypothesis (where species are represented in the same proportion as they are found in the mainland species pool) illustrates the importance of biological characteristics in successful colonisation (Ranta and Ås 1982; Niemelä et al. 1985; Niemelä et al. 1988; Ås et al. 1997). Below I will discuss some of the most often cited biological and environmental explanations put forward for the occurrence of carabid beetles on Baltic islands: dispersal (which is influenced by island isolation and configuration, and matrix effects) and habitat associations of the species (which are influenced by habitat diversity and vegetation types present on an island, and by island size).

Carabid beetle dispersal

Dispersal influences the dynamics and persistence of insular populations, the distribution and abundance of species and the structure of the local community (Den Boer 1990; Dieckmann et al. 1999; Zalewski and Ulrich 2006). Dispersal, i.e., reaching an island, is the first stage of colonisation. Macropterous individuals presumably have much greater powers of dispersal than brachypterous or apterous individuals (Den Boer 1970). This is, however, not the full picture. Macropterous individuals, whether they are from macropterous species or from wing-polymorphic species, do not always possess functional flight muscles, and flight muscles of some species can be reabsorbed after a pre-reproductive flight period (Desender 2000; Matalin 2003). Thus polymorphism of both hind wings and wing muscles, which depends to a large degree on larval nutrition (Nelemans 1987a, b), should be considered together to estimate the dispersal power of carabid beetles (Matalin 2003).

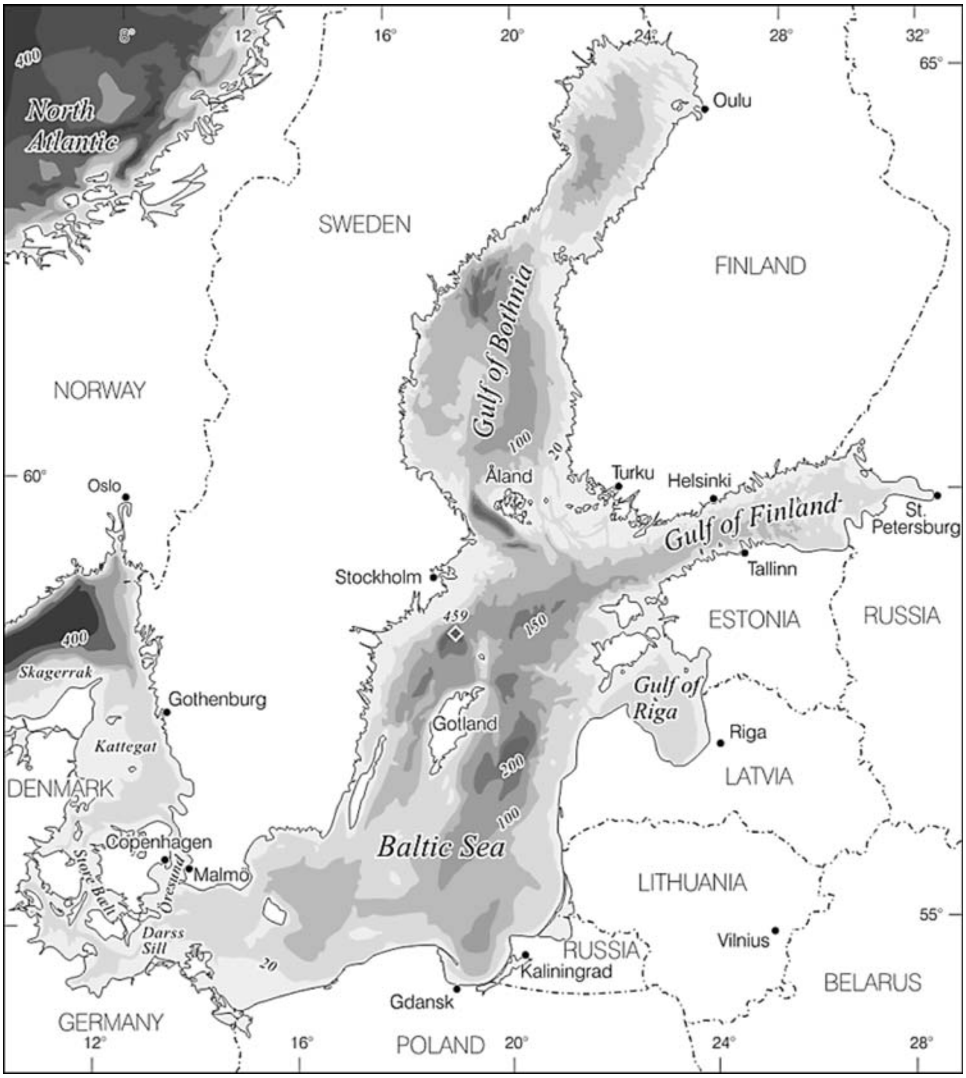

Fig. 1 The Baltic Sea and surrounding countries. Large islands and sea depths are indicated. The author thanks Matti Tikkanen for providing the figure

If flight is the main means by which a carabid species can reach an island, brachypterous or apterous species should be under-represented on islands, particularly highly isolated ones. This is not the case for Baltic islands. Ås (1984) studied carabid beetles on islands at different distances from the mainland in the Stockholm archipelago and showed that the proportion of brachypterous species (0.40–0.67) was significantly higher on islands compared to the mainland (0.18). Ås (1984) furthermore calculated that the expected proportion of brachypterous species increased up to a point approximately 27 km from the mainland, where roughly 61% of the species arriving on an island should be brachypterous, which was supported by the data. Kotze et al. (2000) showed that the mean proportion of brachypterous species on 24 islands (0.27) sampled off the south-western coast of Finland was significantly higher than on the closest mainland source area (0.15). Similarly, the proportion of brachypterous species decreased from 0.33 on small islands to 0.30 on the main island of Åland to 0.12 on the closest Finnish mainland province (Kotze and Niemelä 2002). Furthermore, brachypterous species are amongst the most abundant carabids collected on the islands (Table 1, and Silfverberg 1968; Zalewski and Ulrich 2006), but often with comparable numbers on the mainland (Niemelä 1988b; see also Gutiérrez and Menéndez 1997).

Several mechanisms have been put forward to explain the higher proportion of brachypterous species on Baltic islands. Firstly, carabids are generally poor fliers and the direction of airborne dispersal is highly influenced by wind direction (Lindroth 1949; Ås 1984). Given that the production of wings and functional flight muscles are energetically expensive, that flight itself is energetically extremely demanding, and that these are often, but not always (see Spence 1989; Aukema 1991), at the expense of fecundity (Ås 1984; Roff 1986; Roff and Fairbairn 1991; Zera and Denno 1997; Desender 2000; Langellotto et al. 2000; Langellotto and Denno 2001; Zera 2004), the possession of flight apparatus and flight itself may not be an

Table 1 Most abundantly collected carabid beetles from selected archipelagoes in the Baltic Sea and on lake islands

Species	Studies		1	2	3	3	3	3	4	5	6	7	8	9
	Wings	Size	Baltic Stockholm	Baltic Åland	Baltic Stockholm	Baltic Värgskär	Baltic Tvärminne	Lake, Fin Pihlajavesi	Baltic Åland	Baltic Åland	Baltic Åland	Baltic SW arch	Baltic Åland	Lake, Pol Mamry
Pterostichus niger	M	15–20.5	1/30/443	1/40/97	1/39/301	3/15/714	2/17/60		1/38/129	1/43/335	1/17/587	1/34/5544	2/20/707	3/9/1166
Patrobus atrorufus	B	7.4–10	2/12/181		2/20/150				6/4/14	7/2/16	4/9/311			7/5/571
Trechus secalis	B	3.5–4	3/9/130	6/4/10	3/15/116	4/9/435		1/33/257	2/13/46	2/15/113	3/16/537	8/4/572	1/42/1473	
Dyschirius globosus	B	2.2–3	4/8/214			5/6/280	1/54/191		3/10/35					
Pterostichus strenuus	P	6–7.2	5/6/86											
Calathus melanocephalus	P	6–8.8	6/5/79		4/9/67						5/7/245			
Pterostichus oblongopunctatus	M	9.5–12.6	7/5/72								6/6/220			2/14/1802
Cychrus caraboides	B	14–19		2/12/30						5/4/30		7/7/1061	5/6/220	
Loricera pilicornis	M	6–8.5		3/9/21	6/3/21	7/3/118				8/2/14				
Carabus hortensis	B	22–28		3/9/21		8/2/113	5/3/10	5/4/29	4/6/19	3/13/102	7/4/138	5/7/1161	4/6/228	
Pterostichus nigrita	M	8.8–12.8		5/8/19							8/4/123	9/2/367	8/2/70	
Patrobus assimilis	B	8.8–9		6/4/10								6/7/1093		
Calathus micropterus	B	6.5–8.8				6/5/214	3/8/30	2/24/187	4/6/19	4/6/48		3/9/1415	3/10/348	
Agonum fuliginosum	P	5.5–7.8				2/23/1066			6/4/14	6/2/18		2/12/1903	7/3/102	
Carabus violaceus	B	20–30			5/5/41									
*Agonum obscurum**	P	5–6.5				1/27/1239						4/8/1263	6/4/124	4/8/986
Pterostichus diligens	P	5.3–6.7					4/5/19							
Amara brunnea	M	5.2–6.8						3/13/99						
Agonum viduum	M	7–9						4/12/89						
Calathus fuscipes	B	10–14.4									2/16/558			
Pterostichus melanarius	P	12–18												1/28/3624
Harpalus quadripunctatus	M	9.5–12												5/7/879
Carabus granulatus	P	16–23												6/5/684

Wings: M—macropterous, P—wing polymorphic, B—brachypterous. Size—beetle size range in mm. Values represent; Rank/Percentage of catch from the islands/total number of individuals on the islands

Studies: 1—Ås (1984), 2—Niemelä et al. (1985), 3—Niemelä et al. (1987), 4—Niemelä (1988a), 5—Niemelä (1988c), 6—Niemelä et al. (1988), 7—Kotze et al. (2000), 8—Kotze and Niemelä (2002), 9—Zalewski and Ulrich (2006). Fin, Finland; Pol, Poland

* Other names: *Oxypselaphus obscurus* or *Platynus obscurus*

advantage to carabids on Baltic islands where inter-island distances are generally short (Järvinen and Ranta 1987; Niemelä 1988c) and salinity is low. Indeed, Palmén (1944) calculated that carabids can survive up to five days in brackish water typical of the Baltic without adverse effects on fecundity, during which they can drift up to 10 km (see Ås 1984), and Niemelä et al. (1988) showed that 26 of the 44 species collected on islands in the Åland archipelago have been found in drift material (see also Kotze and Niemelä 2002). Therefore, flight may not be needed for carabids to reach Baltic islands, and brachypterous individuals may be able to use energy reserves directly, and immediately, for survival and reproduction once an island is reached.

Secondly, and related to the point above, Lindroth (1949) argued that for populations which live in small areas, such as islands, surrounded by inhospitable land or water, flying itself constitutes selection against macropterous individuals because the chances of returning to the island are small. Winged individuals of wing-polymorphic or macropterous species may perhaps be superior in getting to an island (via flight, drifting, or both), but once there they stand the obvious risk of being blown off the island, increasing mortality and emigration frequency (Ås 1984; Gillespie and Roderick 2002).

Thirdly, forestry is not practised on small islands and combined with a low degree of human-related disturbances, may partly explain the high occurrences of brachypterous species on small islands (see Ribera et al. 2001; Rainio and Niemelä 2003). These poor dispersers may be relatively good survivors (Kotze and Niemelä 2002; Zalewski and Ulrich 2006), as flightlessness is often a trait selected for on islands (see below).

As such, Baltic islands differ considerably from true oceanic islands. Oceanic islands are usually colonised by species capable of flight, after which-depending on the degree of isolation—there is strong selection for reduced dispersal ability (Chown et al. 1998) and the speciation and adaptive radiation of neo- and palaeo-endemics (Sadler 1999; Emerson et al. 2000; Gillespie and Roderick 2002). Baltic islands, however, are relatively young, not highly isolated, and are low in numbers of endemics (Haila 1990; Ås et al. 1997). No carabid endemics are known from the Baltic although three endemic plant species and a number of endemic subspecies have been described, and polymorphism in the meadow spittlebug (*Philaenus spumarius*) and small-scale differentiation in the allele frequencies at one locus in an island population of the ant *Formica sanguinea* are known (see Ås et al. 1997; Järvinen and Ranta 1987).

The author is not aware of research performed on the genetic structure of carabid populations on Baltic islands, yet genetic differentiation is likely to exist. For example, Desender et al. (1998) showed that random processes such as drift and founder effects are important determinants for the genetic structure of populations of two saltmarsh carabid beetles. The constantly macropterous *Dicheirotrichus gustavii* displays higher genetic diversity and less genetic differentiation between populations than the wing-polymorphic *Pogonus chalceus* (Desender et al. 1998). Western European saltmarshes are relatively young habitats (ca. 6,000 years old)—roughly of the same age as some of the larger Baltic Sea islands—which make studying the genetic structure of carabid beetles of different powers of dispersal on islands of different levels of isolation an interesting prospect.

Baltic islands provide excellent opportunities for studying dispersal-related questions using carabid beetles. For example, the proportion of wing polymorphic species is higher in Fennoscandia than elsewhere (Lindroth 1949; see also Järvinen and Ranta 1987) and polymorphic species are often collected from these islands, sometimes in high numbers (Table 1). Zalewski and Sienkiewicz (accepted) found a threefold increase in the fraction of polymorphic carabid species on lake islands in Poland compared to the mainland. Wing-polymorphic insects are excellent in studying the evolution of dispersal because the non-dispersing brachypterous morph is, presumably, easily recognised (Roff 1986)—but see above. Furthermore, a trade-off may exist between flight capability (i.e. the production and maintenance of wings, flight muscles, flight fuels, and flight itself) and other fitness-related components, such as age at first reproduction and fecundity (Roff and Fairbairn 1991; Denno 1994; Zera and Denno 1997; Langellotto et al. 2000; but see Spence 1989; Aukema 1991).

Desender (2000) showed that in most of the 27 carabid species he studied, a higher proportion of beetles with functional flight muscles than without had unripe as compared to ripe ovaries, indicating that the so-called oogenesis-flight syndrome may be applicable to some, but not to all carabid species (see Desender 1989; Aukema 1991). The following dispersal-related questions warrant investigation on Baltic Sea islands: (1) Are younger islands characterised by higher proportions of macropterous individuals of wing-polymorphic species, as was shown by Zalewski (2004) for lake islands in Poland? Young and unstable habitats are usually characterised by higher proportions of macropterous individuals, as these are the first to colonise such habitats (Den Boer et al. 1980; Roff 1986; Niemelä and Spence 1991; Lövei and Sunderland 1996; Zera and Denno 1997; Langellotto and Denno 2001). (2) Do macropterous individuals of macropterous and wing-polymorphic species disperse before reproduction, and do these individuals reabsorb their flight muscles once a suitable island is reached? Desender

(2000) and Matalin (2003) showed that the dispersal power of carabid beetles differs at different stages of their physiological development; mostly teneral and immature beetles disperse, after which their wing muscles degenerate to facilitate egg development. (3) How many brachypterous individuals reach the islands by drift? This question can be addressed by surveying very small islands. Due to land uplift, many small islands, consisting only of bare rock, exist throughout the Baltic Sea. It is unlikely that carabid populations can persist on these small rocks, but they may act as natural traps (and sinks) for drifting beetles.

Carabid beetle habitat associations

Most carabid species are generalist predators (Lövei and Sunderland 1996), yet species can be classified into specialisation (in terms of niche breadth) and habitat association groups (see Dufrêne and Legendre 1997; Kotze and O'Hara 2003). Once a propagule has dispersed to an island, the next stage of successful colonisation is the establishment of a viable population, which mainly depends on the presence and distribution of suitable habitat. Successful colonisation also depends on finding a mate if the individual is not a gravid female, on the availability of essential resources, and on interspecific predation and competition for food (see Currie et al. 1996). Here I will mainly focus on the availability of suitable habitat in successful carabid beetle colonisation.

With time, land uplift produces larger and higher islands where primary vegetative succession takes place (see Järvinen and Ranta 1987 and references therein). Small islets are characterised by bare rock and pioneer species that are replaced by later successional species with increasing island age and size. Large islands also tend to show a clear zonation from outer, shoreline pioneer communities to an alder belt, then rocky pine forest, continuous forest and finally lush forest towards the island interior (Järvinen and Ranta 1987; Niemelä 1988a, c; Ås et al. 1997). Larger islands, therefore, generally consist of more vegetation types, ranging from unstable shore vegetation to more stable inland forests.

Ås et al. (1997) reviewed a number of case studies from the Baltic Sea and concluded that the only factor common to all studies is that species with wide niche breadths (i.e. generalists) do better on the islands, and that the mean habitat niche breadth of species increases with distance from the mainland. For example, all except the two last-mentioned dominant carabid species on the islands investigated (in Table 1) are of average specialisation to highly eurytopic; none are stenotopic (see Lindroth 1985; 1986; Kotze and O'Hara 2003). Furthermore, by far the most abundant species in most Baltic archipelagoes is *Pterostichus niger* (Schaller, 1783), a eurytopic species characteristic of woodlands, parks, gardens (Lindroth 1986) and agricultural land. Yet, species with specific niche requirements do occur in different vegetation types on the islands. For example, shore environments were mainly occupied by hygrophilous species, typical of open, moist environments and alder forests mainly by forest generalist species (Niemelä 1988a), and field and forest carabids were strictly associated with these environments but generalist species were less strictly associated with any vegetation type sampled (Niemelä and Halme 1992). Furthermore, Niemelä (1988c) found that most of the species collected showed similar habitat associations on Åland and on the small islands (see also Niemelä et al. 1988), but that beetle assemblages were more similar within islands than between them. In all studies mentioned above, most species were found outside their preferred habitat, but in small numbers, and it appears that carabids on small islands use a wide variety of vegetation types, i.e. they are generalists. For example, Niemelä (1988c) showed that five species (which made up 81% of the sample) occurred in all vegetation types sampled on five islands, while three species (30% of the sample) occurred in all vegetation types (the same types as was sampled on the islands) on Åland. This result is supported by a study performed in four archipelagoes (Stockholm, Vargskär, Tvärminne and Pihlajavesi), in which the majority of dominant species on the islands were found in almost all vegetation types (Niemelä et al. 1987).

Habitat affinity does not, however, explain all absences from Baltic islands. For instance, Niemelä et al. (1988) showed that *Pterostichus niger*, *P. melanarius* and *P. versicolor* occurred in several vegetation types on the main island of Åland, but that only *P. niger* was widespread on islands constituting similar vegetation types. Furthermore, striking differences were observed in species distributions in similar vegetation types among four archipelagoes (Niemelä et al. 1987). I will discuss the absence of *P. melanarius* from small islands in detail below, but possible reasons for unexpected absences of species in seemingly suitable habitat patches on small islands include metapopulation dynamics, in the sense that local populations are unstable due to habitat quality differences, different degrees of isolation and stochastic extinction processes (Hanski 1998), differences in dispersal ability among species (see above), smaller and fewer habitat patches on smaller islands (Niemelä et al. 1985; Niemelä 1988c) and more severe conditions on smaller islands. For example, Baltic islands experience frequent droughts (Ås et al. 1997) and sea levels in the gulfs of the Baltic Sea can vary locally by 2.8 m between a low level under high atmospheric pressure conditions and a high level during subsequent cyclonic low pressure (Eronen et al. 2001), which may affect habitats more severely on smaller than on larger islands.

Baltic islands continually increase in size due to land uplift, creating land for more habitat types and for existing habitat types to increase in size (see Järvinen and Ranta 1987). Generally, larger islands have more carabid species than smaller islands, but the rate (z-value) of increase in species richness differs from 0.06 to 0.36 among studies (Ås 1984; Niemelä et al. 1987; Nilsson et al. 1988; Kotze et al. 2000). Habitat diversity is often implicated as a biological alternative to area per se in explaining increased numbers of species on larger islands. Evidence is, however, divided on whether habitat diversity or area per se is responsible for the increased number of species found on larger Baltic islands, mainly because area and habitat diversity are related (Järvinen and Ranta 1987; Ås et al. 1997). For example, Niemelä et al. (1987) found positive correlations between log area and log species number ($z = 0.24$–0.33) in four archipelagoes investigated but could not eliminate the effect of habitat diversity in producing these positive relationships due to higher sampling intensities on larger islands. Similarly, Zalewski and Sienkiewicz (accepted) showed that larger lake islands in Poland host more sub-communities (measured as carabid beetle beta-diversity), which may be a result of habitat diversity.

In an attempt to disentangle the effects of area and habitat diversity on species richness, Nilsson et al. (1988) investigated the species-area relationship (SAR) of carabid beetles on 17 islands (range 0.6–75 ha) in Lake Mälaren, Sweden, where measurements of habitat diversity were unrelated to area. Island area was the best single predictor of carabid beetle species richness, but the authors caution against eliminating habitat diversity as an explanation for the SAR. An alternative explanation could be habitat productivity, or quality, as a higher proportion of wet forests produced more carabid species (Nilsson et al. 1988). Moreover, Kotze et al. (2000) found a surprisingly shallow slope ($z = 0.06$) between area and carabid species richness on islands off the south-western coast of Finland and even though species richness increased with habitat diversity, the relationship was not statistically significant. This result was confirmed by the observation that many of the vegetation types sampled on the islands shared many species, suggesting that movement between vegetation types on islands is easy due to their reduced size on islands (see above).

Even within a single taxonomic group there is no single SAR. For instance, species number in vascular plants was higher on clustered islands than on similar-sized but more scattered islands (Järvinen and Ranta 1987). Kotze et al. (2000) found the opposite for carabid beetles; scattered islands accumulated species at a faster rate than grouped islands, supporting Hanski and Gyllenberg's (1997) hypothesis that islands with between-island colonisation will have a shallower slope than scattered islands that are, presumably, mainly colonised from the mainland. Apart from multiple SARs within single taxonomic groups, an additional factor to be considered is the small island effect (SIE) (Lomolino and Weiser 2001; Triantis et al. 2006), which has not been taken into account in any of the original carabid studies on Baltic islands. The SIE postulates that species richness is independent of island size up to an upper size threshold, beyond which species richness varies in a more deterministic and predictable manner with island area (Lomolino and Weiser 2001; Triantis et al. 2006). Lomolino and Weiser (2001), using breakpoint regression, identified a SIE in five of the six carabid beetle datasets used; with an upper limit of the SIE ranging from 0.6 to 3.1 ha. Triantis et al. (2006) on the other hand, used path analysis and identified a SIE in both carabid beetle datasets used; upper limits of the SIE were 4.3 and 57 ha. This means that nearly half of the 17 islands investigated by Nilsson et al. (1988) and 21 of the 24 (88%) islands investigated by Kotze et al. (2000) fall within the SIE upper limit. These results are of considerable importance for carabid studies on Baltic archipelagoes where the majority of islands are small and consequently likely to fall below the upper limit of the SIE. This means that the richness of species on small islands is probably not influenced by island size and that chance events, creating much variation in the occurrence of species among islands (Niemelä 1988c; Niemelä et al. 1987, 1988; Ås et al. 1997; Ulrich and Zalewski 2007), may be important.

Finally, by integrating the main elements of the island biogeography and niche theories, i.e., area, isolation, stochastic colonisation and extinction processes, habitat heterogeneity and niche partitioning, Kadmon and Allouche (2007) presented an analytical model that provides novel predictions that may be of particular relevance to island communities in the Baltic Sea. For example, the model predicts possible negative and unimodal effects of habitat heterogeneity on species richness, possibly because an increase in habitat heterogeneity increases the number of species in a given area but simultaneously decreases the amount of suitable habitat area available for each species, thus increasing the risk of local extinction (Kadmon and Allouche 2007). Although it seems that carabids on small islands occur in a wider variety of vegetation types as compared to those on the mainland (see above), small islands up to 57 ha (see Kotze et al. 2000; Triantis et al. 2006) do not accumulate species at the expected rate of 0.25–0.35 (MacArthur and Wilson 1967; Järvinen and

Ranta 1987; Rosenzweig 1995). Additionally, habitat diversity seems to be of minor importance in predicting species richness in some of the investigated archipelagoes (Nilsson et al. 1988; Kotze et al. 2000). Furthermore, Kadmon and Allouche (2007) showed a dependency of the slope of the SAR on the levels of habitat heterogeneity and reproduction. At relatively low reproductive rates, increasing habitat heterogeneity increases the slope of the SAR by facilitating species richness of relatively large areas and decreasing species richness of relatively small areas. If carabid species that are able to fly have lower fecundity as compared to brachypterous species (see above), this prediction could be studied on Baltic islands.

The absence of *Pterostichus melanarius* (Ill., 1798) from small Baltic Sea islands

An interesting finding from all carabid beetle studies performed in the Baltic Sea is the absence of *Pterostichus melanarius* from all islands less than 160 ha in size. This species is abundantly collected from most vegetation types on the main island of Åland (ca. 1,000 km^2), Finland (Niemelä et al. 1985, 1986, 1988; Niemelä 1988a, c; Niemelä and Halme 1992; Kotze and Niemelä 2002), and it is the most abundantly collected carabid on the Estonian island of Saaremaa (2,673 km^2) (Talvi 1995). Off the south-western coast of Finland very few individuals (<10) were collected from the large Korpo (ca. 7,000 ha) and Nåtö (371 ha) islands (Kotze et al. 2000). *Pterostichus melanarius* is a wing-polymorphic, eurytopic beetle that occurs in open and forested environments, is favoured by human cultivation, is widespread in Fennoscandia and across Europe (Lindroth 1986), and is a successfully established exotic in North America (Spence and Spence 1988; Niemelä and Spence 1991).

Apart from a seemingly obvious effect of area, several possible, yet unresolved, explanations have been proposed for this species' complete absence from small islands. Firstly, *P. melanarius* may compete for food and be predated upon by the slightly larger and more active *Pterostichus niger* (Niemelä 1988a; Kotze et al. 2000; see also Currie et al. 1996). *Pterostichus niger* is a macropterous, eurytopic species and shares many of its habitat associations and life-history characteristics with *P. melanarius* (Lindroth 1986; Niemelä 1988c). As with *P. melanarius*, *P. niger* is abundant on large islands in the Baltic Sea, but unlike *P. melanarius*, it is highly abundant on smaller islands (Table 1). It is often one of the most abundantly collected species on small islands (Ås 1984; Niemelä et al. 1985, 1987, 1988; Niemelä 1988a, b; Niemelä and Halme 1992; Kotze et al. 2000; Kotze and Niemelä 2002). Interestingly, on small islands in lake Pihlajavesi, Finland, no *P. niger* were collected but a few *P. melanarius* were collected (Niemelä et al. 1987), and *P. melanarius* often outnumbers *P. niger* on large islands (Talvi 1995; Niemelä and Halme 1992).

Secondly, and related to the above, *P. niger* feeds on insect larvae (Lindroth 1986) that may include the larvae of *P. melanarius*. It is not known whether *P. melanarius* also feeds on *P. niger* larvae, but the immature stages of *P. melanarius* may be negatively affected on small islands (see Currie et al. 1996). Niemelä (unpublished) released adult *P. melanarius* individuals on an island previously unoccupied by this species and collected adults, but no recruits, two years after release. Both *P. melanarius* and *P. niger* are autumn breeders and hibernate as third instar larvae, and winter conditions may affect *P. melanarius* larvae more severely than the larvae of *P. niger*. Zalewski (2004) showed that island size affects the populations of autumn breeders more strongly, i.e. it is more difficult for autumn breeders such as *P. melanarius* to persist on small islands. How this affects *P. niger* has yet to be tested, but may not apply because of its high abundance on small islands.

Thirdly, *P. melanarius* may have a reduced power of dispersal as compared to *P. niger*. Matalin (2003) classified *P. melanarius* as dimorphic in terms of wing and muscle development, and *P. niger* as a constantly macropterous species in terms of wing development, but a polymorphic species in terms of wing muscle state. Based on morphometric measurements (length and width of the elytra, maximal length and width of hind wings, live body mass) and number of specimens with macropterous wings and functional flight muscles, Matalin (2003) showed that the index of potential migrants (*Imp*), i.e., the proportion of specimens with the ability to fly, was four times higher for *P. niger* ($Imp = 0.25 \pm 0.09$) than for *P. melanarius* ($Imp = 0.06 \pm 0.02$). If this result applies for these two species in the Baltic region, *P. niger* is likely to colonise islands much more frequently than *P. melanarius*, and may prevent *P. melanarius* from establishing on small islands through competitive exclusion (Niemelä et al. 1987; Niemelä 1988a, b; Niemelä and Halme 1992).

Finally, the absence of some essential resource (see Dennis et al. 2003) may explain the absence of *P. melanarius* from small islands. However, this may be difficult to assess as *P. melanarius* is quite eurytopic, and carabid habitat association is quite broadly defined. For example, and Niemelä et al. (1988) argued that the vegetation composition on the island Björkör, only 4 km from the main island of Åland where *P. melanarius* occurs abundantly, is so similar to that of mainland Åland that variation in the composition of the vegetation cannot explain the absence of *P. melanarius* from it. Or, if passive dispersal via drift is important for the colonisation success of

P. melanarius, salinity may be a possible explanation for its absence from small islands in the Baltic. For example, a few individuals were collected on small islands in the freshwater lake of Pihlajavesi, Finland (Niemelä et al. 1987), and it was the most abundantly collected carabid from 0.01–20.1 ha islands in lake Mamry, Poland ($n > 3{,}500$ individuals; Zalewski and Ulrich 2006; Ulrich and Zalewski 2006).

A changing Baltic Sea landscape—conservation implications

Geophysical data indicate that isostatic recovery will continue in the Baltic area yet for several thousands of years, even though there are uncertainties in the calculated rate of residual uplift. Thus, the lowering trend in relative sea levels will prevail in the northern part of the Baltic for a long time, unless global warming causes a strongly accelerated rise in world ocean level (Eronen et al. 2001). Continual uplift will expose more islands, decrease inter-island distances, increase island sizes and connect islands to one another and to the mainland, but this may be offset by climate change in the Gulf of Finland (Johansson et al. 2004) and in the southern Baltic, where land uplift is considerably slower than in the north (Kont et al. 2003). Salinity may also decrease as a result of both land uplift (decreasing the size of the connection between the Baltic Sea and the North Atlantic) and wetter climates (increased runoff), again depending on the rate of climate change. More, larger and less isolated islands separated by an even lower-salinity matrix are likely to increase the colonisation success of carabid beetles on Baltic islands.

Alternatively, global warming is expected to affect winter conditions in particular, in the Baltic region (Jylhä et al. 2004; Lehikoinen et al. 2006). Winters are becoming milder and more variable, resulting in less and variable snow-depths, and in shorter snow-cover periods. For example, recent winters have been characterised by alternating cold and warm spells (pers. obs.), which may have a considerable negative affect on the survival of hibernating carabids.

One particular vegetation type that has been disappearing from islands in the Baltic Sea since the end of the 18th century is wooded meadows, which are a traditional semi-natural landscape that has been used for the production of hay and leaf fodder, and for grazing, for several millennia (Mitlacher et al. 2002; Hæggström and Hæggström 2003; Rosén and Bakker 2005). A wooded meadow is a vegetation complex characterised by copses of deciduous trees and shrubs alternating irregularly with patches of open meadow, and in terms of vegetation is considered to be among the most species-rich vegetation types on the islands (Hæggström 1988; Mitlacher et al. 2002; Hæggström and Hæggström 2003) and in temperate Europe (Kull and Zobel 1991). After abandonment, wooded meadows become rapidly overgrown by deciduous shrub and tree species. Mitlacker et al. (2002) showed that 87% of the typical grassland species vanished from wooded meadows and were replaced by species characteristic of woodland and disturbed grassland communities. Similarly, carabid species richness, diversity and number of scarce species were highest in wooded meadows on the island of Saaremaa, Estonia (Talvi 1995), and Niemelä (1990) showed that a wooded meadow on Åland yielded almost three times more species than an adjacent, abandoned meadow. The restoration of wooded meadows, using traditional management techniques, cutting of trees and shrubs, mowing, root trenching and controlled grazing, has had some success (Zobel et al. 1996; Mitlacher et al. 2002; Rosén and Bakker 2005), but the almost wholesale abandonment and subsequent succession of wooded meadows to deciduous woodland must have had negative consequences for carabid species richness, locally on individual islands and regionally throughout the Baltic Sea.

Ås et al. (1997) stated that the main reason for preserving archipelagoes is that they often present types of natural vegetation not found elsewhere. Baltic Sea islands are unique due to an eventful and young history, ongoing uplift that results in the formation of more islands in an already highly island-rich landscape, short inter-island distances, a low-salinity matrix and ongoing succession as islands become larger. Indeed, carabid beetles reflect this uniqueness by showing surprising patterns in colonisation success (higher proportions of flightless species on small islands), unexplained absences from small islands (i.e. *Pterostichus melanarius*) and unique assemblage compositions in vegetation types on small islands as compared to seemingly similar vegetation types on larger islands. Furthermore, several species have demonstrated consistent trends of increase (*Agonum obscurum*, *Trechus secalis*) or decrease (*Leistus terminatus*, *Patrobus atrorufus*, *Loricera pilicornis*) from 1982 to 1999, particularly on the main island of Åland (Kotze and Niemelä 2002), and a possible new occurrence since 1999 (*Carabus nemoralis*), indicating a changing Baltic environment.

Islands in the Baltic Sea provide excellent opportunities for studying the mechanisms by which carabid beetles disperse and persist on these islands.

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ORIGINAL PAPER

Conservation of Southern Ocean Islands: invertebrates as exemplars

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Abstract The Southern Ocean Islands (SOI) have an exceptionally high conservation status, and human activity on the islands is low by comparison with more tropical islands. In consequence, overexploitation, pollution and habitat destruction have had little influence on the invertebrate biotas of the islands, although overexploitation of pelagic species has the potential for an indirect influence via reduction of nutrient inputs to the terrestrial systems. By contrast, invasive alien species, the local effects of global climate change, and interactions between them are having large impacts on invertebrate populations and, as a consequence, on ecosystem functioning. Climate change is not only having direct impacts on indigenous invertebrates, but also seems to be promoting the ease of establishment of new alien invertebrate species. It is also contributing to population increases of invertebrate alien species already on the islands, sometimes with pronounced negative consequences for indigenous species and ecosystem functioning. Moreover, alien plants and mammals are also affecting indigenous invertebrate populations, often with climate change expected to exacerbate the impacts. Although the conservation requirements are reasonably well-understood for terrestrial systems, knowledge of freshwater and marine near-shore systems is inadequate. Nonetheless, what is known for terrestrial, freshwater and marine systems suggests that ongoing conservation of SOI invertebrates requires intervention from the highest political levels internationally, to slow climate change, to local improvements of quarantine measures to reduce the rates and impacts of biological invasions.

Keywords Global change-type drought · Indirect interactions · Insect conservation · Marine invasions · Rodents

Introduction

Between 30° and 60° latitude the northern and southern hemispheres differ substantially. In the north, land and water constitute approximately the same surface area. In the south, the land:water ratio is a mere 1:15 (Chown et al. 2004). The vast Southern Ocean dominates this part of the globe. New Zealand, Patagonia and small parts of Australia and Africa comprise the majority of the land. However, within and on either side of the Antarctic Polar Frontal Zone (an area separating two high speed regions of the Antarctic Circumpolar Current, the sub-Antarctic Front to the north and the Antarctic Polar Front to the south) a small number of archipelagos makes up the remainder of the terrestrial area. These are the Southern Ocean Islands (SOI) (Fig. 1).

Given their occurrence right around the Southern Ocean, the islands differ considerably in their geological histories, past and current glacial extents, current climates and vegetation (Table 1). Whilst some of the islands, such as Prince Edward Island, are entirely volcanic, young (<500,000 years), and show no signs of glaciation at the height of the last glacial maximum (LGM), others have a more complex geology and history. Macquarie Island constitutes a raised section of seafloor (Selkirk et al. 1990). The Kerguelen Islands (a large archipelago) are still partly glaciated, and have a complex history associated with the

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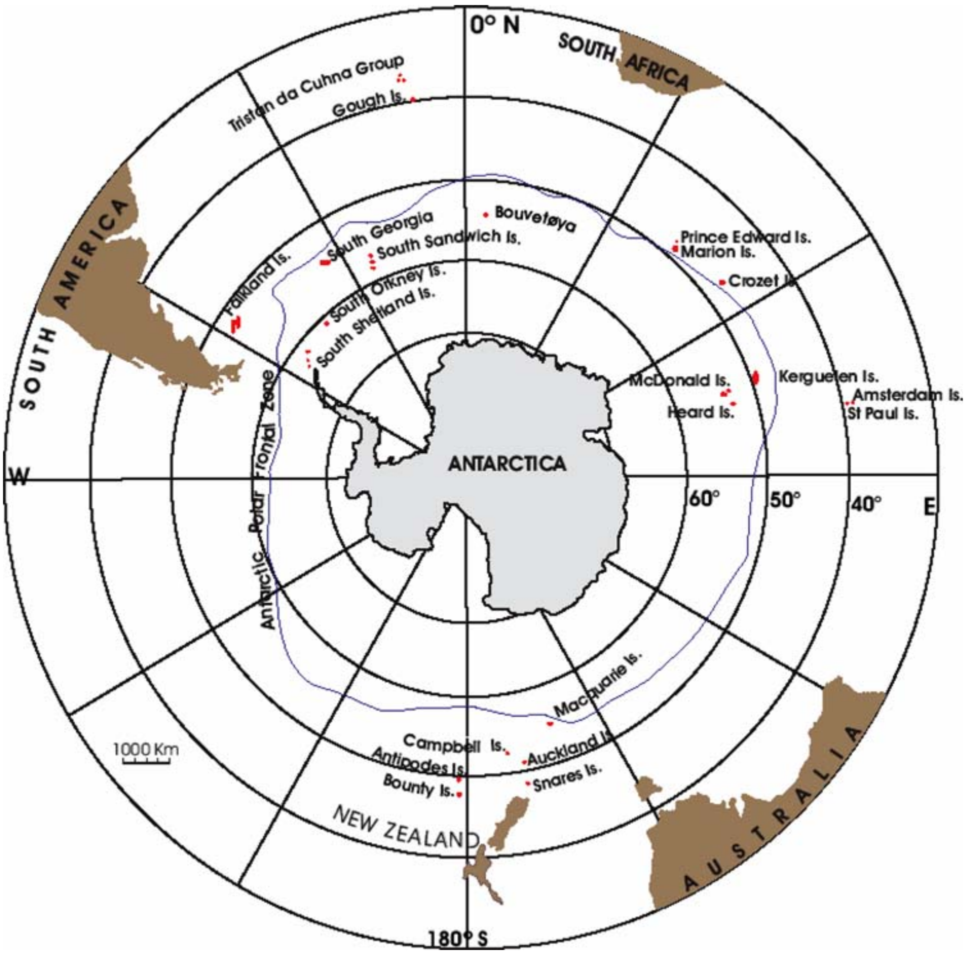

Fig. 1 Schematic map of the position of the Southern Ocean Islands, which straddle the Antarctic Polar Frontal Zone. In this review we have excluded the Maritime Antarctic islands such as Bouvetøya, and the South Orkney, South Shetland and South Sandwich islands (see Chown and Convey 2006, 2007 for additional information)

100 ma (million years) geological evolution of the large igneous province of the Kerguelen Plateau, of which some parts were sub-aerial (i.e. above sea level) at least as far back as 93 ma and consistently for at least 40 ma (Hall 2002; Wallace et al. 2002). The geological history of the Crozet archipelago remains something of a conundrum (Craig 2003).

In terms of climates, similar variation can be found, from the temperate, warmer islands, such as Gough Island and the Auckland Islands, to the north of the Polar Frontal Zone, to the much colder islands south of the zone, such as South Georgia and Heard Island. The islands also differ in the extent to which they are influenced by frontal weather, and in some cases the considerable height of the islands means that the climates on the weather and lee sides of the islands are wholly different (see le Roux 2008 for recent discussion). Nonetheless, the majority of the SOI have highly oceanic climates, and the climates of those islands lying within or to the south of the Polar Frontal Zone are showing a strong warming, and often drying trend in step with global climate change (Bergstrom and Chown 1999; Convey 2006; le Roux and McGeoch 2007).

Given this range of locations, histories and climates, the vegetation also shows marked dissimilarity among the SOI (Fig. 2). For example, Heard Island (53° S) has only 12 vascular plant species and closed vegetation communities only in coastal areas and in some deglaciated valleys (Scott and Bergstrom 2006). Above approximately 50 m in elevation, vegetation is open, and above about 200 m comprises cryptogams only. From about 300 m (depending on position and aspect) the slopes are almost entirely ice-covered. By contrast, Gough Island (40° S) supports 70 species of vascular plants, including trees (*Phylica arborea*, *Sophora macnabiana*) and tree ferns (*Blechnum palmiforme*) at lower elevations, but above ca. 300 m comprises mostly wet heath and moorland vegetation (Wace 1961; Hänel et al. 2005). Similarly, a structurally complex flora can be found at the Auckland Islands (Anonymous 1997), whereas at South Georgia, closed vegetation is mostly restricted to the lowlands (Lewis-Smith and Walton 1975). Whilst differences in the structure of the vascular flora amongst islands are clear, at the majority of islands bryophytes dominate in terms of species richness and have considerable, though perhaps somewhat

Table 1 Location, area, elevation, age, mean annual sea surface temperature, and number of introduced plants and insects on the Southern Ocean Islands (adapted from Chown et al. 1998)

Island	Position (Decimal degrees)	Area (km^2)	Altitude (m)	Age (ma)	SST (°C)	Alien Vascular plants	Alien insects
West Falkland	51.5 S, 60.5 W	3,500	701	2,500	7.67	66	5
East Falkland	51.5 S, 58.5 W	5,000	705	2,500	7.29	78	22
South Georgia	54.25 S, 37.0 W	3,755	2,950	120	1.49	53	8
Tristan da Cunha	37.1 S, 12.25 W	86	2,060	1	15.32	93	37
Nightingale	37.42 S, 12.5 W	4	400	18	15.32	6	4
Inaccessible	37.25 S, 12.75 W	12	600	6	15.32	20	12
Gough	40.33 S, 9.54 W	57	910	6	12.35	24	71
Marion	46.9 S, 36.75 E	290	1,230	0.45	5.53	17	18
Prince Edward	46.63 S, 37.95 E	44	672	0.21	5.59	3	3
Cochons	46.1 S, 50.23 E	70	775	0.4	4.87	6	3
Apôtres	45.97 S, 50.43 E	3	289	5.5	5.11	2	0
Pinguoins	46.5 S, 50.4 E	3.16	360	1.1	4.87	1	0
Est	46.43 S, 52.2 E	130	1,090	8.75	4.75	5	2
Possession	46.42 S, 51.63 E	150	934	8.1	4.78	101	7
Kerguelen	49.37 S, 69.5 E	7,200	1,840	95	3.46	36	13
Heard	53.1 S, 73.5 E	368	2,745	40	1.74	1	1
McDonald	53.03 S, 72.6 E	2.6	230	0.079	1.85	0	0
Amsterdam	37.83 S, 77.52 E	55	881	0.7	15.17	81	18
St Paul	38.72 S, 77.53 E	8.1	268	0.5	14.59	10	9
Macquarie	54.62 S, 158.9 E	128	433	0.7	5.13	5	5
Snares	48.12 S, 166.6 E	3.28	152	120	10.95	2	8
Auckland	50.83 S, 166.0 E	626	668	18	9.22	33	10
Campbell	52.5 S, 169.17 E	113	567	16	7.83	88	19
Antipodes	49.68 S, 178.77 E	21	366	0.5	7.9	2	13
Bounty	47.72 S, 179.0 E	1.35	89	189	9.63	0	0

unappreciated, roles to play in the terrestrial systems, especially at higher elevations (see e.g. Bergstrom and Selkirk 1997; Gremmen and Smith 2008).

Patterns and mechanisms: historical and ecological biogeography

As might be expected, the different geological histories of the SOI have contributed to the identity of the biotas living on them, with the degree of influence of isolation and history depending to some extent on the dispersal abilities of the taxa involved: mobile species such as seabirds are less influenced by large ocean barriers than sedentary species such as insects (Chown 1994; Muñoz et al. 2004; Greve et al. 2005; Chown and Convey 2007). For these reasons, the historical biogeography of the region has been the subject of much contention, with claims both for and against Udvardy's (1987) proposal for a single biogeographic province, 'Insulantarctica', including most of the islands (reviewed in Greve et al. 2005; Chown and Convey 2006). Recent, nestedness and phylogeographic analyses have begun to resolve the areas of contention, showing that an 'either/or' argument for 'Insulantarctica' is too simplistic and ignores important among-taxon variation (e.g. Greve et al. 2005; Stevens et al. 2006). In consequence, much remains to be done to clarify the historical biogeography of the region. Phylogenetic and phylogeographic studies, especially of the arthropods, are likely to help do so in the near future (see e.g. Allegrucci et al. 2006; Grobler et al. 2006; Myburgh et al. 2007).

Taking a more ecological perspective, early work identified glacial extent during the LGM, isolation and persistently low temperatures as the major factors influencing among-SOI variation in the species richness of arthropods and vascular plants (e.g. Gressitt 1970; Abbott 1974; Chown 1990a). More recent work (Chown et al. 1998, 2005) has shown that elements of both classic island biogeography theory (isolation and available area), and the influence of varying energy availability (measured as sea surface temperature) explain variation in richness of terrestrial vascular plants (see Table 1) in keeping with

Fig. 2 Vegetation differs profoundly within and across the Southern Ocean Islands, as a consequence of elevation, manuring effects, exposure, and water availability. These images illustrate the variety of landforms and vegetation types found on the islands. (**a**) Fellfield above the Neumeyer glacier on South Georgia; (**b**) Atlas Cove area of Heard Island showing volcanic sand and a small altitudinal range in vegetation; (**c**) Tafelberg at Marion Island showing mire (yellow), fernbrake (green) and fellfield (grey) areas; two scoria cones are visible in the middle distance; (**d**) Lowland vegetation on Campbell Island with *Pleurophyllum speciosum* flowering in the foreground; (**e**) *Phylica arborea* in fernbush at Gough Island; (**f**) a rata (*Metrosideros umbellata*) thicket on Enderby Island, Auckland Islands. Image (**d**) was taken by Brent Sinclair, the remainder by the authors

species-energy theory (reviews in Gaston 2000; Hawkins et al. 2003; Evans et al. 2004). The situation is more complex for the indigenous insects (Table 1). Depending on the analysis (i.e. including/excluding spatial autocorrelation), distance to the closest continent, indigenous plant richness, area, and sea surface temperature (SST—a surrogate for mean annual land surface temperature) are all correlates of richness (Chown et al. 1998, 2005). Clearly, dispersal capabilities of the insects and isolation of the islands have been significant in influencing the richness patterns (Greve et al. 2005) and energy is likely to have influenced richness via the mechanisms usually proposed, such as increasing numbers of individuals reducing extinction rates of the rarest species and therefore elevating richness (Evans et al. 2004). However, the role of indigenous plant species richness in influencing insect species richness is more controversial. More generally, it has long been maintained that plant richness might have a substantial influence on herbivore richness (e.g. Gaston 1992; Siemann et al. 1998). However, this idea is contentious, with some studies arguing that evidence in favour of a relationship between plant and herbivore richness is perhaps weaker than was once thought, at least at large spatial scales (Hawkins and Porter 2003; Hawkins and Pausas 2004, but see also Novotný et al. 2006). For the SOI it is difficult to determine the nature of the relationship between vascular plant and insect richness. Whilst indigenous plant richness is a strong correlate of insect richness (irrespective of analytical approach), one spatially explicit approach suggests that this is a consequence of similar responses of both groups to island area (Selmi and Boulinier 2001), whilst another does not support this assertion (Chown et al. 2005). Irrespective, the modern analyses demonstrate that in terms of richness variation among islands, SOI plants and insects follow patterns expected from oceanic islands (see Kalmar and Currie 2006). That is, large, high energy, less-isolated islands have the highest richness of insect and plant taxa. Unfortunately, how diversity in the other components of the arthropod fauna (such as spiders, mites and springtails) varies, and what mechanisms might underlie this variation, are not well known, largely as a consequence of poor sampling across all islands in the region (see Pugh 1993, 2004; Pugh and Scott 2002; Pugh et al. 2002 for recent invertebrate faunal catalogues).

Conservation status of the islands

Because the SOI provide the only terrestrial ecosystems at mid- to high southern latitudes across much of the southern hemisphere (Bergstrom and Chown 1999), their conservation value has long been recognized (reviewed in Dingwall 1995; see also Chown et al. 2001; Bergstrom and Selkirk 2007). The island groups discussed here are governed by five different nations: United Kingdom, South Africa, Australia, New Zealand, and France. Unlike Antarctica (which is governed under the Antarctic Treaty System), no international agreements or treaties apply specifically to the Southern Ocean Islands. However, more general international agreements to which the above states are party, such as the Convention on Biodiversity, and the Agreement for the Conservation of Albatrosses and Petrels do apply to the islands (Hull and Bergstrom 2006; Chown et al. 2006). Nonetheless, most of the islands enjoy a high conservation status (de Villiers et al. 2006). The five New Zealand sub-Antarctic island groups (Snares, Bounty, Antipodes, Auckland, and Campbell islands), Heard and McDonald Islands, Gough Island and Macquarie Island are all World Heritage Areas (at the highest IUCN Reserve Status of Category Ia). Several other island groups in the region are also clearly eligible for World Heritage status (Chown et al. 2001), and a nomination for the Prince Edward Islands has been submitted. Macquarie Island is listed as a UNESCO Biosphere Reserve.

At a National level, the New Zealand sub-Antarctic islands are all National Nature Reserves. Macquarie Island and Heard and McDonald Islands (Australia) have the highest reservation status, Nature Reserve and Commonwealth Reserve, respectively, under their governing legislations (State and Federal). Marion and Prince Edward Island (South Africa) are classified as a Special Nature Reserve under South African legislation (National Environmental Management: Protected Areas Act) (Davies et al. 2007). South Georgia has National status (United Kingdom) as a Protected Area, and the Kerguelen and Crozet Islands (France) and Gough Island (United Kingdom) are all National Nature Reserves (de Villiers et al. 2006).

The frequency and intensity of human activity varies across the SOI. At present many of the SOI are visited annually by scientific expeditions (comprising scientists and support staff), and have research and/or meteorological bases occupied throughout the year. The annual number of semi-permanent occupants ranges from 0 to 100 (de Villiers et al. 2006). Unlike most of the islands, the Falkland Islands and Tristan da Cunha archipelago have permanent human settlements and a much more complex set of governance and conservation arrangements.

Tourist vessels visit many of the islands. However, no tourists are allowed to land on the Prince Edward Islands, the Antipodes, Bounty, Snares, Inaccessible or Gough islands. Visits to all other islands require permits that place restrictions on operators, but these vary among the different islands (de Villiers et al. 2006). Permits limit the number of visits per season, number of visitors permitted ashore at once, vessel capacity, number of landing sites, nights ashore, and/or time ashore, and often specify procedures for decontamination prior to shore transfers (such as boot-washing). South Georgia receives the most tourist visitors in a year (5,427 passengers in 2005/2006) (Frenot et al. 2005; de Villiers et al. 2006).

Conservation threats

The Millennium Ecosystem Assessment (MA, 2005) identified habitat transformation, overexploitation, climate change, biological invasion and pollution (including N and P nutrient loading) as the most significant modern drivers of biodiversity loss. For the SOI, habitat transformation and pollution are largely unimportant, and the effects of overexploitation indirect. Habitat transformation is significant only at the permanently inhabited Falkland and Tristan da Cunha islands, and pollution is important in the sense that large-scale acidification of the oceans and the long lifespan of many persistent organic pollutants are having affects around the globe (see e.g. Finizio et al. 1998; Lawton 2007). Likewise, overexploitation of terrestrial organisms is negligible. However, because pelagic species (especially seabirds) contribute large quantities of nutrients to terrestrial systems (e.g. Smith and Froneman 2008), overexploitation in marine systems might have an indirect effect on terrestrial system functioning if seabird populations are severely reduced. Of much more direct significance at the majority of the islands are the effects of biological invasions and climate change, and their interactions.

Climate change

As we have already noted, temperatures are rising at many of the SOI in step with global climate change, and in many cases rainfall is declining (Bergstrom and Chown 1999). The extent of the change in climate varies among islands as might be expected from their diverse geographic locations. For example, the rate of warming over the last 50 years has been slower at Gough Island than at Marion Island (Jones et al. 2003a; Smith 2002). Moreover, climate change is often more subtle than a simple increase in temperature and decline in rainfall might suggest. For example, at Marion Island, the increase in temperature is being accompanied by more clear-sky evenings, leading to an increase in the number and intensity of freeze-thaw cycles (Smith and Steenkamp 1990; Smith 2002). Counter-intuitively, a warming trend is being accompanied by increases in the number of stressful freezing events. It is these subtleties, as well as the general trends, that have important consequences for invertebrate faunas.

To date, few studies have documented direct impacts of changing climates on the indigenous invertebrate faunas of the SOI. Rather, most investigations have either examined the physiological tolerances of particular species and predicted what might be the outcomes of further change, or have used field experiments to determine what the impact of ongoing warming and/or drying might be. In the former case, much work on Marion Island has suggested that warming and drying are unlikely to compromise many indigenous insect species, at least based on data showing considerable desiccation resistance in several species and high critical thermal maxima in others (e.g. Klok and Chown 1997, 2003; Slabber and Chown 2005). However, two investigations suggest that absolute limits are unlikely to provide a complete picture of the effects of changing climates. First, an investigation of egg development rates has demonstrated pronounced thermal sensitivity in the endemic springtail subspecies (probably a species—see Stevens et al. 2006), *Cryptopygus antarcticus travei*, to the extent that egg development does not proceed above 15°C (Janion et al. unpublished data). Another study demonstrated considerable sensitivity of a keystone species, *Pringleophaga marioni* (Tineidae), the caterpillars of which are responsible for promoting nutrient release on the island (Smith and Steenkamp 1992), to repeated low temperature exposures. Increasing freeze-thaw cycles associated with increasing numbers of clear-sky evenings as climates change are likely to have negative consequences for this species (Sinclair and Chown 2005). Later work also demonstrated that wandering albatrosses act as thermal ecosystem engineers for the caterpillars, by promoting survival as a consequence of temperature elevation in the albatross nests (which are occupied for ca. 12 months) where caterpillar densities are high (Sinclair and Chown 2006).

Open-top chamber, temperature elevation trials on the Falkland Islands (Bokhorst 2007) and rain-out shelter trials on Marion Island (McGeoch et al. 2006) have both demonstrated complex responses of the soil arthropod fauna to either warming, or warming and drying, depending on the higher taxon in question. For example, at Marion Island, a drying and warming treatment resulted in a much steeper decline in springtail abundance than in the abundance of mites relative to control sites, but even within these groups responses were individualistic at the species level. Thus, the response to climate change will likely not be a change in the relative positions of present communities or assemblages across the island, but rather re-arrangement of species into wholly novel assemblages (McGeoch et al. 2006). Moreover, the trials also revealed that indigenous and introduced species show different responses to experimental warming and drying treatments. Indeed, the interaction between climate change and invasion is one of the most significant threats to the invertebrates of the SOI islands (see below).

Biological invasions

Southern Ocean Islands are climatically and physically isolated from the surrounding continental landmasses, and have comparatively low human visitation compared with many continental sites (Chown et al. 1998). To a large extent these factors have hindered the establishment of alien species (see Pyšek et al. 2004 for definitions—which include those introduced by humans to one area that have migrated to a nearby one). Although alien species richness is relatively low, it varies substantially among the islands

(Frenot et al. 2005). Some islands, such as McDonald Island, are pristine with no established alien species, whilst others are highly invaded. For example, of the 99 insect species recorded on Gough Island, 71 are established introductions (Gaston et al. 2003).

Intrinsically, introductions are related to human movements. In the case of the SOI, human visits began in the late 1600s, but increased in frequency on many islands from the 1800s with the development of whaling and sealing. In recent years, scientific research and tourist operations have become the dominant form of human activity in the region (Frenot et al. 2005). Whilst contemporary human movements and activities are subject to strict controls to prevent the establishment of non-indigenous species (de Villiers et al. 2006), historical activities were not regulated and this likely led to considerable propagule pressure on occupied islands. Indeed, among the strongest predictors of the numbers of established alien species (plants, insects, birds and mammals) across the SOI are numbers of human occupants per year and energy availability (Chown et al. 2005). Moreover, the historical lack of controls has meant that many of the alien species that established early on have had considerable time to become established and in some cases to shape contemporary island assemblages (Chapuis et al. 1994; Frenot et al. 2005; Greenslade et al. 2007a). In this regard, it is important that a clear distinction be drawn between alien species that have established, but are effectively having little or no impact, and those that are transforming entire ecosystems (see Richardson et al. 2000).

Given their profound influences on invertebrate species and ecosystem functioning, it is the invasive alien species that form the focus of the remainder of this review. We use several case studies to illustrate the effects of invasive species on the invertebrates and ecosystems of the SOI. In some instances, alien invertebrate species are having a substantial impact on other invertebrate species or on system functioning. In other cases introduced mammal or plant species are having an impact on invertebrates, or an interaction between mammals/plants and an invertebrate invader is responsible for the impacts. Finally, we show how climate change is not only exacerbating the impacts of invasive alien species already present on the islands, but also how it seems to be enhancing the ability of new species to establish (see also Frenot et al. 2005).

Invasive alien species and their impacts

Establishment and impact

No island system is static. Rather, islands are characterized by extinction, colonization and evolution. Isolated islands, such as the SOI, typically have low natural colonization rates (Carlquist 1974). However, human activities have substantially changed the natural levels of immigration. For example, it has been estimated that for Gough Island, background rates of colonization were ca. one species every 1,000 years. Now the rate is one species every 4 years (Gaston et al. 2003). Although increased propagule pressure (see Lockwood et al. 2005 for an overview) is undoubtedly part of the reason for the increase in colonization rates over background levels, it also seems likely that the ease of establishment of invertebrates must also be at least partly responsible. Several studies have demonstrated that despite large population sizes, introduced invertebrate species are often characterized by little genetic variation (e.g. Ernsting et al. 1995a; Greenslade et al. 2007b; Myburgh et al. 2007; Lee et al. 2007), suggesting that only one or a few individuals founded the population. Moreover, it has long been argued that parthenogenesis is a trait promoting establishment on these islands so accounting for a relatively high proportion of parthenogenetic species in the introduced insect fauna (Crafford et al. 1986; Hullé et al. 2003; Jones et al. 2003b).

Irrespective, whether the rates of successful colonization are increasing since human occupation of the SOI is much more difficult to establish because repeated, careful surveys have typically not been undertaken on a regular basis at the islands. At Marion Island, this has been done since the mid-1980s and over the past 20 years five new invertebrate colonizations have been documented (Table 2). The

Table 2 Invertebrates that have established at Marion Island since regular surveys commenced in the early 1980s (data from Lee et al. 2007)

Species	Year established	Reference
Plutella xylostella (Lepidoptera, Plutellidae)	~1986	Crafford et al. (1986)
Calliphora vicina (Diptera, Calliphoridae)	~1988	Chown and Language (1994)
Agrotis ipsilon (Lepidoptera, Noctuidae)	~1997	Hänel et al. (1998), Chown et al. (2008)
Aphidius matricariae (Hymenoptera, Braconidae)	~2001–2003	Lee et al. (2007)
Porcellio scaber (Crustacea, Porcellionidae)	~2001	Slabber and Chown (2002)

Lee et al. (2007) suggested that *Trichoplusia orichalcea* (Noctuidae) might have become established, but no larvae have been found population sizes and infrequency of recording of *Calliphora vicina* (Calliphoridae) and *Agrotis ipsilon* (Noctuidae) suggest that neither species might establish permanently. However, both are exceptionally successful elsewhere. A large population of the fly is established at the Kerguelen Islands (Chevrier et al. 1997). Be that as it may, the data are too sparse to detect any trends, though it is noteworthy that three of the species have established despite the adoption of the strict quarantine procedures at the island, in keeping with a predicted increase in the ease of establishment of introduced species as climates ameliorate in the region (Kennedy 1995; Frenot et al. 2005). Strong relationships between energy availability and alien insect richness (Chown et al. 1998, 2005), the restriction of introduced species to low elevations (Gabriel et al. 2001; Hullé et al. 2003), and the clear demonstration that the increase of temperature above a threshold value enabled establishment of *C. vicina* at the Kerguelen Islands (Frenot et al. 2005), provide additional evidence in favour of the prediction. Of course, establishment in no way necessarily means profound impacts on the recipient system. However, several species are now having a considerable influence on terrestrial systems or on other invertebrates.

In 1997, two species of introduced flatworm were found on Macquarie Island (Greenslade et al. 2007b). The more narrowly distributed *Arthurdendyus vegrandis* (Geoplanidae) apparently feeds solely on earthworms. Of the six terrestrial species of earthworm on Macquarie Island, including those living above the high water mark according to Greenslade (2006), four species are regarded as alien, one endemic and one unknown, and all are at least potential prey for the flatworm. The wider ranging *Kontikia andersoni* (Geoplanidae) likely feeds on a range of arthropods, annelids and molluscs. Given that relatively few macroinvertebrate predators occur on Macquarie Island (two flatworm, three spider and six staphylinid beetle species), the continuing range expansion of two predatory flatworms has the potential to exert a profound influence on invertebrate populations at the island. Substantial impacts by introduced invertebrate predators have been documented on other islands, most notably by an introduced carabid beetle species *Trechisibus antarcticus* on indigenous perimylopid beetles on South Georgia (Ernsting 1993; Ernsting et al. 1999; see also below), and by another introduced carabid *Oopterus soledaninus* on populations of indigenous invertebrates at the Kerguelen Islands (Chevrier et al. 1997).

Slugs have been introduced to several SOI (Pugh and Scott 2002), and are likely to have significant effects on system functioning. *Deroceras panormitanum* was first documented at Marion Island in the 1970s (Smith 1992). It has since become widespread and abundant, owing partly to helicopter-assisted transport (slugs adhere to wooden packing cases moved by helicopter) around the island (Smith 1992; Chown et al. 2002). Nutrient cycling in the terrestrial system is mostly through a detritus chain dominated by caterpillars of the indigenous flightless moth *P. marioni*, and by several weevil species (Smith and Steenkamp 1992). However, slugs also release prodigious quantities of nutrients as a consequence of their grazing, but do so such that nutrient release relative to carbon release differs considerably from that of the indigenous species. In consequence, different carbon:nutrient ratios are found in the decomposing substrate, with downstream effects on primary production (Smith 2007).

A final example concerns increases in food web complexity. At most of the isolated SOI, especially the more southerly islands, parasitism is uncommon, with only a few parasitoid species known. Often these are restricted to the littoral zone, parasitizing small kelp flies (e.g. Crafford et al. 1986). Recently, a wasp parasitoid, *Aphidius matricariae*, of an introduced aphid (*Rhopalosiphum padi*), was discovered on Marion Island (Lee et al. 2007). Although the species does utilize an introduced host, the occurrence of both species has added a level of complexity previously missing from vegetated areas on the island (Chown 1990a).

Invasive plants, mammals and invertebrates

Although the relationship between plants and insects is widely acknowledged, few studies have examined these relationships in detail for invasive species of insects (but see Hullé et al. 2003), and fewer still for the impacts of introduced plant species on invertebrate assemblages. One exception is the effects of dense stands of the grass *Agrostis stolonifera* on springtails and mites at Marion Island. Typically, mite abundances are higher and springtail abundances unaffected in the invaded sites relative to the control areas (Gremmen et al. 1998). A more complex interaction between invasive grasses, introduced reindeer (*Rangifer tarandus*) and an introduced predatory beetle and indigenous prey beetle species has been documented for South Georgia (Chown and Block 1997). The introduced predatory carabid, *Trechisibus antarcticus*, appears to be selecting for larger body sizes in the indigenous prey perimylopid *Hydromedion sparsutum* owing to considerable predation pressure (Ernsting et al. 1995b, 1999). However, in those areas where reindeer graze most frequently, size is smaller in *H. sparsutum* adults than where reindeer are absent. In the former areas, reindeer promote the spread of the grazing-intolerant invasive grass *Poa annua* (and in some circumstances the somewhat less tolerant indigenous *Festuca contracta*). Despite substantial ingestion of these grasses, *H. sparsustum* larvae grow poorly on them by comparison with other, less grazing-tolerant indigenous species. In consequence, by promoting the spread of the invasive *Poa annua*, reindeer appear to be selecting indirectly for reduced body size in *H. sparsutum*, whilst selection in the opposite direction is being imposed by the introduced carabid (Chown and Block 1997).

At Macquarie Island, rabbits are likely to be affecting invertebrate populations indirectly by altering vegetation communities (in some cases leading to total denudation). Investigations of invertebrate assemblages has revealed that *Stilbocarpa polaris* (Apiaceae)-dominated herbfields have the highest invertebrate densities, followed by *Poa foliosa* (Poaceae)-dominated tall tussock grasslands and *Pleurophyllum hookeri* (Asteraceae) herbfields (Greenslade 2006), and that among the species most common in these habitats are several indigenous to Macquarie Island (Davies and Melbourne 1999; Greenslade 2006). Recently, the population of introduced rabbits on Macquarie Island has greatly increased, despite early control success (Scott and Kirkpatrick 2008). This increase has been attributed to the complex interactions of several factors including eradication of feral cats in 2000, and resistance to the myxoma virus that was introduced to the island in the 1970s. Rabbits particularly favour the tussock grasses (*P. foliosa*) and large-leaved megaherbs (*S. polaris* and *P. hookeri*) (Copson and Whinam 1998). In the last 7 years, drastic changes in vegetation cover across the island have taken place. In many areas herbfields and tall tussock grasslands have been entirely removed due to intense grazing (Scott and Kirkpatrick 2008) (Fig. 3). In addition, large areas of leaf litter and soil have been reworked by rabbit digging and subsequent (or incidental) erosion. Given the apparent preference of invertebrates for the herbfield and tussock habitats, it is likely that substantial change to invertebrate populations has been effected, although this change has yet to be investigated thoroughly.

Fig. 3 Rabbit-induced vegetation damage on Macquarie Island. Since the eradication of cats and likely also as a consequence of changing climates and reduced efficacy of *Myxoma* virus, rabbit numbers have increased over the past 5 years (Scott and Kirkpatrick 2008), with effects on vegetation and likely on invertebrate assemblages

The effects of introduced mammals are often more direct. Introduced rodents, especially house mice, are having pronounced direct effects on invertebrate (particularly insect) populations on several islands, including Gough (Jones et al. 2003c), Kerguelen (Le Roux et al. 2002), Macquarie (Copson 1986) and Marion (Crafford and Scholtz 1987; Smith et al. 2002) islands. At Marion Island, mice have not only led to substantial declines in populations of their preferred prey (Crafford and Scholtz 1987; Chown et al. 2002), but have also altered ecosystem functioning. By reducing populations of the flightless moth, whose caterpillars are keystone species for nutrient recycling (Smith and Steenkamp 1992), mice have had profound effects on nutrient cycling, plant growth and possibly peat formation (Smith and Steenkamp 1990). Moreover, because caterpillars constitute an important component of the diet of overwintering lesser sheathbills (an indigenous, plover-like bird), populations of these species are also declining (Huyser et al. 2000). In addition, by virtue of their size-selective feeding (Fig. 4), mice are not only changing the size distributions of the weevils on Marion Island (but not on nearby, mouse-free Prince Edward Island, Chown and Smith 1993), but may also have caused introgression of two weevil species that probably speciated sympatrically via size-based, positive-assortative mating (Chown 1990b; Grobler et al. 2006).

Invasions and climate change

As we have noted, several studies have predicted increasing ease of establishment of non-indigenous species as climates on the SOI islands change and as the frequency of human

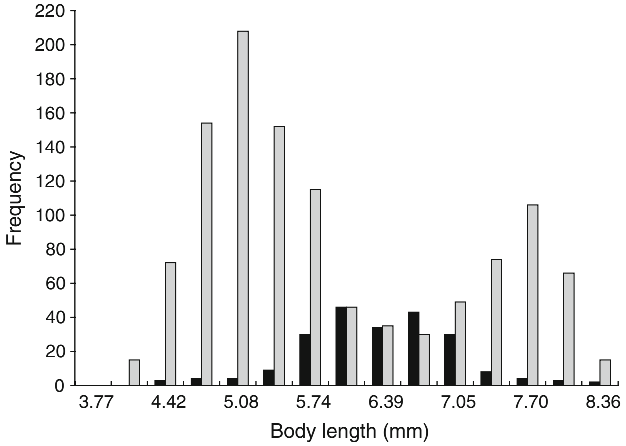

Fig. 4 Frequency distribution of body lengths of two *Ectemnorhinus* weevil species as recorded in 1986/7 on the cushion plant *Azorella selago* on Marion Island (grey bars), with mouse, beetle-size preferences indicated in black bars, which have been estimated from body lengths from prey remains in mouse scats (data from Chown and Smith 1993). It appears that the weevil species have now introgressed (Grobler et al. 2006)

visits increases (see above). However, changing climates are likely also to have direct effects on species already present on the islands in several ways, with important consequences for ecosystem structure and functioning. Physiological data on absolute thermal tolerances and on the relationships between development rate and temperature suggest that not only are the alien species at the island frequently more thermally tolerant than their indigenous counterparts (e.g. Slabber et al. 2007), but also that in response to increasing temperatures, steeper rate-development relationships will mean faster development for alien than indigenous species (Barendse and Chown 2000). For these reasons, and because many of the indigenous species have longer life-cycles (1 year or more) and those of the alien species (Chown et al. 2002), it is expected that the alien species (many of which are invasive—see e.g. Gabriel et al. 2001) will be at an advantage relative to their indigenous counterparts.

Other work has suggested that as a consequence of greater low temperature tolerance, indigenous species are able to occupy higher elevations than alien species (e.g. Gabriel et al. 2001; Slabber et al. 2007), and might possibly have been displaced at lower elevations by large populations of thermally responsive, fast growing invasive species (Jones et al. 2003a, b; Convey et al. 1999; Chown et al. 2002). Increasing temperature may therefore enable invasive alien species to occupy ever higher elevations, with likely detrimental consequences for indigenous species and possibly also for ecosystem functioning. However, the picture may also be much more complicated. For example, currently, the invasive alien slug *Deroceras panormitanum* is restricted to elevations below ca. 250 m (Fig. 5) on Marion Island as a consequence of its inability to tolerate temperatures below its freezing point (ca. −3.3°C) (Lee et al. unpublished data). Whilst a warming trend in mean temperatures might suggest that the slug will colonize higher elevations (vascular plants on which it feeds extend to at least 600 m—Gremmen 1981), with concomitant effects on nutrient cycling, warming is also being accompanied by larger numbers of freeze-thaw cycles. These might, in fact, further constrain the distribution of the slug on the island.

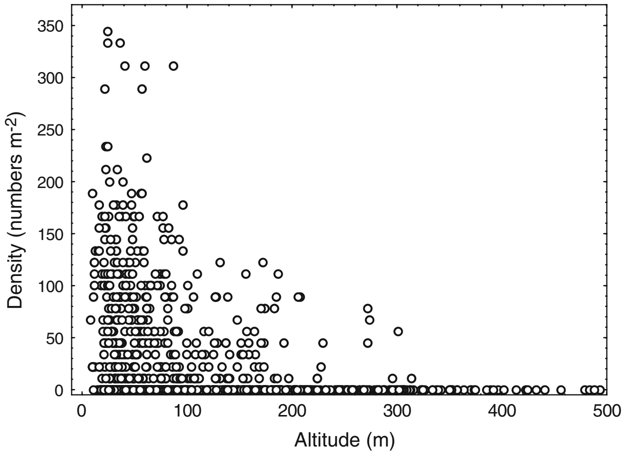

Fig. 5 Densities of the invasive alien slug *Deroceras panormitanum* on Marion Island. Note the rapid decline in maximum density with elevation (Lee et al. unpublished data)

The combination of warming, drying and differential responses to desiccation of indigenous and invasive species constitute a further way in which global climate change will affect the invertebrates of the SOI. Global change type-drought of the kind forecast for many temperate systems (e.g. Easterling et al. 2000; Breshears et al. 2005) is typical also of several SOI (Bergstrom and Chown 1999). On Marion Island, a combination of laboratory studies and field experiments has shown how global change-type drought will likely tip the balance in favour of invasive over indigenous springtails (Chown et al. 2007). In response to thermal acclimation, the magnitude of phenotypic plasticity in the survival of dry (75% relative humidity) conditions does not differ between indigenous and invasive springtails. Rather, the invasive species have longer survival times (at 5 and at 15°C) following acclimation to 15°C, whilst in the indigenous species, the opposite is found (Fig. 6). Field experiments have revealed that in response to a year of dry and slightly warmer conditions, simulated by rain-out shelters (McGeoch et al. 2006, see also le Roux et al. 2005), the indigenous species declined substantially in abundance, whilst the invasive species showed no change (Fig. 6). The combined laboratory and field trials, and data on the distribution of springtails on Marion Island demonstrating the preference of invasive species for lowland areas, suggest that ongoing change of the type forecast for the island (le Roux and McGeoch 2007) will favour the invasive species. What remains to be determined is the extent to which interactions among the indigenous and invasive springtail species will result in displacement of the indigenous species as has been suggested for South Georgia (Convey et al. 1999).

Conclusions and prospectus

At first glance, much seems to be known about the terrestrial invertebrates of the SOI and the ways in which climate change and biological invasions are likely to affect their populations and the ecosystems they form part of. However, the information is spatially autocorrelated. Some islands, such as Marion Island, Macquarie Island, and the Kerguelen Islands are comparatively well investigated. By contrast, for others the invertebrate faunas remain poorly surveyed (e.g. mites on most island groups, springtails on many), and little is known about system functioning. Even for reasonably well-investigated islands, information is

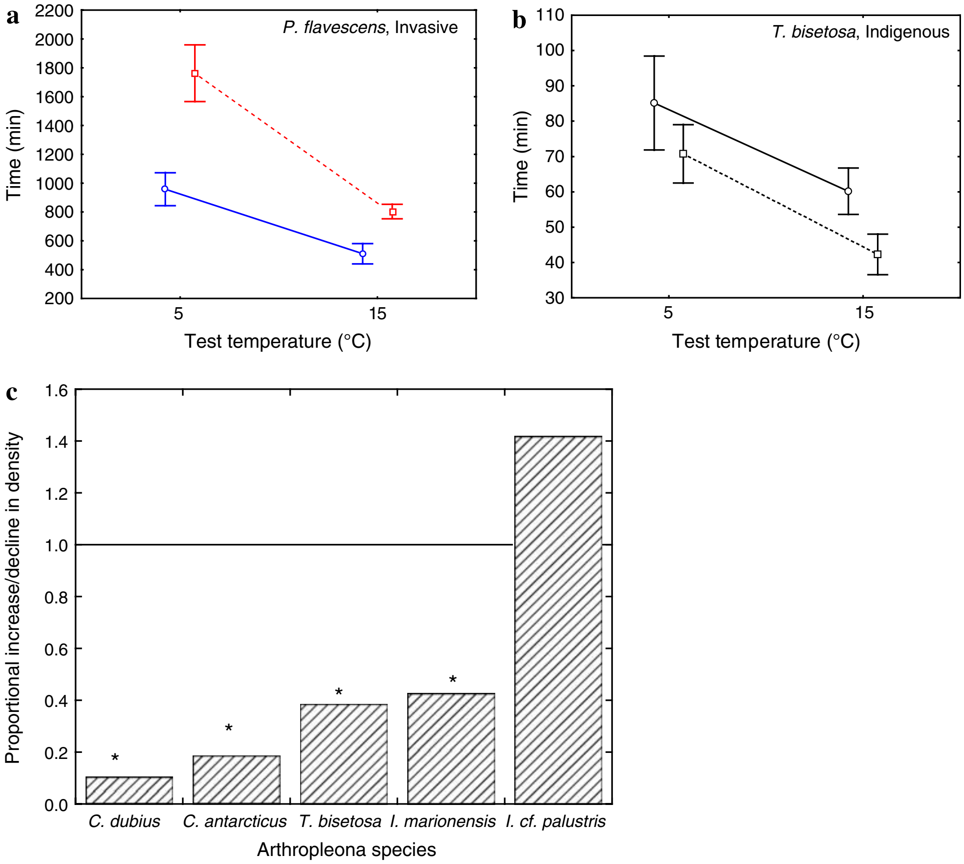

Fig. 6 Survival of dry conditions (75% relative humidity) following acclimation to 5°C or to 15°C by (**a**) an invasive and (**b**) an indigenous springtail species from Marion Island at test temperatures of 5°C (solid line) and 15°C (dashed line). Note that the invasive species performs better following the high temperature acclimation treatment than after the low temperature one. In (**c**) the responses of springtails to experimental warming and drying are shown as proportional abundance relative to controls. Note the decline in abundance of the indigenous species (marked with asterisks). Redrawn from Chown et al. (2007). Species as follows: *Cryptopygus antarcticus*, *Cryptopygus dubius*, *Isotoma marionensis*, *Isotomurus* cf. *palustris*, *Pogonognathellus flavescens*, *Tullbergia bisetosa*

inadequate for systems other than the terrestrial. For example, what the effect of climate change will be on freshwater systems is poorly known, although it is thought that the life history of the South Georgian water beetle *Lancestes angusticollis* will be affected (Arnold and Convey 1998). How warming will influence interactions between freshwater crustaceans and their food resources is unknown. Similarly, the effects of introduced fish on aquatic invertebrates has not been investigated (Frenot et al. 2005), even though it is well known that these species have considerable impacts on invertebrates elsewhere. For marine systems, the picture is likewise patchy. Recent work has demonstrated that ships, smaller marine craft, and plastic debris can act as vectors for non-indigenous species in the region (Lewis et al. 2003, 2006; Barnes et al. 2006), and that species invasive in other parts of the world, regularly travel to and survive conditions throughout the Southern Ocean (Lee and Chown 2007). However, the extent of introductions to marine systems, and how these species, and those indigenous to a given area, might respond to climate change is far from clear. Southerly species living in cold, polar water might be especially sensitive to rising temperatures given their present intolerance of even relatively small acute changes therein (Peck et al. 2006), but the extent to which responses might evolve or to which plasticity might be re-expressed is only now being studied (Seebacher et al. 2005).

These gaps in current information demonstrate that much remains to be done to document and to understand the mechanisms underlying variation in the invertebrate biotas of the SOI. Moreover, they also show that comprehension of the impacts of climate change and invasion, the two major conservation threats to the SOI, is far from fully developed. Nonetheless, an overview of the work available quickly reveals that sufficient information exists for clear initial recommendations to be made concerning mitigation: International agreements to limit climate change globally require more active political and societal engagement, regional quarantine procedures starting at source (i.e. continental departure points) must be tightened to limit further introductions, better surveys are required locally for early detection of new introductions so that eradication can be implemented, and greater attention should be given to managing increasing human use interests in the region. Whilst the ongoing development of protected areas in the Southern Ocean (including large Marine Protected Areas, Lombard et al. 2007) is encouraging, increasing marine exploitation with potential knock-on effects on systems dependent on nutrient inputs from the sea (e.g. Smith and Froneman 2008) is worrying. So too is the fact that dwindling fossil fuel and mineral resources globally will mean increasing consideration of previously uneconomic extractions from ocean plateaus and the seabed. The Southern Ocean Islands will not escape attention as convenient support platforms for such activities. However, it is abundantly obvious that, as some of the most pristine systems on earth, representing habitats unique to the planet, the Southern Ocean Islands have a much greater future value as conservation areas than as convenient staging posts for short-term exploitation of a limited resource base.

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ORIGINAL PAPER

Preliminary conservation status and needs of an oceanic island fauna: the case of Seychelles insects

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Abstract Islands are generally reported to have much higher extinction rates and levels of threat than continental areas. This perception is based largely on studies of vertebrates. A recent assessment of the biodiversity of the Seychelles islands enables the status of a range of taxonomic groups to be compared. A high proportion of the fauna is found to be threatened, with Dictyoptera being the most threatened insect order (51% of 34 native species) followed by Orthoptera (47% of 68 species). Lower levels of threat are found in Diptera (28% of 562 species), Dermaptera (24% of 21 species) and Lepidoptera (21% of 517 species). Differences between the orders relate mainly to distribution patterns, with the most threatened orders having the highest proportions of endemic and restricted range species. The main threats for most orders are habitat deterioration due to invasion by introduced plant species, sea level rise and climate change. These threat factors are different from those reported to affect vertebrates, which are generally considered to be threatened by introduced predators resulting in critically low population sizes. These findings indicate that conservation sources would be more useful and cost effective for insect conservation if directed to habitat maintenance and restoration rather than to alien predator control.

Keywords Climate change · Conservation · Insects · Invasive species · Seychelles

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Introduction

It is widely accepted that island ecosystems are particularly vulnerable to extinction (Mueller-Dombois 1981; Loope and Mueller-Dombois 1989; D'Antonio and Dudley 1995); in support of this is the high rate of extinction of birds and reptiles on islands, compared to continental areas (Baille et al. 2004), with high susceptibility to invasion by alien species (Donlan et al. 2003a; Reaser et al. 2007). Although this is well established in literature there have been no comprehensive surveys of the status of island biodiversity, with studies limited to vertebrates, some plant groups and a small number of conspicuous invertebrate taxa. The invertebrates reported are mainly molluscs threatened with particular invasive predators (Hadfield et al. 1993; Coote and Loeve 2003) and large, charismatic insects such as the New Zealand Weta (Sherley 1998) and the Fregate island giant tenebrionid beetle (*Polposipus herculeanus*) (Ferguson and Pearce-Kelly 2005).

In 2000–2005 the Indian Ocean Biodiversity Assessment (IOBA) provided a comprehensive survey of the biodiversity of the Seychelles islands. This is producing a series of taxonomic reviews and Red List assessments of all the species recorded in Seychelles. These assessments provide a comprehensive review of the status of the insect fauna, allowing this to be compared to existing assessment of the vertebrate fauna in order to answer the question of whether or not island faunas are particularly vulnerable or whether this is an artefact of the small size of vertebrate island populations. The Red Listing process is ongoing. The orders that have been completed are evaluated here.

The Seychelles islands comprise 115 islands in the western Indian Ocean. These form two main groups; the northern granitic islands and the southern, coralline islands. The southern islands are less than 10 m above sea level, representing raised coral atolls or sand cays. This results in limited habitat variation and correspondingly low species diversity. The granitic islands are the remnants of the Seychelles microcontinent which was isolated following the break-up of Gondwanaland 65–100 million years ago. These are high islands reaching 905 m above sea level. This results in great habitat diversity and high rainfall, contribution to the growth of diverse rain forest habitats.

Methods

Collection

During the IOBA collections were made in 135 localities on 52 islands. These included all but three of the islands where collections had been made by previous expeditions and encompassed the recorded range of over 99% of the species recorded before 2000. 78,369 insect specimens were collected, with surveys in both the wet and dry seasons in order to account for any seasonality in abundance or activity of the animals.

Identification

For most families identification was carried out by expert taxonomists. Some families were represented by a small number of species and were identified using existing literature on the Seychelles fauna. Identifications were combined with taxonomic revisions, ensuring that recently collected material data are directly comparable with historical data.

Assessment

Red List assessments of the insects are complete for Dermaptera (21 native species), Dictyoptera (34), Diptera (562), Embioptera (2), Isoptera (7), Lepidoptera (517), Mantodea (5), Orthoptera (68) and Phasmatodea (6). Assessments are ongoing for Coleoptera, Ephemeroptera, Hemiptera, Hymenoptera, Mallophaga, Neuroptera, Odonata, Psocoptera, Siphonaptera, Thysanoptera and Trichoptera.

For the Red List assessment all historical distribution records were compiled, providing a quantified distribution range. Population sizes were not quantified for any taxa. Changes in distribution are indicated by the absence of specimens from historical localities. For species known only from 1 to 2 specimens the significance of this cannot be assessed. However if a species was locally abundant in 1905–1909 but could not be found at that locality in 2000–2005 it was considered to have declined. The IUCN Red List criteria used in the assessments are summarised in Table 1.

In interpreting the criteria each island was considered a separate location. Species which were not found in a location where they had been recorded historically but were collected elsewhere were considered to have declined locally. Other species which were recorded from a historical location but were not located by the present study were considered Data Deficient if recorded from habitat which remains available or if they were known only from a single specimen. Species not located but recorded from threatened habitats (such as marshes) were considered threatened due to the deterioration of that habitat.

Results and discussion

Taxonomy

High levels of threat were found in most orders although there are notable differences in the level of threat between different taxa with high levels of threat in Dictyoptera (51%) and Orthoptera (47%) and moderate levels in Diptera (24%), Dermaptera (24%) and Lepidoptera (21%). The small orders have variable levels of threat: 33% of Phasmatodea, 28% of Isoptera, 0% of Mantodea and Embioptera. In part this relates to the proportion of endemic species, with 24% endemic in Dermaptera, 49% in Leidoptera and 51% in Diptera, 87% of Dictyoptera and 59% in Orthoptera, in the largest orders. Levels of endemism are again variable in the smaller orders: 100% of

Table 1 IUCN Red List criteria used in the Seychelles assessments

Factor	Measurement	Critical points	Criterion
Number of locations		1 (CR), <5 (EN), <10 (VU)	B1&2a
Geographic range	Extent of occurrence	<100 k^2 (CR), <5000 km^2 (EN), <20,000 km^2 (VU)	B1
	Area of occupancy	<10 km^2 (CR), <500 km^2 (EN), 2,000 km^2 (VU)	B2
Declines	Extent of occurrence		B1bi&2bi
	Area of occurrence		B1bii&2bii
	Quality of habitat		B1biii&2biii

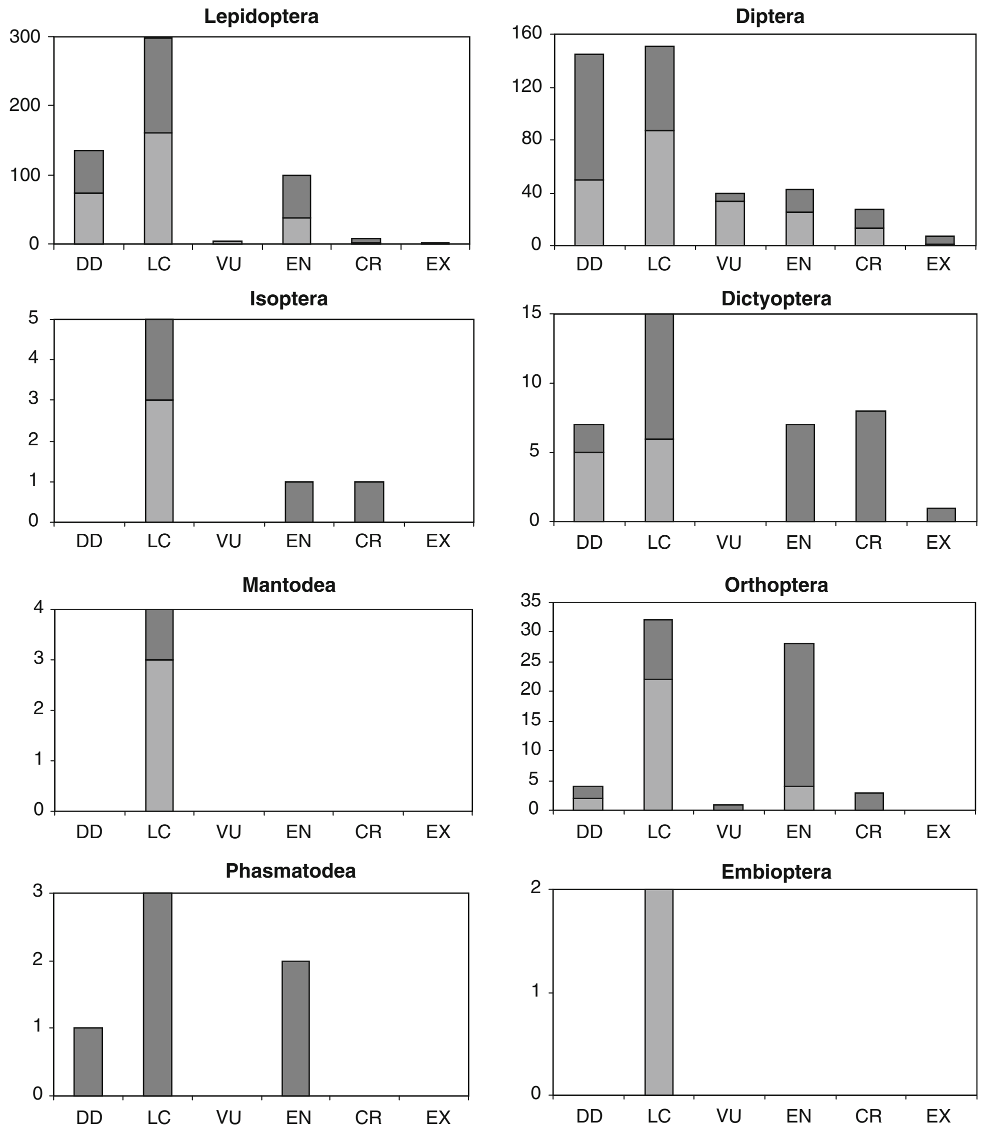

Fig. 1 Numbers of threatened species of Seychelles insects. Grey bar—indigenous species, black bar—endemic species

Phasmatodea, 57% in Isoptera, 25% in Mantodea, and 0% of Embioptera. Within all groups the endemic species have higher levels of threat than indigenous species, largely due to their more restricted distributions, reflected by the differences in average area of occupancy and especially extent of occurrence (Figs. 1, 2).

Geography

Different geographical areas also have different levels of threat, with higher levels of threats in the coral islands than the granitics for Lepidoptera (52%, compared to 32%), Diptera (68% compared to 15%) and Dictyoptera (57% compared to 55%). In contrast the Orthoptera have fewer threatened species on the coral islands (35%) than the granitics (46%). Too few species of the other taxa are present on the coral islands for meaningful comparison. These differences can be equated to the composition of the fauna: most Diptera and Lepidoptera on coral islands do not occur on the granitics, being southern atoll endemics of Afro-Malagasy colonists; coral island Dictyoptera are restricted to a small number of mainly endemic species, again with very few shared with the granitic islands; the Orthoptera have a higher proportion of taxa shared with the granitic islands, dominated by the wide-ranging acridid grasshoppers and tetrigid katydids.

Threats

Although the main threats to species on coral and granitic islands are ongoing or projected declines in the area of suitable habitats in the granitic islands this is largely due to habitat deterioration caused by alien plant species. In the coral islands the threat is predominantly from projected sea level rise as 90% of the land area of these islands is no more than 1 m above sea level. Habitat degradation due to

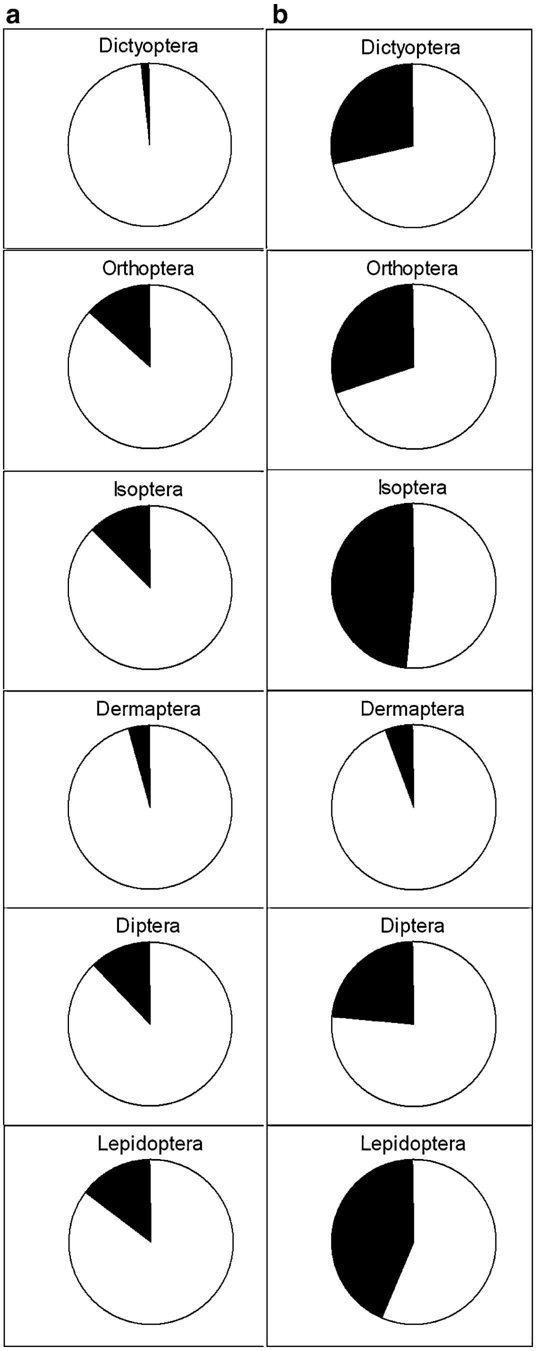

Fig. 2 Comparison of ranges (km^2) of endemic and indigenous species: (**a**) extent of occurrence; (**b**) area of occupancy. White = mean range of indigenous species; black = mean range of endemic species. Orders are ranked by degree of threat (order with the highest proportion of threatened species first)

invasion by the alien plants *Cinnamomum verum*, *Psidium cattleianum* and *Falcataria moluccana* is the major threat for most taxa; 67% of threatened Lepidoptera, 69% of threatened Dictyoptera and 78% of threatened Orthoptera. This is followed by sea level rise (Lepidoptera 30%, Dictyoptera 19% and Orthoptera 22%), development (12% of threatened Dictyoptera), climate change (Lepidoptera 2%, Orthoptera 3%) and association with restricted range taxa (Lepidoptera 2%). Close association with particular food plants contributed to threatened status within Phasmatodea where the two threatened species are both Endangered by restricted range combined with habitat deterioration, both have close food plant associations—the birds nest fern *Asplenium nidus* in the case of *Casuius scotti* and endemic palms in the case of *Graffaea seychellensis*. Of the Lepidoptera three indigenous species are threatened due to a restricted association with a Vulnerable plant species (*Epermenia* cf. *moza* associated with *Schefflera procumbens*, *Herpetogramma licarsisalis* with *Pseuderanthemum tunicatum* and *Bocana* sp. with *Procris insularis*), or a Critically Endangered animal species (*Crypsithyrodes concolorella* associated with the Seychelles sheath tailed bat *Coleura seychellensis*).

Diptera are the only order that does not fit this pattern. In this group the main threat is sea level rise (68% of threatened species) followed by habitat deterioration (39%) and climate change (2%). This difference may be an artefact of the relatively high proportion of Data Deficient Diptera, which comprise 35% of species, compared to 6–24% in other orders. The Data Deficient species are predominantly (76%) species known from a small number of specimens from one locality. For these the data are too limited to allow identification of any habitat association; they may be threatened or even extinct but cannot be assessed on the available information.

One of the most threatened habitats in Seychelles is marsh habitat; this has been largely drained and the few remaining areas are being drained and developed rapidly. Of the 14 Lepidoptera associated with marshes 86% are threatened and 100% of the 37 marsh associated Diptera, of the other groups studied here few are associated with marshes—only 2 Orthoptera (both Least Concern) and only one Dictyoptera (Critically Endangered).

Development affects two species of cockroach (*Delosia ornata* and *Hololeptoblatta pandanicola*). Recorded extinction levels are low; 1 Diptera, 2 Lepidoptera and 1 Dictyoptera may be extinct. Actual extinction levels may be higher as a high proportion of taxa have not been located since 1909 but are not listed as extinct as they may survive in unexplored areas of habitat. These are listed as Endangered if associated with a deteriorating habitat or Data Deficient if known just from a single specimen.

The varied effects of geographical distribution and ecology on threatened status are shown by a comparison of the Lepidoptera families. Within the Lepidoptera particularly high threat levels are apparent in the Tineidae (62% of 47 species) and Oecophoridae (55% of 21 species). These are diverse families of small moths, with high levels of narrow geographical endemism, including many island radiations (Robinson and Tuck 1997). Low levels of threat are found in the widespread grass-associated Pterophoridae (0%) and in the equally widespread Geometridae (0%). The effects of dispersal ability allowing wide distributions and of polyphagy are shown by the low threat levels for the Nocutidae (8%) and Nolidae (14%). Other families of large Lepidoptera with active flight are more specific in their larval feeding habits and have higher levels of threat, such as the Nymphalidae (27%), Arctiidae (31%) and Sphingidae (31%).

The highest recorded levels of threat (i.e. the highest proportion of threatened species) are found on tropical islands (Mueller-Dombois 1981; Loope and Mueller-Dombois 1989; D'Antonio and Dudley 1995). This is reflected in bird data where over half the world's threatened birds are island species (Baille et al. 2004). These comparisons are based largely on data for vertebrates, for which the main threats are invasive species. Two thirds of island birds are threatened by invasive species (Baille et al. 2004), almost all of which are mammalian predators. It is widely accepted that island faunas (and endemic species in particular) are threatened by introduced predators, as reported for birds (Blackburn et al. 2004, 2005; Jamieson 2006). It is often stated that island endemics have evolved in the absence of predators (e.g. Groombridge 2007). Whilst this is true of bird faunas with regard to mammalian predators and for some islands, it does overlook reptile predators on other islands and does not apply to most invertebrates which are subject to a range of invertebrate and avian predators even in the absence of native mammals. Accordingly this cannot be considered a general explanation for the vulnerability of island taxa. This susceptibility to the impacts of invasives are thought to be due to attributes such as reduced dispersal ability and low population sizes. Island species are generally assumed to have lower dispersal abilities, due to reduced willingness to disperse or reduced flight abilities (Reaser et al. 2007).

Flightlessness is rare in the Seychelles fauna, but has been recorded in birds (one species), beetles (10 species) and cockroaches. As noted above, threat levels are high in the Dictyoptera and this may correspond to a tendency to wing reduction and loss in the endemic cockroaches. No flightless species have been identified in any of the other groups studied here; females of some Diptera are flightless, but these are introduced (Phoridae) or widespread intertidal species (Chironomidae). As a generalization reduced flight ability is not an explanation for the high threat levels faced by Seychelles insects, although it may be an additional factor for a small number of species.

Island populations are generally smaller than continental ones, which combined with isolation makes island ecosystems highly sensitive to disturbance (Reaser et al. 2007). Population size may be particularly important as it has been suggested that genetic factors (principally inbreeding) are important in the decline of island populations, with island populations having lower genetic diversity than continental ones (Frankham 1998, 2005; Frankham et al. 2002; Spielman et al. 2004; Groombridge 2007). Some studies suggest that although extinction due to genetic factors such as inbreeding may be significant it may also be slow in comparison with rapid declines due to predation (Jamieson et al. 2006). Other influences include low population growth rates and additional effects of habitat loss contributing to genetic deterioration (Jamieson 2006).

In common with other island groups, Seychelles vertebrates are largely threatened by factors leading to critical population size (Gerlach 2007). There is no evidence that similar factors apply to any of the insects evaluated here although predation has been speculated to affect Orthoptera (Matyot 1998). Population declines due to introduced predators were considered a risk for the flightless Fregate giant tenebrionid beetle *Polposipus herculeanus* but this has not been substantiated (Gerlach 2005). The status of this species is currently being re-evaluated. Some large invertebrate species have high population densities on rat-free islands but are scarce (or absent) on the largest islands. The distributions of such species as the Seychelles giant millipede *Sechelleptus seychellarum*, the whip-scorpion *Phrynicticus scaber* and the large snail *Stylodonta unidentata* superficially appear to be influenced by rats but this is disproved by the survival of substantial populations of these species on Silhouette island where rats are highly abundant. Their absence from the largest islands (Mahé and Praslin) may be due to the introduced tenrec *Tenrec ecaudatus* which may be assumed to be a significant alien predator on those two islands. Thus predation may be a significant factor for some large invertebrate species when faced by a particular predator, but the impacts have not been reliably demonstrated to date. Invasive insects may also have caused population declines, but this is similarly speculative. The absence of any conclusive evidence of invasive ant impacts beyond short-term impacts of temporary population explosions in the crazy ant *Anoplolepis longipes*, has been suggested to be due to the undetected impacts of earlier introductions of species such as *Pheidole megacephala* in the nineteenth and twentieth centuries (Gerlach 2004). The lack of unequivocal examples of critical population sizes as threats to Seychelles insects may be due in part of a lack of information on invertebrate population sizes or may reflect higher population densities in invertebrates. This is supported by the assessments of Mollusca where population sizes have been estimated (Gerlach 2006); although threat levels are high (61%), none is listed as threatened based on critical population sizes, rather they are threatened by the habitat (98%) and climate (12%) factors identified here for insects.

Invasives are considered to be the main causes of extinction on islands (Veitch and Clout 2002; Donlan et al. 2003b). For the Seychelles fauna this results predominantly from habitat deterioration, with introduced predators being a significant factor only in some vertebrate species. This suggests that conservation efforts focusing on invasive predator control may do little to halt biodiversity loss. More attention needs to be paid to maintaining functional ecosystems and restoring degraded areas. Healthy ecosystems may be more resilient to disturbance and such resilience is essential to minimise future problems; it has long been noted that climate change may exacerbate the impacts of invasions.

Although extinction rates are high on islands (Mueller-Dombois 1981; Loope and Mueller-Dombois 1989; D'Antonio and Dudley 1995) few species have become extinct in Seychelles. Periods of major habitat loss may have caused unrecorded extinctions (especially when lowland areas were cleared during the early years of human settlement in the early 1800s and in the late nineteenth century and early twentieth centuries when coconut plantations were expanded. The low numbers of extinctions over most of the twentieth century reflect a reduction in rate of conversion of forests to plantations. Since the 1770s invasive species have been spreading and since the late twentieth century they have caused major modifications of habitat structure. The problems faced by Seychelles biodiversity are further exacerbated by rapid increases in infrastructure development. This is placing increasing stress on an already seriously compromised ecosystem. In this situation it is probable that the historically low extinction rate will rise in the near future.

Appendix

Appendix List of threatened insects included in the present study

Class	Family	Species	Seychelles Red List status
Lepidoptera	Tineidae	*Erechthias calypta*	VU (D2)
		Erechthias methodica	EN (B1abv,2abv)
		Erechthias molynta	EN (B1abv,2abv)
		Erechthias polyplaga	VU (D2)
		Erechthias trichodora	EN (B1abv,2abv)
		Amphixystis crobylora	VU (D2)
		Amphixystis cyanodesma	CR (B1abv,2abv)
		Amphixystis ensifera	VU (D2)
		Amphixystis fricata	EN (B1abv,2abv)
		Amphixystis ichnora	EN (B1abv,2abv)
		Amphixystis lactiflua	EN (B2abiii)
		Amphixystis nephalia	EN (B1abv,2abv)
		Amphixystis polystrigella	EN (B1abv,2abv)
		Amphixystis rhothiaula	VU D2
		Amphixystis rorida	EN (B1abv,2abv)
		Amphixystis roseostrigella	VU (D2)
		Opogona florea	VU (D2)
		Opogona heliogramma	CR (B1abv,2abv)
		Opogona sacchari	EN (B1abv,2abv)
		Afrocelestis lochaea	EN (B2abiii)
		Crypsithyrodes concolorella	VU (D2)
		Tinea coronata	EN (B1abv,2abv)
		Tinea cursoriatella	LC
		Tinea milichopa	VU (D2)
	Gracillariidae	*Acrocercops angelica*	EN (B1abv,2abv)
		Caloptilia tirantella	VU (D2)
		Cuphodes luxuriosa	EN (B1abv,2abv)
		Cuphodes tridora	VU (D2)
		Parectopa parolca	EN (B1abv,2abv)
	Oecophoridae	*Pachnistis fulvocapitella*	EN (B1abv,2abv)

Appendix continued

Class	Family	Species	Seychelles Red List status
		Bigotianella menaiella	VU (D2)
		Bigotianella simpsonella	VU (D2)
		Bigotianella tournefortiaecolella	VU (D2)
		Chanystis syrtopa	VU (D2)
		Anachastis digitata	VU (D2)
		Cophomantella cubiculata	VU (D2)
		Paraclada tricapna	CR (B1abiii)
	Blastobasidae	*Blastobasis intrepida*	EN (B1abv,2abv)
	Gelechiidae	*Apocritica chromatica*	VU (D2)
		Helcystogramma effera	EN (B1abv,2abv)
		Thiotricha tenuis subtenuis	EN (B1abv,2abv)
	Momphidae	*Ascalenia isotacta*	EN (B2abiii)
		Cosmopteryx flavofasciata	EN (B1abv,2abv)
		Cosmopteryx mimetis	EN (B1abv,2abv)
		Lymnaecia superharpalea	VU (D2)
		Stagmatophora acris	EN (B1abv,2abv)
		Stagmatophora hieroglypta	EN (B1abv,2abv)
	Metachandidae	*Metachanda coetivyella*	VU (D2)
		Metachanda columnata	VU (D2)
		Metachanda crypsitricha	EN (B1abv,2abv)
		Metachanda glaciata	CR (B1abv,2abv)
		Metachanda hydraula	CR (B1abv,2abv)
		Metachanda noctivaga	EN (B1abiii,2abiii)
		Metachanda plumbaginella	EN (B1abv,2abv)
	Epermeniidae	*Epermenia* cf. *moza*	VU (D2)
	Lyonetiidae	*Lyonetia probalactis*	EN (B1abv,2abv)
	Heliodinidae	*Epicroesa* sp.	VU (D2)
		Stathmopoda glyphanobola	VU (D2)
	Pyralidae	*Glaucochrais muscela*	EN (B1abv,2abv)
		Crocidolomia pavonana	EN (B1abv,2abv)
		Noorda blitealis	EN (B1abv,2abv)
		Achyra massalis	EN (B1abv,2abv)
		Syllepte derogata	EN (B1abv,2abv)
		Cadarena pudoraria	EN (B1abv,2abv)
		Cnaphalocrocis trapezalis	EN (B1abv,2abv)
		Eurrhyparodes tricoloralis	EN (B1abv,2abv)
		Herpetogramma licarsisalis	VU (D2)
		Herpetogramma phaeopteralis	EN (B1abv,2abv)
		Lamprosema charesalis	EN (B1abv,2abv)
		Lamprosema delhommealis	EN (B1abv,2abv)
		Mimudea ablactis	EN (B1abv,2abv)
		Piletocera basalis	EN (B1abv,2abv)
		Pycnarmon diaphana	EN (B1abv,2abv)
		Syllepte sabinusalis	VU (D2)
		Stemorrhages sericea	EN (B1abv,2abv)
		Ancylosis niveicostella	VU (D2)
		Ematheudes nigropunctata	EN (B1abv,2abv)
		Ptyobathra irregularis	VU (D2)

Appendix continued

Class	Family	Species	Seychelles Red List status
		Pyralis manihotalis	EN (B1abv,2abv)
	Choreutidae	*Anthophila gratiosa*	VU (D2)
		Anthophila quincyella	VU (D2)
	Tortricidae	*Cryptophlebia caeca*	VU (D2)
		Olothreutes conchopleura	CR (B1abiii,2abiii)
		Olothreutes hygrantis	VU (D2)
	Arctiidae	*Argina astraea*	EN (B1abv,2abv)
		Exilisia subfusca	VU (D2)
		Mahensia seychellarum	VU (D2)
		Utetheisa lotrix	VU (D2)
		Utetheisa pulchella	VU (D2)
	Noctuidae	*Progonia patronalis*	EN (B1abv,2abv)
		Acontia zelleri	VU (D2)
		Gesonia pansalis	EN (B1abv,2abv)
		Rhesala moestalis	EN (B1abv,2abv)
		Bocana sp.	VU (D2)
		Porphyrinia cf. ragusanoides	VU (D2)
		Spodoptera cilium	EN (B1abv,2abv)
	Nolidae	*Celama tarzanae*	VU (D2)
		Maceda mansueta	EN (B1abv,2abv)
	Sphingoidea	*Cephonodes tamsi*	CR (C1)
		Macroglossum alluaudi	VU (D1)
		Nephele leighi	Extinct ?
		Temnora fumosa pekoveri	VU (B1abiii,2abiii)
	Hesperiidae	*Pelopidas m. mathias*	VU (D2)
	Nymphalidae	*Euploea mitra*	EN (B1abv,2abv)
		Junonia rhadama	VU (D2)
		Phalanta philiberti	Extinct
Isoptera	Kalotermitidae	*Glyptotermes scotti*	EN (D2)
		Procryptotermes fryeri	CR (D2)
Dictyoptera	Blatellidae	*Miriamrothschildia* sp.	EN (B12abiii)
		M. aldabrensis	EN (B12abii)
		M. biplagiata	EN (B12abiii)
		M. mahensis	EN (B12abiii)
		Margatteoidea amoena	Ex ?
		Hololeptoblatta minor	EN (B12abiii)
		H. pandanicola	CR (B12abiii)
		'Theganopteryx' grisea	CR (B12abiii)
		'T.' liturata	CR (B12abiii)
		'T.' lunulata	EN (B12abiii)
		'T.' minuta	EN (B12abiii)
		'T.' scotti	CR (B12abiii)
		Delosia ornata	CR (A3c, B12abi,ii,iii)
		Sliferia similis	CR (B2abiii)
		Balta crassivenosa	CR (B12abiii)
	Nocticolidae	*Nocticola gerlachi*	EN (B2abiii)
	Blattidae	*Neostylopyga rhombifolia*	VU (D2)
	Polyphagidae	*Holocompsa pusilla*	CR (B12abiii)

Appendix continued

Class	Family	Species	Seychelles Red List status
Dermaptera	Anisolabididae	*Antisolabis scotti*	EN (B2abiii)
		A. seychellensis	CR (B2abiii)
	Forficulidae	*Hypurgus ova*	VU (D2)
	Spongiphoridae	*Chaetolabia fryeri*	CR (B12abiii)
		Chaetospania gardineri	EN (B12abiii)
Orthoptera	Mogoplistidae	*Arachnocephalus medvedevi*	EN (B2abi,ii,iii)
		A. subsulcatus	EN (B2abi,ii,iii)
		Ectatoderus aldabrae	EN (B2abi,ii,iii)
		E. nigriceps	EN (B2abi,ii,iii)
		Ectatoderus squamiger	EN (B2abi,ii,iii)
		Ornebius stenus	EN (B2abi,ii,iii)
		O. syrticus	EN (2abi,ii,iii)
		Malgasia sp.	EN (2abi,ii,iii)
	Gryllidae	*Gryllapterus tomentosus*	EN (B12abiii)
		Phaeogryllus fuscus	EN (B12abiii)
		Phalangacris alluaudi	VU (D2) ?????
		Seychellesia longicercata	EN (B2abiii)
		S. nitidula	CR (B2abiii)
		S. patellifera	EN (B2abiii)
		Chorthippus parvulus	EN (B2abiii)
		Trigonidium (Metioche) bolivari	EN (B2abiii)
		Z. major	EN (B2abiii)
		Scottiola sp.	EN (B12abiii)
		S. salticiformis	EN (B12abiii)
		Fryerius aphonoides	EN (B2abiii)
		Orthoxiphus nigrifrons	EN (B2abiii)
		Phaloria (P.) i. insularis	EN (B2abiii)
		Subtiloria succineus	EN (B2abiii)
	Tettigonidae	*Brachyphisis visenda*	EN (B2abiii)
		Odontolakis cf. *sexpunctatus*	EN (B12abiii)
		Plangia ovalifolia	EN (B2abiii)
	Acrididae	*Pternoscirtus aldabrae*	EN (B2abiii)
	Tetrigidae	*Coptotiggia cristata*	CR (B12abiii)
		Amphinotus (?) nymphula	EN (B2abiii)
		A. (?) pupulus	EN (B2abiii)
		Procytettix fusiformis	CR (B12abii,iii)
		P. thalassanax	EN (B2abiii)
Phasmatodea	Ionchodidae	*Carausius scotti*	EN (B12abiii)
	Platycranidae	*Graffaea seychellensis*	EN (B2abiii)
Diptera	Sciaridae	*Epidapus pallidus*	VU (D2)
		Lobosciara adebratti	VU (D2)
		Pseudolycoriella setigera	VU (D2)
	Cecidomyiidae	*Asinapta northi*	VU (D2)
		Seychellepidosis spinosus	EN (B12abiii)
		Lepidodiplosis filipes	VU (D2)
	Culicidae	*Uranotaenia nepenthes*	VU (D2)
	Ceratopogonidae	*Forcipomyia psilonata*	EN (12abiii)
		Forcipomyia sexannulata	CR (12abiii)

Appendix continued

Class	Family	Species	Seychelles Red List status
		Forcipomyia vesicula	EN (12abiii)
		Forcipomyia pulcherrima	EN (12abiii)
		Forcipomyia hutsoni	EN (12abiii)
		Dasyhelea cogani	EN (12abiii)
		Dasyhelea fenerivensis	EN (12abiii)
		Dasyhelea hutsoni	EN (12abiii)
		Dasyhelea inconspicuosa	EN (12abiii)
		Dasyhelea monosticta	EN (12abiii)
		Dasyhelea nigricans	EN (12abiii)
		Dasyhela tamsi	CR (12abiii)
		Culicoides adamskii	EN (12abiii)
		Culicoides leucostictus	CR (12abiii)
		Metacanthohelea cogani	EN (12abiii)
		Stilobezzia spirogyrae	EN (12abiii)
		Nilobezzia scotti	CR (12abiii)
		Bezzia africana	EN (12abiii)
		Bezzia ornatissima	CR (12abiii)
	Chironomidae	*Tanypus complanatus*	VU (D2)
		Larsia pallidissima	VU (D2)
		Clunio gerlachi	VU (D2)
		Semiocladius brevicornis	VU (D2)
		Pseudosmittia triangular	CR (12abiii)
		Pseudosmittia remigula	VU (D2)
		Tanytarsus sp. n.	VU (D2)
		Tanytarsus pallidulus	VU (D2)
		Polypedilum brunneicorne	EN (12abiii)
		Polypedilum glabripenne	VU (D2)
		Polypedilum melanophilum	VU (D2)
		Chironomus seychelleanus	EN (12abiii)
	Psychodidae	*Clogmia* n. sp.	VU (D2)
		Trichopsychoda cf. *africanus*	VU (D2)
	Scatopsidae	*Rhegmoclemina botulus*	VU (D2)
	Tipulidae	*Idiocera aldabrensis*	EN (12abiii)
		Erioptera maculosa	EN (12abiii)
		Atypophthalmus mahensis	CR (1abiii)
		Orimarga fryeri	EN (12abiii)
	Stratiomyiidae	*Cardopomyia robusta*	EN (12abiii)
		Odontomyia sp.	EN (12abiii)
		Oplodontha pulchripes	EN (12abiii)
	Bombyliidae	*Geron dilutus*	EN (12abiii)
		Geron seychellarum	VU (D2)
		Anthrax johanni	EN (12abiii)
		Exoprosopa aldabrae	EN (12abiii)
		Micomitra famula	EN (12abiii)
		Villa aldabrae	EN (12abiii)
	Asilidae	*Trichardis nigrescens*	EN (12abiii)
	Dolichopodidae	*Aldabromyia plagiochaeta*	EN (12abiii)
		Amblypsilopus pallidicornis	EN (2abiii)

Appendix continued

Class	Family	Species	Seychelles Red List status
		Austrosciapus sp. S41	EN (12abiii)
		Ethiosciapus prysjonesi	EN (12abiii)
		Mascaromyia leptogaster	EN (12abiii)
		Mascaromyia sp. S40	EN (12abiii)
		Hydrophorus praecox	VU (12abiii)
		Thinophilus indigenus	EN (12abiii)
		Hercostomus sp. S48	EN (12abiii)
		Lichtwardtia aldabrensis	EN (12abiii)
		Paraclius solivagus	EN (12abiii)
		Tachytrechus tessellatus	EN (12abiii)
		Medetera pachyneura	EN (12abiii)
		Diaphorus sp. S11	EN (12abiii)
		Diaphorus sp. S45	EN (12abiii)
		Acropsilus errabundus	EN (12abiii)
		Chaetogonopteron marronense	VU (D2)
		Chaetogonopteron seychellense	VU (D2)
		Chaetogonopteron aldabricum	EN (12abiii)
		Sympycnus allotarsis	EN (12abiii)
	Hybotidae	*Parahybos iridipennis*	EN (12abiii)
	Phoridae	*Chonocephalus modestus*	VU (D2)
		Dohrniphora papuana	EN (12abiii)
		Megaselia aldabrae	EN (12abiii)
		Megaselia extans	VU (D2)
		Megaselia frontata	VU (D2)
		Megaselia pseudomera	VU (D2)
		Megaselia senegalensis	EN (12abiii)
		Megaselia sp. A	CR (12abiii)
		Megaselia sp. B	CR (12abiii)
		Puliciphora exachatina	CR (12abiii)
	Pipunculidae	*Eudorylas semiopacus*	EN (12abiii)
	Muscidae	*Atherigona cornicauda*	EN (12abiii)
		Atherigona orientalis	VU (D2)
		Coenosia setalis	EN (12abiii)
		Limnophora sp.	EN (12abiii)
		Lispe bengalensis	EN (12abiii)
		Lispe sp.	EN (12abiii)
		Lispe sp.n.	EN (12abiii)
	Hippoboscidae	*Olfersia aenescens*	EN (12abiii)
		Olfersia spinifera	EN (12abiii)
	Platystomatidae	*Naupoda inscripta*	VU (D2)
	Tephritidae	*Philophylla seychellensis*	EN (12abiii)
		Psednometopum aldabrense	EN (12abiii)
		Taomyia ocellata	Extinct ?
	Lauxaniidae	*Homoneura funebricornis*	EN (12abiii)
		Homoneura laticosta	EN (12abiii)
		Homoneura mahensis	EN (12abiii)
		Homoneura terminalis	EN (12abiii)
	Clusiidae	*Heteromeringia nigrifrons*	EN (12abiii)

Appendix continued

Class	Family	Species	Seychelles Red List status
	Agromyzidae	*Cerodontha piliseta*	EN (12abiii)
		Ophiomyia centrosematis	EN (12abiii)
	Asteiidae	*Asteia lambi*	EN (12abiii)
		Phlebosotera striata	EN (12abiii)
	Xenasteiidae	*Xenasteia seychellensis*	EN (12abiii)
		Xenasteia aldabrae	EN (12abiii)
	Chloropidae	*Anatrichus erinaceus*	EN (12abiii)
		Caderema femorata	CR (12abiii)
		Conioscinella dissimilicornis	EN (12abiii)
		Chloropsina sp.	VU (D2)
		Oscinella acuticornis	EN (12abiii)
		Pseudogampsocera scutellata	EN (12abiii)
		Epimadiza rugosa	EN (12abiii)
		Epimadiza sp.	EN (12abiii)
		Fiebrigella atritibia	EN (12abiii)
		Lagaroceras sp.	EN (12abiii)
		Pselaphia sp.	EN (12abiii)
		Tricimba armata	EN (12abiii)
	Milichidae	*Enigmilichia dimorphica*	EN (12abiii)
		Leptometopa nilssoni	EN (12abiii)
	Canacidae	*Isocanace briani*	EN (12abiii)
		Nocticanace actites	EN (12abiii)
		Nocticanace flavipalpis	EN (12abiii)
		Tethina ochracea	EN (12abiii)
	Ephydridae	*Allotrichoma breviciliatum*	VU (12abiii)
		Atissa sp.	VU (12abiii)
		Ceropsilopa lacticella	EN (12abiii)
		Schema aldabricum	VU (12abiii)
	Drosophilidae	*Leucophenga* sp. a	VU (12abiii)
		Drosophila vallismaia	VU (12abiii)
		Scaptodrosophila sp. h	VU (12abiii)

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ORIGINAL PAPER

Insect conservation in early succession on islands: lessons from Surtsey, Iceland, and the Krakatau Archipelago, Indonesia

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Abstract Early successional communities on islands may include specialised aeolian-based pioneer arthropods scavenging on aerial fallout on volcanic lava or ash. Some such species appear to be restricted to such extreme habitats. Persistence of such species may be governed by volcanic activity and their future thus be beyond the control of people. Surveys to determine their presence elsewhere are needed to determine their possible status as refugees in later successional stages, and as a basis for any more informed conservation measures. Insect colonization patterns on Surtsey and Anak Krakatau are briefly reviewed and contrasted to indicate the background to insect community formation on remote islands.

Keywords Aeolian community · Colonization · Lava · Oceanic islands · Volcanism

Introduction

Much habitat and resource management for insect conservation focuses on pre-climax successional stages, commonly with a primary aim of maintaining particular seral communities as the milieux within which insect species of conservation interest thrive. Management plans for many individual insect species in temperate regions emphasise tactics such as to 'control encroachment' of shrubs or to sustain particular grassland or herbfield associations as plagioclimax communities, and so to curtail the processes of natural succession and maintain habitat suitability. Most such plans involve secondary successions following human interventions, and the particular associations involved dictate aspects and desirable trajectories of management, with the key foci often being particular seral plant resources needed by a targeted insect. Management commonly necessitates a deliberate mosaic scale approach to ensure availability of a particular suite of successional stages on a site. However, and reflecting the rapid turnover of species, the earliest stages within secondary succession can be difficult to sustain and even defining the suite of pioneer insect species that depend on these may be difficult. Some additional clues may be sought from studies on primary succession.

The early stages of development of insect assemblages, based on initial colonization of new ground, are an intriguing source of ecological knowledge. In a few widely separated places, such primary successional processes have been detected and monitored to varying extents on ground newly formed from volcanic activity, and in places where the source of insect colonists, and their modes of arrival, may be inferred reasonably reliably. Numerous situations involving colonisation of bare ground substrates on continents and islands differ widely in their relevance, but in most of these, potential colonists are available nearby, and the 'bare ground' may already be biologically fecund as including seed beds and other propagules. Some successional studies after volcanism have been on ash deposits or lava flows on continents (such as Mt St Helens, Washington: Edwards 1996) or islands (as on Hawai'i), where potential colonists abound nearby. Others have been on entirely new terrain, as complete 'new' oceanic islands, usually with arrivals from colonisation sources considerably farther away, and studies of these more remote environments may be particularly informative.

In this paper, insect colonisation of two very different oceanic islands (Surtsey, off Iceland in the North Atlantic,

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and Anak Krakatau, in the Sunda Strait of Indonesia) is compared and discussed. Every such 'new' island will be unique, with subsequent biological events influenced by extent of isolation and the variety of arriving organisms. True replication is impossible, but each such case may also contribute to a wider basic understanding of the complex ecological processes involved.

Surtsey is perhaps the most intensively documented case of community development on a new island, where, following its initial emergence from the sea in 1963, annual visits by scientists have provided a clear and detailed picture of subsequent biological events (Fridrikkson 1975; Snorri Baldursson and Alfheidur Ingadóttir 2006). Another, far distant from Surtsey but with considerable parallels to it, is Anak Krakatau, Indonesia. These cases were discussed in detail by Thornton 1996, 2007), and this short account draws on the latter summary, in particular, to examine the possible relevance of such knowledge to conservation planning on new oceanic islands and in parallel biotopes elsewhere. Many such stages are transient, and are replaced rapidly by more complex systems as successions proceed and additional resources become available. Nevertheless, in general, those later-formed habitats can be exploited initially only by insects arriving as new colonists to the island, with the later mosaic dynamics on an island reflecting changes such as re-establishment of pioneer environments by volcanic activity. These may then be replenished by colonists from more proximal sources than areas far across water. Any subsequent conservation not reliant on continued recolonisation or additional colonisations necessitates the retention of such early successional stages within a mosaic of systems progressing toward more complex communities, and in which later-arriving species may, in turn, establish, thrive and in some cases lead to loss or displacement of the pioneers as ecological strategies change (Southwood 1977). In some continental disturbance regimes (scree slopes, floodplains, as examples) the major players in such successions can be defined with reasonable confidence from knowledge of the local biota.

Following the explosion of Krakatau in 1883, the three remaining island remnants in the archipelago, Rakata, Panjang and Sertung, have undergone succession for more than a century to produce a variety of forest types and other vegetation. The trajectories of those successions were discussed by Whittaker et al. (1989, 1992), and summarised also by Thornton (1996, 2007). Additionally, a completely new island, Anak Krakatau ('Child of Krakatau') emerged from the sea in the centre of the caldera in 1930 and, eventually, has stabilised as a younger island which is still active volcanically. Together, the islands allow study of a hierarchy of successional processes involving insects as (1) comparison of the three older islands after around a century of succession, with the putative source areas (Java and Sumatra) each about 40 km distant, to either side of Sunda Strait, and (2) the younger succession on Anak Krakatau, perhaps nested within the above, and with source areas only about 2–4 km away. Anak Krakatau was devastated by eruptions in 1952, when all vegetation was destroyed, and severely damaged also in 1970–1971. It is important as one of very few tropical islands in which aspects of insect colonisation and assemblage development can be assessed from their earliest stages, and recovery of the biota from severe later perturbations also appraised. Background information on invertebrate colonization of the Krakataus is given by Thornton and New (1988) and Thornton (1996), with numerous more specific papers referred to there and in more recent summaries such as Tagawa (2005) and Thornton (2007). Ecological aspects of insect colonisation were summarised by New and Thornton (1992b), and the case for treating colonisation of Anak Krakatau as a 'model within a model' discussed further by Thornton et al. (1992).

The development of insect assemblages on Surtsey and Anak Krakatau is recapitulated briefly below, to exemplify some of the possible trajectories, and their place in understanding conservation need.

Surtsey

Detailed information on the formation and development of Surtsey, and on the comprehensive biological surveys undertaken there throughout its existence, is provided in the recent nomination of the island for inclusion in the UNESCO World Heritage List (Snorri Baldursson and Alfheidur Ingadóttir 2006). Up to 2004, a total of 335 invertebrate species, 249 of them insects (including

Table 1 Insects and related groups recorded from Surtsey until 2004 (from Snorri Baldursson and Alfheidur Ingadóttir 2006)

Group	No. of identified species
Collembola	24
Protura	1
Hemiptera	7
Thysanoptera	3
Phthiraptera	1
Neuroptera	1
Coleoptera	22
Diptera	136
Siphonaptera	1
Trichoptera	4
Lepidoptera	21
Hymenoptera	28
Total	249

Collembola and Protura: Table 1), had been found on Surtsey. Diptera were by far the most species-rich order. One weevil (*Ceutorhynchus insularis*) was described from specimens found on an island near Surtsey, and later discovered also in the Hebrides. Establishment of a colony of gulls (dominated by lesser black-backed gull, *Larus fuscus*, but with other species also present) in forb-rich grassland toward the south of the island is associated with heightened diversity and abundance of invertebrates in that area. A few insects, such as the staphylinid *Atheta graminicola*, appear completely dependent on the gull colony site and have not been found elsewhere. Conversely, the carabid *Amara quenseli* prefers barren tephra substrates. It is known also from the 'helicopter pad', where gulls tend to congregate and to enrich the soil, so inducing development of vegetation similar to that on their breeding colony site. Another of the few abundant insects, the thysanopteran *Taeniothrips atratus*, occurs on its sole food plant, sea sandwort (*Honckenya peploides*).

The first insect recorded on Surtsey was a midge (*Diamesa zernyi*) in May 1964. It, and others, were presumed to have arrived by air, from Iceland or other islands in the Westman group. However, long-distance migrants were also amongst the early arrivals, with the noctuid moth *Autographa gamma* probably from the European mainland. In contrast, taxa such as the Collembola and sole proturan were found in driftwood and floating clumps of turf washed ashore on Surtsey's beaches. The carabid *A. quenseli* is common in Iceland and was first found on Surtsey in 1967.

Early establishment of most insect arrivals was prevented by lack of resources. The earliest resident species include the fly *Heleomyza borealis*, larvae of which feed on fish and bird carcasses, and the midge *Holocladius variabilis*, breeding in shallow tidal pools. With development of permanent vegetation and colonies of breeding seabirds, invertebrate richness increased from the early 1970s and, particularly, after establishment of the major gull colony in 1985. Most insects appear to have arrived by 'natural' means, with importation of organisms controlled strictly during the whole period of Surtsey's existence. Despite these precautions, two species appear to have been introduced by people. Both have been found within the research hut area—the synanthropic fly *Drosophila funebris* and the lathridiid beetle *Lathridius minutus*.

A number of early-recorded Collembola have probably not survived on the island, with a survey in 1995 revealing only eight species, six of them newly recorded, with many of the 16 species recorded previously not then found.

Uniquely amongst islands, Surtsey has in principle been strictly protected since it emerged from the ocean, with human pressures limited to annual visits by scientists and the fauna and flora documented thoroughly and disturbed very little. Such detailed surveys have provided a relatively thorough understanding of community development and early succession. The limited infrastructure, representing human disturbance, comprises a helicopter pad (built in 1993) and a small field hut (1985), with an abandoned lighthouse base (late 1980s) scheduled for removal in 2007. Anthropogenic disturbance is therefore minimal, with tourists not allowed to land, but despite such care introductions by people cannot be entirely ruled out. The nearest inhabited island, Heimaey, is about 18 km away.

Conservation of Surtsey has thus been based on (1) a high level of protection from invasion and damage and (2) strict non-intervention in natural successional processes. The insect assemblages are low in species richness and, reflecting the regional climate, may never become very rich. Their development has reflected opportunistic arrivals and colonization, accompanied by considerable turnover of species. As a de facto 'Strict Nature Reserve: a protected area managed mainly for science' since 1965, Surtsey is genuinely a sanctuary of global significance for increasing our understanding of foundation island communities of insects at higher latitudes, and their post-arrival fates.

Anak Krakatau

Dammerman (1948) made a strong plea to biologists to monitor the development of communities on Anak Krakatau (AK) as effectively as possible, in part to compensate for the lack of equivalent effort following the major eruption of Krakatau in 1883. Unfortunately, this regular monitoring did not occur, and knowledge of Anak Krakatau's flora and fauna has accrued more sporadically and opportunistically, and in the context of highly incomplete documentation of the likely source pools of species, including insects, on the three older islands of the archipelago, and on Java and Sumatra. Lack of data from the early years of AK's existence was countered by apparently complete destruction of biota in 1952, and most information available was accumulated during the 1980s and early 1990s, over which period some patterns of the ecological characteristics of successful early insect colonists emerged. The taxa recorded commonly reflect dispersal capability and opportunity, with a strong filter effect evident in some groups. As examples:

(1) The termites found on AK and on older islands of the archipelago are all species that nest in wood, rather than in soil (Abe 1984). Yamane et al. (1992) attributed this to the fact that colonies of such taxa may survive in drift wood over long distances; some such taxa were found in wood on the beaches of AK.
(2) The Krakataus almost completely lack swarm-founding social bees and wasps, possibly reflecting that

> swarms may not remain cohesive over long ocean flights. Most species of these groups of Hymenoptera present are solitary colony-founders. The sole exception, the bee *Apis dorsata*, is known to make long trips in swarms, unlike other species of *Apis* recorded from Java and Sumatra.

In other cases, the spectrum of taxa present reflects availability of resources. Maeto and Thornton (1993) assessed probable host relationships of the 102 parasitoid braconid wasps recorded from the archipelago. The fauna of AK was very distinctive and biased heavily toward koinobiont endoparasitoids of Lepidoptera. AK lacked koinobiont endoparasitoids of Hemiptera, Coleoptera and Diptera, although 31 species of these guilds were found on other islands. The lack of dipteran parasites was attributed to the relative lack of Diptera on AK, whereas Lepidoptera are far more strongly represented as possible hosts to parasitoids that were considered mainly oligophagous rather than narrowly host-specific.

The most completely documented insects, butterflies (New and Thornton 1992a; New et al. 1988), are represented largely by species characteristic of coastal or near-coastal vegetation, and that occur in more open environments on the islands. Many butterflies found appear to be recent arrivals on AK. Of the 44 species recorded in 1990, 18 had apparently arrived since 1986 (New and Thornton 1992a). Some of these species were not recorded from the older islands, and so are presumed to have emanated from Java or Sumatra or, closer but some 15 km away, the island of Sebesi to the north of the archipelago.

Butterfly richness was assessed by transect inspections in the three vegetated areas of AK in 1990, and correlated strongly with vegetation life forms. Highest richness (31 species, 26 of them considered as ‘resident’) occurred in the well developed *Casuarina equisetifolia* woodland with defined grassland (*Ischaemum muticum*) areas on the Eastern Foreland (Fig. 1). Richness was lowest (nine species, seven resident) in the youngest vegetation, predominantly grassland with a few scattered small *Casuarina* on the Northern Foreland, and intermediate (18 species, 17 resident) between these. No butterfly species was confined to the minimal richness area, and all resident species are taxa associated with transitional seral stages. Later survey in 1992 revealed 32 butterfly species, all recorded earlier from AK. However, by late 1995, following 3 years of volcanic activity, only eight species were found (Thornton et al. 2000).

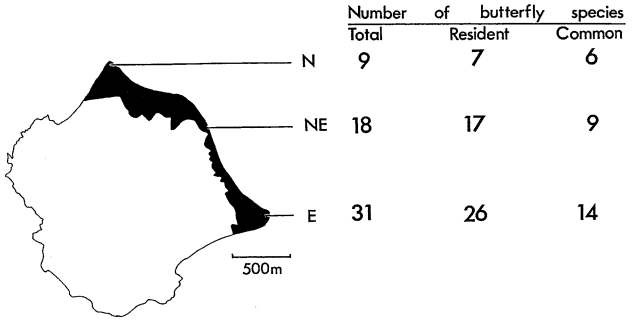

Fig. 1 Butterfly richness pattern on Anak Krakatau, Indonesia, in relation to successional stage of vegetation (vegetated areas in black). The three areas indicated are E (Eastern Foreland), NE (Northeast Headland), and N (Northern Foreland) and form a transition from oldest to youngest in that sequence (from New and Thornton 1992a, reproduced with permission from the Lepidopterist’s Society)

The trend in butterfly distribution noted above, with increasing richness as the habitats age and move toward more established woodland, was mirrored in a broader study of arthropods on *Casuarina* in the three main vegetated areas of AK, where Turner (1997) showed increased biomass and abundance, reflecting both the age of the trees and the complexity of their surrounding vegetation. Such subsets are implicitly linked with periods available for succession, with the asynchrony between areas related directly to volcanic activity. Such direct correlations are not marked in the older forest assemblages on the three older islands (New and Thornton 1992b). It seems that a high proportion of the butterflies on the archipelago are not truly deep forest forms, so that even the most advanced assemblages present on the older islands still represent an ecologically depauperate subset of those present to either side of Sunda Strait. New and Thornton (1992b) suggested for butterflies (and, by analogy, possibly also some other insect groups dependent on vegetation) that a high proportion of the ‘early successional stage/high dispersal ability/tendency’ source pool taxa had reached the islands, whereas a more specialised ‘late successional stage/low dispersal ability/tendency’ suite had scarcely done so. However, on AK it remains unclear whether some of the former group are maintained there mainly by frequent immigration events or are more permanent residents. As in numerous other studies of invertebrates on islands, distinguishing ‘arrivals’ from ‘colonists’ is difficult. Some butterflies on the Krakataus appear to have colonised on several occasions, as early successional vegetation stages re-established after volcanic episodes. From the irregular monitoring that has occurred, these are species with sequences of ‘recorded –not recorded –recorded’ on successive occasions. For such conspicuous insects, focused surveys on such small areas are likely to be reasonably reliable; for most other invertebrates, ‘new records’ are correspondingly more difficult to interpret.

Unlike Surtsey, successions on AK have not been founded wholly on vegetation, but have included aeolian components feeding as scavengers or predators on arthropod ‘fallout’ from the aerial plankton. Considerable diversity of such consumers can be found on bare lava flows (Thornton et al.1988). A population of

Speonemobius crickets was one of the most characteristic components of this aeolian fauna in the 1980s (New and Thornton 1988), and these communities thus show considerable parallels with those supporting the related *Caconemobius* on Hawaii (Howarth 1979). As the first major colonizing plant on areas with such aeolian communities on AK, *Saccharum* (forming dense tussocks or clumps) may accelerate community development by intercepting airborne organisms, without itself being an obligatory resource for these.

However, our ability to monitor and interpret such developmental patterns on AK is increasingly difficult. Unregulated and unmonitored tourism and other visitation continue to increase, mostly by people with little appreciation for the delicacy of the environment, and progressively clouds the pictures available from seral changes in a fully insulated environment. In contrast to Surtsey, AK has never been protected in practice from such disturbance, and the anthropogenically introduced or facilitated components of its biota are sometimes relatively obvious. Thus, the antlion *Myrmeleon frontalis* (although recorded earlier from the older islands) was apparently absent on AK in the mid 1980s, but Turner (1992) found it there in 1990, with larvae forming characteristic pits under the raised floor of a small wooden shelter constructed by the Indonesian authorities, where a favourable habitat was presented by human activity. The shelter was destroyed by volcanic activity commencing late in 1992, and numbers of antlion pits declined successively in 1993 and 1994, to zero in 1995, when the site was filled with ash (Thornton 1996). Likewise, a small concrete trough built to collect rainwater in the late 1980s harboured odonatan larvae soon afterwards, as the only ‘permanent’ fresh water body on the island. By 1992, the trough was dry and overgrown, and by 1993 it was buried under ash. In both these cases, human-facilitated introductions or colonisations of insects preceded extirpation from natural events.

A number of exotic plant species were introduced deliberately to AK in the late 1980s (including foodplants such as papaya, cucurbits and coconut), as well as weeds by accident. The trend noted by Thornton et al. (1990) of future surveys revealing progressively increased effects of human intrusion rather than of natural processes seems highly likely.

Discussion

As Thornton (1996, 2007) emphasised, recently formed islands such as Anak Krakatau and (in a very different environment) Surtsey are important natural laboratories for the study of community assembly. Unlike lands in most parts of the world, their communities must develop from zero, and the successions noted above have occurred over few decades of island existence, and from distant source pools. They have provided significant understanding of how insect communities may be founded and persist in such isolated areas and, thus, may provide clues to the roles of natural regeneration processes, or of restoration, in such areas. The initial environments were devoid of vegetation, and colonization trajectories on AK and Surtsey both follow traditional succession as vegetation develops. However, a second successional trajectory is founded on aeolian input on AK. There, and paralleling volcanic disturbances on the much older Hawai’ian archipelago and the Canary Islands (Ashmole and Ashmole1988, Ashmole et al. 1992), the scale of volcanic activity has the potential to extirpate or to foster production of mosaic habitats with a variety of early successional stages and assemblages based on either or both of the major pathways, over relatively small distances. Production of kipukas is also the production of reservoir habitats, areas from which organisms may need to disperse only very short distances to colonise re-establishing succession at some later time, and from where the initial filter effect may be relaxed. Parallel conditions and events on continental areas (such as Mt St Helens, Washington: Edwards 1996, 2006) also exemplify this putative rescue effect which, of course, is widespread in response to many forms of local disturbance. However, in the nature of rapid turnover in early succession, many of the species subject to volcanic extirpation are likely to be those which would not persist over the long term, and for which conservation effort would necessitate planned successional rejuvenation. On an archipelago scale, AK might act thus for species on the three older islands.

Conservation of habitat mosaics is a central theme of landscape ecology, but much of the relevant information on continental areas has emphasised the values of later successional vegetation (such as forests) that harbour far greater insect richness than relevant here. The most intensively studied earlier successions have largely been grassland, with particular attention to the roles of grazing and fire as conservation management tools. The pioneering successions noted here add further to understanding development of insect communities on newly formed volcanic islands, and the variety of processes that may influence this. Many of the pioneer insect species in the secondary successional communities outlined above, most of these outcomes of disturbance regimes, are common elsewhere and may be widespread and typical *r*-strategists. However, some of the most abundant species in primary successions (such as the crickets depending on aeolian inputs on Anak Krakatau) are not yet known elsewhere. Likewise, Hawaiian aeolian scavengers—crickets, an unusual lygaeid bug (*Nysius wekiuicola*) and lycosid spiders—are clearly derived from related species on the archipelago (Howarth 1987). On the island of Maui, caterpillars of a flightless oecophorid moth (*Thyrocopa apatela*) feed on windborne vegetable fragments trapped in silken webs: Thornton (2007) referred to it as having evolved 'the lifestyle of a kind of vegetarian spider'. The long evolutionary history of the Hawai'ian islands has fostered massive development of specialised endemic species. This contrasts with the recent development of AK, on which endemism is highly unlikely, rendering the presence there of species unknown elsewhere likely to be a collecting artifact. However, the unusual ecological scenarios afforded by volcanic activity on new islands indeed reveal unusual and specialised insect species.

These insects (and other arthropods) are not known from other environments, so that these presumed pioneer communities include highly specialised species with striking and unusual ways of life and which merit conservation both as highly localised species and as constituting unusual assemblages in ecosystems founded in dramatic and unusual ways. Their conservation, seemingly, must depend largely on the natural events attending recurrent volcanic activity to maintain the mosaic habitats in which they are found. Human intervention in such events can be only minimal, and such insects may not be 'manageable' in any conventional conservation terms. Some of the species appear to be quite common in the rather extreme pioneer environments in which they have been found, and it is presumed that they may persist in low numbers within the later successional mosaics and may indeed be present in localised refuges there. Further investigation and survey of their distributions is a prerequisite for any more focused conservation of these elusive species.

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ORIGINAL PAPER

Issues and implications for research on disturbed oceanic islands illustrated through an ant survey of the Cocos (Keeling) Islands

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Abstract An inventory of invertebrates is crucial to the development and implementation of conservation and restoration programs on small oceanic islands, which are among the most threatened ecosystems on earth. We use a survey of ants (Formicidae) on the Cocos (Keeling) Islands to illustrate issues that hinder detailed understanding of biodiversity and the origins of the invertebrate fauna and associated changes since human settlement on the islands. The ant fauna surveyed consisted of exotic ant species, most of which had been introduced to the islands via human activity. Some of these species, like the Yellow Crazy Ant (*Anoplolepis gracilipes*) have the potential to build to large numbers, particularly in conjunction with scale insects, and alter the relatively intact ecology and fauna of North Keeling Island. The absence of baseline information on the invertebrate fauna, the identities and locations of earlier collections, and the introduction of exotic invertebrates since human settlement compromised our ability to determine which invertebrate species are native to the island and the changes in species composition that have occurred since human arrival.

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Introduction

The Cocos (Keeling) Islands are an Australian external territory situated in the north-eastern Indian Ocean (12° S 96° E). The islands, discovered by William Keeling in 1609 and subsequently visited by Dutch, English and Swedish ships, were not permanently inhabited until 1826 when Alexander Hare established approximately100 Indomalayan workers on Pulu Selma (Home Island). Subsidiary camps on other larger islands were later established (Gibson-Hill 1947). Despite their isolated location, the Cocos (Keeling) Islands were settled because of (1) their convenient location for ships travelling between Asia and Europe via the Cape of Good Hope; (2) the establishment of a commercial copra industry between 1834 and 1987 after which it became commercially unviable; (3) the construction of a telegraph relay station (1901–1966); (4) a World War II military base; and (5) in recent years, as a home for the descendents of the Malay copra industry workers, a tourist resort, and a nature conservation reserve.

Currently only two of the islands are inhabited: Pulu Selma (Home) and Pulu Panjung (West), both of which were settled in 1826. Settlements were established on other islands (Pulu Luar [Horsburgh], Pulu Atas [South], Pulu Tikus [Direction] and Prison Island but subsequently abandoned; Pulu Keeling (North Keeling) was settled only for a short period. While the current population totals only several hundred people, numbers reached 10,000 during World War II when the islands were used as a military base, with an airstrip built on Pulu Panung in 1944 (Bunce 1988).

The 22 vegetated islands of the atoll contain approximately 130 species of vascular plants with about half of them native, but no endemic plant species have been described (Williams 1994). This native flora is thought to have reached the islands by natural dispersal via wind, ocean currents, birds and bats. There are 69 introduced plant species that are predominantly on the larger settled islands. Pulu Keeling was originally densely covered with large timber trees, including *Pisonia grandis* and *Cordia subcordata*, with an understorey dominated by coconut palms (*Cocos nucifera*). The island provides valuable breeding grounds to a large number of seabirds, for example, Pulu Keeling comprises the largest remaining breeding ground for the Red-footed Booby (*Sula sula*) in the Indian Ocean (Barker et al. 2004). The main vegetation on other islands is *Pemphis acidula* (tea tree) at higher elevations and pioneer coconut palms, as well as some coarse grasses (Wood-Jones 1912). The pre-settlement vegetation has been modified for coconut plantations (Williams 1994), which are now abandoned. Another key feature of the islands is the poor state of their soils. On all islands, except Pulu Keeling, soil formation is mainly due to the decomposition of coconut husks. Across the atoll the abundance of earthworms is low; however the large land crab (*Cardisoma carnifex*) burrows and undermines the coconut husks which then rot. Other species of land crabs take the fibre into their burrows and bury it. On Pulu Tikus, even with coconut palms, there has been little accumulation of soil (Wood Jones 1912).

Studies on oceanic islands around the world have documented the effects of invasive species in some detail. Island systems allow the examination of the biological drivers of change and ecosystem function at species level largely due to the depauperate biota which allows identification of the impacts of individual species on island communities and function (Wardle 2002). Islands are unique allowing scientists the ability to document the effects of invasive species on the current flora and fauna and examine patterns of colonisation.

Knowledge of the ant fauna on the Cocos (Keeling) Islands has been documented via a number of papers and scientific reports. The first ant species was detected by Darwin (1839) who noted thousands of individuals of a small species of ant under the loose dry blocks of coral. In a more recent survey in 2001, 15 species of ants were collected, 11 of which had not been previously recorded from the islands (Slip and Comport 2001). The distribution of ants was 10 species on Pulu Selma, 8 each on Pulu Panjung and Luar, 6 species total across the 11 southern islands (Atas, Labu, Siput, Pandan, Wak Banka, Cepelok, Kembang, Blekok, Wak Idas and Ampang), and 5 species on Pulu Keeling.

One well-known tramp species that has caused considerable damage to island communities is the Yellow Crazy Ant (*Anoplolepis gracilipes*). The invasive potential of this species has been well documented on islands including Christmas Island and the Seychelles (Hill et al. 2003; O'Dowd et al. 2003; Gerlach 2004; Abbott, 2005). On Christmas Island, it forms mutualisms with the honeydew-secreting cryptogenic lac insect *Tachardina aurantiaca* (Kerridae) and the introduced *Coccus celatus* (Coccidae) which lead to population explosions of both ants and scale insects with dramatic impacts on local biota (O'Dowd et al. 2003; Abbott and Green 2007; Davis et al. 2008).

In June 2005, a survey of the terrestrial invertebrates was undertaken on selected islands within the Cocos (Keeling) complex. One of the aims of the study was to document the invertebrate fauna of the islands to assist their conservation. The survey unveiled a number of logistical and technical issues that hindered the inventory, and these are discussed in relation to documenting the invertebrate faunas of oceanic islands that have been heavily disturbed by human settlement. The ants collected during the 2005 survey are used to illustrate some of these issues.

Survey methods

The Cocos (Keeling) Islands (Figs. 1 and 2) are 2,400 km northwest of the North West Cape in Australia, 960 km southwest of Java and 975 km west of Christmas Island (Williams 1994; Woodroffe and Berry 1994). They are located in the humid tropical zone, with predominantly Southeast Trade Winds, and occasional cyclones. The main climatic features are an annual rainfall between 850–3,300 mm, relatively uniform temperatures from 18–32°C and a mean daily wind speed of 4.7–8.1 m/s (Falkland 1994). The terrestrial invertebrates of the islands were surveyed from 1–24 June 2005.

Our aim was to use standardised collecting techniques across the main islands, although adverse weather conditions limited access and led to unequal sampling effort across the islands. The sites and methods for the full survey are outlined in Neville et al. (2007); only results for ants are presented here.

Transects (each 30 m long) were set up on Pulu Panjung (6 transects, with two in coconut, grassland and *Scaevola taccada*), Pulu Tikus (4 transects, with two in coconut and *S. taccada*), and Pulu Selma (5 transects, with two in grassland and *S. taccada* and one in a domestic garden). Logistic difficulties prevented use of transects on Pulu Luar and Keeling. Pitfall trapping, water pan collection, and sweep netting were undertaken across the transects, following Neville and Yen (2007). Other collecting techniques included Malaise traps, light traps, direct searching, and litter extraction.

Pitfall and water traps were set out for four days. Pitfall traps consisted of a glass test-tube (diameter of 1.8 cm) set into a fixed PVC pipe sleeve (Majer 1978) with a 50:50 mixture of 70% ethanol and propylene glycol to kill and preserve invertebrates. Traps were placed out on a 2 × 5 grid located at the centre of each transect, with traps placed

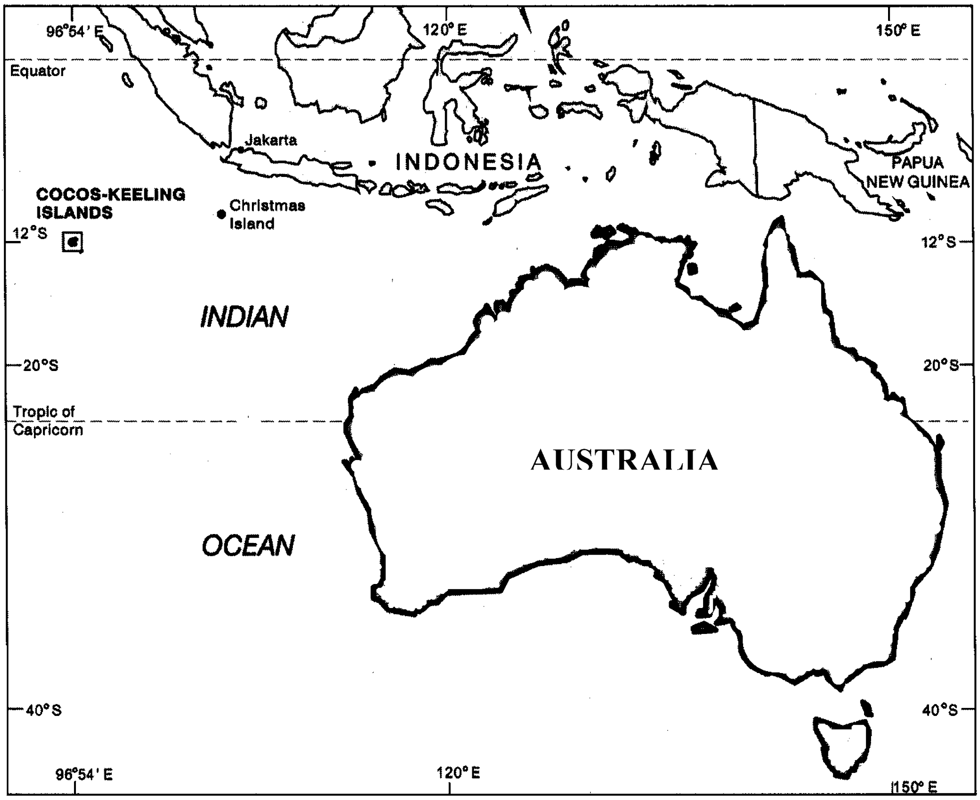

Fig. 1 Location of the Cocos (Keeling) Islands in relation to Australia and Indonesia (adapted from Parks Australia 2004)

5 m apart. Water traps were 12.5 × 20 × 7.5 cm plastic containers painted internally with yellow enamel. Three water traps were placed at each transect, 5 m beyond each end and one at the midpoint of each transect. Invertebrates from surrounding vegetation were collected by sweep netting (45 cm diameter opening). Four sweep samples were collected at each transect, two by walking the 30 m distance along each outer edge of the transect from one water trap to the other and two by walking 30 m at right angles to each transect.

Invertebrates were also hand-collected directly from vegetation and litter. Direct searching collected invertebrates from foliage, bark, and leaf litter for 30 min. Malaise traps were used primarily on Pulu Panjung and Pulu Keeling. Litter was also collected in 30 × 30 cm quadrats across a number of sites, sieved using a Rietter sieve, and then placed in Winkler sacks to extract the invertebrates into ethanol. Light traps, consisting of a white bucket supporting a fluorescent tube, were set out on Pulu Panjung, Selma, and Keeling at dusk and operated throughout the night. The first collection was destroyed by Yellow Crazy Ants (*Anoplolepis gracilipes*) so thereafter ethanol was added to the collection bucket.

Anoplolepis gracilipes—the Yellow Crazy Ant survey

A survey of the Yellow Crazy Ant on Pulu Keeling was targeted towards areas of the island with *Pisonia* or mixed *Pisonia* forest and parts of the island that had been reported to be invaded by the Yellow Crazy Ant, *Anoplolepis gracilipes* (Slip and Comport 2001). Ant surveys were based on existing transects used for seabird surveys, and comprised belt transect lines I, K, C, and P. In each contiguous 20 × 10 m quadrat along each transect, ant activity on the forest floor was determined in two ways. First, a bait station (using grape jam and a sardine piece) was placed in each quadrat and all ants at the bait were counted and identified after 30 min. Secondly, five 10 cm^2 laminated cards were placed in five haphazardly selected locations within each quadrat (Abbott 2005). Ant activity was estimated by counting the numbers of ants crossing each card over 30 s (0 = no ants, 1 = 1, 2 = 2–5, 3 = 6–10, 4 = 11–20, 5 = 21–50, 6 = 51–100, 7 = 101–200, and $8 \geq 200$). Arboreal ant foraging activity was assessed by estimating ant abundance (0 = no ants, 1 = 1–10, 2 = 11 = 50, 3 = 51–100, and $4 \geq 101$ ants) on each of five trunks of *P. grandis* in each quadrat.

Survey findings

A total of 21 ant species were identified across the atoll (Table 1). Species richness was higher where sampling was most intensive: 17 ant species were recorded from Pulu Panjung, 15 from Pulu Selma, and 12 from Pulu Tikus. Of the total species, 19 are introduced tramp ant species (Campbell

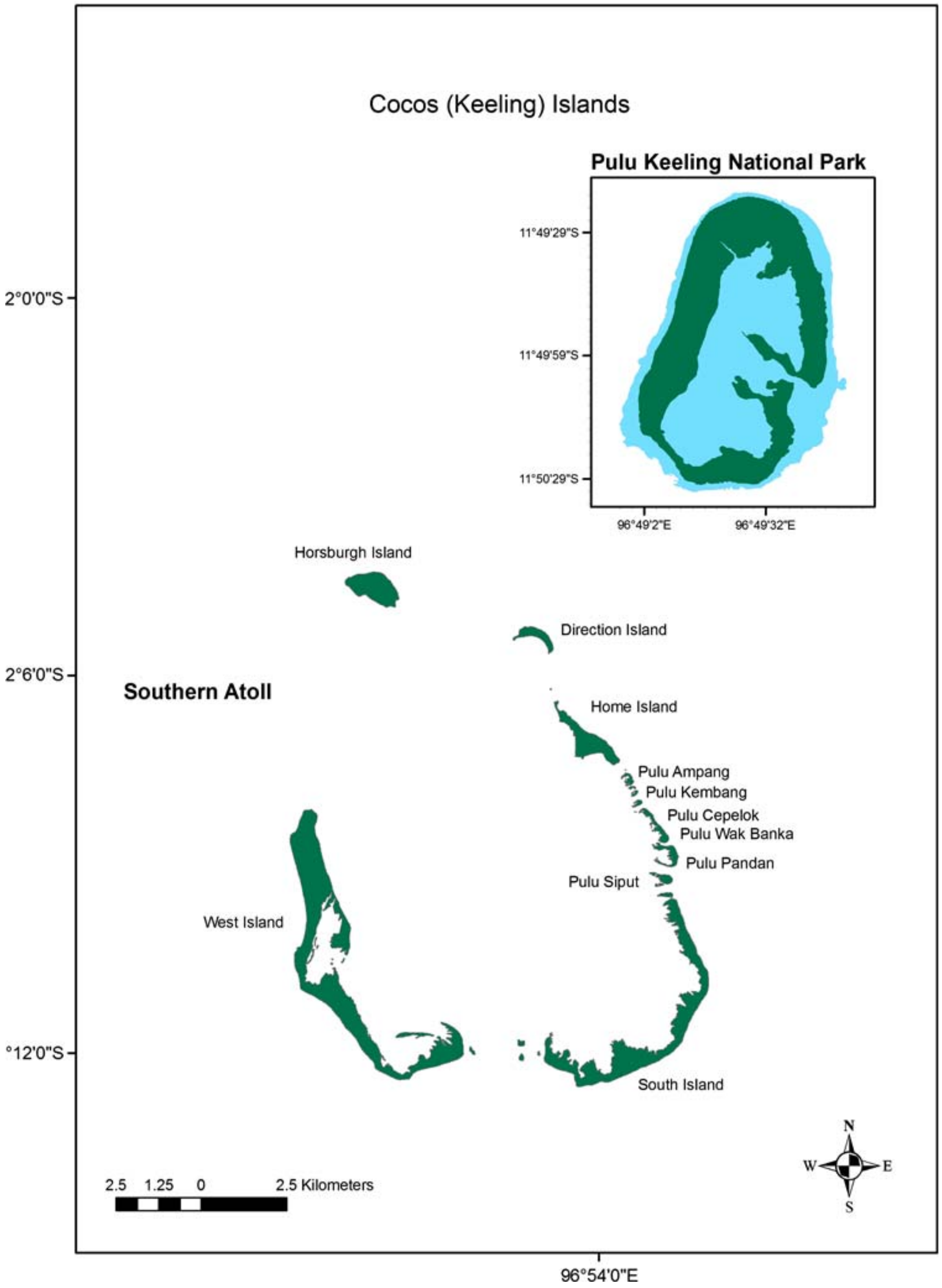

Fig. 2 The Cocos (Keeling) Islands (From Parks Australia 2008)

TG 1964, Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology, "unpublished"; A. Andersen, "personal communication"). The two remaining ant taxa, *Camponotus* sp. and *Pheidole* sp., require further taxonomic assessment to resolve their status.

Two groups of ants could not be identified to species level including the *Camponotus* and *Pheidole* groups. These two genera are difficult to resolve taxonomically due to the high species richness within the groups (Campbell TG 1964, Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology, "unpublished"). *Pheidole* has approximately 53 described species within Australia and 898 worldwide, while *Camponotus* has 128 described species in Australia and 1518 worldwide (Shattuck 2000) although the actual number of species within these two groups may be much higher than these reported figures. While currently identified as *Cardiocondyla nuda*, *Monomorium talpa* and *Platythrea wroughtonii*, these species are taxonomically confused and hence may actually be different species although would still be considered exotic (A. Andersen, personal communication). Recent taxonomic revision has also seen the genus *Quadrastruma* clumped within the genus *Strumigenys* (Andersen pers. comm.) further demonstrating the taxonomic complexities

Table 1 Relative abundance of ant species collected using all survey methods from four large islands in the southern atoll and on Pulu Keeling in the Cocos (Keeling) Islands

Ant species	Pulu Panjung (West Island)	Pulu Selma (Home Island)	Pulu Tikus (Direction Island)	Pulu Luar (Horsburgh Island)	Pulu Keeling (North Keeling Island)
Dolichoderinae					
Ochetellus glaber	0.001	0.038	0.000	0.000	0.000
Tapinoma melanocephalum	0.028	0.014	0.007	0.055	0.000
Technomyrmex albipes	0.016	0.091	0.065	0.087	0.132
Formicinae				0.000	0.000
Anoplolepis gracilipes	0.293	0.171	0.191	0.068	0.392
Camponotus sp.	0.114	0.070	0.079	0.011	0.000
Paratrechina bourbonica	0.138	0.105	0.144	0.093	0.014
P. longicornis	0.015	0.181	0.180	0.052	0.000
Myrmicinae				0.000	0.000
Cardiocondyla nuda	0.009	0.001	0.000	0.000	0.000
Monomorium latinode	0.028	0.002	0.023	0.036	0.101
M. talpa	–	0.002	0.000	0.000	0.000
Pheidole megacephala	–	0.001	0.000	0.000	0.000
P. sp.	0.053	0.025	0.131	0.164	0.277
Solenopsis geminata	0.001	0.000	0.000	0.000	0.000
Strumigenys 'emmae'	–	0.000	0.002	0.000	0.000
S. 'godeffroyi'	0.001	0.000	0.000	0.000	0.000
Tetramorium bicarinatum	0.103	0.083	0.171	0.415	0.024
T. lanuginosum	0.172	0.215	0.002	0.011	0.020
T. similimum	0.022	0.000	0.005	0.000	0.000
Ponerinae				0.000	0.000
Hypoponera sp.	0.001	0.000	0.000	0.000	0.000
Odontomachus simillimus	0.015	0.000	0.000	0.008	0.041
Platythyrea wroughtonii	0.000	0.001	0.000	0.000	0.000
No. of individuals	1156	1240	444	366	296
No. of species	17	15	12	11	8

All species, with the possible exceptions of *Camponotus* sp. and *Pheidole* sp., are known tramp ants

of scientific research. The use of published taxonomic keys can often lead to inaccurate taxonomic identifications as recent revisions are not followed.

Anoplolepis gracilipes—the Yellow Crazy Ant survey

One well-known invasive tramp species that has caused considerable damage to island communities is the Yellow Crazy Ant (*Anoplolepis gracilipes*) (Wetterer 2005). Its impacts have been documented on islands, including Christmas Island and the Seychelles in the Indian Ocean where it forms mutualisms with introduced honeydew-secreting scale insects (Kerriidae and Coccidae) that lead to large impacts on island biota (Haines et al. 1994; Hill et al. 2003; O'Dowd et al. 2003). On islands elsewhere, the Yellow Crazy Ant and other invasive ants, including *A. gracilipe*s, *Pheidole* and *Tetramorium* spp., have been implicated in dieback of *Pisonia grandis* (Hill et al. 2003; Krushelncky and Lester 2003; Smith et al. 2004; Kay et al. 2003; Handler et al. 2007).

The Yellow Crazy Ant was found on all surveyed islands and was even hand-collected from Prison Island (a total area of 0.02 km^2). Across the atoll, this ant forages on vegetation where it collects nectar from plants such as *Morinda citrifolia*, *Scaevola taccada* and *Argusia argentea*. On Pulu Keeling, *Anoplolepis gracilipes* was widespread along the survey transects, but activity as assessed by card counts was low, averaging <1 ant per 30 s^{-1}. However, activity indices of 6 to >200 ants 30 s^{-1} on cards in contiguous quadrats in two transects indicates that this ant is patchily abundant. Average activity counts were many times lower than those seen in supercolonies of the Yellow Crazy Ant in rainforest of Christmas Island (e.g. 13–135 ants 30 s^{-1}, Abbott 2005). Of special concern are the high activities along transects C and K, which run through one of the main infestations of Yellow Crazy Ants on Pulu Keeling (Slip and Comport 2001). Activity of the Yellow Crazy Ant on the boles of *P. grandis* was usually nil to low. However, in quadrats with high ant activity on the ground (i.e., along Transects C and K), the Yellow Crazy Ant was abundant on some boles of

P. grandis suggesting that the ant is using some resources in the *Pisonia* canopies. Nevertheless, we found no evidence of honeydew-secreting scale insects on leaves of these trees at any survey sites suggesting that associations with honeydew-secreting scale insects are not well developed.

Discussion

Ant survey

The ant fauna of the Cocos (Keeling) Atoll was found to contain 21 species of ants, 6 more than previously recorded. Ants previously not recorded by Slip and Comport (2001) include *Tapinoma melanocephalum*, *Quadrastruma* (=*Strumigenys*) *'emmae'*, *Strumigenys 'godeffroyi'* and *Platythyrea wroughtonii*. The other two species belonging to the genera *Camponotus* and *Pheidole* cannot be clearly determined due to taxonomic impediments. Some confusion also exists over ants placed within the genera *Monomorium* and *Paratrechina* where different nomenclature has been used when identifying the species. This highlights the importance of comparing specimens from previous studies with the current survey to ensure taxonomic impediments can be overcome and a true picture of the invertebrate fauna achieved. As one would expect, the highest species richness of ants was found on islands where intensive sampling of the fauna occurred, employing multiple trapping techniques. At this stage, the ant fauna of the less intensively sampled islands cannot be fully determined, and the absence of some species may be directly related to low sampling effort and few collection methods. Further survey of the ant fauna across the islands is required to fully document the presence/absence of the ant fauna. The one conclusion drawn from the 2005 survey was that no ant species collected to date appears to be native.

With each additional survey of the islands, higher richness of ants has been documented. Charles Darwin first reported ants on the Cocos atoll in 1836 (Darwin 1839). In the penultimate survey of ants on the atoll a total of 15 species were collected, 11 of which had not been previously reported from the islands (Slip and Comport 2001). Higher numbers of ant species were found in our survey. Interestingly, the greatest increase in the detection of ant species occurred on Pulu Panjung which increased from 8 species (Slip and Comport 2001) to 17 species during this survey. The richness of the ant fauna also increased from 10 species to 15 on Pulu Selma. Both Pulu Panjung and Selma support human settlements, with an international airport on the former and a seaport on the latter. The increased number of tramp species in our survey of these islands is probably a result of recent arrival and establishment through movement of cargo and passengers, although greater sampling effort on Pulu Panjung and Pulu Selma could contribute to greater species richness of ants. Sample effort was lower on other islands, but species richness was also higher than in previous surveys.

Three invasive alien ant species with well-known impacts, *Anoplolepis gracilipes*, *Pheidole megacephala*, and *Solenopsis geminata*, are present on the atoll. Two of these, *A. gracilipes* and *P. megacephala*, are listed by the Invasive Species Specialist Group of the IUCN as among 100 of the world's worst invaders (Lowe et al. 2004). The distributions of *P. megacephala* and *S. geminata* appeared restricted to single islands, but *A. gracilipes* is widespread across the atoll. *A. gracilipes* was at relatively low abundance on most islands, many times lower than those seen in supercolonies of rainforest on Christmas Island (Abbott 2005). However, counts were high in some patches of *Pisonia grandis* forest in Pulu Keeling National Park, reaching abundances seen in supercolonies on Christmas Island. This is an important conservation concern, since on other oceanic islands *A. gracilipes*, *P. megacephala*, and *Tetramorium* spp. are associated with large populations of scale insects, particularly *Pulvinaria urbicola*, that are implicated in canopy dieback of *Pisonia grandis* (Hill et al. 2003; Smith et al. 2004; Kay et al. 2003; Handler et al. 2007). If such outbreaks of scale insects should occur in *Pisonia* forest on Pulu Keeling this could degrade nesting sites for seabirds, including the Red-footed Booby, *Sula sula*. Furthermore, *A. gracilipes* is known to affect abundance, behaviours, and reproductive success of birds on Christmas Island and in the Seychelles (Feare 1999; Davis et al. in press).

These results show that tramp ant species are widely distributed across Pulu Keeling. An extensive survey is needed to fully document the spread of the tramp ant species and the potential impact they will have. Strict quarantine regulations should be enforced to limit further exotic species becoming established on the island. A survey of the scale insects will also help determine the potential impact of *A. gracilipes* and other invasive ants in the future and assess the potential for supercolonies to form across the islands.

Limitations to Island fauna analyses

The current composition of the invertebrate fauna of the Cocos (Keeling) Islands is a result of (1) the natural colonisation of the islands; (2) the history of human settlement and associated activities; (3) exotic invertebrate introductions; and (4) effects of exotic invertebrates on native species. Attempts to inventory the invertebrate fauna are hampered by (5) fragmented historical records and location of collections, (6) taxonomic issues, and (7) efficiency of surveys.

The composition of the invertebrate fauna on small islands is determined by (1) their degree of isolation; (2) modes of colonization; (3) geological time since islands were formed; (4) size of the islands; and (5) disturbances (both natural and anthropogenic). An important characteristic of oceanic islands are long periods of isolation (Gillespie and Roderick 2002). The biota will be dependent upon immigration, extinction, and speciation, and how these are disrupted by more recent historical factors (humans). At the same time, islands are under greater threat of losing native species because their small size and depauperate faunas mean they are more vulnerable to habitat change, introduced species, disease and climatic factors (Simberloff 2000).

Identifying tramp ants on oceanic islands has its difficulties, but they are a relatively well studied group, and there is considerable background information available to assess the ants of the Cocos (Keeling) Islands. However, the issue is more complex with the remaining terrestrial invertebrates, and similar difficulties arise when trying to determine which species are native to these islands. Information on the terrestrial invertebrates of the Cocos (Keeling) Islands is scattered in the scientific and grey literature, and this information is presented to reinforce the issues faced when surveying heavily disturbed islands.

Natural colonisation of the islands

Wood-Jones (1912) suggested that the natural modes of transport to the islands for invertebrates are either by air or water. The South East Trade Winds meant that predominant wind direction is east to south east for all months. Winds from the north, NE, SW, W and NW occur for less than 6% of the time (Falkland 1994), however these could be an important factor in the introduction of invertebrates from the closest landmasses to the north and north east (Wood-Jones 1912).

History of human settlement and associated activities

Human settlement resulted in habitat alteration and the import of building materials, soil for agriculture, plants for food and gardens, and exotic animals (either intentionally or unintentionally including pigs, goats, chickens, rats, mice, deer, rabbits, sheep, dogs, cats, and some birds (Gibson-Hill 1947). Material was imported for small scale agriculture to supplement fishing. Pulu Luar was inhabited in 1826 and established to grow fruit and vegetables for the inhabitants of the other islands (Gibson-Hill 1947). The lack of soil on the islands resulted in importation of soil from Mauritius, Singapore, and Christmas Island (Wood-Jones 1912; Gibson-Hill 1950c) possibly introducing many exotic species.

Exotic invertebrate introductions

Gibson-Hill (1950c) suggests that the insect fauna at the time of human settlement was limited, and the rapid increase in species richness was due to exotic incursions from trading ships and the establishment of fruit and vegetable plants. Wood-Jones (1912) speculates that many species of cockroaches, ants, scorpions, centipedes, spiders, crickets, beetles and moths were brought by humans. The list of taxa known to be cosmopolitan, transported across the tropics in ships, or associated with human habitation includes: spiders, centipedes, scorpions, cockroaches, land molluscs; buffalo and dog ticks, Heteroptera, dermestid beetles, the Copra beetle, and scenopinid and ceratopogonid flies (Wood-Jones 1909; 1912; Abbott 1950; Gibson-Hill 1950c, d; Murray and Marks 1984; Kelsey 1989). The lack of quarantine regulations has resulted in the introduction of many cosmopolitan tramp invertebrate species that have been transported by ships across the world. Bellis et al. (2004) suggest that the most probable mode of access to the Cocos (Keeling) Islands was arrival on or in plant material, although some species are commonly dispersed over long distances by wind, birds or bats.

There was an attempt to control the rhinoceros beetle, a pest of coconut palms, by introducing a predatory beetle, *Pachylister chinensis*, from Fiji (Anonymous 1964). This species was released on Pulu Tikus, Selma and Panjung, but apparently did not become established. The Commonwealth Scientific and Industrial Research Organisation (CSIRO) also introduced other parasites and predators to control the rhinoceros beetle during 1960–1961, but they also did not become established (Anonymous 1964).

An interesting dilemma involves taxa described from specimens collected on the Cocos (Keeling) Islands and whether they are endemic or more widespread. This includes *Nogodina bohemani* (Izzard 1959), *Nysius usingeri* (Izzard 1959) and *Dasyhelea intonsa* (Debenham 1987), while Holloway (1982) described a moth (*Luceria jowettorum*) and an endemic subspecies of moth (*Utetheisa pulchelloides darwini*) and Braby (2000) lists the endemic subspecies of lycaenid butterfly *Catopyrops ancyra exponens.* While Gibson-Hill (1950c) suggested that the majority or all of the Lepidoptera were introduced by man, Holloway (1982) believes that the fauna includes both natural colonisation by long distance dispersal and introduction by man. He based this on the lower proportion of pest species such as those found in the Geometridae.

It is likely that a significant proportion of the terrestrial invertebrates have been introduced to the Cocos (Keeling) Islands since human settlement. The modes of transport have been outlined earlier, but the most common methods are direct importation from ships, in imported items such as plants and food stuffs, and associated with domestic animals. Some domestic animals such as pigs and sheep are no longer maintained. Hence the loss of the pig louse collected by Campbell (1952) but not present in 1964 (Campbell TG 1964, Entomological survey of the Cocos (Keeling)

Islands. CSIRO Division of Entomology, “unpublished”). Gibson-Hill (1950c) collected four species of dung-eating scarab beetles, but Campbell (1964, Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology, “unpublished”) did not find any and suggested that the cessation of sheep grazing was the reason for their absence.

Effects of exotic invertebrates on native species

Exotic invertebrates can have devastating impacts on community structure and ecosystem function which appear to be magnified on small oceanic islands. O’Dowd et al. (2003) discussed the impact of the Yellow Crazy Ant (*Anoplolepis gracilipes*) on Christmas Island causing destruction of red land crab populations which led to habitat changes including seedling recruitment and litter accumulation. The association of Yellow Crazy Ants with honeydew-secreting scale insects amplifies and diversifies their impact on systems (Simberloff and Von Holle 1999; Richardson et al. 2000; Abbott and Green 2007). *Anoplolepis gracilipes* now dominates the Christmas Island ecosystem forming supercolonies of the highest density recorded to date (Abbott 2005). This introduced species has also led to the displacement of some ant species from infested zones (Abbott 2006), although abundance and species density of other ant species has increased following invasion by the Yellow Crazy Ant because removal of the land crab has resulted in litter build-up that provides suitable microhabitat for these additional ant species (DJ O’Dowd, “unpublished data”). The presence of Yellow Crazy Ants on all of the surveyed Cocos (Keeling) Islands indicates that this species is of concern to the diversity and conservation of the invertebrate fauna of the islands and their associated ecosystem functions.

Fragmented historical records and location of collections

Invertebrate records from the Cocos (Keeling) Islands are difficult to verify as in many cases, the current location of specimens is not known or they have been lost. Darwin (1839) collected 13 species of insects in 1836; of which some specimens are in the Natural History Museum in London (Smith 1987). Forbes collected insects from 18 January–9 February 1879, but his collection was lost on the return trip to Java (Forbes 1885).

The first major collection of the insects was by Wood-Jones (1909, 1912). He spent 15 months on the islands (June 1905–September 1906 on Pulu Tikus and January 1907 on Pulu Selma) collecting approximately 94 species. Gibson-Hill stayed from 20 December 1940—November 1941 and visited Pulu Keeling on 30 January and 7–8 July 1941. Gibson-Hill collected about 220 species and deposited most of his specimens at the Raffles Museum in Singapore in 1941, but acknowledges that some have been lost.

Campbell (1952; 1964, Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology, “unpublished”; 1966, Mosquito control—Cocos (Keeling) Islands. CSIRO Division of Entomology “unpublished”; 1966, Rhinoceros beetle (*Oryctes rhinoceros* L.) in the Cocos (Keeling) Islands. Dept. of Territories, “unpublished”) surveyed the atoll primarily for health and quarantine reasons when it was proposed to use the Cocos (Keeling) Islands as a possible stop-over when flying between Australia and South Africa. He collected between 23 May–21 June 1952 (collecting 1–2,000 specimens and approximately 145 or 154 insect species) and between the 8 November–1 December 1964 (collecting a further 2,000 insect specimens and some other invertebrates). This material is lodged in the Australian National Insect Collection (ANIC) in Canberra. Some of Campbell’s information was summarized in Anonymous (1964). Paton et al. (Paton R, Navaratnam SJ, Khair G 1981, Pest and disease survey, Cocos (Keeling) Islands, Department of Primary Industry, Canberra, “unpublished report”) surveyed the atoll when establishing a quarantine station on Pulu Panjung. In the insect study, eight species of soil nematodes and eight species of litter molluscs were listed. Bellis et al. (2004) conducted a survey for pests of field crops in May 2000 defining a pest as “an insect reported to feed on commercial plant species or products thereof or, in the case of ants, reported to cause environmental disruption or are pests of households.” They collected on Pulu Selma and Panjung and the material is lodged in the ANIC. They collected an additional seven pest species to those listed by Campbell (1964, Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology “unpublished”), mainly sap sucking insects (two species of aphids and four species of scale insects) as well as the Banana root weevil (*Cosmopolites sordidus*).

Taxonomic impediments

Examination of the previously cited references suggests that approximately 360 species of terrestrial invertebrates have been recorded from the Cocos (Keeling) Islands. This figure has to be considered with caution because (1) some species may have been recorded more than once under different species names; (2) taxonomic revisions may have seen the lumping of some species (the converse also applies); (3) many of the recorded species names cannot be checked because either specimens were not collected or collected specimens have been lost. Much of Gibson-Hill’s material was described in notes and publications (Gibson-

Hill 1950a, b, c), but much is thought to have been destroyed at the Raffles Museum during World War 2 (Williams 1990) although 12 specimens of his beetles have been located in the Natural History Museum (London).

Taxonomic impediments were found with the results presented with specimens currently identified as *Cardiocondyla nuda*, *Monomorium talpa* and *Platythyrea wroughtonii* to be taxonomically confused and hence may actually be different species (Andersen pers. com.). Taxonomic revision has also seen the genus *Quadrastruma* recently clumped within the genus *Strumigenys* (Andersen pers. comm.) further demonstrating the taxonomic complexities of scientific research. Basing species descriptions on past collections needs verification to ensure appropriate species names still apply.

Efficiency of the surveys

There is the question on how comprehensive the collecting efforts have been on the Cocos (Keeling) Islands. This is related to practical issues such as time spent on the islands, access (Pulu Keeling is difficult to access for example, even though Gibson-Hill spent nearly 12 months on the islands, he only had three days on Pulu Keeling), and the range of collecting techniques utilised. Since Darwin's initial collection, each additional collecting effort on the islands has added more species to the list. This is partly due to time (more time spent on collecting usually results in additional species being found), the use of different collecting techniques resulting in the collection of different groups, and recent exotic colonisations (whether natural or mediated by humans). The June 2005 survey collected 34 invertebrate orders, six of which had not been recorded previously (Neville et al. 2007). This either indicates that the islands have not been fully assessed in terms of documenting the invertebrate fauna, and/or introduction of new species are still occurring.

The transport of equipment to isolated oceanic islands is often difficult, restricting collection methods that can be employed for the assessment of invertebrate assemblages. Equipment needs to be prepared months in advance and delays in shipping and transport can hinder collections. Transport of dangerous substances must also be taken into account, often delaying the movement of goods. Access to remote islands is also problematic. During the 2005 survey of the Cocos (Keeling) Islands, transport to Pulu Keeling was delayed three times through unsuitable weather conditions. All collecting equipment had to be moved by hand on and offshore. Hence, timing with tides and weather conditions was vital for the collection of invertebrates from North Keeling. These delays meant a total of two days collection over the three week period, reducing the survey of invertebrates dramatically.

Conclusions: implications for future research

A survey of the terrestrial invertebrate fauna of selected islands of the Cocos (Keeling) atoll was undertaken during June 2005. The aim of the survey was to update information of the invertebrate fauna, to initiate an understanding of invertebrate monitoring principles and methods amongst Parks Australia staff working on the islands, and to provide some suggestions on future research and management needs associated with invertebrates.

Conserving invertebrates and restoring their habitats requires baseline information on the fauna. Cocos (Keeling) Islands are an example of a group of heavily disturbed small islands, although there is potential for some bench mark from Pulu Keeling. The development of management plans for Pulu Keeling, and possible restoration on the other islands, relies on quarantine and possible elimination of invasive species. However, historical records, including extant collections from the islands, need to be considered; unfortunately much of the historical information has been depleted, lost or has not been reported in a way that can be examined at a later date. This can be seen in the case of Gibson-Hill (1950a, b, c).

One of the more difficult aims of the 2005 survey was to identify which species were native and which were exotic and introduced since human habitation of the islands. The information available makes it difficult to provide any accurate estimates, although it can be stated that a large proportion of the invertebrates collected would be exotics.

The main problems faced by the 2005 survey team were the (1) lack of a baseline data on invertebrate assemblages; (2) the massive changes to the islands since human settlement; and (3) introduced invertebrates. These problems are compounded by (1) the isolated nature of the islands hindering frequent field trips; and (2) difficulty of access to Pulu Keeling, the remaining island with remnant native vegetation (Gibson-Hill 1948).

In order to conserve the native invertebrates of the Cocos (Keeling) Islands, several steps are recommended: (1) entry of exotic invertebrates be minimized by quarantine controls on imports; (2) invertebrate surveys over the whole year to assess temporal changes; (3) a more detailed study of invertebrates closely associated with native plants or with the bird colonies on Pulu Keeling; and (4) lodgement of specimens collected into a few designated depositories for ease of study.

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ORIGINAL PAPER

Conservation status and needs of butterflies (Lepidoptera) on the Torres Strait Islands

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Abstract The geographical affinities of the butterfly fauna of the islands of Torres Strait are outlined. The region forms a complex area of transition between New Guinea and Australia, and several taxa are not yet known from either adjacent mainland. Lack of published biological and distributional data renders it difficult to allocate any such taxon to a conservation status other than 'Data Deficient', but current threats related to human land uses and the likely sea level rises from future climate change emphasise the need for conservation planning. Complex systems of land tenure and difficulties of effective monitoring impinge on the establishment of effective reserves in the region.

Keywords Biogeography · Connectivity · Dispersal · Land bridge · Land tenure

Introduction

Torres Strait separates the island of New Guinea (comprising Papua New Guinea and the Indonesian province of Papua) from Australia. It developed between 8,000 and 10,000 years ago (Doutch 1972), but now forms a potential barrier spanning about 130 km between the nearest mainland points of Papua New Guinea (PNG) and the northernmost part of Australia, Cape York (Queensland) (Fig. 1). The region has received considerable attention from biologists, anthropologists and geographers, because of its spectrum of roles as 'Bridge and Barrier' to the biota of Australia and New Guinea (Walker 1972).

Torres Strait includes a large number of islands, with the archipelago forming a set of potential stepping stones from within about 5 km of PNG toward Australia, and either facilitating or impeding dispersal of organisms between the regions, in both directions. As Taylor (1972) summarised for insects, Torres Strait and Cape York is a 'region of interdigitation' between the two faunas. Taylor suggested that Torres Strait itself might be neither a significant barrier to insect dispersal, nor a major discontinuity between faunas, with the rainforest/savannah interface amongst the most important governors of faunal change.

Barriers to movement of terrestrial arthropods across Torres Strait include distance between islands, and between islands and mainlands, landforms (Jennings 1972), climatic gradients (Nix and Kalma 1972), vegetation types (Webb and Tracey 1972), plant associations (Taylor 1972) and land use. The main traditionally cultivated crops, bananas and yams (Beckett 1972), are well-known food plants for insects including butterflies (Common and Waterhouse 1981) that were believed to be used by butterflies for "island-hopping" across Torres Strait. A number of plant families and species are found on both mainlands (Australia and New Guinea), and many are shared only with those islands closest to the mainlands (Hoogland 1972). An important barrier to the dispersal of herbivorous insects across Torres Strait is therefore likely to be absence of food plants at their likely destinations.

Most of the islands have both English and more local names, as indicated in the legend to Fig. 1. They range in size from around 23-km diameter (Prince of Wales Island, or Muralug) to tiny coral atolls of less than a hectare in

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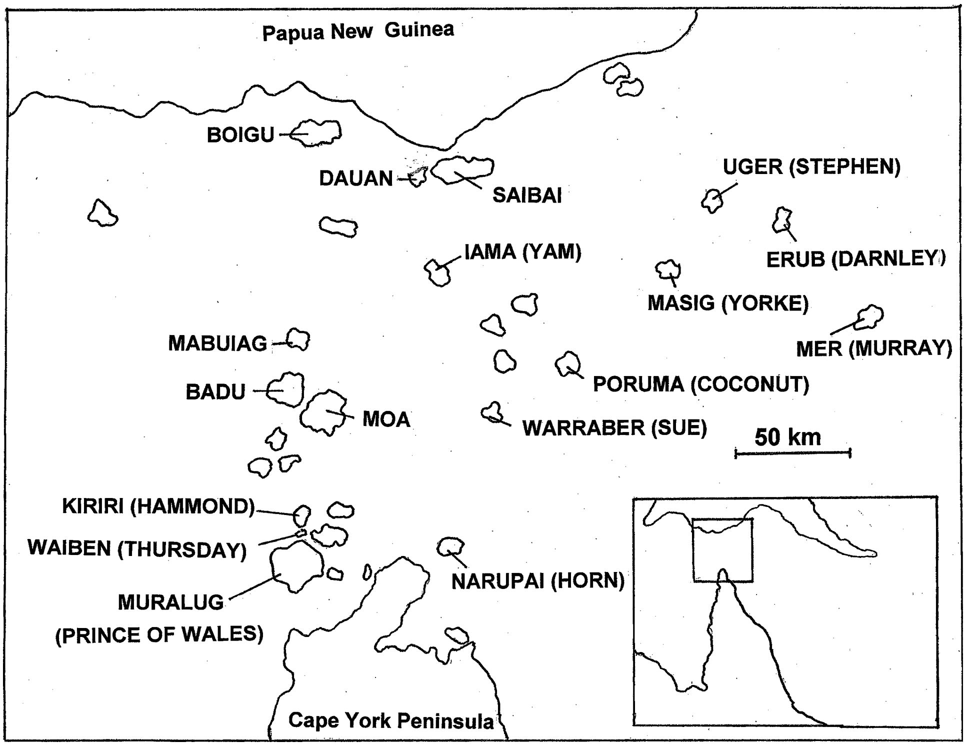

Fig. 1 Map of Torres Strait, showing main islands with names of selected islands

extent. Beckett (1972) recognised four categories of inhabited islands: (1) small but high volcanic islands covered in dense vegetation, all at the eastern end of the group; (2) small low sandbanks, raised on coral reefs and sparsely vegetated, most of them in the centre of the group; (3) large low-lying swampy and sparsely vegetated islands, with the category represented only by Saibai and Boigu; and (4) mainly larger high rocky islands, almost bare on the hills but lightly vegetated at lower levels: this category includes most of the western islands. The administrative centre for the islands, Thursday Island (Waiben), supports around half of the approximately 6,500 residents, with people living also on 16 of the more northerly islands. The geology and ecosystems of the southern islands are most similar to those of Cape York. The entire archipelago comprises several geographical groups based on the larger islands of each (Fig. 1): the western islands (Badu, Moa, Mabuiag), northwestern islands (Boigu, Dauan, Saibai), eastern islands (Ugar, Erub, Mer; these are Stephens, Darnley, and Murray, respectively), central islands (Masig, Poruma, Warraber, Iama; these are Yorke, Coconut, Sue and Yam, respectively), and southern islands (Thursday, Prince of Wales). The area is administered through the Torres Strait Treaty (signed December 1978), an agreement between Australia and PNG that defines the boundaries between the two countries. The major boundary is the 'Seabed Justification line' (Fig. 2) but 15 islands to the north of this line also 'belong' to Australia, each with territorial sea of three nautical miles from their coastline. A 'Protected Zone' encompasses much of the Strait, and allows Torres Strait Islanders and people of PNG to continue their traditional ways of life and helps to protect the biota of this complex region, without the need for passports to travel between the various islands. The treaty includes obligations on both parties to protect and preserve indigenous fauna and flora, specifically through (1) identification of endangered species; (2) protective measures; (3) prevention of introduction of harmful foreign species; (4) control of noxious species of fauna and flora and (5) exchange of information and consultation between the parties (Article 14, see Laffan 1991).

The importance of Torres Strait for butterfly conservation became apparent during our compilation of Australia's Action Plan for Butterflies (Sands and New 2002). A number of taxa reported could not be appraised reliably because of uncertainty over their status as vagrant or resident on particular islands, relevant in deciding whether they are in fact even Australian taxa. In this paper, we summarise the current difficulties of determining this status, and emphasise the importance of the islands as a faunistic link. This is likely to assume greater relevance for conservation in the future, when some of the low-lying islands are likely to succumb (or be reduced substantially in area) to sea level rises resulting from climate change. Recent attempts by Australian lepidopterists to document the butterfly fauna of the islands more fully have led to accumulation of considerable new information, under collecting authorisation from various island community

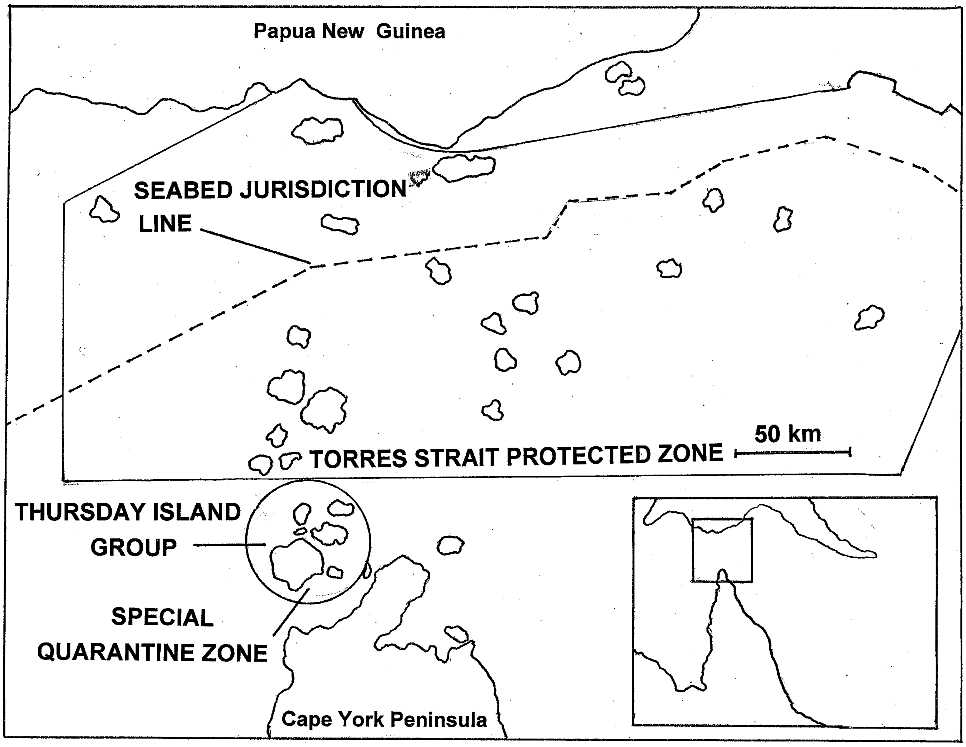

Fig. 2 Map of Torres Strait, with indication of some formal boundaries relevant to pursuing conservation. The solid line bounding much of the central area of the strait encloses the 'Protected Area', and the dashed line is the major boundary between Australia and New Guinea: see text. The area around the Thursday Island group is a Special Quarantine Zone

councils, and the status of some of the taxa necessarily treated as anomalous by Sands and New (2002) has become clearer. Of all insect groups, butterflies have received most attention worldwide but methods to determine their meaningful conservation status in Australia required appraisals different to the established methods used for other "animals" (Key 1978; Sands and New 2002). The summary given here will allow future information to be appraised more fully as an aid to detecting future movements of species, for example in response to climate change.

Butterfly monitoring in Torres Strait is important also for a different reason. Part of the practical importance of the islands for conservation has been the realisation that they are potential stepping-stones to facilitate the arrival in Australia of invading species from New Guinea. Some of these are important pests. Thus, the screwworm fly (*Chrysomyia bezziana* Villeneuve) is a potentially devastating pest of livestock in northern Australia and is well established in southern PNG. Fears that it could get to Australia either by its own volition, in smuggled livestock, or via open wounds on stock or people prompted substantial quarantine efforts across the Strait. More recently, one (of rather few) economically important pest butterflies (the banana skipper, *Erionota thrax* (L.)) has been the subject of biological control measures in PNG. It is suspected to have been introduced to New Guinea (Parsons 1998), and could have devastating effects on Australia's banana industry should it arrive. Waterhouse and Norris (1989) commented that the water gaps across Torres Strait are 'probably well within the flight range of adults', and any detection of this distinctive skipper in the region may trigger action to prevent its ingress, possibly with unplanned side-effects on non-target butterflies. Daru, Bristow and Marakara Islands in Torres Strait are the parts of Papua New Guinea, where fauna and flora are most similar to those occurring on the mainland immediately to the north. The banana skipper is well established on the PNG mainland at the edge of Torres Strait and on Daru Island, where there are moderate densities of bananas. Establishment of the butterfly on the Australian islands may have been prevented by low densities of the food plants and the movement of plants being regulated by Australian quarantine officials.

Butterflies of the Torres Strait Islands

In general, butterfly collecting in Torres Strait has been rather sporadic and uneven, with some islands receiving far more attention than others (Lambkin and Knight 1990), reflecting their ease of access, and 'promise' to hobbyists. Nevertheless, as at 2002, a total of 176 butterfly species or subspecies had been recorded from the islands (Table 1), with 41 taxa (including several subspecies of rather dubious status) not having been found elsewhere in Australia. Several other taxa have been reported since then (Table 2). Many of the taxa are amongst the resident fauna of tropical

Table 1 Butterflies (Numbers of 'taxa', i.e. species and subspecies) reported from Torres Strait Islands (TSI) by 2002 (summarised from Sands & New 2002)

Family/Subfamily	No. taxa	TSI only	Conservation significance	Northern Australia[a]	Widespread in Australia[b]
HESPERIIDAE					
Coeliadinae	4	0	0	2	2
Pyrginae	3	1	1	2	0
Trapezitinae	6	0	0	4	2
Hesperiinae	22	2	0	15	5
PAPILIONIDAE					
Papilioninae	13	5	0	4	4
PIERIDAE					
Coliadinae	7	1	0	1	5
Pierinae	10	2	1	3	5
NYMPHALIDAE					
Acraeinae	1	0	0	0	1
Amathusiinae	2	2	1	0	0
Argynninae	3	1	0	2	0
Charaxinae	3	1	1	1	1
Danainae	17	6	2	5	6
Libytheinae	1	0	0	1	0
Limenitinae	3	0	0	3	0
Nymphalinae	12	1	1	3	8
Satyrinae	9	2	1	4	3
Tellervinae	2	1	0	1	0
LYCAENIDAE					
Liphyrinae	1	1	1	0	0
Polyommatinae	37	11	10	11	15
Theclinae	20	4	5	14	2
Total	176	41	24	76	59

[a] Queensland, Northern Territory, Northern Western Australia

[b] More southerly states within range

northern Australia, and others known mostly from New Guinea. Table 1 includes 23 taxa listed by Sands and New (2002) as having conservation interest. All were then categorised as data deficient, reflecting lack of knowledge of their resident status in Torres Strait, and all but one of the more recently noted taxa (Table 2) share this ambiguity. The recent exception is the hesperiid *Cephrenes moseleyi* (Butler). This skipper has now been confirmed as a breeding resident on Dauan (Lambkin 2007). However, it is much less common than the related *C. trichopepla* (Lower), which breeds on coconut palm on almost all the inhabited islands.

Assessment of conservation status depends on sound taxonomy, and a problem in Torres Strait is that overlapping forms of some poorly understood butterfly taxa lead to ambiguities or uncertainties of species or subspecies recognition. Thus, our understanding of *Euploea* (Nymphalidae) remains incomplete, with a number of forms poorly documented. In a considerable advance in interpreting the validity of some members of this genus in the region, Lambkin and Knight (2007) showed that *E. leucostictos* (Gmelin) and *E. netscheri erana* (Fruhstorfer) are residents on some northern islands. Until then, *E. n. erana* had been known from a single male (Dauan: Johnson and Valentine 1997), and *E. leucostictos* from very few specimens. *E. leucostictos* is probably also restricted to Dauan, but there is suggestion that a resident population may also be present elsewhere on Murray (treated as the group of Mer and small nearby islands), with resident status inferred from the fresh condition of captured adult butterflies (Lambkin and Knight 2007). Perhaps the most intriguing aspect of *Euploea* in the Strait is the occurrence of a possible sympatric zone between the two putative subspecies of *E. tulliolus*, which may in reality represent species forming a hybrid zone between the PNG *E. t. dudgeonis* Grose-Smith and the Australian *E. t. tulliolus* (F.). Individuals of intermediate appearance occur on Daun and Yam (Fig. 3) (Lambkin and Knight 2007).

Dispersal and establishment from mainlands

Some Torres Strait butterfly taxa are sedentary and local. Others disperse readily, and are distributed more widely.

Table 2 New Guinea butterflies recorded since 2002 from Torres Strait Islands

Taxon	Island(s)	Resident	References
PAPILIONIDAE			
Graphium codrus medon	Dauan	Probable	Lambkin & Knight 2005
NYMPHALIDAE			
Cyrestis achates nedymnus	Dauan	Probable	Lambkin & Knight 2005
Euploea alcothoe misenus	Saibai, Dauan, Boigu, Darnley	Yes	Lambkin 2001, 2005
LYCAENIDAE			
Arrhopala philander gander[a]	Dauan, Saibai	Yes	Lambkin & Knight 2005 Meyer et al. 2005
Hypochrysops chrysargyrus	Saibai	?	Lambkin & Knight 2005
Cephrenes moseleyi	Dauan, Saibai	Yes	Lambkin & Knight 2004 Lambkin 2007

[a] Enumerated in Table 1, but then identified only as '*Arrhopala* sp.'

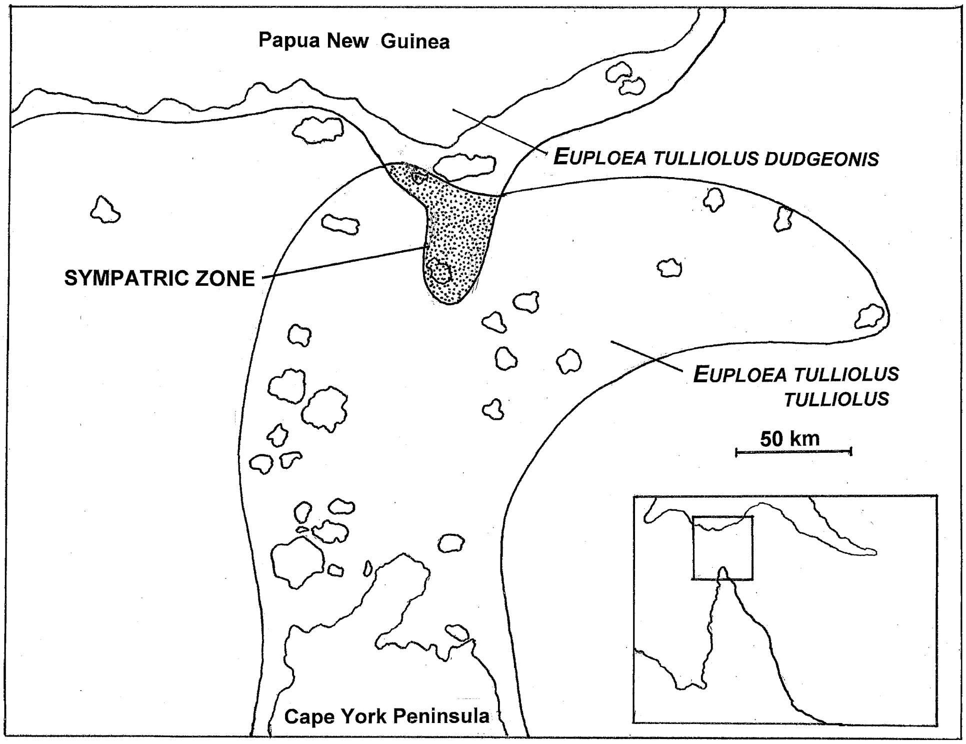

Fig. 3 The boundaries of two subspecies of *Euploea tulliolus* in Torres Strait: *E. t. dudgeonis* occurs in New Guinea, and *E. t. tulliolus* extends northward from Australia. They are sympatric in a small area (hatched). (Map based on Lambkin and Knight 2007)

These intrinsic differences may affect movement between islands or between islands and the mainlands, as well as the influence of local wind intensities and directions. The ability of butterflies to establish and subsequently maintain populations after immigration depends both on presence of suitable food plants and on climate at the receiving locality. In order to establish, an immigrant species must have sufficient founders and encounter habitats supporting adequate supplies of specific food plants, limited detrimental disturbance, and lack undue competition from other species or impacts by natural enemies. Several butterflies from Torres Strait indicate cases where establishment of species on islands may be temporary. For example, *Appias albina* (Boisduval) has always been considered "rare" in the Northern Territory (Australia) and the Torres Strait Islands. It may be an occasional migrant from PNG to Torres Strait islands and perhaps also to Cape York Peninsula, where it breeds intermittently. These predictions (unpublished) are based on observations of migratory behaviour in PNG where it is a common and widespread species (Parsons 1998).

Braby (2004) suggested that *Melanitis amabilis* Fruhstorfer (Nymphalidae) was 'probably extinct' on the Torres Strait islands (Darnley Island). The related *M. constantia* (Cramer) is known to persist on Murray Island. Both are uncommon species, although with seasonal apparency in

PNG. They have similar food plant requirements but *M. amabilis* is always crepuscular (Parsons 1998) and tends to occupy denser rainforest habitats than *M. constantia.* In consequence, it is less apparent. The former may be a temporary resident whereas *M. constantia* is firmly established on Murray Island. Similarly, *Taenaris catops* Fruhstorfer is probably a temporary resident on the Torres Strait islands, even though the food plants are widely distributed. In PNG *T. catops* is a rainforest-adapted species but is often seen many kilometres from shore travelling between islands (M. Sands pers. comm. 2007). The hesperiid *Tagiades nestus korela* Mabille has been confirmed to be resident on Dauan Island (Valentine and Johnson 2005). It is unlikely to be threatened, because its larval food plants, yams (Dioscoriaceae), are widely cultivated as vegetables. *Nacaduba pactolus cela* Waterhouse & Lyell was considered data deficient by Sands and New (2002). However, no threats have since been identified and caterpillars feed on buds and flowers of *Terminalia catappa* (Sands unpublished), which is widely distributed in gardens and behind beaches in PNG, sites generally free of disturbance.

The junctions between subspecies in Torres Strait may be quite abrupt or their ranges overlap. For example, the distributions of the typically Australian danaine subspecies, *Danaus affinis affinis* (F.) and the distinctive PNG subspecies, *D. a. gelanor* (Waterhouse & Lyell), overlap on the northern islands (Braby 2000). Similarly, *Euploea tulliolus tulliolus* and *Euploea tulliolus dudgeonis* appear to occupy the same islands (Lambkin and Knight 2007).

Taxa endemic to Torres Strait Islands

It is not surprising that the diversity of butterfly and food plant species increases with proximity to the two mainlands. Several butterfly taxa of Australian origin are restricted to the southern islands of Torres Strait while others of PNG origin are only known from Australian islands close to the PNG mainland. Several taxa in Torres Strait are morphologically intermediate between the Australian and PNG subspecies but have not been described formally as separate subspecies. Other populations, although distinctive, show a gradient of change in the species from one side of Torres Strait to the other. For example, the subspecies *Hypochrysops narcissus sabirius* (Fruhstorfer), from Cape York and the southern islands of Torres Strait, differs from the central island populations on Moa and Badu, while the populations from the northern islands more closely resemble *H. n. eratosthenes* from the PNG mainland. In *Hypochrysops polycletus*, individuals from Darnley Island differ from both subspecies *rovena* Druce from the Australian mainland and subspecies *rex* (Boisduval) from the PNG mainland (Sands 1986). The Murray Island population may better be considered an endemic subspecies with conservation values to be determined, because it is likely that no similar populations occur elsewhere in Torres Strait or on mainland Papua New Guinea. Similarly, specimens of *H. elgneri* from the northern Torres Strait are closest to subspecies *elgneri* (Waterhouse & Lyell) from PNG but they also have some characteristics of the Australian subspecies *barnardi* Waterhouse.

The recent geological and geographic history of the land bridge between the Australian mainland and Papua New Guinea (Walker 1972) helps to explain why very few taxa (Table 3) are endemic to the Torres Strait islands. Notwithstanding their youth, the islands support a range of taxa that are “intermediate” in their appearance when compared with mainland populations, or when compared with adjoining island populations. When significantly distinctive they may be recognised as subspecies, for example *Euploea alcathoe misenus* Miskin or as distinct species, for example, *Hypolycaena litoralis* Lambkin, Meyer, Brown and Weir, known only from Torres Strait islands. The specific distinction and identity of *H. litoralis* was made clearer by its sympatry with the closely-related *H. phorbas* (F.), known also from mainland Queensland and the remainder of theTorres Strait islands. It is possible that *H. litoralis* occurs on mainland New Guinea as well as Torres Strait, but *H. phorbas* and its subspecies require revision (see Parsons 1998) before the several subspecies occurring in Papua New Guinea and Papua, Indonesia are revised. The conservation status of *H. litoralis* remains Data Deficient until it is formally assessed for possible threats on Boigu, Dauan, Saibai and Yam Islands. However, due to its wide distribution on these islands it is unlikely to qualify as “threatened”.

Misidentifications have affected the predicted distributions for some species, especially *Euploea* spp. For example, a specimen of *E. modesta lugens* Butler from Thursday Island was shown by Meyer et al. (2004) to be *E. crameri crameri* Lucas, whereas *E. modesta lugens* was recorded from Murray Island only after the correct identifications had clarified their distributions.

Criteria for determining conservation status

Land use and tenure are always relevant when determining threatening processes for species of fauna and flora. Of the 274 islands in Torres Strait only two islands are formally protected for fauna, namely Round Island (as a Conservation Park) and Possession Island National Park. About 17 islands were occupied by people during early years of European contact and these would have undoubtedly been subjected to substantial changes in land use, including

Table 3 Butterfly taxa endemic and/or assessed as data deficient on Torres Strait Islands

Taxon	Island(s)	References
PAPILIONIDAE		
NYMPHALIDAE		
Euploea leucostictos	Dauan, Saibai, Murray	Lambkin and Knight 2007
E. netscheri erana	Dauan, Saibai, Murray	Lambkin and Knight 2007
E. modesta lugens	Murray	Sands and New 2002, Meyer et al. 2004
Melanitis constantia constantia	Murray	Johnson et al. 1994 Sands and New 2002
PIERIDAE		
Appias albina albina	Moa, Thursday, Prince of Wales	Braby 2000
LYCAENIDAE		
Hypochrysops polycletus ssp.[a]	Darnley	Sands 1986
H. narcissus ssp.	Moa, Badu	Sands 1986
Hypolycaena littoralis	Boigu, Dauan, Saibai	Lambkin et al. 2005
Nacaduba pactolus cela	Darnley, Murray	Johnson et al. 1994
Jamides nemophilus nemophilus	Darnley, Murray	Sands and New 2002
Nothodanus schaeffera caesius	Murray	Meyer et al. 2005
HESPERIIDAE		
Tagiades nestus korela	Darnley	Sands and New 2002 Valentine and Johnson 2005

[a] Referred to as *H. polycletus rex* by Waterhouse (1932)

clearing vegetation for villages, crop cultivation, and burning. It is not known if natural vegetation was deliberately set aside from disturbance, for protecting medicinal plants or for other purposes.

Fire is potentially a threatening process for local butterfly species on many of the Torres Strait islands when the insects are established in small areas with no refuges. The threat of fire would apply mostly to grassland and dry forest-adapted species but may also apply to rainforest when these areas are deliberately burnt during periods of dry weather. Uncontrolled use of fire and weed invasions were recognised by Sands and New (2002) as potentially major threatening processes for *M. constantia* on Murray Island, for example.

No butterflies putatively restricted to Torres Strait were considered threatened or lower risk by Sands and New (2002) but several were considered data deficient because of lack of information on biology and on likely tangible threats. Few species have since been considered of conservation concern despite many new records from Torres Strait. Conservation assessments for butterflies in Torres Strait will need to be based in part on determining threats and potentials for threat abatement for each taxon although, of course, some threats wrought by land use patterns and potential sea level changes transcend individual taxa. For many species or subspecies this assessment can only be done if the likelihood of sustained residency on an island is first understood. This assessment necessitates much fuller information than currently exists on the presence, stability, fluctuations and abundance of each food plant species as a prelude to appraising threat. Threats would be expected to differ somewhat according to intensity of human interference and land uses on each island, and their sustainability also reflect likelihood of sea level rises and inundation. Most islands with substantial butterfly faunas are relatively high, and will not be lost entirely, but the continued presence of critical resources for butterflies may not be assured. However, without this information, together with addressing other lacunae in ecological understanding of most of the taxa involved, many butterflies can only be retained as Data Deficient at present. For evolutionary clarification, each distinctive island population needs recognition as an important "link" between related taxa from neighbouring islands, or between islands and the mainlands, so that conservation status incorporates their roles as 'evolutionarily significant units', by which distinctive populations should be evaluated as if they were accorded formal taxonomic status. The significance of the basaltic communities dominated by PNG flora on the volcanic Murray, Darnley, Yam and Dauan, as well as their proximity to mainland PNG, cannot be underestimated when determining conservation values. Protection of representative plant communities is the most appropriate action to be taken by the Australian authorities, in collaboration with local residents. The status of 'Nature Refuges' is available under Queensland legislation for unique non-government-owned ecosystems, and this categorisation may be a valuable means to help protect sensitive areas on many of the Torres

Strait Islands. However, effective monitoring of both individual species and wider conservation values may be difficult. Unclear land tenure systems will need to be investigated carefully in order to facilitate this protection, together with assuring the goodwill of the local residents, so that both 'biological' and 'political' matters will be important components of any effective management plan for the area. Maintenance of anthropogenic mosaics of habitats on the islands may be critical to sustain some taxa.

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ORIGINAL PAPER

Climate variability, biological control and an insect pest outbreak on Australia's Coral Sea islets: lessons for invertebrate conservation

Penelope Greenslade

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Abstract Distant tropical coral sand islets in the Coral Sea have remained isolated from major human interference since their relatively recent inception. As a result they have highly impoverished faunas and floras consisting only of species capable of long distance dispersal. Despite this bias, they have established some degree of stability or equilibrium. In the 1990s, it became apparent that a scale insect, *Pulvinaria urbicola* Cockerell and at least one species of attendant ant, *Tetramorium bicarinatum* (Nylander) were undergoing a population explosion on two of these islets causing damage to *Pisonia grandis*, a tree important as a nesting site for sea birds. The same phenomenon as in the Coral Sea, (Coringa Herald group), was recorded about the same time in the Capricorn group of islets (Great Barrier Reef), on Palmyra Atoll and Samoa in the Pacific and in the Seychelles (Indian Ocean). Control measures, the application of systemic insecticides, poisoning of attendant ants and introduction of biological control agents were applied to some islands. Pest numbers subsequently fell, often within months, even where no control measures were applied, suggesting that the population decline was a natural phenomenon on some sites and not the result of recent invasions. It is suggested that climate variability is likely to be a contributing factor. Rising sea surface temperatures that reduce prey available to sea birds so causing a lower nitrogen input to soils during nesting activities, together with drier conditions, are likely to have put *Pisonia* trees under stress. Stressed trees mobilise nutrients making them more vulnerable to attack by herbivores. If climate variability is an indirect cause of the pest outbreak, it is important to carefully assess the benefits and disadvantages, both environmentally and economically, of any control measures, especially when biological control agents are concerned, the effects of which are irreversible.

Keywords *Pisonia grandis* · *Pulvinaria urbicollis* · Attendant ants · Sea surface temperatures · Biological control

Introduction

Australia's territories in the Coral Sea consist of three groups of coral sand islets, the Herald and the Magdelaine Cays and the Coringa Islets, collectively called the Coringa Herald Group (Fig. 1a,b). These islets are around 400 km due east of Cairns and are designated Class 1A reserves because of the large populations of sea birds and turtles that nest on them. The Commonwealth of Australia administer the islands and government staff, accompanied by biologists, make regular visits, at least twice a year, to monitor, among other variables, sea bird and turtle populations and any human activities. Nearly 20 species of sea birds nest in the Coringa Herald group, either on the ground or on low vegetation. On some of the larger islands, forests of the tree, *Pisonia grandis* R.Br., provide a nesting resource that is heavily used by the Black Noddy, *Anous minutus* Boi and by shearwaters, *Puffinus pacificus* (Gmelin), who excavate burrows beneath the trees.

Pisonia grandis has a widespread distribution in the Indian and Pacific Oceans but is only found on small, usually isolated, islands and where there is a large population of nesting sea birds. It is classified as an endangered species in Australia because only small stands (in total area 190 ha) occur in the country. Most populations occur on islands in

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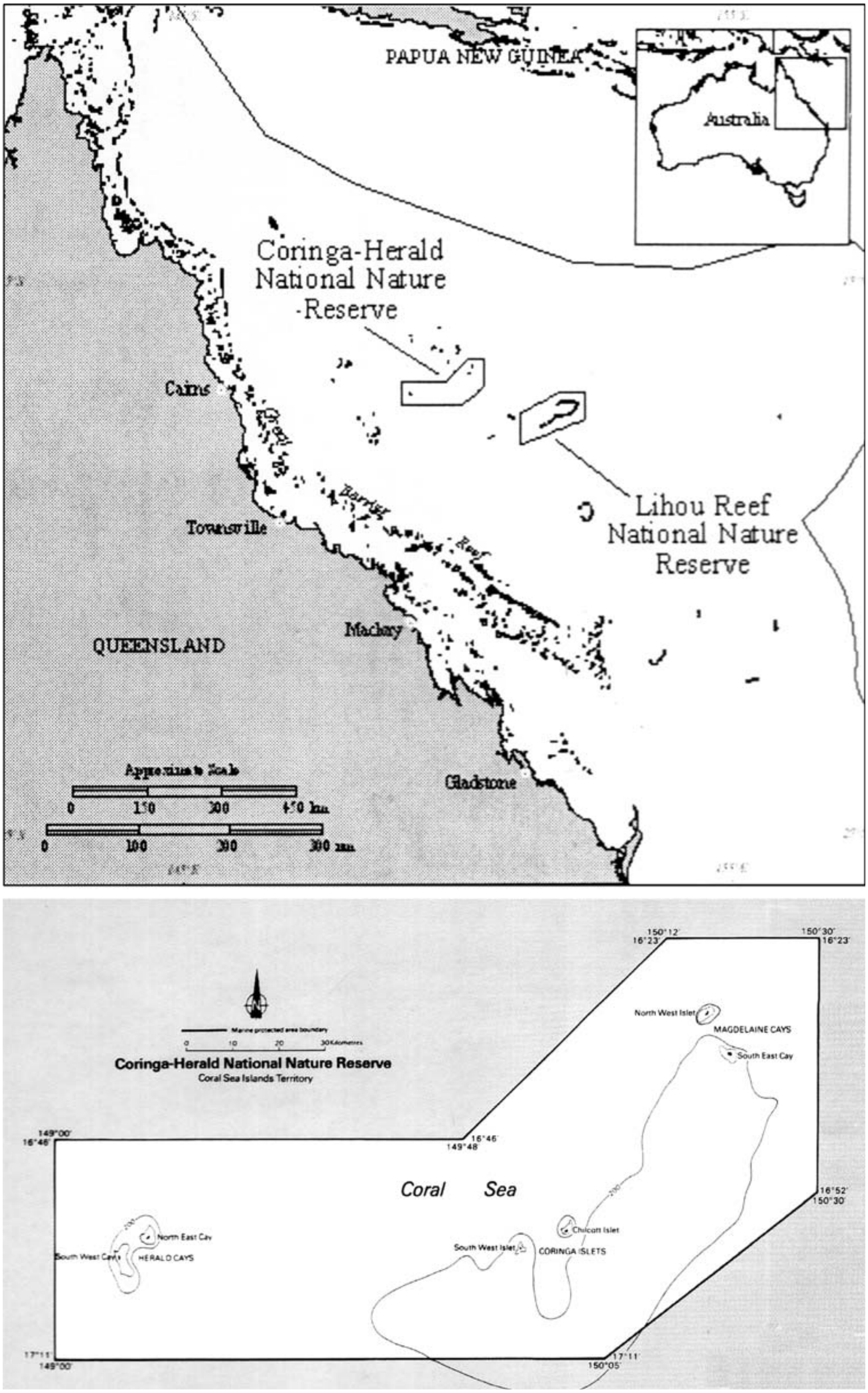

Fig. 1 (**a**) Location of Australia's Coral Sea territory; (**b**) islets of Australia's Coral Sea territory. Copyright Department of Environment and Water Resources, Canberra, Australia

the Coral Sea and Great Barrier Reef. The tree grows vegetatively. Seeds are highly adhesive and are spread by birds even over long distances, and there is only rare local recruitment by seedlings (Burger 2005). One reason why this species is limited in distribution is because it is dependant on a high input of nutrients from guano, provided during nesting activities by Noddies and other species. It has been calculated that, on average, over 100 gm of nitrogen m^{-2} yr^{-1} are deposited by birds on *Pisonia* forest soil (Chambers et al. 2005). Although the trees have adaptations

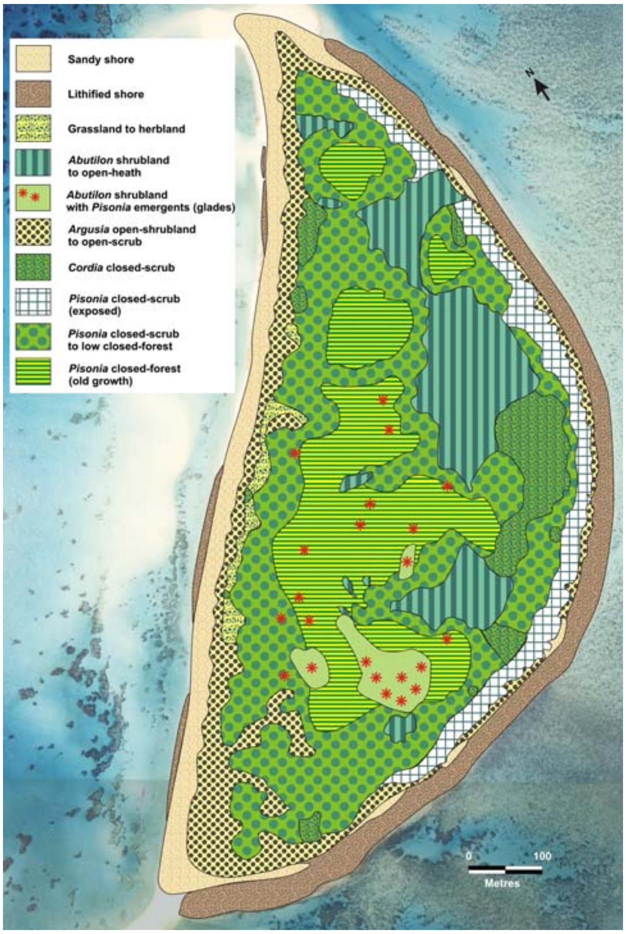

Fig. 2 Vegetation map of North East Herald showing distribution of *Pisonia* trees and invasion of low shrubland in gaps. From Batianoff et al. (2007). Copyright Department of Environment and Water Resources, Canberra, Australia

that allow them to tolerate some degree of desiccation by losing leaves and becoming dormant, it also appears that they are dependant on a lens of fresh water beneath the sand. Only islets with dimensions of about 60 m, such as North East Herald Cay (NEH), which is just over 500 m wide at the largest point, provide suitable conditions for a lens to develop (Fig. 2) (Batianoff et al. 2007). Eleven per cent of Australia's *Pisonia* trees now occur in the Coringa Herald group on NEH and Magdelaine Island.

The biological control programme

In 1991 (Coringa Islet) and later, in 2001 (NEH), it was noticed that defoliation, followed by dieback, of *Pisonia* was occurring in the group and it appeared to be due to an infestation of the coccoid scale insect, *Pulvinaria urbicola* Cockerell, a species native to the West Indies and exotic to Australia (Smith and Papacek 2001a). As the scale had not been observed before damaging trees, it was assumed that it had only recently invaded the islands and entomologists studying the problem suggested that the scale had been transported to the island by birds (Smith and Papacek 2001a). Further observations in 2001 confirmed that tree was extinct on Coringa, they were dying at a fairly rapid rate on NEH and that *Pulvinaria* numbers had increased 150 fold since 1997 on NEH. It was therefore decided to apply control measures for *Pulvinaria* in order to protect the tree habitat for nesting birds. The most effective, practical and economical method was considered to be the introduction of a biological control agent (BCA) as it had been noted that no parasitoids and only one, somewhat ineffective, coccinellid beetle were already present. Another Australian coccinellid beetle, *Cryptolaemus montrouzieri* Mulsant, had been widely used for control of pest scale in other regions (Waterhouse and Sands 2001) and was available commercially, so a programme to introduce the species to islands where *Pisonia* trees were under threat was instigated (Smith et al. 2001).

By 2001 when the decision was made to import *C. montrouzieri*, all but one *Pisonia* tree on Coringa, where there was a flourishing stand in the 1960s (Heatwole 1979; Heatwole et al. 1981), had already died and the only other island affected at that time was NEH. This island is considered to have developed from a coral reef about 6,000 years ago. A range of vegetation types occur on it; grassland, herbland, shrubs and *Pisonia* forest (Fig. 2). The forest occupies 27 ha or about a quarter of the island's area (Batianoff et al. 2007). NEH has never been permanently inhabited and is little visited. Indigenous people do not seem to have utilised the island nor are there any harvestable guano deposits on it. Tourists are rare. *Cryptolaemus montrouzieri* was introduced to the island in late 2001. Scale numbers have been monitored regularly since 2001 along eleven transects across the island by counting pest numbers on leaves. Twelve months after the introduction of the coccinellid beetle, numbers of scale had dropped to less than half the original level (Freebairn 2007) (Fig. 3). There was a slight increase in 2004 but again numbers fell and scale was virtually undetectable from late 2004 to mid 2006 and numbers were still low in 2007 (Freebairn 2007). *Cryptolaemus* was present throughout this time in what was assumed to be a self-sustaining population but several thousand individuals were still being released twice a year. The programme was consequently deemed to be a success (Smith et al. 2004).

Constraints

An examination of old records showed that *Pulvinaria* was likely to have been on Coral Sea Islands for at least 20 or so years and was probably not a very recent invasion (Greenslade 2007). A record from Cato Island in

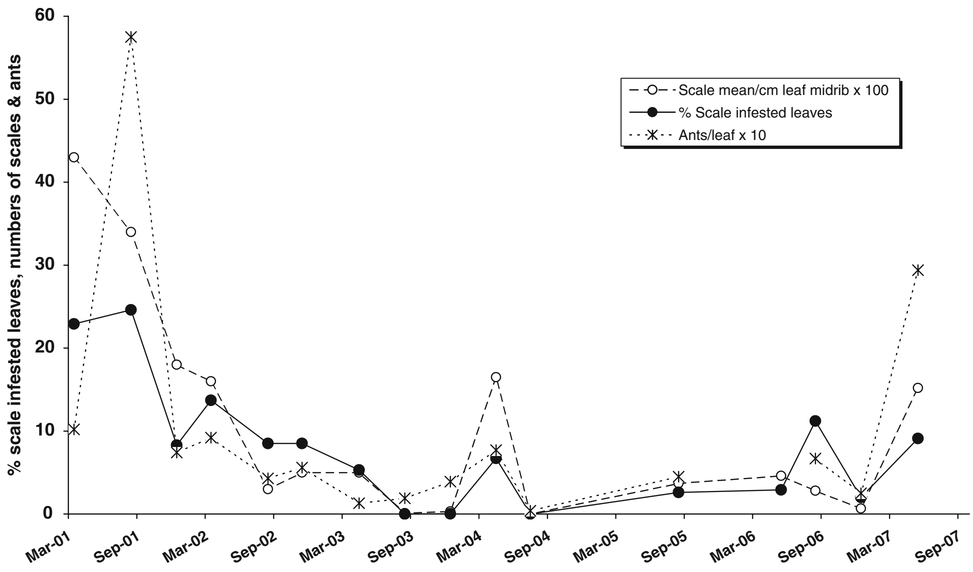

Fig. 3 Numbers of *Pulvinaria urbicola* and *Tetramorium bicarinatum* on *Pisonia grandis* recorded on North East Herald from 2001 to 2007 from Freebairn (2007). Copyright Department of Environment and Water Resources, Canberra, Australia

November 1982 (Hill 1982) was identified by P. Gullan as *Pulvinaria* sp. and likely to be *P. urbicola* as no other species of the genus is known from neighbouring regions. Recently, Queensland Parks and Wildlife Service (2007) also considered the species to have been present in the Capricorn group for many years. As crawlers (immatures) of the scale are readily dispersed long distances on wind currents, even up to 1,000 km away (L. Cook, pers. comm.), it was likely that the scale probably occurred on many Coral Sea and Capricorn group islands from at least the 1980s onwards, albeit in low, possibly undetectable, numbers. Native predators or parasitoids controlling populations were noted on some islands in the Capricorn group but at least on Tryon Island they did not appear to be controlling scale populations. Unknown biotic or abiotic factors must have been maintaining low numbers earlier. *Pulvinaria urbicola* is common in Queensland where it has a wide host range including a number of plants common and widespread in the region (Smith and Papacek 2001a). The population explosion in the Coral Sea only seems to have occurred in the mid 1990s and the species only became conspicuous because of the damage it was causing to *Pisonia* forests. Taking this evidence into account, it therefore appears that the pest problem was not due to a recent invasion but a population explosion of a species that was already present in low numbers. There must therefore be an alternative explanation for the apparently sudden increase in scale population.

A complicating factor was that the scale was heavily attended by the ant, *Tetramorium bicarinatum* (Nylander), another species considered exotic to Australia with a native range restricted to South East Asia (Shattuck and Barnett 2001). A species of *Tetramorium*, probably this species but identified as *T. simullimum*, was first collected on NEH 40 years ago (Heatwole 1979). Numbers of this ant on NEH in May 2007 were so high on the ground, in dead timber and on trees and shrubs, that abundance of other invertebrates was suppressed in places where the ant was active (Greenslade and Farrow 2007). Even as late as 1997, ant numbers were quite low. A comparison of pitfall and catches from NEH in 1997 and 2007 suggests that ant numbers have increased nearly 100 fold over the last 10 years. In 1997, pitfalls caught an average of 7.2 ants per trap over one day while in 2007, numbers were in some places several hundred per trap day (P. Greenslade, unpublished results). Although *T. bicarinatum*, considered a pantropical tramp species, occurs on mainland Australia, it is not known to be invasive there as it appears to be a poor competitor (B. Heterick, pers. comm.). However, on NEH in 2007, it was observed that there were no competitive species and no specialised predators of ants, such as reptiles, present (Greenslade and Farrow 2007). Once monitoring began in 2001, it became clear that the populations of both scale and ant increased and decreased in tandem (Fig. 3) and the same factor that caused an increase in scale numbers was indirectly also affecting ant numbers.

As noted above, *P. grandis* is not restricted to Australia and it occurs widely in the Indian and Pacific Oceans. It now appears that trees on such widely separated islands such as Bird Island in the Seychelles (Hill et al. 2003), the Palmyra Cay south of the Hawaiian Islands (Handler et al. 2007), an island in the Samoa group as well as three islands in the Capricorn group of Australia, Tryon, Heron and Wilson (Olds et al. 1996; Queensland Parks and Wildlife Service 2007), were also dying from damage caused by the same scale at various times over a 12 year period (Table 1). Moreover, several tramp ant species, but always including *T. bicarinatum*, were found to be attending the

Table 1 Islands suffering population explosion of *Pulvinaria* scale and their parameters

Island	Date scale population explosion	Size	Latitude	Area of *Pisonia* forest
Tryon	Aug 1993	2.5 km × 1.5 km	23°15′	None (1993 onwards)
Chilcott	1997	163 km^2	17°00′ S	None (2001 onwards)
North East Herald	1997	0.34 km^2 5 m	17°01′	25–27 ha (2007)
Bird, Seychelles	2006	0.6 km × 1.4 km 101 ha 5 m alt	3°53′ S	2,000 trees (2006)
Palmyra	2002–2005	<5 km^2 2 m alt	5°53′.6″ N	27.3 ha (2002), 18.2 ha (2005)
Samoa			13°35′	?
Wilson	2006	1 km × 1.5 km	23°18′	2.4 ha
Heron	2006	0.9 km × 0.3 km	23°26′	?dominant

scale in large numbers. Different control measures had been applied on some of these islands, systemic insecticides in the Palmyra group (W. Smith pers. comm.) and *C. montrouzieri* and ant baiting in the Capricornia group (J. Olds, pers. comm.). On some islands, no control measures had been applied but on all for which there are records, including those in the Palmyra group (W. Smith, pers. comm.), numbers of scale later fell, except on Coringa and Tryon, regardless of what control measure had been applied. This suggests that the reduction in numbers of the scale on NEH might not have been solely due to predation by *Cryptolaemus*.

Possible causes of the outbreak

Because the affected islands are at widely separated longitudes, of different sizes and subject to different abiotic and biotic influences, it is possible that the same phenomena, operating widely at low latitudes in Pacific and Indian Oceans, caused the pest population explosion. The most likely cause is climate variability. Aspects of climate variability that could be influential are rising sea surface temperatures, increased frequency and depth of El Nino events during the last 15 or so years as suggested by Donaldson (1994) and/or increasing drought as shown in the Palmer Drought Severity Index (Lough 2007). Donaldson (1994) also suggested that erosion of fringing, protective *Argusia* shrubs from a fungus disease as well as cyclone damage, causing gaps in the forest cover, could also be considerations. However, it is not clear whether the fungus has invaded before or after death of *Argusia*. On the other hand, cyclone damage was recorded on NEH in the early 1990s and it also affected the *Pisonia* forest on Coringa prior to the pest explosion (M. Hallam pers. comm.) and so may have been, with other variations in climate, a contributing factor. Although a contributing cause for the population explosion is likely to be climate variability, the mechanism through which climate could be operating to cause the widespread pest outbreaks is not immediately obvious.

The closest weather station to NEH is on Willis Island. Meteorological records have been made on the island since 1921 and show a series of drier than average rainfall years from 1991 to 1995 (Fig. 4) followed by five wetter than average years from 1996 to 2000. Rainfall is strongly seasonal in the region with most rain falling in summer (January to March) and much less rain in winter and spring (May to November) (Fig. 5). Stress from lack of water is therefore most likely in the seven months centred on winter. It is significant that the years of lowest rainfall since 1922 in winter on Willis were 2004 for July and August and 2003 for September (BOM 2007). In addition, nine of the wettest months ever recorded on Willis were 1955 or earlier, indicating a trend to drier conditions over a fairly long period in the region.

As regards the availability of subterranean freshwater, no measurements have been made on NEH, but the death of trees at the edges of the groves, at sites most likely to experience drought stress rather than in the centre, would indicate a possible reduction in this lens. Notably Smith and Papacek (2001a,b) recorded trees on the northern fringes of the forest were the first to die (Batianoff et al. 2007) although an earlier record suggests that the infestation began in the southern end (M. Hallam, pers. comm.)

Climate variability and sea birds

Congdon et al. (2007) studied Noddies on Michaelmas Cay and showed a negative relation between the El Nino index and numbers of breeding pairs (Fig. 6). These authors also demonstrated a negative relationship between sea surface

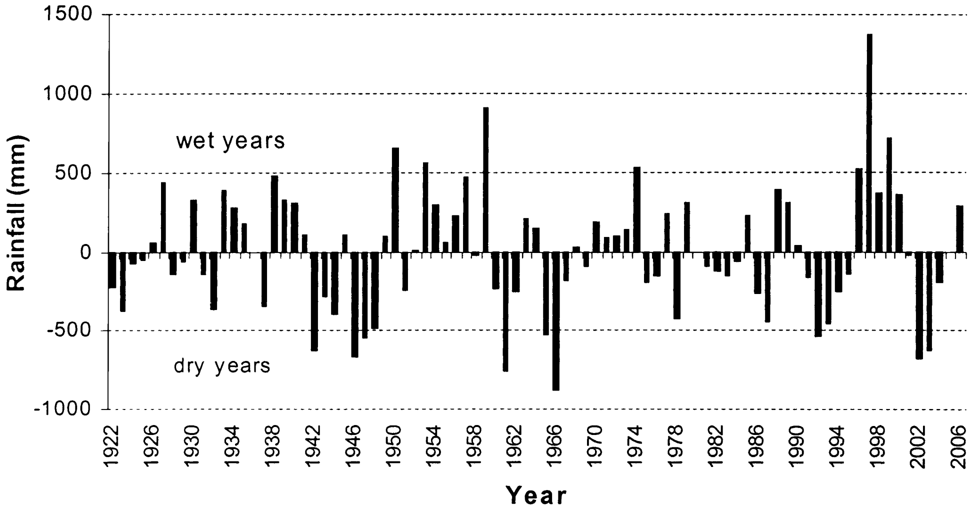

Fig. 4 Annual rainfall on Willis Island from 1922 to 2006. From Bureau of Meteorology, 2007

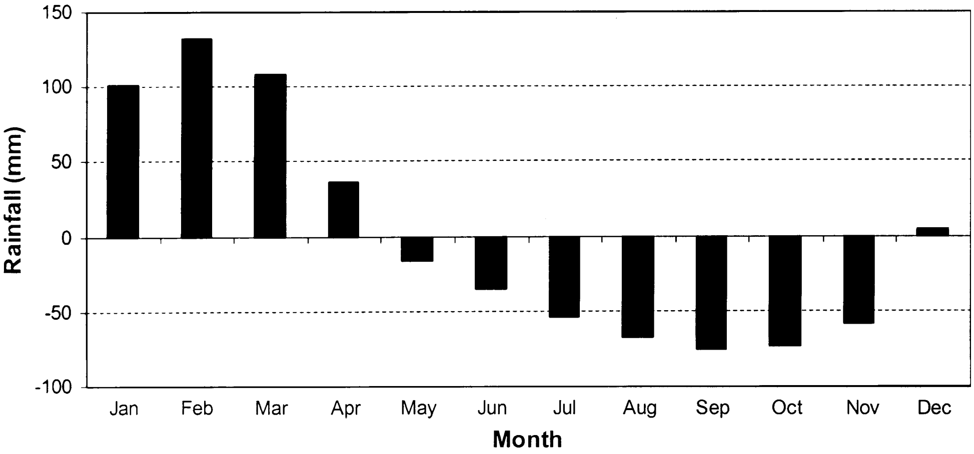

Fig. 5 Distribution of rainfall by month on Willis Island. From Bureau of Meteorology, 2007

temperatures at Heron Island and feeding frequency, meal mass and chick mass in 2005. Related data (Batianoff and Cornelius 2005) recorded reductions of over 95% in nesting populations of Common Noddy on Raine Island (Great Barrier Reef) over the last 24 years and Baker (unpublished results quoted in Congdon et al. 2007) showed that there had been significant gradual declines, equivalent to possibly more than six to seven per cent per annum, in populations of Black Noddies on NEH since 1992 (Fig. 7). A change in diet was suggested as the cause on Raine Island (Batianoff and Cornelius 2005).

Although sea surface temperatures have not been measured at Willis Island, it is known, from hindcast modeling, that they have been rising steadily in the Great Barrier Reef over the last 250 years (Fig. 8). Congdon et al. (2007) suggest that the significant change in numbers of Noddies on Michaelmas Cay appears to be related to population crashes at the time of the exceptionally long 1997 to 1998 El Nino event (Fig. 8). During El Nino, associated higher sea surface temperatures in the western Pacific reduce nutrient upwelling from below, lowering populations of plankton so leading to reductions in food availability for hatchlings (Congdon et al. 2007). When El Nino conditions last for many months, as they did in the protracted event of the 1990s, more extensive ocean warming occurs. This is concurrent with the time the first pest outbreaks were noted on Australia's Coral Sea Islands and Capricorn group. Given that climate variability over the whole Indian and Pacific Oceans is not uniform and that biotic and abiotic differ between the islands are considerable, it is not surprising that the pest outbreaks that have been recorded occurring on islands in the different regions are over a longer period (Table 1).

Consequences

The resulting two major stresses on *Pisonia* trees, that is reduced fertiliser from birds together with water stress, particularly in winter, are likely to result in a mobilisation of nutrients within the tree so making it more attractive to herbivorous insects. A self-perpetuating cascade effect

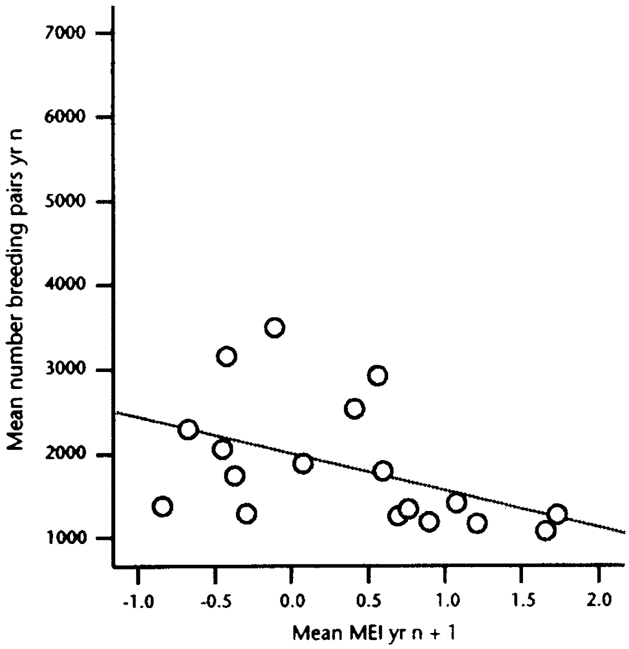

Fig. 6 Significant negative relationships between mean annual multivariate El Niño Index (MEI) in year $n + 1$ and mean annual numbers of breeding pairs of common noddies breeding at Michaelmas Cay in year n39 (reproduced with permission from Congdon et al. 2007)

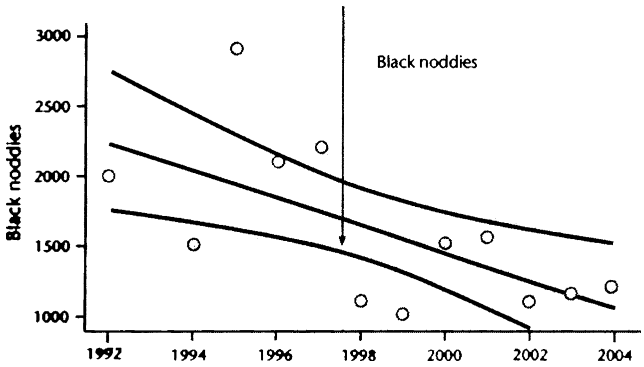

Fig. 7 Decline in numbers of Black Noddy populations at North East Herald Cay in the Coral Sea Marine Protected Area between 1992 and 2004 (Baker et al. unpublished data) after Congdon et al. (2007). Vertical line indicates timing of the 1998 El Nino event (reproduced with permission from Congdon et al. 2007)

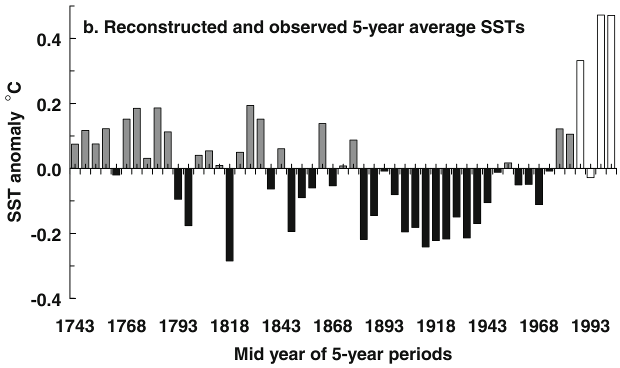

Fig. 8 Reconstructed (1741 to 1985) and observed (1985 to 2005) average 5-year sea surface temperature anomalies (from long-term average) for the GBR. This coral series ends in 1985. Observed warming (1977 to 2006) minus (1871 to 1900) summer (grey) and winter (black) sea surface temperatures in the north, central and southern GBR. All differences significant at the 5 percent level. Greatest warming observed in winter (reproduced with permission from Lough 2007)

could then have developed with the increase in scale accompanied by an increase in attendant ant populations and parallel reduction in other surface living invertebrates because of predation by ants. This seems to have occurred, where records are available, whether scale parasitoids and/or predators were present or absent. A similar cascade event caused by climate change has been described for another terrestrial ecosystem (Eveleigh et al. 2007) and also for a marine environment (Lenihan et al. 2001). Given this possible scenario, the lower number of Noddies nesting on NEH in the last 10 years is not due to the declining viability of the *Pisonia* forest but rather the reverse, that is the lower number of Noddies has indirectly caused the pest outbreak and subsequent tree decline.

Risks of biological control agents

There is ample evidence of the benefit of introducing BCAs to control pests but there are also many examples of where they have had unpredicted and damaging effects (Kuris 2003 and included references). In particular, the introduction of non-specific predatory arthropods, such as *C. montrouzieri*, has been criticized in the literature recently by Snyder and Evans (2006) and Handler (2007) because of the considerable potential for adverse effects. Specifically, Snyder and Evans (2006) recommended that intentional introductions of such BCAs as coccinellids be discontinued because of their unpredictable effects on non-target organisms.

It is normal that such introductions to Australia from overseas to be preceded by a rigorous risk assessment that includes testing on a range of non-target organisms that they are likely to encounter and those which are related to the target species but no account is made of the potential and real risk of host shifts. Introductions within the Australian territory are free of such requirements. Such applications are subject to review by environmental but not by quarantine agencies. Moreover, intentional introductions of BCAs to small islands in fragile equilibrium with small, disharmonic faunas, run a risk of having a greater impact than in larger, more diverse areas (Howarth and Ramsay 1991). This is because the high numbers of an alien species released at one time have the potential to impact more drastically on the existing *status quo* as there are so few species present to provide ecosystem resilience.

Parasitoid biological control agents

In August and December 2001, three wasp parasitoids, *Coccophagus ceroplastae* (Howard) and *Euryschomyia flavithorax* Girault and Dodd and *Metaphycus* sp. were introduced to NEH (Smith and Papacek 2001b) to contribute to the control of *Pulvinaria*. The latter two species were confirmed as established shortly afterwards and the first one at a later date (Smith and Papacek 2002). As these parasitoids are specific for scale, and there are no other susceptible species on NEH except for *Pulvinaria* and a mealy bug, *Ferrisia malvastra* (McDaniel), these introductions appear to be benign although whether they have had any effect in reducing populations of *Pulvinaria* has not been assessed. It should be noted that although adverse effects on the ecosystem have not been detected, this does not equate to proof of total absence of impact.

Smith and Papacek (2002) also mooted the introduction of hymenopterous parasitoids to control several species of migratory defoliating moths (Sphingidae) that were causing severe defoliation of a number of plants including *Cordia subcordata* Lam. as well as *Pisonia*. Accordingly, *Trichogramma pretosum pretiosum* Riley and *Trichogramma carverae* Oatman & Pinto, were released in 2002. These authors also recommended using viruses and *Bacillus thuringiensis* Berlinger (Smith et al. 2004, Smith and Papacek 2002, 2004). Both wasps are fairly unspecific and will parasitise moths belonging to a range of families. There are probably up to fifty species of native moths on NEH (Donaldson 1994) that could be affected by the parasitoids. Further introductions of these parasitoids are inadvisable because large populations of some of these defoliating moths periodically invade from the mainland under specific weather conditions (Farrow 1984) and parasitoids will not be able to control these high populations over the single generation that they remain on the island. More serious is their effect on other susceptible and benign moths native to the island.

The replanting of *Pisonia* seedlings on islands from which it has been recently lost, which has been suggested and was attempted on Coringa but failed, is also not advisable as it is unlikely to succeed without protection from pest damage, without establishing that sufficient manuring with occur from visiting birds and especially if water tables have changed.

The way forward

Firstly, the effect on non-target organisms from all BCAs on these islands, not considered previously, should now be assessed in detail as the data so far available is based on one brief visit of three days to NEH. On this island, the only other species providing prey for the beetle appears to be the mealy bug, *F. malvastra* (Greenslade and Farrow 2007). Populations of this species do not appear to be impacted to any extent and the mealy bug is allowing the coccinellid to survive when populations of the scale are low, but further work needs to be done here.

The native invertebrate fauna of all the Coral Sea Islets is little known at species level. On NEH, data collected on a brief visit in 2007 suggests that it probably consists of just over 100 species with Coleoptera, Hemiptera, Acari and Collembola being the most speciose groups (Greenslade 2007; Greenslade and Farrow 2007). Even with our current limited knowledge, the fauna seems to largely consist of widespread species with no endemics, and so is of low conservation significance although the maintenance of ecosystem integrity is of high importance because of the dependence of sea birds on it. Although the total effect of any BCA on the native fauna cannot be assessed at present, it is likely that some effect on ecosystem stability and function will result from these introductions. Clearly the effect of more than one BCA combined is likely to be greater than each one individually.

Secondly, the evidence is strong that *Cryptolaemus* does appear to be preventing the complete annihilation of the *Pisonia* forests by scale at times of particular stress such as during an extreme El Nino event and periods of lack of fresh water on NEH (Freebairn 2007). In support of this is that on Coringa Island a healthy grove of *Pisonia* was present in the late 1960s (Heatwole 1979; Heatwole et al. 1981) but now no trees remain. The last stand of 20 or so trees present in the 1990s were all dead by 2002 being badly affected by *Pulvinaria* before *Cryptolaemus* or parasitoids were introduced (Smith and Papacek 2002).

An alternative view is that if the pest outbreak is the result of climate variability, it might not be desirable to continue to conduct releases of *C. montrouzieri* on NEH. The least interventionist policy would be to leave the island to develop a new but different equilibrium and so continue to experience occasional population explosions of species followed by a slow recovery close to the previous equilibrium as it probably has done in the more distant past. Also it is possible that *Pisonia* might even colonise naturally on those islands from which has been reduced or eliminated as on Bird Island all *Pisonia* were removed to make way for coconut plantations which were abandoned in 1970. Thirty or so years later there were 2000 *Pisonia* trees on the island showing a very rapid rate of recolonisation (Hill et al. 2003).

Considering the points made above it seems on balance that the introduction of *Cryptolaemus* to NEH should continue for the present; cost is low and no custom visits to the island are necessary as the beetle can be carried on the regular official visits to monitor sea birds. The apparent limited effect detected on non-target organisms and the likely beneficial effect in enabling *P. grandis* to survive during especially adverse weather conditions are additional factors to support continuation of the control measures. However the BCA programme should be reviewed regularly, at least every five years.

Final words

Intentional introductions of BCAs to small islands in the future should be preceded by a risk assessment taking into consideration the total fauna. This means, of course, that an inventory of species must be compiled and ecological studies carried out on faunal community composition and species distribution, abundance and other aspects of biology of the species present. This recommendation should be widely applied in order to protect native invertebrate faunas, in particular on small islands.

A further consideration is that these islands are only a few metres above sea level. NEH has a maximum altitude of 5 m. Sea levels are thought to have risen 195 mm since 1870 and appear to be rising at the rate of 1 to 2 mm per year but in some places the rate is higher (Lough 2007). It is not clear how long the lens of fresh water will be retained on NEH which adds another stress to the *Pisonia* trees. In addition if, as predicted, there will be an increased intensity of cyclones in the region (Lough 2007), it is possible that loss from damage to *Pisonia* trees will occur.

Much effort is currently being put into modeling possible changes in pest species abundances and distributions as a result of climate variability. It should be noted that the phenomenon described here is likely to have been an unpredicted and probably an unpredictable effect of climate change. In spite of modeling efforts there will, no doubt, be more of these unpredicted cascade effects in future.

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ORIGINAL PAPER

Grasshopper outbreak challenges conservation status of a small Hawaiian Island

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Abstract A tiny (63.1 ha) and uninhabited Nihoa Island within the Hawaiian Archipelago is situated 250 km NW of Kauai. It is a part of Papahānaumokuākea National Marine Monument established in 2006 and jointly administered by NOAA, USFWS, and the State of Hawaii (Department of Land and Natural Resources). The island's known terrestrial biota include 26 vascular plant species, 27 bird species, and 243 arthropod species. Approximately half of the species are endemic to Nihoa or indigenous to Hawaii. Four plant species and two resident bird species are federally listed as threatened or endangered species. Gray bird grasshopper *Schistocerca nitens* has occurred on the main Hawaiian Islands since 1964 and was first reported from Nihoa in 1977. In 2002–2004, there was an outbreak of this grasshopper that aggravated the drought and denuded most of the island's vegetation. Since then, grasshopper numbers crashed, most probably due to insufficient soil moisture for embryonic development. With subsequent rains, the island's vegetation recovered. During the USFWS expedition to Nihoa in October 2006, grasshopper population assessments were undertaken. Based on 18, 300 × 2 m transect counts, the Nihoa grasshopper population was estimated at 19,430 ± 10,360 individuals. Laboratory rearing of *S. nitens* revealed that its development occurs without diapause. Potentially, the grasshopper can produce as many as four annual generations on Nihoa, although it is likely that only two generations occur. This article reviews the implications of fluctuations in *S. nitens* population dynamics for island flora and entomo- and avifauna, in particular, for the endangered endemics, the insectivorous Millerbirds. Potential threats to the island's biota and challenges for conservation are discussed.

Keywords Nihoa · *Schistocerca nitens* · Alien species · Oceanic Island · Endangered species

Introduction

Northwestern Hawaiian Islands and their biota

Extending 2,400 km across the north-central Pacific Ocean, the Hawaiian Islands are the most isolated group of high islands on earth and are summits of giant submarine volcanoes. The chain is progressively older in a NW direction and began over 70 million years ago (Howarth and Mull 1992). Besides the better-known main Islands (Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii), the Hawaiian Archipelago includes several small Northwestern Hawaiian Islands (NWHI) (Fig. 1). These remote Pacific islands contain the largest coral reef system in the U.S. and some of the most pristine underwater habitats in Hawaii. Because they are a protected wildlife sanctuary, marine life in waters surrounding the NWHI exhibits some of the highest biodiversity levels per unit area in Hawaii (Evenhuis and Eldredge 2004). Terrestrial biota on these islands includes numerous endemic plants and animals, particularly arthropods (Gagné and Conant 1983; Conant et al. 1983). Vegetation assemblages in the less disturbed NWHI represent the best remaining examples of their kind in Hawaii, allowing us to imagine how the vegetation cover of the main islands may have looked like before these habitats were devastated by anthropogenic influences, introduced herbivores and invasive weeds.

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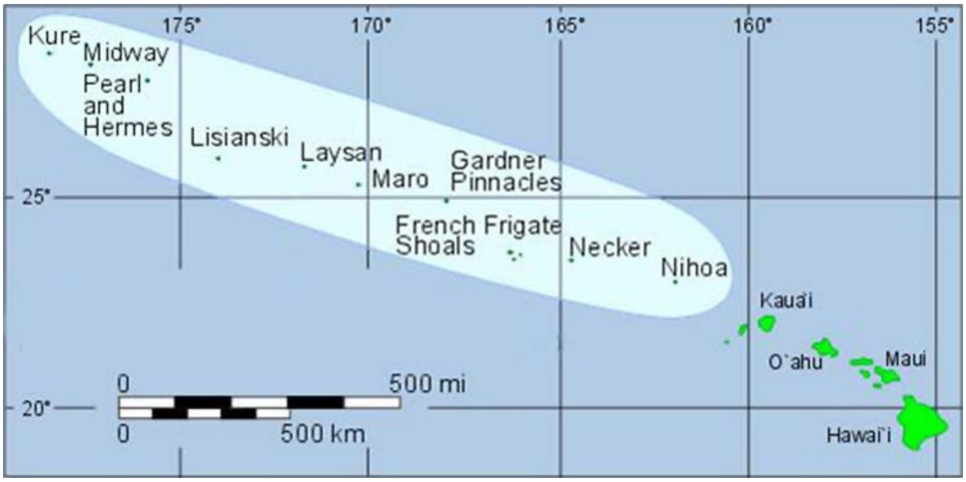

Fig. 1 Northwestern Hawaiian Islands

Nihoa's terrestrial biota: a unique assemblage

Nihoa is the southernmost NWHI island (Fig. 2). It is situated 250 km NW of Kauai. Nihoa is a remnant of an ancient volcanic crater with an emerged land area of 63.1 ha (1.35 by 0.45 km). Geologically, it is the youngest island among the NWHI, with an age calculated at 7.3 million years (Clague 1996). Populated by myriads of birds, it was once known as "Bird Island" (Clapp et al 1977). Unlike most of other NWHI, Nihoa was spared from guano mining and bird feather hunting in the 19th century, and its sparse human settlements were abandoned before the late 1700s (Emory 1928). This contributed to preserving a unique island biota, which is possibly the most intact and the most diverse within the NWHI (Conant et al. 1983). Although Nihoa's area (63.1 ha) amounts to only 0.0038% of the Hawaiian Islands total land area, it contains a remarkably large proportion of biodiversity among the islands. Nihoa's 184 insect and 27 nesting bird species represent respectively 2.2 and 14.8% of the total number of species of these classes in Hawaii (Table 1). More than half of Nihoa's insects are either endemic to the island or indigenous to the Hawaiian Archipelago (Nishida 2001, 2002; Evenhuis and Eldredge 2004). The island's flora includes 26 vascular plants species of which 17 are indigenous and 3 endemic (Christophersen and Caum 1931; Conant 1985). Four of Nihoa's plant species are listed as endangered (Evenhuis and Eldredge 2004). An

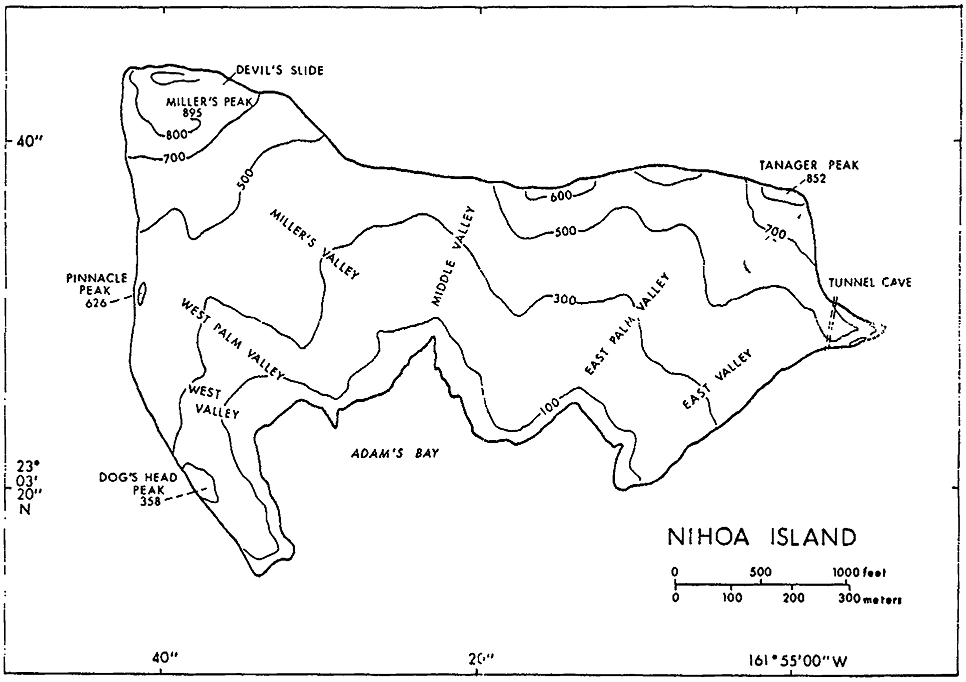

Fig. 2 Nihoa Island (from Clapp et al. 1977)

Table 1 Number and proportion of species from Nihoa compared to all of Hawaii (updated from Eldredge and Evenhuis 2003; Evenhuis and Eldredge 2004)

Taxonomic group	Nihoa	Hawaii total	% of total
Flowering plants	26	2,142	1.2
	END 3 (12%) NIS 6 (23%)	END 896 (42%) NIS 1,139 (53%)	
Insects	184	8,155	2.2
	END 20 (11%) NIS 89 (48%)	END 5,233 (64%) NIS 2,782 (34%)	
Other arthropods	59	1,060	5.6
	END 7 (12%) NIS 15 (25%)	END 295 (28%) NIS 573 (54%)	
Nesting birds	27	183	14.8
	END 2 (7%) NIS 8[a] (30%)	END 63 (34%) NIS 55 (30%)	
Area (ha)	63.1	1,663,600	0.0038

[a] Visitors/migrants; END—species endemic to Nihoa only; NIS—nonindigenous species that do not naturally occur in the Hawaiian Islands and have arrived either accidentally or intentionally through biological control efforts, agricultural imports, etc

additional indigenous plant species, *Solanum nelsonii*, is currently a candidate for listing as endangered or threatened (USFWS 2007).

Invasive organisms: a threat to island ecosystem

Ocean islands are fragile ecosystems that can be easily and often irrevocably damaged by introducing alien organisms. Due to the restricted land area, Nihoa's resident bird, vascular plant, and terrestrial invertebrate populations are small and at constant risk of extinction (Gagné 1988). A purposeful or inadvertent introduction of an alien organism could devastate native vegetation and trigger a chain reaction decimating associated bird and arthropod populations. Observations over the past few decades showed a steady increase in non-native species (Evenhuis and Eldredge 2004). Among them, a recent (2002–2004) outbreak of the Gray bird, or Vagrant grasshopper *Schistocerca nitens* (Thunberg 1815) (Orthoptera: Acrididae) (Fig. 3), was a particular concern because of its potentially devastating impact on Nihoa's biodiversity, especially plants, birds and insects (Gilmartin 2005). Island visits during 2002–2004, revealed that grasshopper damage to vegetation was extremely high. Most plants constituting the island's vegetative cover (*Sida fallax*, *Chenopodium oahuense*, *Solanum nelsonii*, *Portulaca villosa* etc.), together with the endangered species *Sesbania tomentosa* and *Schiedea verticillata*, appeared completely devoid of foliage; even the leaves of the relict and endangered Nihoa fan palm (*Pritchardia remota*) were noticeably chewed (Wegmann et al. 2002; Culliney 2004; Liittschwager and Middleton 2005) (Fig. 4).

Grasshopper infestation could also impact Nihoa's avifauna (Gilmartin 2005). While the majority of the island's nesting birds are marine or shore birds, there are two endemic resident song birds, Nihoa Millerbird (*Acrocephalus familiaris kingi*) (Fig. 5) and Nihoa Finch (*Telespiza ultima*). Because of their small population, both were added to the U.S. Endangered Species List in 1967. The insectivorous Nihoa Millerbird (the common name reflects its preferred food, "miller moths"—noctuids from genera *Agrotis*, *Helicoverpa*, etc.) appeared to be threatened most by the alien grasshoppers. In the past, a similar bird from Laysan Island (*A. f. familiaris*) became extinct between 1916 and 1923 when introduced rabbits destroyed the island's vegetation and, consequently, decimated the island's insect fauna (Ely and Clapp 1973; Morin et al. 1997; Rauzon 2001).

Endemic insect species, such as the Nihoa conehead katydid (*Banza nihoa*) (Orthoptera: Tettigoniidae), Conant's giant Nihoa tree cricket (*Thaumatogryllus conantae*) (Orthoptera: Gryllidae), Nihoa Rhyncogonus weevil (*Rhyncogonus exsul*) (Coleoptera: Curculionidae; Fig. 6) and others, might also be threatened by *S. nitens* outbreaks (Gilmartin 2005). Numerous endemic insects (particularly, the orthopterans), and thousands of nesting birds, as non-targets, make any actions aimed at reducing the population of *S. nitens* on Nihoa problematic.

Nihoa conservation status

Until recently, Nihoa Island was managed by the U.S. Fish and Wildlife Service (USFWS) as part of the NWHI wildlife preserve. In June 2006, all NWHI were declared the Papahānaumokuākea National Marine Monument, which became the largest single area dedicated to conservation in U.S. history and the world's largest protected marine area. The new monument is managed in a three-way partnership by USFWS, National Oceanic and Atmospheric Administration (NOAA), and the State of

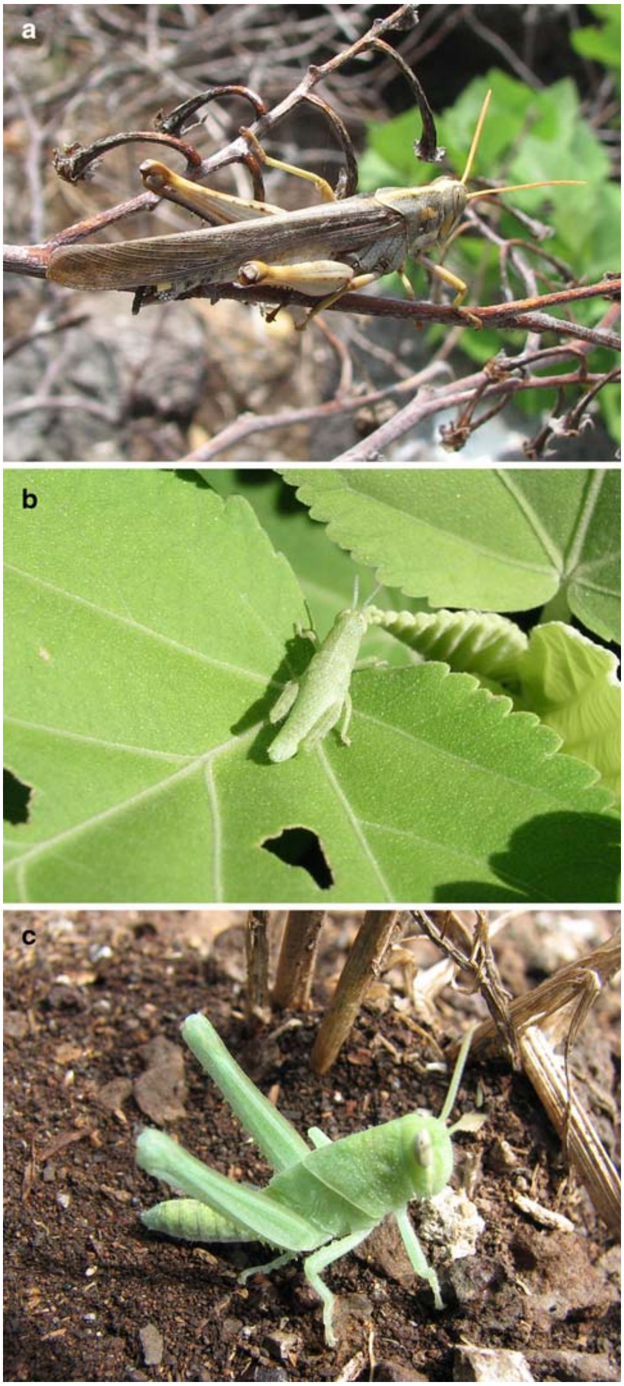

Fig. 3 Grasshoppers *S. nitens* from Nihoa (photos A. Latchininsky) (**a**) adult female (**b**) second instar nymph on *Sida fallax* leaves (**c**) fourth instar nymph

Hawaii (Department of Land and Natural Resources). In 2007, it was included in the U.S. World Heritage Tentative List (US NPS 2007). Nihoa visits are restricted to scientific expeditions by special permit only. Because of the extremely treacherous landing, such visits are usually limited to only one or two per year by a team of four or fewer scientists. I participated in one such expedition in October

Fig. 4 Damage to Nihoa fan palm *Pritchardia remota* by grasshoppers *S. nitens* in 2004 (photo Benton Pang)

Fig. 5 Nihoa Millerbird *Acrocephalus familiaris kingi* (photo A. Latchininsky)

Fig. 6 Nihoa endemic weevil *Rhyncogonus exsul* (photo A. Latchininsky)

2006, with a primary purpose of assessing the grasshopper situation and monitoring the arthropod fauna on the island.

Objectives of this study were: (1) to quantitatively assess the population of *S. nitens* on Nihoa; (2) to examine the parameters of its life cycle under laboratory conditions; (3) to identify critical ecological factors affecting its population dynamics on the island; (4) to estimate its actual or potential impact on Nihoa's vegetation, birds and arthropods; and (5) to consider, if necessary, *S. nitens* population management options that would not adversely affect other arthropods on the island.

Materials and methods

Site description

Detailed descriptions of Nihoa can be found in Clapp et al. (1977), Conant (1985), Rauzon (2001) and Evenhuis and Eldredge (2004). In brief, the island is located at roughly 23°3.6′ N and 161°55.4′ W. It is characterized by steep slopes, rocky outcroppings, six well developed valleys, and precipitous cliffs. Its two highest points are situated in the NW corner (Miller's Peak, 269 m) and in the NE corner (Tanager Peak, 256 m) (Fig. 2), making it the tallest among NWHI. The northern, eastern and western sides of the island are sheer sea cliffs, 10–265 m high. The southern side features a wave-cut terrace which provides a landing site. One small sandy beach is at the SW end of the island, and is frequented by groups of the endangered endemic Hawaiian monk seal (*Monachus schauinslandi*). Nihoa's climate is dry subtropical, probably close to that of French Frigate Shoals, with average yearly temperatures around 24°C and annual rainfall of about 750 mm (Morin et al. 1997; USGS 2006). There are no fresh water sources on the island, although rains create 5–7 temporary seepages in the valleys and depressions.

Nihoa's vegetation is dominated by dry, scrub-type low shrubs of *Sida fallax*, *Chenopodium oahuense*, *Solanum nelsonii*, and *Sesbania tomentosa* (Christophersen and Caum 1931). In two valleys, there are Nihoa fan palm (*Pritchardia remota*) groves with trees reaching 6 m in height. At higher elevations, rocks are covered by clumps of a native grass, *Eragrostis variabilis* (Conant 1985).

Grasshopper population assessments

During my stay on the island, between 11 and 22 October 2006, several grasshopper population assessment methods were attempted (Onsager and Henry 1977; Thompson 1987), but none of them appeared to be satisfactory for Nihoa's conditions. Taking into account the complicated relief, dense vegetation cover, and relatively low abundance of *S. nitens* in October 2006, the following method was selected. I calibrated my walking speed at approximately 300 m/h and counted all adult grasshoppers flushed out of the vegetation in the 2 m wide visual field, advancing along a more or less straight line for one hour. Each transect covered a 600 m^2 area. In total, 18 transect counts were accomplished between October 12 and 21, 2006. In two of the 18 transects, I counted both adults and nymphs. The transects sampled the entire island except its western extremity known as Dog's Face where, according to different observers, the grasshoppers were less abundant than elsewhere on the island (Wegmann et al. 2002). Approximate transect locations are shown in Fig. 7.

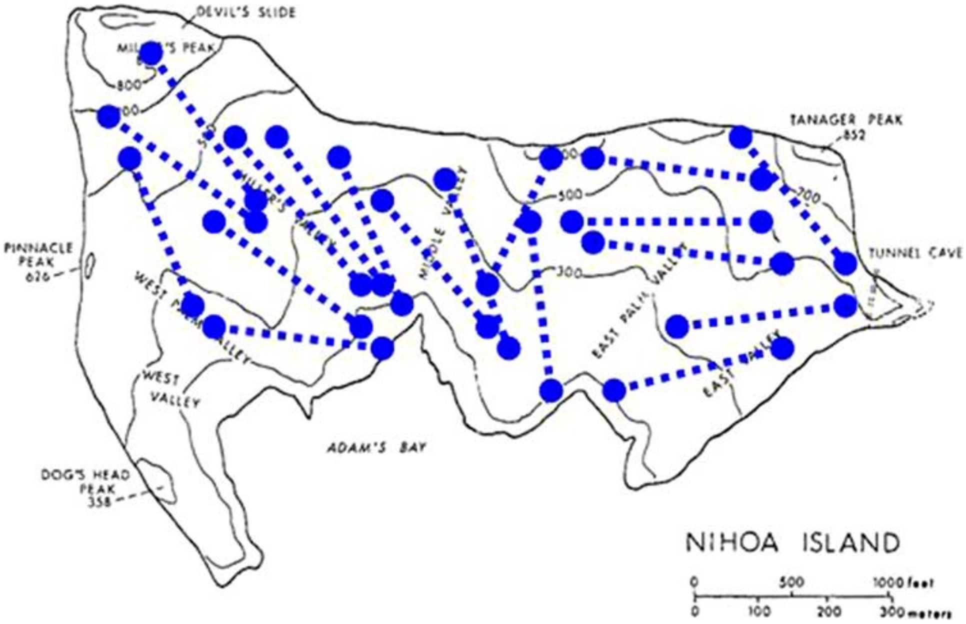

Fig. 7 Location of 18 transects used for *S. nitens* counts in October 2006

Results of the counts were expressed in terms of descriptive statistics (Southwood 1987) and then extrapolated for the entire area of the island (63.1 ha).

S. nitens life history under laboratory conditions

S. nitens life cycle parameters were studied in the University of Wyoming (Laramie, WY, USA) entomology laboratory. Fourteen mid- to late instar nymphs of both sexes were brought alive from Nihoa. Constrained by technical difficulties until September 2007, the grasshoppers were kept in 25 × 25 × 25 cm wooden cages with plastic front sliding panels and mesh sides at a constant temperature of 30 ± 1°C and a 24-h light. Grasshoppers bred successfully under these conditions; however, such regime was not realistic for Nihoa. Beginning in September 2007, the grasshoppers were transferred to larger (50 × 50 × 50 cm) aluminum cages with mesh sides and plastic front panels with sleeves. Cages were kept in controlled climate cabinets (Percival Scientific, Model E-36X) at a temperature of 28 ± 0.5°C at daytime (12 h) and 22 ± 0.5°C at night (12 h), which approximated the weather conditions on the island (Conant and Morin 2001). Plastic cups with moist soil were offered for oviposition. Fresh food was replaced daily; food plants included a variety of foliage species such as lettuce, cotoneaster, hibiscus, dandelion, sweet clover, red clover, crab apple, avocado, various thistles and others.

Results and discussion

How did *S. nitens* reach Nihoa?

S. nitens is thought to be a recent introduction to Nihoa. Its distribution area extends from northern South America through Mexico and the southwestern United States (Capinera et al. 2004). The grasshopper was first captured on the main Hawaiian Islands in 1964 (Anonymous 1965a) and identified initially as *Schistocerca vaga* (Scudder 1899) by J. W. Beardsley (Anonymous 1965b). It was first reported from Nihoa under the name of *S. nitens* in 1977 (Beardsley 1980). In 2000, the grasshoppers became numerous enough to warrant concern expressed by Nishida (2001). In 2002 and 2004, scientists visiting the island were confronted by numerous grasshoppers that denuded 90% of the island's vegetation (Wegmann et al. 2002; Culliney 2004). In 2003 and 2005, however, the grasshopper numbers seemed to decrease, and the island's plants showed signs of recovery (Gilmartin 2005; Wegmann 2005). In April and October 2006, Nihoa's vegetation appeared lush and green, and the grasshopper population was relatively low. Observations in March 2007 revealed abundant island vegetative cover and low grasshopper numbers (Rowland et al. 2007). In August 2007, the grasshopper numbers remained low but the vegetation dried out significantly (Marc MacDonald pers. comm. 2008).

S. nitens appeared to reach Nihoa from the main Hawaiian Islands following trade winds without human influence. Grasshopper and locust species from the genus *Schistocerca* Stål are large, strong flyers with a notorious migratory potential. In 1988, swarms of Desert locust (*S. gregaria*) crossed the Atlantic Ocean covering 5,000 km from West Africa to the Caribbean Islands in 10 days (Kevan 1989; Ritchie and Pedgley 1989). For its part, *S. nitens* was found on Socorro Island situated about 500 km off Baja California, which suggests the ability to colonize from the mainland (Song et al. 2006). Nihoa is located only 250 km NW from the island of Kauai and with favorable trade winds, the grasshoppers could cover the distance in a day or two. On the mainland, an adult female of *S. nitens* (identification confirmed by Dr. Hojun Song, BYU) was captured in August 2007 near Cheyenne (WY), about 1,000 km north off the limit of the known distribution area for the species.

S. nitens is found on other NWHI such as Necker and French Frigate Shoals (Beardsley 1980; Nishida 2001). More recently, the progression to the NW resulted in *S. nitens* findings on two even more remote locations of NWHI—Laysan (John Schmerfeld pers. comm., 2006) and Lisianski (Jon Sprague pers. comm., 2007 via Beth Flint), which are located 1,500 km NW from Nihoa. Should they be considered alien? Or is this a natural process in the expansion of their distribution area?

Howarth and Mull (1992) consider "alien" the insect species that were inadvertently or purposefully brought to the Hawaiian Islands by humans. Most specialists believe that the initial arrival of *S. nitens* on the main Hawaiian Islands was a human-aided migration (Nishida 2001; Evenhuis and Eldredge 2004). This opinion was based on the fact that the first specimen of *S. nitens*, a gravid female, was captured on Coast Guard base at Sand Island, Oahu (Anonymous 1965a). However, published accounts of the first collections of *S. nitens* from Oahu are not unequivocal. Several days after the initial specimen capture, numerous adult males and females were captured within the same area and "many additional grasshoppers were seen" (Anonymous 1965b). Rather than an accidental introduction, which is typically restricted to a limited number of specimens, the picture of numerous adult grasshoppers flying together in the same area appears more consistent with swarm's arrival. Interestingly, all attempts to find the grasshoppers near the docks or at the airport—traditional sites of new species' introductions on Oahu—failed (Anonymous 1965b). Although the possibility of ship hitch-hiking cannot be completely ruled out in the initial arrival of *S. nitens* to the main Hawaiian Islands, wind-assisted migration seems an equally plausible hypothesis. Reaching Nihoa from the main islands unassisted is also likely.

Examples of two well-known insect migrants may give some weight to this point of view. In October 2006, I caught a Painted Lady butterfly (*Vanessa cardui*) on Nihoa, which was the first ever record of this species from the island. Also, on several occasions, I observed a dragonfly (possibly a green darner *Anax junius*). On one of these occasions the dragonfly was laying eggs in a seepage pond. The dragonfly observation appears particularly interesting because although fresh water supplies are meager and intermittent on Nihoa, several species of chironomids and other aquatic dipterans have been recorded on the island (Evenhuis and Eldredge 2004). Therefore, the possibility for a dragonfly to establish a resident colony on the island cannot be ruled out entirely. In 2004, a dragonfly was seen on Nihoa also (Culliney 2004).

Historical records of *S. nitens* on Nihoa and other NWHI are summarized in Table 2. Since its initial appearance on Oahu, the grasshopper made an impressive progression in the NW direction.

Quantitative assessments: how many grasshoppers are there on Nihoa?

The total number of adult *S. nitens* observed during the 18 transect counts was 133 (Table 3). Extrapolated to the area of Nihoa (63.1 ha), the estimated total adult population of *S. nitens* on the island consisted of 7,772 ± 4,144 individuals (95% confidence interval). Unlike adults, visual estimates of nymphal populations were more difficult because of their smaller size, cryptic coloration, and tendency to remain in the dense foliage even when disturbed. Two attempts to count all developmental stages of grasshoppers along the 300 m transects on October 17 and 19 yielded 21 adults and 32 nymphs, and 11 adults and 16 nymphs, respectively. Thus, the number of nymphs was approximated as being 1.5 times higher than the number of adults. Hence, the estimated nymph total on the island was 11,658 ± 6,216 individuals, and the total nymphs plus adults was 19,430 ± 10,360.

It is interesting to compare these findings with the only previous quantitative estimate of *S. nitens* population (Wegmann et al. 2002). Wegmann did his counts on September 8, 2002, when the grasshoppers appeared to be numerous, and “nine-tenths of Nihoa’s vegetative cover was nude, stripped of all leaves, buds, flowers and seeds” by the grasshoppers (*l.c.*). The author made six, 50 m long transect surveys sweeping the tops of the vegetation with an insect net (50 cm diameter opening) every 2 s. The collections yielded 4, 8, 5, 1, 1, and 1 grasshopper respectively (developmental stages not indicated). Assuming that, (1) he conducted his sweeping 0.5 m to the right and 0.5 m to the left from the center line of the transect, and (2) he collected *all* available grasshoppers, this would mean each transect covered 50 m^2, and the mean count for the transect would be 3.333 ± 2.875 individuals, which corresponds to 42,062 ± 36,282 grasshoppers on the entire island. These numbers are approximately two times higher than my calculations in October 2006 (19,430 ± 10,360). The grasshoppers must have been especially active between 9:55 and 10:45AM when Wegmann did his survey, and most probably, he was only able to catch a fraction of the grasshopper population, while many of them, especially adults, escaped capture. If this was the case, the actual grasshopper population on Nihoa in September 2002 was much (maybe, several times) higher.

Grasshopper *S. nitens* life history on Nihoa: how many annual generations are possible?

During my first days on the island (October 12–14), grasshoppers were represented by two distinct age cohorts: early (first and second, rarely third) instar nymphs and adults. During my last days (October 18–22), the grasshopper population was represented mostly by mid- to late instar (third to fifth) nymphs and senescent adults. Among the adults, males outnumbered females by approximately 5:1, which may indicate the end of the adult life span (see e.g. Latchininsky and Launois-Luong 1997). Other aging signs such as missing hind legs, dull coloration and worn out wing tips were also common. Several captured adults soon died in the vials. The presence of young nymphs together with senescent adults indicates that *S. nitens* on Nihoa exhibit continuous development, without quiescence or diapause. Senescent adults seen in October probably hatched about 3 months earlier, i.e. in mid- to late July. Subsequent generations should have hatched in early January, 2007 and another in late March or April. This prediction was confirmed by Rowland et al. (2007) who observed adults and hatchlings in late March 2007. In theory, the grasshopper may produce up to four annual generations on the island. In reality, this number may go down if winter temperatures are significantly lower and the soil is dry delaying grasshopper embryonic development.

Laboratory rearing of *S. nitens*: what are the life-cycle parameters?

Between November 2006 and January 2007, the *S. nitens* colony produced five successive generations under

Table 2 Historical records on *S. nitens* on Nihoa and other NWHI (compiled from different sources)

Year	Month, date	*Schistocerca nitens* population	Vegetation state	Observer or Reporter; Reference
1964	August 3, 1964	Specimen found on Sand Island, Oahu	NA	Anonymous (1965a)
	August 10, 1964	Confirmation of establishment (second specimen collected from Sand Island)		Anonymous (1965b)
1977	?	Specimen(s) found on Nihoa	NA	Collector George Balazs; Beardsley (1980)
1977	August 14	Specimen collected from Necker	NA	Collector George Balazs; Beardsley (1980)
1983	?	Specimen(s) found on Nihoa	NA	Wayne Gagné (1983) (G. Nishida pers. comm.)
1997	? (few hours on the island)	Numerous grasshoppers observed	NA	Beth Flint (in Gilmartin 2005)
2000	September 9–21	Numerous specimens observed and collected by G. Nishida	Very dry conditions. Some shrubs left leafless by *S. nitens*; concern about vegetation damage expressed by G. Nishida	Nishida (2001); Beth Flint (in Gilmartin 2005)
2000	September 24–27	Reported from Necker and French Frigate Shoals	NA	Nishida (2001); Evenhuis and Elderidge (2004)
2001	September 1	Low numbers	NA	Alexander Wegmann (in Wegmann et al. 2002)
2002	September 2–9	Extremely high. A total estimate for the island (recalculated by A. Latchininsky based on A. Wegmann's 6 transect counts): 42,062 ± 36,282	9/10 of island's vegetation denuded. Three patches of *Schiedea* grazed to root level. Fans, stems, seed cases and bark of *Pritchardia* chewed	Alexander Wegmann (in Wegmann et al. 2002)
2003	?	Numbers are lower than in 2002	Verdant plant community	Gilmartin (2005)
2003	August (?)	High *S. nitens* numbers	Many damaged plants	Liittschwager and Middleton (2005)
2004	August 29–September 1	Extremely high. 70+ grasshoppers accumulated on orange peel in 20 min. Grasshoppers seem to converge on patches of remaining green vegetation	*Sesbania*, *Sida*, *Pritchardia* and other plant species are severely damaged. Twigs are often girdled. *Eragrostis variabilis* is generally less attacked although some leaf blades are 50% chewed. Some *Sesbania* shrubs are surprisingly healthy amid completely defoliated plant community	John Culliney (Culliney 2004)
2004	August 13 and September 4 (?)	Very high grasshopper numbers	Island's vegetation is devastated	Liittschwager and Middleton (2005)
2004	September 4	Two nymphs found on Necker	Healthy, green vegetation	John Culliney (Culliney 2004)
2005	Late June (2 h on the island)	No grasshoppers seen	Verdant plant community	Alexander Wegmann (Wegmann 2005)
2005	August 13–20	Low grasshopper numbers. Two adult females, 7 adult males, 2 moderate size nymphs, and 2 small nymphs were collected. The nymphs were found in Devil's Slide	Very lush vegetation despite August being a "dry season"	Pete Oboyski (Oboyski 2005)
2006	April 1–9	Low grasshopper numbers: a total of 9 individuals seen by four observers over 9 days	Vegetation is green, only a few old *S. nitens* chew observed	Natalia Tangalin and Stefan Kropidlowski (in Kropidlowski 2006)
2006	October 11–22	Moderate to low grasshopper densities observed. Age: mostly 1–3 instar nymphs and adults. Population estimate: 7,772 ± 3,954 adults (based on 18 transect counts) and 11,658 ± 5,931 nymphs. Total adults plus nymphs: 19,430 ± 9,885	Lush, green vegetation all over the island. No signs of fresh *S. nitens* chew on *Pritchardia*. Some insignificant damage (shot-holes) to leaves of *Sida*, *Solanum* and *Sesbania*	Alexandre Latchininsky (Latchininsky 2006)

Table 2 continued

Year	Month, date	*Schistocerca nitens* population	Vegetation state	Observer or Reporter; Reference
2006	October 11–22	Reported from Laysan	NA	John Schmerfeld observed a Laysan finch catching an adult *S. nitens* (pers. comm.)
2007	March 16–25	Low grasshopper numbers. Only 14 individuals were observed along 54 Millerbird and finch transects. Adults and nymphs are observed, including hatchlings on 3/21. Higher densities in the SE part of the island	Lush, green vegetation with little or no insect damage. However, plants of *Sesbania* showed noticeable damage, especially in the eastern part of the island, presumably by grasshoppers	Ian Jones (in Rowland et al. 2007)
2007	June (22?)	An adult captured and photographed on Lisianski	NA	Jon Sprague (pers. comm. 2007 via Beth Flint)
2007	Mid-July to mid-September	Low grasshopper numbers: one adult flushed out of vegetation every 15 min. Sometimes localized concentrations of 3–4 adults within few m. Increased grasshopper numbers in mid-September	Very dry vegetation. *Sida* and *Sesbania* almost entirely absent. Green pockets of *Solanum nelsonii* and *Chenopodium oahuense* present	Mark Alexander MacDonald (pers. comm. 2008)

Table 3 Transect counts of *S. nitens* on Nihoa in October 2006

Date	Transect # and Adult count
October 12	#1–1
October 13	#2–8, #3–6, #4–10
October 15	#5–3, #6–2
October 16	#7–4
October 17	#8–9, #9–12
October 19	#10–12, #11–15, #12–5, #13–6
October 20	#14–8, #15–13
October 21	#16–7, #17–8, #18–4
Total	18 transects, 133 adults

laboratory conditions. Nymphal development included five instars. At 28 ± 0.5°C (12 h D) and 22 ± 0.5°C (12 h N), the time from hatching to adult emergence ranged from 32 to 40 days, with males completing their nymphal development 3–5 days earlier than females. Mating started 8–12 days after fledging and females began laying eggs 7–10 days after mating. Females laid egg-pods every 10–15 days during their life span, which in some individuals extended more 150 days. Each egg-pod contained on average 66.25 ± 20.36 eggs with a minimum of 32 and a maximum of 97 eggs (Table 4). Egg-pod structure was typical for the genus *Schistocerca*: it consisted basically of eggs with some white foam secretion without any protection (hard walls) from adverse conditions. Egg viability and duration of the embryonic development largely depended on soil moisture. In the cages kept under the constant air temperature of 30 ± 1°C, when the soil was moistened every other day, eggs started to hatch in about 14 days. If the soil was moistened only once a week, hatching occurred about one month after oviposition. If the soil was maintained dry, the eggs succumbed from desiccation and no hatching occurred. Further research is needed to estimate how long the eggs would remain viable in dry soil.

Table 4 Number of eggs in *S. nitens* egg-pods from grasshoppers reared under laboratory conditions at constant temperature 30 ± 1°C

N	Number of eggs in egg-pod
1	32
2	97
3	68
4	74
5	55
6	86
7	52
8	66
Average	66.25 ± 20.36

Which ecological factors are critical for *S. nitens* population dynamics?

Grasshopper population on Nihoa in October 2006 consisted of relatively low numbers but appeared healthy and exhibited a high reproductive potential. After a population explosion in 2004, grasshopper numbers crashed, most likely due to extreme drought and lack of food, but the numbers seen in October 2006 may reflect an early "bouncing back" situation. The "boom and bust" population fluctuations are typical for other *Schistocerca* species, and, confined to a limited area, such oscillations may even be more pronounced on Nihoa. In the recent past, grasshopper numbers appeared high in 2002 and 2004, but relatively low in 2003, 2005, April and October 2006, as well as in March and August 2007 (Table 2). A fragile equilibrium between vegetation and the primary herbivores (grasshoppers) may be shattered if rainfall continues to be scarce for a prolonged period (several weeks). In such a case, quick vegetation drying combined with rapid grasshopper population growth may result in considerable damage to the island's ecosystem. However, based on what was observed in 2002–2007, this process appears to be reversible and the island's natural, self-regulatory mechanisms have thus far managed to overcome the grasshopper population explosions.

At this point, data are insufficient regarding the potential role of natural enemies in population regulation of *S. nitens*. Egg predation by an alien beetle, *Trox suberosus*, should not be excluded as a species from the same genus (*T. procerus*) is well known for its detrimental impacts on grasshopper eggs in Africa (Greathead et al. 1994). Predators or parasitoids of nymphs and adult grasshoppers appear to be scarce, being limited to arachnids and Millerbirds.

It is likely that grasshopper numbers crashed after the 2004 peak due to egg desiccation in the soil. Recent visits to Nihoa suggest that its climate exhibits seasonality, with higher temperatures and long dry periods from mid-spring to mid-autumn while the other half of the year appears to be cooler with increased precipitation. Laboratory observations confirmed that *S. nitens* does not exhibit embryonic diapause, an adaptation that allows more temperate grasshopper species to survive long periods of unfavorable weather conditions. While dry and hot weather is beneficial for nymphs and adults, the *S. nitens* eggs laid in the soil require moisture for successful development. Without moisture, the eggs of another species from the same genus, *S. gregaria*, cannot survive more than 60 days (Duranton and Lecoq 1990). Apparently, *S. nitens* has similar constraints in its life cycle. This duality in ecological requirements appears to produce a "built-in" auto-regulating mechanism in the grasshopper population dynamics. Prolonged hot and dry weather would contribute to a build-up of grasshopper numbers with a 100-fold increase possible in just one generation, although more likely there would only be a 20- to 30-fold increase. Furthermore, drought would cause grasshoppers to concentrate on the few remaining green patches, increasing plant damage. After a certain period, excessive drought would cause massive egg losses, and the grasshopper population will collapse. Unfortunately, all these considerations remain largely speculative because regular weather monitoring was absent on Nihoa until the first six Hobo weather stations were deployed in April 2006.

On Laysan Island, 12 years of meteorological observations revealed significant fluctuations in rainfall among years (400–1,600 mm) and between months (36–120 mm), with the maximum annual precipitation falling in winter and the minimum in summer (Athens et al. 2007). If a similar rainfall pattern is likely for Nihoa, an excessively long dry period from February until August may become critical for the grasshopper population dynamics due to insufficient soil moisture for embryonic development. A drought occurred on Laysan during 2002–2004. Nihoa over the same years also appeared to experience a precipitation deficit (see descriptions of vegetation state in Table 2). While initially the dry and hot weather contributed to faster grasshopper development and a population increase, the continuing drought resulted in the dramatic crash of the grasshopper numbers due to embryonic mortality. In 2005–2006, Nihoa's vegetation recovered from the drought and the grasshopper attack. Surviving *S. nitens* maintained relatively low population densities in 2006 and 2007.

S. nitens feeding preferences: which plants are at risk?

High numbers of *S. nitens* observed in 2002 and 2004 resulted in severe damage to Nihoa's vegetation. Particularly affected were *Sida fallax* (Malvaceae), *Sesbania tomentosa* (Fabaceae), *Solanum nelsonii* (Solanaceae), *Chenopodium oahuense* (Chenopodiaceae), *Schiedea verticillata* (Caryophyllaceae), and *Pritchardia remota* (Arecaceae) (Fig. 4) (Gilmartin 2005). The native grass *Eragrostis variabilis* (Poaceae) was less frequently attacked by the grasshopper (Culliney 2004). Indeed, although *Schistocerca* grasshoppers are polyphagous (for example, the diet of the Desert locust includes over 600 plant species from all major families (Uvarov 1977)), they exhibit a marked predilection towards forbs and reluctantly feed on grasses. This apparently is also true for *S. nitens* and while on the island it refused to feed on *E. variabilis*. Under the laboratory conditions in Wyoming, *S. nitens* fed on plants from Malvaceae, Asteraceae, Fabaceae, Rosaceae, Chenopodiaceae and, less willingly, Salicaceae and

Poaceae; certain Apiaceae plants were rejected. Based on field observations in October 2006, the feeding preferences of *S. nitens* on Nihoa could be ranked as follows, from the most to the least appetizing species: *Sida fallax* > *Sesbania tomentosa* > *Solanum nelsonii* > *Chenopodium oahuense* > *Schiedea verticillata* > *Pritchardia remota*.

Extrapolating from dietary preferences knowledge of other grasshopper species from genus *Schistocerca*, it is possible to hypothesize that most of Nihoa plant species from broad-leaved families should be included in the circle of *S. nitens* food sources. Besides the species mentioned earlier, this list should include *Sicyos pachycarpus* (Cucurbitaceae), *Chamaesyce celastroides* (Euphorbiaceae), *Rumex albescens* (Polygonaceae), *Tribulus cistoides* (Zygophyllaceae), *Portulaca* spp. (Portulacaceae), *Ipomoea* spp. (Convolvulaceae), and the critically endangered (if not extinct) *Amaranthus brownii* (Amaranthaceae), which was last reported from Nihoa in 1983 (Conant 1985; USFWS 2006). In my opinion, among the four endangered plants of Nihoa, it is *A. brownii* that should be considered most vulnerable to grasshopper depredation, followed by *S. verticillata, S. tomentosa* and *P. remota*. I base this ranking on: (1) actual and likely *S. nitens* feeding preferences, and (2) plant species population size on the island. Indirectly, this assumption regarding *A. brownii* can be supported by observations on *S. gregaria* feeding related by Predtechensky (1935). During a severe Desert locust invasion in the former Soviet Union in 1929, at one occasion hatching occurred within a weedy cotton field. The weeds included 11 species from six plant families. Scientists collected a large quantity of *S. gregaria* young nymphs and placed them on cotton plants. However, after some time, all of the nymphs invariably were found feeding on a single weed species, *Amaranthus angustifolium*.

Behavior of *S. nitens* on Nihoa: an adaptation to the island habitat?

Usually, bright green *S. nitens* nymphs were found basking and feeding on leaves of the shrubs *Sida fallax, Sesbania tomentosa*, or *Solanum nelsonii*. Frequently, several young instar nymphs were observed on one plant, sometimes on just one leaf. When disturbed, the nymphs usually jumped off the plant down to the ground and continued jumping until they were a safe distance from the predator, after which they climbed up a shrub again. This tendency to stay in the canopy rather than on the ground is quite typical for many *Schistocerca* species. Adults, however, often exhibited different behavior, basking not only on the plants but on the ground as well. When disturbed, the adults usually made an escape flight and landed either on vegetation or on the ground. Such flights were relatively short, between 3 and 10 m only. This is different from many other *Schistocerca* species, (e.g., *S. americana*) which often fly considerable distances from the source of disturbance (Capinera et al. 2004). Such reduction in escape flight distance may be a useful adaptation to the small-size island habitat preventing the grasshoppers from being blown into the ocean. However, other observers have not noted this tendency (M. MacDonald, pers. comm.))

Grasshoppers and Millerbirds: are the birds at risk?

In 2002–2004, *S. nitens* severely defoliated Nihoa's vegetation, especially the shrubs of *S. tomentosa*, *S. fallax* and *Ch. oahuense*. Millerbirds nest in these plants (Conant et al. 1983; Morin et al. 1997) and thus may have been negatively impacted by the grasshoppers. Indirectly, Millerbirds may suffer from a grasshopper outbreak because plant defoliation may reduce numerous herbivore insect populations that constitute the birds' main food. It is known that the devegetation of Laysan, coupled with the effects of guano mining, resulted in the extinction of the Laysan Millerbird (*Acrocephalus familiaris familiaris*) along with two other endemic birds, the Laysan rail (*Porzana palmeri*) and the Laysan honeycreeper (*Himatione sanguinea freethi*) (Ely and Clapp 1973; Conant et al. 1983; Conant and Morin 2001).

Millerbird counts on Nihoa in 2006 showed that the grasshopper impact, as a food resource, was potentially positive and the birds likely benefited from high grasshopper numbers in previous years. Kropidlowski (2006) estimated 746 Millerbirds on the island in April 2006, and Beth Flint's (pers. comm.) counts in October 2006 (741) came close to this. Both numbers are record highs for Nihoa during 40 years of observations (Fig. 8). Carrying capacity (K) on the island for this species is estimated at 600 birds (USFWS 1984); although, Conant and Morin (2001) consider this number a substantial overestimate and advance a more reasonable $K = 380$. As such, Millerbird numbers in 2006 almost twice exceeded the island's carrying capacity. This is a marked increase from 1994 and 1996, when Millerbird estimates remained well below 200 (Morin et al. 1997). In 2002, when the grasshopper population was high, the Millerbird population was estimated at about 450, while in 2005, when virtually no grasshoppers were found in June, Millerbird estimates dropped below 200. In March 2007, after a relatively "low" grasshopper year 2006, the Millerbird numbers were estimated at 427 (Rowland et al. 2007; Fig. 8). Although more data on the population dynamics of both, the Millerbirds and the grasshoppers are needed to warrant statistically supported inferences, the changes in Millerbird population might reflect the grasshopper fluctuations on the island.

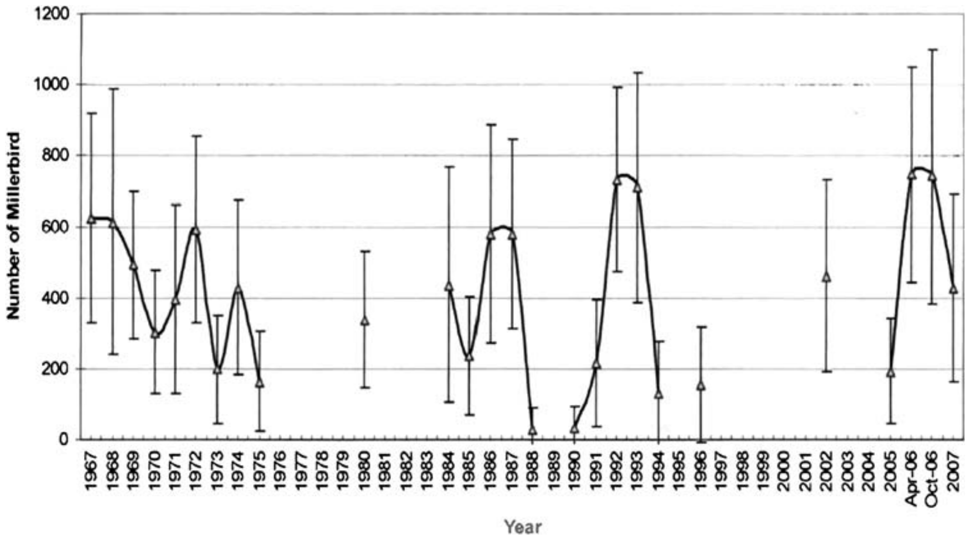

Fig. 8 Nihoa Millerbird population estimates 1967–2007 by USFWS, 95% confidence interval (from Morin et al. 1997) updated by data from Kropidlowski (2006) and Rowland et al. (2007)

My observations on Nihoa Millerbirds in October 2006 did not reveal feeding on grasshoppers, although it was documented in the past (Morin et al. 1997). It may be that grasshopper numbers were too low and did not represent an attractive and easy-to-obtain food source. Judging from bird and the grasshopper sizes, it is reasonable to expect that grasshopper nymphs, especially the young instars, would be manageable prey for the Millerbirds. This is probably true for adult male grasshoppers as well because they are much smaller in size than females: male body length is 24–46 mm and female body length is 40–66 mm (Capinera et al. 2004). Adult females (~3 g) are probably too large for the Millerbirds (~18 g) to consume in one piece. Successful Millerbird feeding on a *S. nitens* nymph was documented by Culliney (2004). At high numbers, grasshoppers (particularly nymphs) provide an abundant and accessible food source for the birds (Wegmann in Liittschwager and Middleton 2005), which may produce more than one clutch per year during its nesting period from January to September (Morin et al. 1997). There is no doubt that the grasshoppers are among the favorite foods for Millerbirds: *S. nitens* body parts were found in 69% of the bird's fecal samples analyzed between 1980 and 1993 (Morin et al. 1997).

The second Nihoa endemic and endangered songbird, the Nihoa Finch did not seem to be impacted by the grasshopper outbreak. They are approximately 10 times more numerous than Millerbirds (Conant et al. 1983) and the recent fluctuations in their numbers (see Rowland et al. 2007) did not appear to exhibit any trend. Unlike Millerbirds, the omnivorous, and ecologically adaptable finches survived the devegetation of Laysan in the past.

Are Nihoa's endemic insects threatened by *S. nitens*?

Coupled with drought, the Gray bird grasshopper outbreak in 2002–2004 led to significant defoliation on Nihoa. In turn, this could have produced a severe impact on the arthropods that depend on the island's vegetation. I observed several Nihoa endemic insects in October 2006. Nihoa Rhyncogonus weevil (*Rhyncogonus exsul*) adults feed primarily on the same plants as those preferred by *S. nitens*: *S. tomentosa*, *Ch. oahuense, S. fallax* etc. It was reasonable to expect that the weevil's population would decrease after losing its food sources to the grasshopper. However, adult weevils were common in October 2006 and, according to Rowland et al. (2007), in March 2007. UV light collections in October 2006 yielded two different click beetles (probably, endemic *Itodacnus* spp.) species, several endemic noctuid moths species as well as oecophorid moths from genus *Thyrocopa*. At the same time, despite a significant effort, I was not able to find Nihoa's three orthopteran endemics: Nihoa conehead katydid *Banza nihoa*, Conant's giant Nihoa tree cricket *Thaumatogryllus conantae* or Nihoa giant rock cricket *Caconemobius nihoensis*. The latter inhabits the splash areas, so it is unlikely to be affected by *S. nitens*. *Thaumatogryllus conantae*, however, appears to be confined to a limited habitat, the so-called Devil's Slide in the NW part of the island (Evenhuis and Eldredge 2004). Vegetation there was impacted by the grasshoppers, so it is possible that the cricket's numbers decreased after the grasshopper outbreak. At this point, I do not have data regarding the potential impact of the grasshopper outbreak on the endemic Nihoa katydid *Banza nihoa*, which is the only Nihoa insect included in the IUCN Red List (listed as "vulnerable" meaning it is "facing a high risk of extinction in the wild in the medium-term future") (IUCN 2007). Without further and more detailed observations, it is impossible to provide any insight regarding the impact of *S. nitens* on other endemic Nihoa insects.

Nihoa's ecosystem after the grasshopper invasion: what happened, what to expect and what can be done?

The *S. nitens* outbreak in 2002–2004, which devastated Nihoa's vegetation, was considered a threat to biodiversity and a challenge to conservation (Gilmartin 2005). Impacts on several endemic and endangered plant species appeared to be particularly pronounced. Since then, and through at least March 2007, grasshopper numbers crashed and the island's vegetation, including the endemics, has recovered. Moreover, the available (although admittedly fragmentary) data on the Millerbird population showed that the grasshoppers might have provided a plentiful food source allowing the birds to increase their population. In this respect, the grasshopper invasion may be considered as beneficial to these critically endangered birds. High Millerbird numbers may allow USFWS to consider the plans of translocating some birds to Laysan Island (Conant and Morin 2001; Fleischer et al. 2007), a conservation measure that is only possible during high-population years (Morin et al. 1997).

It is not clear how the grasshoppers affected the population dynamics of other Nihoa herbivores (primarily arthropods). Food source depletion during the grasshopper outbreak might have decreased the numbers of many Lepidoptera, Coleoptera, Hemiptera and other plant feeders. However, observations in October 2006 showed that several noctuid species, as well as the endemic weevil *Rh. exsul* were quite common, despite their apparent competition with *S. nitens* for resources.

Collecting the detailed meteorological data from April 2006 through present, along with future scientific expeditions will help clarify questions regarding the *S. nitens* life cycle on Nihoa as well as biotic and abiotic factors governing its population dynamics. Further laboratory studies on the impact of soil dryness on the grasshopper egg viability may elucidate factors limiting the insect's reproductive potential. The state of Nihoa's vegetation can be monitored using remotely sensed data. High resolution satellite imagery (e.g. SPOT) would be instrumental in early detection of vegetation changes on the island.

If the grasshoppers produce another outbreak in the future, should we take measures to reduce their numbers? Because of the complicated island relief and rich flora and fauna, eradication would not be possible. Traditional grasshopper control options, such as chemical spraying or biological insecticides, are hardly viable on Nihoa given the logistical constraints, potential severe non-target effects and risks of bringing exotic microorganisms (Gilmartin 2005). One possible alternative is to use stations with insecticidal baits strategically placed in areas of grasshopper concentrations. Baiting has reduced non-target impact and provides environmental and logistical advantages over conventional anti-grasshopper spraying (Latchininsky and VanDyke 2006). However, any control method on Nihoa should be applied with maximum diligence, only as a last resort; and its consequences should be closely monitored.

Should *S. nitens* be considered alien, with all the legal consequences of such a status? As it was shown earlier, published accounts of the grasshopper's arrival on Oahu (Anonymous 1965a, b) are not convincing and they leave room for different interpretations. A recent natural expansion in the distribution range (Table 2) of this highly mobile insect impressed even those specialists who did not question its alien status in the past: "given the distances *S. nitens* has managed in the NWHI, and the general track of hurricanes coming up from Mexico, I don't think we could fully discount the possibility that they could manage the distance with the aid of storms" (Gordon Nishida pers. comm., 2008).

Nihoa has survived disasters in the past. In 1885, a landing party accompanying Princess Lili'uokalani accidentally started a fire that consumed virtually all Nihoa fan palms on the island (Clapp et al. 1977). The palms have recovered, and in April 2006 there were 1,042 adult trees and 1,718 seedlings (Kropidlowski 2006). Maybe, the grasshopper outbreaks on Nihoa should be considered not as destructive plagues of alien invaders, but as self-regulating natural processes, similar to forest fires, which might be beneficial for the island's ecosystem in the long run. *S. nitens* populations on Nihoa and other NWHI should be closely monitored to better understand their impact on the islands' biota. Control measures should be avoided unless grasshopper numbers become overwhelming for a prolonged period (several weeks in a row). At lower population densities, grasshoppers are known to increase plant production, accelerate nutrient cycling (Belovsky and Slade 2000), contribute to soil building (Belovsky et al. 2000), and provide food source for numerous animals, primarily birds (McEwen et al. 2000).

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ORIGINAL PAPER

History of weta (Orthoptera: Anostostomatidae) translocation in New Zealand: lessons learned, islands as sanctuaries and the future

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Abstract Establishing new populations by transferring founder individuals from source populations has been effective for managing the recovery of many threatened species including some weta (Orthoptera: Anostostomatidae) in New Zealand. These large-bodied flightless insects are 'flagship species' for insect conservation in New Zealand and many are rare or threatened. The declining abundance of most weta species, particularly giant weta, can be attributed to the introduction of mammalian predators, habitat destruction, and habitat modification by introduced mammalian browsers. New populations of some weta have been established in locations, particularly on islands, where these threats have been eliminated or severely reduced in order to reduce the risk of extinction. Some populations were established to provide food for endemic vertebrates, ecosystem restoration and ready access for the general public. We illustrate how methods for both transferring weta and monitoring them have become more sophisticated by using a series of case studies. Other transfers of weta not included in the case studies are also summarised. We conclude by re-iterating the importance of documenting the transfer and post-release monitoring for all insect transfers, both for biogeographical reasons and to provide information to improve future transfers.

Keywords Orthoptera · Anostostomatidae · New Zealand · Threatened species · Insects · Recovery · Restoration

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Introduction

In nature, populations are continually expanding or contracting their natural geographic range. Human activities have vastly changed species distributions, to the point where deliberate transfers of plants and animals have become commonplace in pursuing conservation objectives. Where a species is threatened, the need to lessen the risk of extinction often makes it desirable to establish new populations of a species, beyond the boundary of its known threats (JCCBI 1986; Sherley 1995; Hodder and Bullock 1997; New 2000; Hambler 2004). Many translocations and reintroductions are made as part of ecosystem restoration programmes and perhaps, in rare cases, to provide food for a critically endangered species (Wingate 1985; New and Sands 2002; Ringwood et al. 2004). In New Zealand, the first transfers for conservation purposes were made in the 1890s and involved birds. Most subsequent transfers also involved birds although many have also involved reptiles and frogs (McHalick 1998; Atkinson 1990; Saunders 1995). In contrast, relatively few invertebrates have been transferred although the number globally is gradually increasing (New and Sands 2004; Seddon et al. 2005; Hochkirch et al. 2007). Weta, large wingless anastostomatid orthopterans, have been the most often transferred insects in New Zealand, and frequently to predator-free islands. In this paper, we review progress and the lessons learned from translocations of weta over the last 30 years to illustrate the sequence of improvements and increased sophistication in the techniques used. The most recent advances are associated with acquiring rapid and accurate feed-back on the success of these operations.

New Zealand weta are ideal subjects for transfer projects because their biology and behaviour is relatively well known, many can be captive-bred, and as the examples below show, many appear to establish readily after being moved to new locations (Field 2001). They are a distinctive iconic component of the New Zealand fauna, being large-bodied (35–75 mm body length) and long-lived (2–3 years) and, in many cases, have succumbed to the invasion of mammals into New Zealand. The term 'weta' is the indigenous name given to these cricket-like insects by Maori and, in the tradition of their language, it is used as both singular and plural. There are four New Zealand genera within the Family Anostostomatidae: *Deinacrida* are commonly referred to as 'giant weta'; *Hemideina* are 'tree weta'; *Motuweta* are 'tusked weta'; and *Hemiandrus* are the 'ground weta'. A trend towards gigantism can be a characteristic of isolated island faunas that have evolved in the absence of mammalian predators and competitors (Daugherty et al. 1993). Giant weta have been referred to as 'invertebrate mice' due to a combination of their characteristics including their frequently large size, nocturnal foraging behaviour, omnivorous habits, use of diurnal retreats, and polygamy, while even their droppings are often confused with those of small mammals (Ramsay 1978).

Given that the fauna and flora of New Zealand evolved in isolation in the absence of mammals apart from bats, the introduction of mammals, particularly carnivores, caused the extinction of many species and increased the risk that more could become extinct (Daugherty et al. 1993).

New Zealand is an archipelago of approximately 735 islands: 6 are between 10,000 and 100,000 ha; 23 between 1,000 and 10,000 ha; 57 between 100 and 1,000 ha; and approximately 646 are smaller than 100 ha (Parkes and Murphy 2003). A review by Atkinson and Taylor (1992) concluded that rats reached at least 113 (33.5%) of the 337 islands over 5 ha. Successful eradication campaigns have now removed rodents from 90 islands ranging in size from Maria Island (1 ha) to Campbell Island (11,300 ha) (Towns and Broome 2003). Such predator-free islands present ideal opportunities to conserve threatened species and they have been widely used to protect native birds and reptiles ever since the first translocation of 300 kakapo birds (*Strigops habroptilus*) to Resolution Island, Fiordland, by Richard Henry in the1890s (Butler 1989).

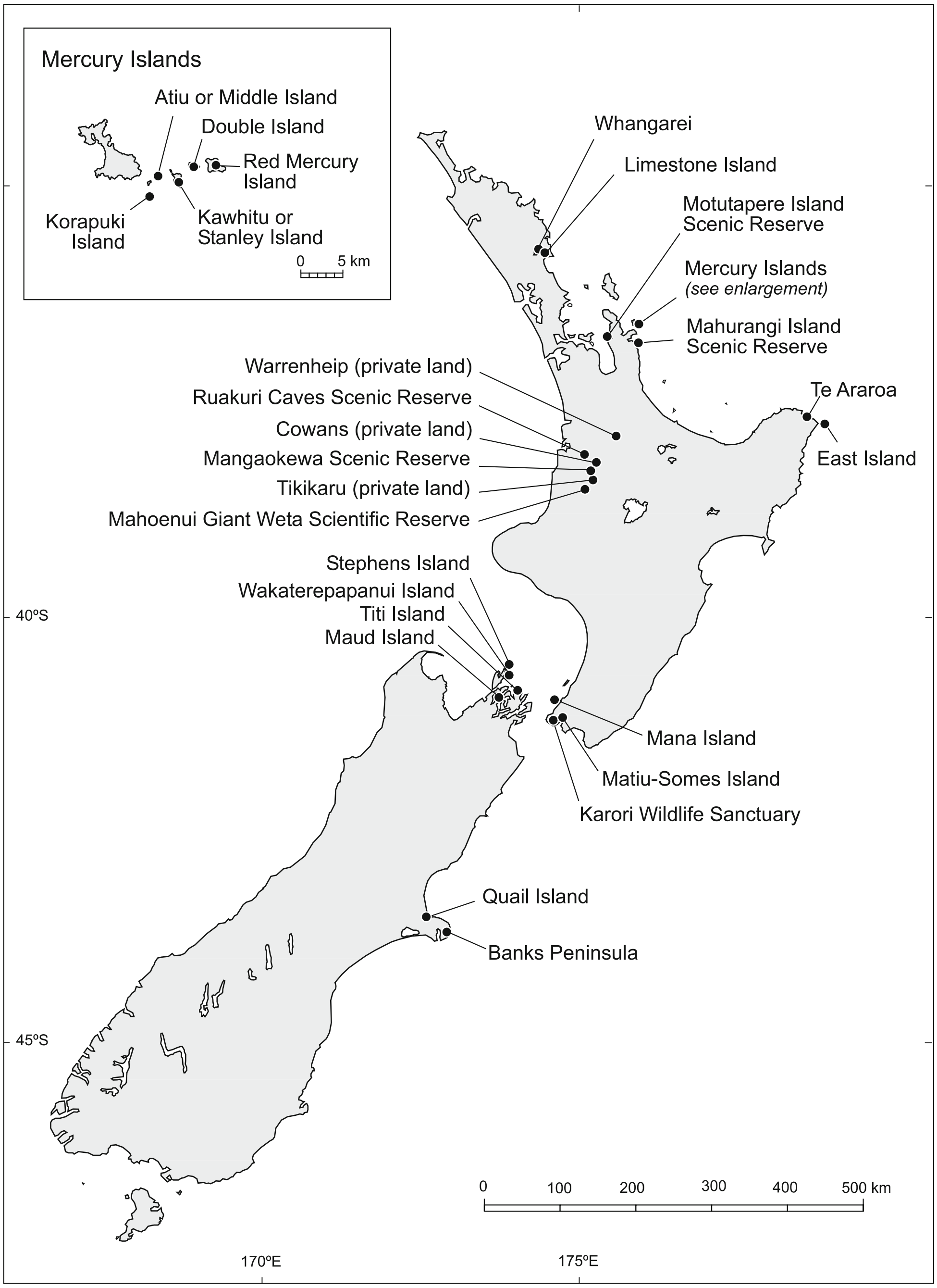
Translocating native species, particularly in New Zealand, has become an important aspect of conservation management and there has recently been a proliferation of translocation-related publications (Seddon et al. 2007). However, there is a clear taxonomic bias in transfer projects and only 9% involve invertebrates (Seddon et al. 2005). Indeed, until the 1990s, nearly all transfers of insects worldwide involved butterflies (New et al. 1995); other invertebrate groups, such as Coleoptera and Orthoptera, are only now being considered (e.g. Knisley et al. 2005; Berggren 2007; Parrish and Stringer 2007; Pearce-Kelly 2007; Seddon et al. 2007).

A wide variety of terms have been used to refer to transfers of animals for conservation and this has caused some confusion in the literature (Hodder and Bullock 1997; JNCC 2003). We follow IUCN (1998) where a re-introduction is a transfer of a species to an area that was once within its historical range; a translocation is the transfer of wild individuals from one part of their present range to another; supplementation is the addition of individuals to an existing population; and a conservation introduction is a transfer outside its recorded distribution. However, we use the term transfer in the following account when we do not know if a transfer is a translocation, a reintroduction or an introduction. This has been necessary because in New Zealand, the ranges of many threatened invertebrates became restricted soon after the arrival of humans, leaving no evidence of their former distributions and transfers are now usually made to localities where they were likely to have been present.

Case study 1: Transfer by release followed by intermittent monitoring in subsequent years

One of the first intentional transfers of insects in New Zealand involved Mahoenui giant weta (*Deinacrida mahoenui*). Two populations of this large (adult body length of 50–62 mm) dark-brown, long-legged weta were discovered in 1963 (Sherley and Hayes 1993). While one population is now presumed extinct, weta are common at the other, the Mahoenui giant weta Scientific Reserve (Fig. 1). Most weta in this 240 ha reserve inhabit gorse (*Ulex europaeus*), a seral thorny shrub that became a weed after it was introduced into New Zealand for hedgerows in pastureland. The prickly foliage apparently provides the weta with both food, shelter and protection from mammalian predators (Sherley and Hayes 1993; McIntyre 2001). This habitat was managed using cattle and feral goats, both normally considered pests on conservation land, in order to retain the gorse and prevent regeneration of native plants. Elsewhere, native vegetation does not offer the same protection against predation by rodents as does gorse-dominated vegetation. However, the dense dry dead foliage associated with gorse creates a high fire risk so weta were transferred to other

Fig. 1 Locations of known weta transfers in New Zealand



localities to reduce the risk of losing the species should the reserve burn (Sherley and Hayes 1993; Sherley 1995, 1998). The transfers involved 2,050 individuals in 32 releases at 7 locations between 1989 and 2002 (Table 1). All of the transfer locations were legally protected and had similar habitat to the Mahoenui Giant weta reserve: five were mainland sites and two were islands. Most weta were collected from the wild, transported to the release sites, and let go usually into bushes at densities and with age structures similar to those where they were found. For example, adult pairs found together were released alongside each other at a release site. At one site, Mangaokewa Scenic Reserve, a total of 220 captive-bred weta were also released, together with 467 wild collected weta (Table 1).

Occasional follow-up searches were made 10–26 months after the transfers, to determine survivorship at three of the transfer locations (Sherley 1995) but elsewhere, no surveys were done until Watts and Thornburrow (accepted) made substantial searches at all 7 release sites. They reported that Mahoenui giant weta survived at four locations but were readily found only at locations where introduced mammalian predators (rats) had been removed at Mahurangi

Table 1 Weta transfers in New Zealand

Species	Donor location	Transferred to	No.	Date	Monitoring	Population status
Deinacrida rugosa	Mana Island	Maud Island	43	Sept 1977	Yes	Wild-wild transfer: Successful 1992[a]
	Mana Island	Matiu-Somes Island	34 & 28	Mar & Apr 1996	Yes	Wild-wild transfer: Successful 2007[b]
	Maud Island	Titi Island	92 (30M, 62F)	Feb 2001	No	Wild-wild transfer: Status not confirmed
	Stephens Island	Wakaterepapanui, Rongitoto Islands	42 (5M, 13F, 24J)	Oct 2003	No	Wild-wild transfer: Status not confirmed[c]
	Nature Land, Nelson	Wakaterepapanui, Rangitoto Islands	13 (7M, 6F)	May2004	Yes	Captive-bred for release: Status not confirmed[c]
	Matiu-Somes Island	Karori Wildlife Sanctuary	100 (25M, 75F)	Feb 2007	Yes	Wild-wild transfer: Status not confirmed
Deinacrida mahoenui	Mahoenui giant weta Scientific Reserve	Mangaokewa Scenic Reserve	687 (9 transfers)	Feb 1989–Mar 2000	No	Wild-to-wild and captive-bred-to-wild transfer: 1 weta found, population not viable 2007[d]
	Mahoenui giant weta Scientific Reserve	Cowan's—private land	374 (5 transfers)	Dec 1989–Oct 1992	No	Wild-to-wild transfer: Unsuccessful 2007[d]
	Mahoenui giant weta Scientific Reserve	Ruakuri Caves Scenic Reserve	179 (11 transfers)	Dec 1993–Mar 2000	No	Wild-to-wild transfer: Unsuccessful 2007[d]
	Mahoenui giant weta Scientific Reserve	Mahurangi Island Scenic Reserve	295	Dec 1993	No	Wild-to-wild transfer: Successful 2007[d]
	Mahoenui giant weta Scientific Reserve	Motutapere Island Scenic Reserve	54	Apr 1998	No	Wild-to-wild transfer: Unsuccessful 2007[d]
	Mahoenui giant weta Scientific Reserve	Tikikaru—private land	123 & 50	Mar 2000 & Mar 2001	No	Wild-to-wild transfer: 1 weta found, not a viable population 2007[d]
	Mahoenui giant weta Scientific Reserve	Warrenheip—private land	100, 100 & 87	Nov 2001, Mar 2002 & Apr 2002	No	Wild-to-wild transfer: Successful 2007[d]
Motuweta isolata	Middle Island	Double Island	82	May–Sept 2001	Yes	Captive-bred for release: Successful 2006[e]
	Middle Island	Red Mercury Island	50	May–Sept 2001	Yes	Captive-bred for release: Successful 2006[e]
	Middle Island, Double Island	Korapuki Island	200	Jul 2007	Yes	Captive-bred for release: Status not confirmed
	Middle Island, Double Island	Stanley Island	200	Jul 2007	Yes	Captive-bred for release: Status not confirmed
Hemideina thoracica	Double Island	Korapuki Island	52	May 1997	Yes	Wild-wild transfer in retreats: Successful 2005[f]
	Te Araroa	East Island	55 (8M, 32F, 15J)	Nov 2002	No	Wild-wild transfer: Successful 2007[g]
	Whangarei	Limestone Island	100	Apr 2000	No	Unknown[h]

Table 1 continued

Species	Donor location	Transferred to	No.	Date	Monitoring	Population status
Hemideina crassidens	Mana Island	Matiu-Somes Island	33 (14M, 19F)	Apr 1996	Yes	Wild-wild transfer in retreats: Successful 2000[i]
	Mana Island	Matiu-Somes Island	26 (7M, 19F)	Aug 1997	Yes	Wild-wild transfer in retreats: Successful 2000[i]
Hemideina ricta	Banks Peninsula	Quail Island	28	Jan 2005	Yes	Wild-wild transfer in retreats: Status not confirmed[j]

M, male; F, female; J, juvenile (gender not determined)

[a] Meads and Notman (1992)

[b] Watts et al. (in preparation) 2007

[c] Mike Aviss, Department of Conservation, personal communication (2008) and Gail Sutton, Naturelands Nelson, personal communication (2008). Weta release in May 2004 were progeny from 10 captive giant weta collected from Stephens Island. This captive population at Naturelands has been allowed to die off

[d] Watts and Thornburrow (accepted)

[e] Stringer and Chappell (2008)

[f] Green (2005)

[g] Two *H. thoracica* seen during seabird monitoring in Mar 2007

[h] Clarke (2001)

[i] *H. crassidens* populations established as monitoring begins May 2000

[j] Bowie, Lincoln University, personal communication (2007)

Island (23 ha) and at Warrenheip (16 ha) (Watts and Thornburrow accepted). Warrenheip is on mainland and is enclosed by a predator-proof fence designed to prevent mammals from re-invading.

Case study 2: Transfer by initial release in a cage followed by liberation into the wild

This method was explored by Sherley (1998), with Mahoenui giant weta as an alternative to releasing insects directly into the wild. The intention was to allow the founder insects to reproduce within a cage while protected from predators, and once this was successful lift the mesh sides to allow the progeny to disperse. A total of 179 weta were collected from Mahoenui giant weta Scientific Reserve between 1993 and 2000, and liberated on 11 separate occasions within a cage (6 m × 10 m × 3 m high) containing gorse at Ruakuri Caves Scenic Reserve (Table 1). Establishment was unsuccessful (Watts and Thornburrow submitted), partly because predator control was inadequate and possibly because the exclosure became too hot.

The only post-release monitoring method available for the first two case studies was based on searching for the insects. However, the efficacy of this method depends on observational skills of the searchers and it can provide unreliable results if unexperienced searchers report no sightings. The following case studies aimed both to develop more reliable survey and monitoring techniques and to improve the likely success rate of transfers.

Case study 3: Transfer and monitoring using artificial retreats

Our third example involves transferring tree weta (*Hemideina* species, adult body length 50–70 mm) whereby artificial retreats were used both to facilitate the actual transfers and to monitor the weta populations after the transfers. This was first used with Wellington tree weta (*H. crassidens*) in 1996 and 1997 in a transfer from Mana Island (217 ha) to Matiu-Somes Island (25 ha). Subsequently, in 1997, Auckland tree weta (*H. thoracica)* were transferred from Double Island (33 ha) to neighbouring Korapuki Island (18 ha) within the Mercury Islands group (Green 2005) (Table 1). Both transfers were part of the restoration plans for these islands after introduced rodents were eradicated from them (Towns and Atkinson 2004; Department of Conservation 1998). These weta are the two most common tree weta species in New Zealand (Gibbs 2001) and their transfers formed parts of a broad range of significant faunal elements that are planned for return to these islands.

For the Matiu-Somes Island transfer, artificial retreats containing single cavities (Ordish 1992) were attached to trees on Mana Island and left for about 6 months to be colonised by weta. These retreats, together with their resident weta (33 individuals in total), were then transferred to and attached to trees on Matiu-Somes Island (Table 1). The transfer was first monitored in May 2000, when a series of new artificial retreats, providing 120 artificial galleries, were placed around the release area. Occupancy of these retreats, and a network of new retreats with multiple galleries (Trewick and Morgan-Richards 2000), was then checked monthly for 6 years and each adult weta encountered was individually numbered in order to follow their progress as they established on the island. Initial expansion of the population was rapid, with numbers in a subset of 56 galleries reaching 73 by March 2001 and 138 by March 2003. Thereafter, weta numbers in artificial galleries declined in the release area to 17 in 2005 and 22 in 2006. A further series of artificial retreats, distributed around the island, revealed that colonisation was spreading throughout shrub-land that was regenerating. By 2005, the highest densities were in a new focal area approximately 400 m south of the release site.

Not only did the distribution of weta over the island change between 2000 and 2005, but a major morphometric change occurred. Initially, the rapidly expanding colonising population was characterised by an unusually high frequency (38%) of diminutive male adults. These are individuals that have precociously become sexually mature in their 8th instar, with a head size that is half the length of a fully developed adult male in its 10th instar (Spencer 1995; Gibbs 2001). No adult males as small as these were present in the donor population on Mana Island, where all are 9th or 10th instars. Males of this polygynous species rely on their head weaponry for achieving a dominant position in the gallery hierarchy that exists in normal tree-weta populations (Field and Deans 2001; Kelly 2005). It appeared that although the transferred population on Matiu-Somes had increased rapidly into a new habitat, it was possibly under some kind of environmental stress. This interpretation was borne out by trends at the southern end of the island, where the tree-weta again assumed a size distribution approaching those on Mana Island. We suspect that nutrition may be an important factor for determining size at maturity and that for some reason, their release site was deficient (although it allowed rapid expansion) but the weta have now found an optimal location where their full lifestyle can be exploited.

In the Mercury Islands, smaller artificial retreats were used to transfer and monitor tree weta populations on both the donor island and the destination island (Green 2002).

Two hundred wooden retreats each with a single gallery were attached to trees 1–2 m above the ground on Double Island in December, 1996 (Green 2005). By May 1997, half the retreats were occupied with one or more weta and 39 of them, containing 52 adult weta, were transferred to Korapuki Island where they were attached to trees. Weta were not handled during the transfer, and the transfer was completed within 1 day to minimize possible stress to the insects.

The donor weta population on Double Island was monitored twice yearly for 3 years following the transfer by examining 200 retreats. By November 1997, occupancy of these retreats had reached 65% and thereafter varied between 32% and 64%. The high occupancy rates indicated that the removal of 52 weta had no apparent adverse effects on the donor population.

The transferred population on Korapuki Island was also monitored twice annually after the transfer using additional wooden retreats as well as short lengths of bamboo with smaller internal cavity diameters (Green 2005). All retreats were attached to trees in and around the release site. One week after the release 75% of the adult weta were still present in the retreats, 5 months later 68% were present, and by February 1998 only 31% of the adults remained. The first juveniles (10) appeared in the bamboo retreats in February 1998. Thereafter, the numbers of weta in retreats steadily rose to reach a 10-fold increase 4 years after the release. Weta were also observed in natural retreats both within the release site and beyond this.

Case study 4: Monitoring individuals of a rare weta after their release

This example involves establishing additional populations of the very rare Mercury Islands tusked weta (*Motuweta isolata*, adult body length 46–73 mm), to reduce the chances of accidental extinction while, at the same time, contributing to the restoration of the fauna of other Mercury Islands. In this case, the released weta were repeatedly located after the transfer to determine how long they survived, and a monitoring plan was established to confirm if they became established.

These weta were vulnerable because only one small population on Middle Island (13 ha) remained. Population estimates between 1990 and 1993, when the weta were most frequently seen, were of 75–178 mid-sized to adult individuals. Little was known of the autecology of the species because of their extremely cryptic behaviour: they dig shallow underground chambers where they remain for many days or weeks and usually emerge to feed on other invertebrates on moonless nights that are warm and humid (McIntyre 2001; Winks et al. 2002). Given a lack of contrary biogeographic evidence, it was assumed that the tusked weta once inhabited all the larger Mercury Islands before the arrival of commensal Pacific rats brought by Polynesians because the Mercury Islands formed a single island ~6,500 years ago (Towns 1994). However, Middle Island remained free from rats, allowing the survival of this remarkable weta (McIntyre 2001).

The transfers initiated by the New Zealand Department of Conservation were designed to ensure the long-term survival of this species. A Middle Island Tusked Weta Recovery Group was set up in 1990 whose aim was to establish additional populations on nearby islands from which introduced mammals have been eradicated (Towns and Broome 2003). A successful captive-rearing method was developed by Winks and Ramsay (1998) following advice from Gibbs (1990) that there were too few tusked weta on Middle Island to harvest for wild-to-wild transfers. A total of 134 weta were then reared from one male and two females collected in 1989 (Winks et al. 2002) and transferred to Double Island (33 ha) and Red Mercury Island (225 ha) between 2000 and 2001. These two transfers were intended as experiments using small numbers of weta to determine if they survived after release. The intention was to follow the released insects as much as possible to gauge the likelihood of their surviving at the release site. If these transfers were successful, more transfers were planned using larger numbers of weta.

Most tusked weta were liberated as half-grown juveniles with fewer being larger juveniles or adults: 81% were released under artificial cover objects (ACOs) made from plant-pot saucers and the remainder were released in holes made in the ground. As with tree weta, the ACOs were provided as artificial retreats, although those for tusked weta were aimed at mimicking the underground chambers made by these weta in the wild (McIntyre 2001; Winks et al. 2002). Some weta did use ACOs after release, which afforded an easy and convenient monitoring method. However, the numbers under ACOs varied erratically, generally reduced with time, and were restricted to the release group. The results did, however, show that some weta that were released as juveniles grew into adults and that these adults survived for up to 7 months. This indicated that the new habitats could support the weta and this was confirmed because they also reproduced successfully, and by 2006 had passed through up to 3 generations on both islands (Stringer and Chappell 2008).

Additional monitoring methods were also explored. These included the use of adult weta equipped with harmonic radar transponders and miniature radio transmitters to lead searches to other weta when the weta paired. Both techniques had been used previously on insects in New Zealand: Lövei et al. (1997) first used harmonic radar on carabid beetles whereas Richards (1994) developed the technique of using miniature radio transmitters on weta in 1991. Both techniques were considered more appropriate for locating tusked weta when they were widely dispersed but when they were present in moderate to high densities the best method for monitoring them was to search plots by scraping the topmost layer of soil off. This revealed the insects in their shallow underground galleries and has the potential to give estimates of absolute density (Stringer and Chappell 2008). Plot searches will now be used on a biennial basis to monitor these populations in the foreseeable future.

In this case, surveys were undertaken on both islands before the transfers were made to establish if these weta were not already present. In the previous case studies, weta were either assumed to be absent because of the presence of predators and a lack of sufficient protective habitat (case studies 1 and 2) or the islands were so frequently visited they were known to be absent because of an absence of the distinctive stridulation made by the adult weta (Field 2001).

There is however, a potential problem with these transfers because the weta that founded the new populations originated from only one male and two females collected from Middle Island. While these three weta happened to be among the last tusked weta seen on Middle Island, it is possible they still survive there in very low numbers. However, if they are ever seen again in any numbers on Middle Island, the intention is remove additional breeding stock to supplement the existing populations on Double Island and Red Mercury Island for genetic reasons (Stringer and Chappell 2008). In the meantime, to reduce the extinction risk still further, six individuals from the expanding Double Island population were removed for captive rearing and 200 of their progeny released onto each of Korapuki Island and Stanley Islands (200 individuals onto each island) in the Mercury Island Group during 2007 (Table 1).

Case study 5: Studying post-transfer dispersion behaviour

Finally, we examine a recent transfer of 100 adult Cook Strait giant weta (*Deincrida rugosa*, adult body length 54–67 mm), to restore the fauna of a mainland area enclosed by a predator-proof fence (Karori Wildlife Sanctuary, Wellington) in February 2007. This was the first time Cook Strait giant weta had been transferred from an offshore island to a mainland site, from which they had been extinct for over 100 years. The transfer was conducted after all mammalian predators, apart from mice (R. Empson, personal communication, 2007), had been eradicated from within the fenced sanctuary. The transfer was well documented with morphometric data recorded for each transferred weta. Detailed information was obtained on the movements and survival of these insects after they were released because there are no data on how any weta behave after release. Furthermore, little was known of their survival in the presence of mice and the suite of endemic avian predators that exist in Karori Wildlife Sanctuary. Intensive daily and nightly monitoring was conducted over two months for 20 weta equipped with miniature radio transmitters. All weta were located daily and it was only rarely that the precise position of a weta could not be determined because of concealment in difficult habitat such as under a pile of fallen trees. The results indicated that 25% of the radio-tracked adult weta died towards the end of the 2-month study, probably of natural causes. None were consumed by predators. Males moved on average 33 m per night with a maximum distance of 295 m, while females travelled on average 12 m per night (Watts et al. in preparation). These weta travelled substantially further than expected based on a study of resident Cook Strait giant weta that was carried out on Mana Island, the original donor population for this species (M. McIntyre, personal communication). In addition, the study by Watts et al. (in preparation) successfully developed a new method for monitoring giant weta after they are released using radio telemetry.

Transfers of other weta species

We conclude with a summary of all other transfers of anostostomid weta known to us. The information was obtained from a literature search that included grey literature such as unpublished Government file reports and information provided directly by the people who made the transfers (Table 1).

Three other species of weta have been involved in transfers in New Zealand in addition to the transfers detailed above (Table 1). These additional transfers involved six islands, and on eight occasions where weta were transferred, they were moved between islands. On another occasion the transfer was from the mainland to East Island (Table 1). For example, Cook Strait giant weta was transferred from Mana Island to Maud Island (267 ha) in 1977 and from Mana Island to Matiu-Somes Island in 1996 (Table 1). Weta are now abundant on both the donor islands and are now being considered as donor populations for further transfers. While there was a single transfer of 13 captive bred weta to Wakaterepapanui Island in May 2004 (Table 1), the captive population at Nature Land has not been maintained (G. Sutton, personal communication). One visit to Wakaterepapanui Island has not been successful in finding weta (Department of Conservation unpublished report January 2007) so there is no indication of whether the transfers have been successful. The Auckland tree weta transfer to East Island in 2002 may have resulted in an established population although this requires verification because two weta were seen incidentally in 2007 during a sea-bird monitoring trip.

In all but one of these additional transfers of weta the main reasons given for the transfers were (1) establishing another population of an endangered or threatened species, and (2) restoration of the original native island community before human-induced modification (such as introduced rodents). The exception was the transfer of Auckland tree weta to East Island in 2002. This was done to provide a food source for tuatara (*Sphenodon punctatus*) when they are released there in the future. There was also a research component associated with the transfer of Banks Peninsula tree weta (*H. ricta*) to Quail Island. The intention is to monitor weta abundance on the island and compare it with mainland populations where predators are present in an attempt to infer what the effects of predation are on this species. In addition, samples were taken from the released weta for future genetic analysis to document the effect of a genetic bottleneck on the long-term establishment success of the population.

Discussion

The importance of islands in New Zealand insect conservation

In New Zealand, there is an obvious advantage to using islands free of introduced mammalian predators for conserving threatened species: the predator-free status of islands is easier and more cost efficient to maintain than are areas on the mainland. Nevertheless conserving threatened invertebrate species by transferring them to islands is still in its infancy. A database of transfers in New Zealand up to 2002 held by the Department of Conservation lists 98 attempted transfers of 30 species of birds, 40 attempted transfers of 12 species of reptiles, but only 14 transfers of invertebrates, including 6 species of weta. All of the invertebrate transfers involved islands. However, the first documented transfer of an invertebrate in New Zealand for conservation purposes was the 1934 release of a giant land snail, *Placostylus hongii*, onto Motuhorapapa Island in the Noises group (Powell 1938). This is well before the first reptile was transferred in 1942 but long after the first transfer of a bird in 1890. All six invertebrate transfers recorded on the Department of Conservation database were after 1996, indicating that transferring invertebrates to islands is becoming a more frequent.

Early transfers of weta were aimed at species conservation but more recently ecosystem restoration has also become an important aim. The latest releases, that were outlined in case study 5 and the release of the Mercury Islands tusked weta to Ohinau Island, have the additional objective of making the weta accessible to the public, which has a growing interest in and awareness of weta, especially the larger species. Increasing numbers of predator-free areas are also being established on the New Zealand mainland and there is now a growing demand to have examples of iconic insects present. For example, there are now 34 different private conservation projects in the North Island involved in creating mammal-free areas or areas where mammals are controlled to low densities (Burns, Landcare Research, personal communication, 2007) and all wish to introduce native birds and reptiles as soon as possible to attract visitors and funding. Many of these projects are likely to focus on invertebrates in the future and this should be encouraged to provide easy access to the general public and help increase their awareness of both weta and invertebrate conservation in general. In contrast, access to islands administered by the Department of Conservation is usually restricted to people doing research or management because every visit increases the risk of re-invasion by introduced mammals or other pests, weeds or diseases despite the strict biosecurity procedures that must be followed.

Future transfers of weta can present important research opportunities. Such research could be directly applicable to the introductions themselves, such as those in case studies 3 and 4; to related topics, such as in case study 5; or to helping answer more fundamental questions in ecology and evolutionary biology, as suggested by Sarrazin and Barbault (1996). With respect to weta transfers, the most pressing need is to investigate the genetic implications of highly restricted founder populations and this is planned for tusked weta where samples are available from the three parent weta used to establish the captive-breeding programme. So far no weta transfers have been planned as experiments in the sense of Armstrong et al. (1994) where simultaneous releases are made to treatment and non-treatment locations to address a specific question. The transfers of Mahoenui weta do provide some evidence of the effect of mammalian predators on the survival and establishment of this weta, but we follow the recommendations of Armstrong et al. (1994) and Seddon et al. (2007) of taking an experimental approach in future, whenever possible. This is certainly possible when common insects are involved. Details of past transfers can also provide valuable information on long-term establishment in relation to the number of insects released and we re-emphasise the importance of documenting as much information as possible relating to a transfer and, in the case of invertebrates, including the precise locations where the animals were collected and released; the number, sex and life-history stages of the individuals released; how the animals were caught, moved and released; and the personnel involved with all aspects of the transfer. We also advocate that a genetic sample is taken from each of the released insects wherever possible. In insects with long antennae, such as weta, this could be a small section of the antenna. Surveys made at the release sites before and after a release should also be fully recorded. Such documentation is either prescribed or implied by the procedures given in guides for transferring animals (IUCN 1998; Cromarty 2002; JNCC 2003).

Advances in planning and procedures

The early transfers of weta were motivated by one or a few individuals seeking to conserve a species by establishing multiple populations of that species. Sometimes this involved releasing weta to new locations outside their known biogeographic range. Examples are the transfers of Mahoenui giant weta to Mahurangi and Motutapere Islands, where both are probably outside the historical range of this species (Watts and Thornburrow submitted). There was little or no consultation with external agencies such as indigenous people or even at a national level within the organisations where the individuals worked who did the transfers. In the case of the transfers to Mahurangi and Motutapere Islands, permission was first obtained by the Waikato Conservancy of the Department of Conservation (DOC), but there were no pre-transfer surveys of the release sites and little planning was done for the transfers. In these cases it was assumed that the species did not occur on these islands because rats had been present and they were likely to have caused the local extinction of this species (if, indeed, they occurred there in the first place). An unfortunate aspect of these early transfer efforts was the virtual lack of post-transfer monitoring to determine how long the insects survived and it was left to the distant future to determine whether new populations established or not.

Today transfers for conservation purposes within New Zealand involve comprehensive proposals that are subjected to formal review and approval processes. These proposals also require justification in terms of appropriate species recovery and restoration programmes (Cromarty 2002). This process is applied to all species that are listed as threatened, including insects (Hitchmough et al. 2005), as well as to other animals to protected areas but is often ignored for transfers of common species to non-legally protected areas, and thus these are often poorly documented. Transfers of common species should follow the same procedures as described above not only to understand better why some transfers succeed while others fail, but also to document the changes in species distribution and to help ensure future options for the transfer sites are not compromised.

New Zealand has a long history of transferring threatened vertebrate species onto predator-free islands. Such transfers have undoubtedly played a crucial role in securing the survival of many species, particularly birds. In many cases the islands were once seen simply as safe-havens for these vertebrates and little or no consideration was given to the effects on the indigenous fauna of the islands themselves. This may have compromised the potential for future transfers to some islands. After all, islands, especially those with quality habitat suitable for native species introductions, *are* a finite resource. Each time a new vertebrate is established on an island, it increases the potential difficulties for establishing invertebrates there in the future and it may even reduce the options of which invertebrates may be moved there. We foresee an increasing need to facilitate the establishment of threatened invertebrate species in areas where the native insectivorous vertebrate species could actively work against the invertebrate species' establishment. As an example, during a recent release of two beetle species on Lady Alice Island, Hen and Chicken group, large cages were constructed to protect the beetles from predation by resident reptiles as well as the insectivorous birds that had previously been established there. The intention was to release the beetles' progeny after they reproduced (Parrish and Stringer 2007). The techniques used in recent successful transfers (Case studies 3, 4 and 5) may also have to be adapted to facilitate the survival of weta when they are transferred to other islands that now include a suite of native vertebrate insectivores, or at least to mitigate the effects of these predators so as to ensure establishment. Increasingly effective monitoring methods also provide opportunities for exploring possible changes due to small initial population size such as demographic stochasticisty and Allee effects. In New Zealand, transfers of weta to islands are certainly leading the development of reintroduction biology for invertebrates by exploring and exploiting a variety of transfer and monitoring methods that may have applications to other conservation initiatives involving invertebrates in the future.

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ORIGINAL PAPER

Possible rescue from extinction: transfer of a rare New Zealand tusked weta to islands in the Mercury group

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Abstract The rare Mercury Islands tusked weta, *Motuweta isolata* (Orthoptera: Anostostomatidae), a large flightless insect originally confined to 13 ha Middle Island in the Mercury Islands, New Zealand, was last seen there in January 2001. Half-grown or larger insects from a captive-breeding programme were released onto nearby Red Mercury Island (34 ♀, 16 ♂) and Double Island (65 ♀, 19 ♂) in 2000 and 2001 to reduce the potential for accidental extinction. Most (108) were released under individual artificial cover objects (ACOs)—clear Perspex discs under plastic plant-pot saucers—and 26 were placed in artificial holes in soil. Usually <10% were found again under ACOs for up to 18 months including 7.5 months as adults. Adults, found in 2005 and 2006, were 1st to 3rd generation island-bred weta (lifespan 1.7–3.2 years). Ongoing monitoring is planned to confirm long-term success. Inbreeding depression is likely so supplementation from Middle Island is required but they may be extinct there. Scraping the soil to expose weta in underground galleries was the best monitoring method. Few were found by searching with lights at night but adults could be located by following other adults equipped with harmonic radar transponders or micro-transmitters.

Keywords Relocation · Island conservation · Monitoring · Harmonic radar · Radio-tracking

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Introduction

Conservation managers sometimes face the dilemma of how to proceed when a threatened animal becomes scarcer and the reason is not known. This occurred with the rare Middle Island tusked weta, *Motuweta isolata* (Orthoptera: Anostostomatidae), a large carnivorous flightless insect (adult body length 46–73 mm; mass 8.6–34 g) that occurred only on Atiu or Middle Island (13 ha), in the Mercury Islands, New Zealand (Fig. 1). With fewer than 200 large juveniles and adults estimated to be present early in the 1990s (McIntyre 2001), it was critically endangered. When numbers later plummeted an attempt, documented here, was made to establish the species on two nearby islands, Double Island and Red Mercury Island. These weta were found only by searching at night and little was known of their ecology and habitat requirements (McIntyre 2001) so experimental transfers were made to test if the insects survived and at the same time new monitoring methods were tested on the insects that were released (Stringer 2005).

Transferring animals is well established in conservation management although this has been done mostly with vertebrates (New 1995). The relatively few published examples with insects do, however, include other species of New Zealand weta (Meads and Notman 1992; Sherley 1998; Green 2002). Nowadays more insects are being transferred or considered for transfer as increasing attention is focused on their conservation (New and Sands 2004; Hochkirch et al. 2007) and there are also guidelines and recommendations for such procedures (e.g. Anon 1986; IUCN 1998). In addition, there is an extensive literature on the intentional transfer of insects for a variety of other purposes such as biological control, pasture improvement, food production, or as pets (e.g. Doube and Macqueen

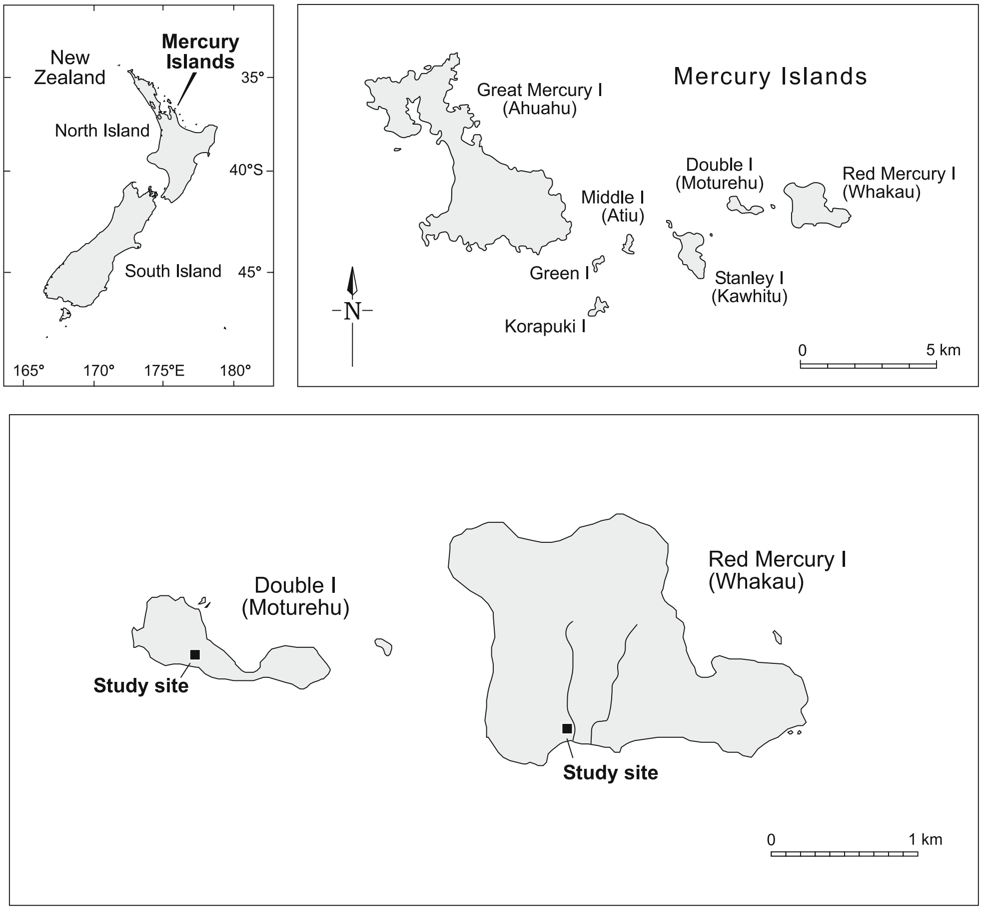

Fig. 1 Map of the Mercury Islands showing the islands mentioned in the text and the positions where tusked weta, *Motuweta isolata*, were released onto Double Island and Red Mercury Island

1991; Howarth 1991; Morris et al. 1991; Cooper 2004; Crane 1999).

In general, a good knowledge of an insects' autecology is considered essential if transfers are to succeed (e.g. Samways 1994; New 1995; Holloway et al. 2003) but this entails considerable research time. Even then, many transfers fail and often for unknown reasons (Oats and Warren 1990; Cameron et al. 1993; Fischer and Lindenmeyer 2000). We planned to maximise the information obtained by attempting to monitor weta after they were released to assess their survival. Reproductive success was also assessed but this took longer because of the 2–3 years generation time (Stringer et al. 2006). Most weta were released as juveniles that could not be followed individually because any marks or tags on cuticle are lost at moulting. Instead, they were released under artificial cover objects (ACOs) with the expectation that some would remain there and allow us to monitor them. This seemed likely because this weta lives in individual underground chambers and repeatedly returns to them at night after feeding on other invertebrates (McIntyre 2001; Winks et al. 2002). ACOs can provide a fast and cost-effective monitoring method that does not harm the animal. They can also increase detection rates for rare and cryptic species whilst incurring minimal habitat damage (Lettink and Cree 2007 and references therein).

Other monitoring methods tested were searching plots and using adult weta equipped with harmonic radar transponders (HR transponders) and micro-transmitters to lead us to other untagged weta they paired with. Lastly, as a precaution in case none of the weta were found again, some were released into a predator-proof cage on Red Mercury Island and followed using all of the monitoring methods. In addition, the behaviour of these caged insects immediately after their release was also investigated using infra-red time lapse video to check if they do return to their burrows. Trays of suitable oviposition substrate were provided so we could determine when they started ovipositing.

These experimental transfers were made possible because Winks and Ramsay (1989) developed a method for captive-rearing tusked weta. Their work was initiated by the Mercury Islands Tusked Weta Recovery Group which was formed in 1990 by the New Zealand Department of Conservation soon after the vulnerable status of this insect was recognised. The aim was to establish additional populations of this weta on other islands to reduce the chance of accidental extinction. The decision to start a captive-breeding programme followed a report by Gibbs (1990) that there were too few weta on Middle Island to effect wild-to-wild transfers. As a result, two females and one male weta were collected from Middle Island in 1998 (Winks et al. 2002) to captive breed insects for the experimental transfers described here. The intention was to make additional transfers of weta captive-bred from a larger number of insects collected from Middle Island if the experimental transfers were successful. However, the three weta collected for captive rearing were amongst the last 9 to be seen on Middle Island following a severe drought in 1993–1994. None have been found there since January 2001 despite 11 unsuccessful searches involving 308 person hours of searching over 34 nights up to January 2007. These insects may still be present in very low numbers because they are difficult to find—they can remain in their chambers for many weeks and usually emerge only on moonless nights when it is calm, warm and humid (McIntyre 2001; Winks et al. 2002; Stringer 2006). This behaviour, together with this insect's rarity, explains why *M. isolata* was not discovered until 1970 (Johns 1997), despite its large size.

Methods

Transfer sites

Double Island (Moturehu, 33 ha) and Red Mercury Island (Whakau, 225 ha) (Fig. 1) were chosen for the relocations because this tusked weta probably originally occurred on all of the Mercury Islands—they were a single island ~6,500 years ago when sea levels were lower (Hayward 1986; Towns 1994). We consider the transfers are likely to be re-introductions using IUCN (1998) terminology, but we use the term 'transfer' here because evidence of the former distributions of most New Zealand insects disappeared following the habitat destruction that occurred after humans arrived. It is believed that tusked weta disappeared from most of the Mercury Islands after Pacific rats (*Rattus exulans*) colonized them and that they survived only on Middle Island because it remained rat-free. Middle Island lacks free water, is largely surrounded by cliffs and humans have never lived there (McIntyre 2001). However, Double Island and Red Mercury Island are now rat-free following eradications in 1989 and 1992 (Towns and Broome 2003). An additional aim for establishing tusked weta on other Mercury Islands was to help restore the islands, as far as possible, to their probable pre-human state (Towns et al.

Table 1 Numbers of captive-bred tusked weta, *Motuweta isolata*, released onto Red Mercury Island and Double Island

Place	Date	No. Weta			Stage	Source
		Male	Female	Total		
Red Mercury cage	1 May 00	3	3	6	Half grown	Captivity
Red Mercury release site 1	2, 5 May 00	15	29	44	Half grown	Captivity
	26 Apr 01	1	2	3	Adult	Red Mercury cage[a]
	26 Apr 01	0	2	2	Adult	Captivity
	14 Oct 01	0	1	1	Adult	Red Mercury cage[a]
Red Mercury release site 2	23 Sep 02	6	9	15	Half grown	Captivity
	31 Mar 03	2	0	2	Adult	Captivity
Double Island release site	5, 18 May 00	11	33	44	Half grown	Captivity
	25 Sep 00	0	17	17	Large nymph	Captivity
	24 Jan 01	2	0	2	Sub-adult	Red Mercury cage[b]
	22 Apr 01	0	8	8	Adult	Captivity
	22 Sep 01	6	7	13	Adult	Captivity

All weta released in the cage on Red Mercury Island were progressively removed and released onto Red Mercury Island or Double Island

[a] Released from cage onto Red Mercury, to prevent predation on hatchlings

[b] Transfer to Double Island to increase male sex ratio

1990; Towns and Broome 2003). The flora and vertebrate fauna of these islands are listed by Cameron (1990), Campbell and Atkinson (1999), Towns et al. (1990) and Lynch et al. (1972). Double Island is similar to Middle Island in that it is relatively dry and lacks streams whereas Red Mercury Island, with a permanent stream, was chosen in case *M. isolata* prefers moist sites, as suggested by McIntyre (2001).

Release of weta

First generation tusked were, captive-reared as described by Winks et al. (2002), were released when half grown or larger (body lengths >1.5 cm) in 2000 and 2001, and 17 second generation captive-bred weta were released >500 m away from the first release site on Red Mercury Island in 2002 and 2003 (Table 1, Fig. 1). Most were released individually in depressions dug in the ground and covered with numbered ACOs consisting of clear Perspex discs underneath plastic plant-pot saucers (Table 1, Fig. 2). The Perspex discs allowed observation to ensure that the weta were not trapped. All ACOs were left at the same locations during the study and later releases were made under ACOS that weta had vacated. The remaining weta (six on Double Island, 20 on Red Mercury Island and two in the cage) were released individually into artificially made holes ~3 cm in diameter by 10 cm deep, then the openings were covered with leaf litter (Table 1).

On Red Mercury Island, 24 ACOs were set 4–6 m apart in a zigzag pattern within the area indicated in Fig. 3a. This area sloped up from the edge of the moist stream flat. In addition, 16 release holes were made 2–5 m apart in an irregular grid pattern amongst the ACOs near the bottom of the slope. On Double Island, 22 ACOs were used initially

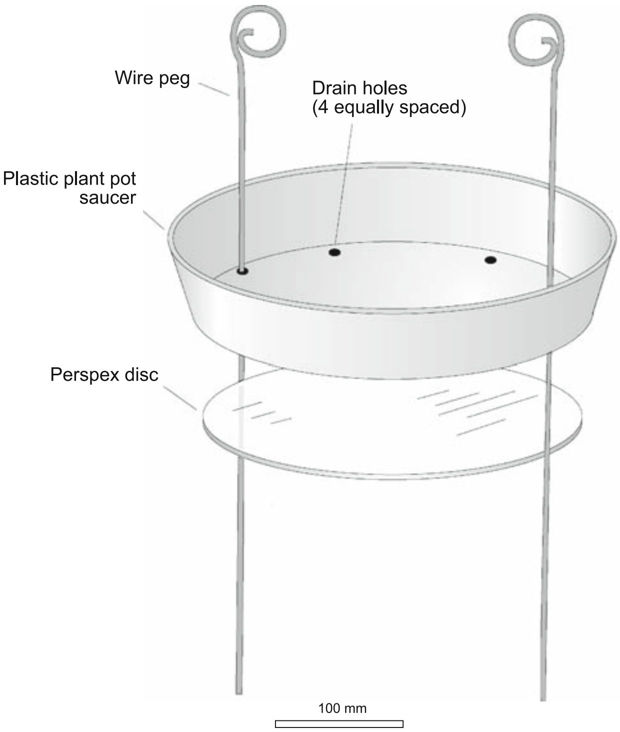

Fig. 2 Artificial cover object (ACO) used for releasing tusked weta under. Each ACO consists of a plastic plant-pot saucer (250 mm diameter) that overlies a Perspex disc

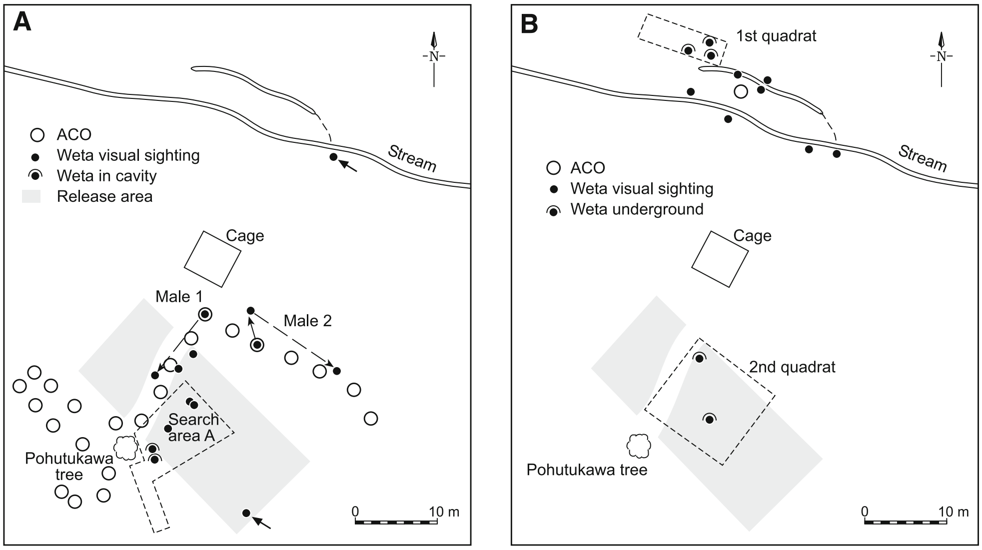

Fig. 3 Maps of the study area on Red Mercury Island showing the positions of the cage and where tusked weta, *Motuweta isolata*, were released and later found. The locality of the study area is shown in Fig. 1. (**a**) Positions are shown where tusked weta were released under artificial cover objects (ACO) or into artificial holes, and where tusked weta were found in April 2001 (indicated by arrows) and March 2003 during searches at night or by searching plots. In addition, the positions are shown where two adult male weta equipped with transmitters moved to after their release in April 2001. (**b**) Positions where tusked weta were found during searches at night and by searching plots in April 2005

set 3–6 m apart in an irregular grid pattern on a small, level area of moist soil (Fig. 4) but another 26 ACOs were added between these in April 2001.

Monitoring

The ACOs were checked whenever the islands were visited (May, September 2000; January, April, September, December 2001; January, March, April, September and December 2002; March 2003, April 2005; May 2006) and other search methods were used intermittently within 30 m of the release areas. Visual searches were made during moonless periods of the night using powerful lights. Searching plots involved carefully scraping the top ~0.5 cm of soil off over measured areas to reveal weta in their underground chambers. The plots varied in size from 25 to 100 m^2 and were situated where the surface was not densely covered with tree roots. The approximate developmental stage (instar number) of juveniles and adults was determined from measurements (±0.02 mm) made with calipers of the pronotum length and occasionally the metafemur and/or metatibia lengths (Stringer et al. 2006).

Tracking weta with harmonic radar and radio transmitters

HR transponders, each consisting of an attachment base of thin sheet copper shaped to fit the pronotum, a diode (HP5082-2835) and an aerial of fine stainless steel (Fig. 5a), were attached to adult weta with 'Supa Glue' (Selleys Pty Ltd, Padstow, Australia) after lightly scuffing the pronota with fine sandpaper. A hand-held harmonic radar unit (Type R5P1, Recco AB, Sweden) was used to locate them (Lövei et al. 1997). Single stage transmitters (~1.7 g; Sirtrack Ltd., Havelock North, New Zealand) were glued to HR transponders already attached to adult weta using a neutral curing silicone adhesive (Selleys Roof & Gutter Sealant, Selleys Pty Ltd., Padstow, Australia) (Fig. 6b) 4–6 h before weta were released, to allow the adhesive to partially set. A receiver (model FM16, Advanced Telemetry Systems, Isanti, USA) and Yagi directional aerial was used to locate them.

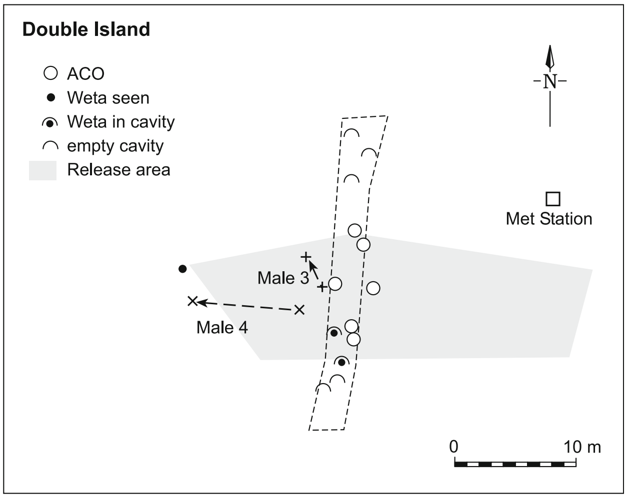

Fig. 4 Map of the study area on Double Island showing where tusked weta, *Motuweta isolata*, were released under artificial cover objects (ACO) or into artificial holes, and where tusked weta were found in March 2003 during searches at night and by searching plots. The positions of only 6 of the 48 ACOs that were in or near the area of soil searched are shown. In addition, the positions are shown where two adult male weta equipped with transmitters moved to after their release in March 2003. The locality of the study area is shown in Fig. 1

Releasing and monitoring tusked weta in a predator-proof cage

The predator-proof cage was modified from a design by Aviss and Roberts (1994) and enclosed an area of 22.5 m^2. It was situated in a small clearing under a continuous canopy of mixed broadleaf forest near the release site on Red Mercury Island with moist soil but where it was unlikely to flood (Fig. 3). Ground cover vegetation (mostly kawakawa *Macropiper excelsum*, and *Coprosma* spp.) was kept trimmed from touching the cage.

Six ACOs and four oviposition trays were initially placed inside the cage and four additional ACOs were added in April 2001. The oviposition trays, two plastic trays (410 mm × 300 mm × 60 mm high) and two plastic food containers (170 mm × 170 mm × 90 mm high) with numerous 0.5 mm diameter drainage holes, were filled with moistened commercial potting mix of equal volume of peat and pumice. The trays were placed on the ground but the food containers were dug in to ground level.

Three weta in the cage were monitored continuously during the second and third nights after being released using a custom-made portable time-lapse infra-red video recording system (incorporating a National Panasonic videotape recorder, Model AG-1070DCE and VPC-505 micro camera and lens). Illumination was provided by infra-red light-emitting diodes.

The oviposition trays were searched for eggs once the released weta became adult but this was discontinued when the first eggs were found to avoid damaging them. All adult weta were later released outside the cage to limit the number of eggs laid in the cage and to prevent adults from eating the juveniles. Once the first hatchling was found, the cage was left undisturbed for 13 months to prevent damage by trampling and to allow the juveniles to grow sufficiently large to be easily found.

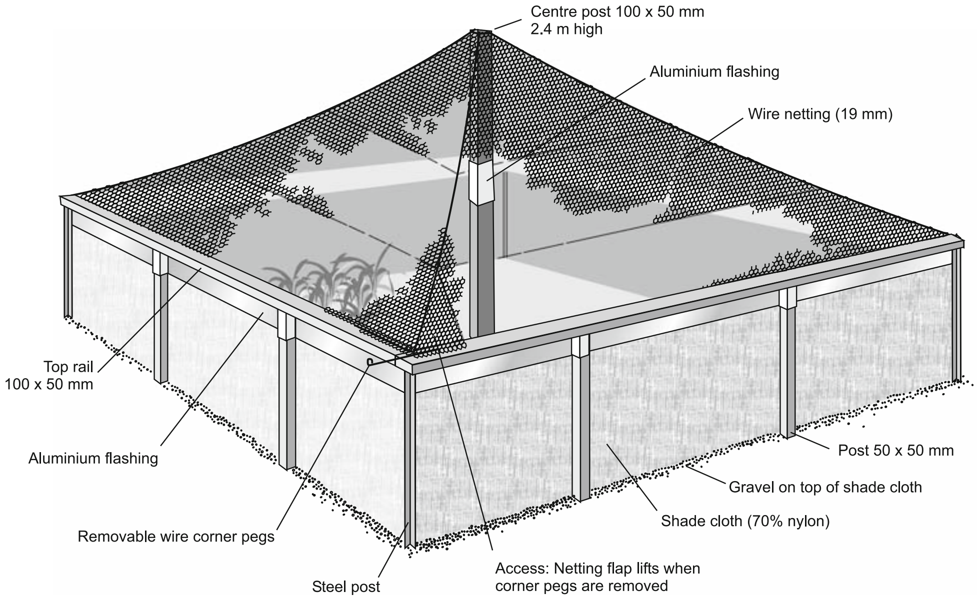

Fig. 5 Details of the cage constructed on Red Mercury Island to retain tusked weta, *Motuweta isolata*, and exclude large predators. The cage covered an area of 22.5 m^2. Construction details are given in the text

Fig. 6 Adult male tusked weta, *Motuweta isolata*. (**a**) With an harmonic radar transponder attached to the pronotum. The roof of the underground chamber has been opened to observe the weta. (**b**) With a transmitter attached to a harmonic radar transponder, which in turn is attached to the pronotum. (Photos by C. Watts)

Results

Numbers of weta released

A total of 84 captive-bred tusked weta were released on Double Island, 44 were released onto Red Mercury Island and 6 were released into the cage in 2000 and 2001 (Table 1). Most were half grown ($n = 94$, instars 4–5), 17 were large juveniles (instars 8–10), and 23 were adults (instars 10–11). All six were eventually released from the cage: two of the males were released on Double Island to increase the number of males there (Table 1) and the four females, together with two from captivity, were released on Red Mercury Island to make a total of 50 released there.

Behaviour of weta after release in the cage

All four weta released under ACOs and one of those released into an artificial hole constructed smooth-walled chambers during the first night. All were found in these chambers each day over the next 3 days. The other weta left its hole during the first night and did not return. The three weta recorded with time-lapse video emerged during the second night after release but none emerged during the third night. The two weta under ACOs emerged at 20:15

and 20:26, and returned 49 min and 4 h later, respectively, whereas the weta in the hole emerged at 21:52 and then returned eight times remaining inside from 36 s to 4 min before it finally entered at 23:35 and closed the entrance. All three weta followed quite different routes when leaving and returning to their chambers.

Testing monitoring methods using released weta

ACOs

All weta released into the cage were found under ACOs on three occasions and half were found on one occasion. Numbers under ACOs outside the cage on Red Mercury Island progressively diminished until none were present after 7 months. On Double Island, after an initial rapid reduction, the proportion of released weta found under ACOs varied erratically from 1.6% to 13% over 20 months (Fig. 7). The number of times individual ACOs were occupied in sequence also varied: 20 were occupied once, 8 were occupied twice, three were occupied three times and one was occupied 5 times. The overall median occupation period was 22 days (range 6–339 days). Weta were also found under previously unoccupied ACOs on 16 occasions and, on Double Island, one weta and 12 empty chambers were found under new ACOs that had not been used to release weta.

Searching at night

Searches were made for released weta during only three nights in April 2001 on Red Mercury Island. One juvenile was found in the release area and an adult was found next to the stream 25 m from the release area during a total of 11 person search hours (Fig. 3a).

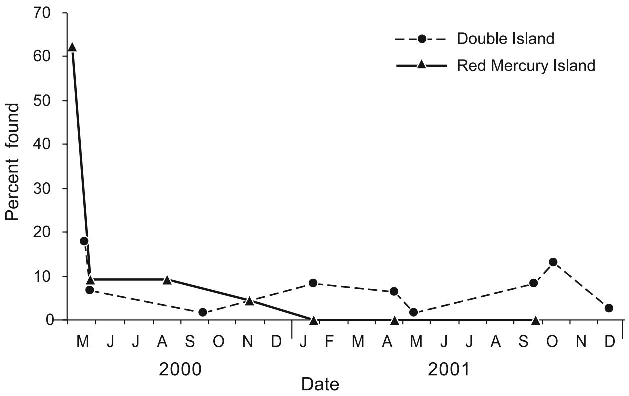

Fig. 7 Percentages of tusked weta found under artificial cover objects following releases on Double Island and Red Mercury Island. Percentages relate to numbers of released weta

Searching plots

Plot-searches were investigated by searching the entire cage on two occasions. Five of the 6 weta present were found the first time (January 2001) and three of 4 still present were found the second time (April 2001). Both searches took approximately one person hour excluding the time taken to measure weta.

Locating weta with harmonic radar transponders and micro-transmitters

Harmonic radar was first used in the cage in April 2001 after HR transponders were attached to a male and two female adults found during the plot-search. On this occasion, an adult female not found during the plot-search was located in a cavity under a large tree root together with the HR-tagged male. All three insects with HR transponders were then released outside the cage on Red Mercury Island but none were found again although one of the transponders was found near the stream in September 2001 after it had become detached.

Two searches with harmonic radar were made on Double Island after HR transponders were attached to six adult females in April 2001. Four weta were located again during the first search in September 2001: one was in a chamber with two adult males near the edge of the release area (it was copulating with one male) and three were under ACOs. During the second search in October 2001, only two of the females were found again and both were under ACOs. On both occasions, the harmonic radar searches were extended c. 10 m uphill and 5 m downhill from the release area but no weta were detected outside the release area.

Micro-transmitters, attached to HR transponders, were used on two occasions. The first involved two adult males and two adult females that were released under ACOs outside the cage on Red Mercury Island in April 2001. The next day, one male was found in a chamber together with an unmarked adult male and an unmarked female weta. This chamber was under a tree root 9.2 m uphill from the ACO where the weta was released. The male remained in this chamber until 26 April 2001 when it was captured and the micro-transmitter was recovered. The female was also in the chamber but the unmarked male had left. The second tagged male moved 8.4 m downhill from where it was released and was found the following day resting, partly visible, amongst dead leaves next to a fallen branch. It moved a further 6.4 m into an empty bird burrow the next night where it remained until it was captured on 26 April 2001 and the radio-transmitter removed (Fig. 3a). Both males were returned to captivity for breeding. Both females with micro-transmitters remained where they were released until the 26 April 2001 when the radio-transmitters were removed but the HR transponders were left attached. These females were left under the ACOs where one was found dead on 22 September 2001 but the other female was never seen again.

Confirming reproductive success

The cage

Two eggs were found in an oviposition tray in the cage in April 2001 providing the first indication that weta had started to breed. A first instar tusked weta was then found under an ACO in the cage in April 2002, and this was followed by five large juveniles (instars 8–9) in March 2003, one adult (instar 11) in April 2005 and an adult (instar 10) and juvenile (instar 9) in July 2006.

Red Mercury Island

At the first release site, no island bred weta were found under ACOs but juveniles were found in March 2003. Both juveniles and adults were found in April 2005 by searching at night and searching plots (Table 2). All 6 weta found at night in 2003 were near the release site whereas in 2005 one was in the release area and 5 were near the stream (Fig. 3a, b). Results from searching plots indicated that in 2005 weta were approximately twice as abundant near the stream as in the release area. No weta were found when a plot of only 25 m^2 was searched in 2006 because of time limitations.

At the second release site, three large juveniles were under ACOs in March 2003 but none were present in April 2005 and May 2006. No weta were found at this site during a brief night search or when a plot of 20 m^2 was searched in April 2005. No further plot searches were attempted here because a network of tree roots covered the ground.

Table 2 Captures of *Motuweta isolata* weta on two of the Mercury Islands, New Zealand

Place	Year	Plot-search No. weta/50 m^2	Night search No. person hours/weta
Double Island	2003	3.4 ($n = 2$)	14.7 ($n = 1$)
	2005	2.4 ($n = 3$)	–
	2006	5.2 ($n = 8$)	–
Red Mercury Island	2003	1.4 ($n = 2$)	0.53 ($n = 6$)
	2005	1.9 ($n = 5$)	0.44 ($n = 8$)
	2006	–	– ($n = 14+$)

The weta were the progeny of weta released in 2000 and 2001

Double Island

No weta were found under ACOs after the released weta had died although an adult male was found in a chamber next to an ACO in May 2006. One juvenile was found during the only night search in March 2003, two juveniles were found when a plot was searched in March 2003 and both juveniles and adults were found in plots in April 2005 and May 2006 (Table 2).

No new weta were found when two males equipped with HR transponders and micro-transmitters were released for three days on Double Island in March 2003. These males were found each day in depressions they had excavated under piles of leaves and sticks, 2.5 m and 8.6 m from where they were released. Both were returned to captivity for captive-breeding purposes.

Discussion

These experimental releases demonstrate that tusked weta can breed and survive on both Double Island and Red Mercury Island. All of the released weta would have become adult by April 2001 and then have died naturally within a year so the large juveniles found in March 2003 were their progeny, one to 1.5 years old. Given that their lifespan is usually 1.7–3.2 years or longer when eggs delay hatching for a year (Stringer et al. 2006), then by 2006 the progeny would have completed at least one and possibly up to three generations on these islands.

All weta released in 2000 and 2001 were a single cohort so the presence of adult weta on both Red Mercury Island and Double Island in 2005 and 2006, and the range of instars (6th–11th) present there in March 2003 and April 2005 indicate that the generations had become asynchronous. It is possible that weta from the second release site on Red Mercury Island may have moved to the first release site but weta at both sites should have been at approximately the same developmental stages (both were second generation progeny from those captured for captive-breeding). Asynchrony between generations was expected from the wide variation in life-span observed in the laboratory (Winks et al. 2002; Stringer et al. 2006). In addition, eggs could potentially be laid over a period of 8–9 months if adults are present from late February–March until October–November as reported on Middle Island (McIntyre 2001). The adults of other anostostomatids may occur throughout the year (Cary 1981; van Wyngaarden 1995; Leisnham et al. 2003) and as such, these together with tusked weta have a wider seasonal range than many other lowland orthopterans in New Zealand (Ramsay 1978). In the case of *M. isolata*, the long period when adults are present is likely to be at least partly due to both sexes having individuals that mature at different instars and therefore have different developmental periods (Stringer et al. 2006).

The indications are, from Red Mercury Island, that *M. isolata* prefers living near streams as does its close relative *M. riparia* (Gibbs 2002). In 2005 weta were about twice as abundant in plots near the stream as in the release area, and more were seen near the stream than elsewhere at night. In addition, observations made by a kiwi monitoring team on Red Mercury Island in 2006 indicate that the weta are expanding their range because they reported finding them ~43 m downstream and up to 73 m upstream from the release area (R.M. Colbourne, H.A. Robertson, A.S. Holzapfel and P. de Monchy, pers. comm.). We have no indication of range expansion on Double Island because all searches were made near the release site.

Testing new monitoring methods

Using these experimental transfers to test a variety of potential ways for finding weta led to a better monitoring method, plot-searching, and it also maximized the amount of information gained by allowed us to follow the progress of weta after they were released. One method that did not occur to us was using footprint tracking tunnels. This could clearly work because tusked weta footprints, identifiable by shape and size, were found in one of the tracking tunnels used to warn of rodent incursions on Red Mercury Island in February 2007 (de Monchy 2006).

ACOs

ACOs were the least successful long-term monitoring method that we investigated because no weta were found under those outside the cage after December 2001. However, they were useful for following the weta that were released by confirming that some survived for up to 20 months and developed into adults (Fig. 7). This was possibly due, in part, because individual weta probably used the same chambers repeatedly over many nights. Our results show that tusked weta will desert chambers and that they may construct new chambers under ACOs that have never been previously been occupied by weta. We did not confirm that weta that returned to the chambers were the same each time because they were not individually marked but it is possible they do because other anostostomatids as well as closely related gryllacridids are known to do this (Townsend 1995; Hale 2000; Jamieson et al. 2000; Hale and Bailey 2004). Some gryllacridids even discriminate between their own nests and those of conspecifics (Lockwood and Rentz 1996). Our observations also suggest that *M. isolata* may not need to retrace their outward paths when returning to their chambers and such behaviour suggests that long-term memory of olfactory and visual cues, or even path integration, may be involved as reported for other orthopteroid insects (Beugnon and Campan 1989; Greenfield et al. 1989; Hale and Bailey 2004; Rivault and Durier 2004).

The potential advantages of using ACOs for monitoring (Lettink and Cree 2007) and their successful use with a variety of animals (e.g. Kjoss and Litvaitis 2001; Houze and Chandler 2002; Wakelin et al. 2003; Lettink and Patrick 2006) merit further investigation with tusked weta. One possibility worth exploring is whether keeping the soil immediately surrounding the ACOs clear of leaf-litter affects occupancy. This follows because the ACOs in the cage, where falling leaves were intercepted by the mesh roof, continued to be occupied, whereas ACOs outside the cage became progressively buried in leaf-litter and were eventually no longer occupied. We acknowledge there are other possible explanations for this such as the higher density of ACOs in the cage than outside, and that weta outside can disperse.

In New Zealand, other anostostomatids have successfully been monitored by lifting numbered rocks or by attaching artificial wooden refuges to trees (e.g. Ordish 1992; Jamieson et al. 2000; Trewick and Morgan-Richards 2000; Bleakley et al. 2006). We took the obvious step of releasing weta under the ACOs that were also intended for monitoring them, but we know of relatively few instances where this has been reported for other species—examples include transfers of tree weta (*Hemideina* species), tuatara and burrowing sea birds (Bell 1995; Priddel and Carlile 1995; Ussher 1998; Green 2002; Bowie et al. 2006). However, artificial shelters of varying sorts have long been associated with successful transfers of other insects, both unintentionally, as with pest species such as some ants, and intentionally, as in the case of honey-bees (Crane 1999; Holway et al. 2002).

Searching plots

Searching plots was a relatively effective way of finding weta when they are not widely dispersed but it caused considerable habitat disturbance. The method can potentially provide an estimate of weta abundance, but we did not do this because of time limitations and, on Red Mercury Island, because dense surface roots prevented randomization by restricting where plots could be located.

Searching at night

Comparing the numbers of tusked weta seen at night in different locations cannot be used to obtain a reliable estimate of relative abundance because little is known about how tusked weta activity varies with environmental factors. Despite this, observations from night searches on both islands (Table 2) indicate they may be more abundant in the vicinities of the release areas than they are on Middle Island where each weta was found on average every 86.7 person hours at the same time of year between 1998 and 2001 (Stringer unpublished data).

Locating weta with harmonic radar transponders and micro-transmitters

We suggest that following adult weta tagged with HR transponders and/or micro-transmitters is most suitable for locating new weta when they are widely dispersed. However, it involves locating weta over several days and is dependent on some adult weta being available to tag. We know of no previous studies where insects equipped with radio-transmitters or HR transponders were used for locating conspecifics but the technique is used to locate mammals (e.g., Taylor and Katahira 1988; McIlroy and Gifford 1997).

Conclusions

The chances of survival for *M. isolata*, at least in the medium-term, have been increased by these transfers, and the species may even have been saved from extinction if it has disappeared from Middle Island. The ultimate aim was to establish self-sustaining populations of these weta on other islands, but the released insects represent the progeny of only few individuals so inbreeding depression is likely. However, we believe that this species already had low genetic variability because the population on Middle Island was small (McIntyre 2001), and because reductions in numbers are likely to have occurred there repeatedly during previous droughts. Nevertheless, the intention is to undertake annual searches of Middle Island and, if sufficient numbers ever occur there again, to collect more for captive-breeding to supplement the transferred populations. In the meantime, we can only hope that both transfer populations are increasing fast enough to prevent any further loss of genetic variation (Allendorf and Luikart 2007).

The transfers were successful largely because of the following. First, a recovery group was formed which initiated the ecological and behavioural investigations of McIntyre (2001), the research into captive-breeding. It also made the decision to use the first weta produced from the captive-breeding programme in the present experimental transfers. Second, the early success in developing a captive rearing method by Winks and Ramsay (1998) was crucial in making the transfers possible. And lastly, the release sites were close to Middle Island so similarities in climate and vegetation cover probably contributed to the weta's survival (Sarrazin and Barbault 1996). Luck was also involved: the three weta collected for captive-breeding happened to be amongst the last seen on Middle Island (Winks et al. 2002; Stringer 2006) and if this weta is now extinct on Middle Island, then it is indeed fortunate that the transfers did succeed.

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ORIGINAL PAPER

Population studies and conservation of Jamaica's endangered swallowtail butterfly *Papilio* (*Pterourus*) *homerus*

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J. R. Parnell · T. C. Emmel

Abstract This is an 18-year study of the endangered *Papilio* (*Pterourus*) *homerus*, adding substantial information to our scanty knowledge of its ecology. The contraction of a once contiguous but narrow population on a single Caribbean island carries the serious threat of extinction. There are now two populations or probably metapopulations, effectively isolated from each other. The butterfly's larvae feed on *Hernandia catalpaefolia* and *H. jamaicensis*, both endemic to Jamaica, and development takes ~84 days from egg to the emerged adult. Adult numbers fluctuate rapidly, with peaks in July/August each year. Egg distribution was studied at three spatial levels: the food item (leaf cluster), the patch (tree) and the habitat (each valley). Major causes of developmental mortality were *Chrysonotomyia*, a eulophid parasitoid of the eggs, and bacterial infection of the larvae and pupae. Critically, the mortality from this wasp was lower in undisturbed forest than in the area disturbed by agriculture, this finding having important consequences for conservation. Although there was no evidence of a decline in numbers over the last century, we believe this is an artefact due to collectors working only at the periphery of its distribution. Even assuming that its population densities have not changed, the contraction of its usable habitat implies a similar reduction in average numbers and the small populations are susceptible to disaster. The efforts of researchers, NGOs, and Government agencies have greatly increased the level of awareness, making the people in some key areas the 'protectors of the species'.

Keywords Egg parasitoids · Physical factors · Polymorphism · Natural deception · Population dynamics · Spatial distribution · Rare species · Metapopulations

Introduction

It is almost axiomatic in insect ecology that the majority of species have low abundance and hence would rank in the long tail of the species abundance curve derived from a faunal sample (Williams 1964) and often would be regarded as endangered, were they sufficiently well known and or appreciated. While rare species are a majority, studies on their ecology are, perhaps paradoxically, sparse. Hence, there is a great need for further research on rare species both to improve our understanding of the causes of the endangered status and to obtain a more balanced view of insect ecology and population dynamics. Furthermore, the development of comparative population studies along the species abundance curve would lead to a better integration of autecology and synecology (Jones and Lawton 1994), with the practical result of a better understanding of the principles of conservation.

Such research is possible only in certain circumstances because, of course, there will be a paucity of data. Firstly, there are those studies in which the researcher is not constrained by time or finance. In this happy situation a long-term study in which the data gradually build up may be undertaken, although such situations are rare in a world of short term grants and or publish or perish imperatives

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(Emmel 1995; Parsons 1992). Secondly, there are those in which favourable features of the rare species facilitate its study. For example, in the solitary wasp *Monobia mochii* Soika, found in southern Jamaica, Ittyeipe and Taffe (1982) were able to describe its distribution and present a life table because the artefacts in its cells built up over many generations, thus effectively multiplying its extant population density. The use of traces in the study of insect populations, is a very fruitful one (Varley 1947; Beaver 1966; Freeman 1976; Jayasingh and Freeman 1980; Garraway and Freeman 1981; Watmough 1983). In the present case, emphasis was placed on an assessment of the density and distribution of the eggs as a means to maximise the data; nevertheless, the time taken to collect even these data was considerable.

The Papilionidae contains over 500 world species, with their greatest diversity in the tropics (Scriber et al. 1995). *Papilio* (*Pterourus*) *homerus* F., one of eighteen species in this sub-genus, which has a largely New World distribution, is the largest swallowtail in that region, and is confined to Jamaica. While formerly found in several areas of wet limestone and lower montane forest, its present distribution has contracted to two forested regions (Emmel and Garraway 1990; Turner 1991). It is now listed as endangered by the IUCN (Collins and Morris 1985), and is of conservation concern (Emmel and Garraway 1990; Garraway et al. 1993), with specimens illegally changing hands for high prices.

There is a western population where the parishes of St. Elizabeth, St. James and Trelawny meet in the Cockpit Country and, some 125 km to the east, a probably larger population centered on the junction of the Blue Mountains and John Crow Mountains in the parishes of Portland and St. Thomas (Emmel and Garraway 1990; Garraway et al. 1993). While it is clear that there has been a reduction of its geographic distribution, its numbers in the eastern population, at least, appear at present to be relatively stable. Apart from the butterfly's natural dynamics, this is the result of recent governmental legislation, and the work of NGOs, and individual conservationists to conserve the indigenous forest and from the fact that considerable areas of its present distribution are extremely inaccessible.

The present study is a continuation of a long-term project initiated by Garraway and Parnell (1984), which aims to improve our knowledge of this magnificent butterfly and hence be better able to make recommendations for its conservation. It also makes a contribution to our limited knowledge of the ecology of rare species.

Methods

Study areas

The bulk of the fieldwork was undertaken on the eastern population, at the area of Millbank known as Fishbrook in the Rio Grande valley (Fig. 1, see also Emmel and Garraway 1990). Ancillary observations and data were recorded subsequently until the time of writing. At Fishbrook there were three adjacent sampling stations along wooded or partly wooded (30–70% cover) riverine valleys. These valleys drain from the ridge of the John Crow Mountains, which is about 1,050 m elevation at this point, and flow in an approximately westward direction into the Rio Grande at about 250 m elevation. They are between 2.2 and 1.8 km long but were not accessible in their upper reaches. They have an average gradient of about 15–30° in the lower reaches and much higher in the upper reaches where the streams contain a series of waterfalls. They were selected because of the relative abundance of the food plant *Hernandia catalpaefolia* Britton and Harris. White River (WR) was sampled for 0.72 km to a final elevation of 285 m, and Island Spring (IS) for 0.96 km to a final elevation of 275 m. These two sites had 30–35% cover and were considered disturbed. Bruck Foot (BF) (means "broken leg", attesting to the difficult terrain) was sampled for 1.30 km to a final elevation of 585 m. With a 70% forest cover it was considered to be undisturbed.

Further observations of the eastern population were made at Millbank (elevation 220 m), Muddy Spring, (250 m), Bowden Pen, (300 m), Cuna Cuna Pass (750 m) and Corn Puss Gap (680 m). Rainfall in the area occupied

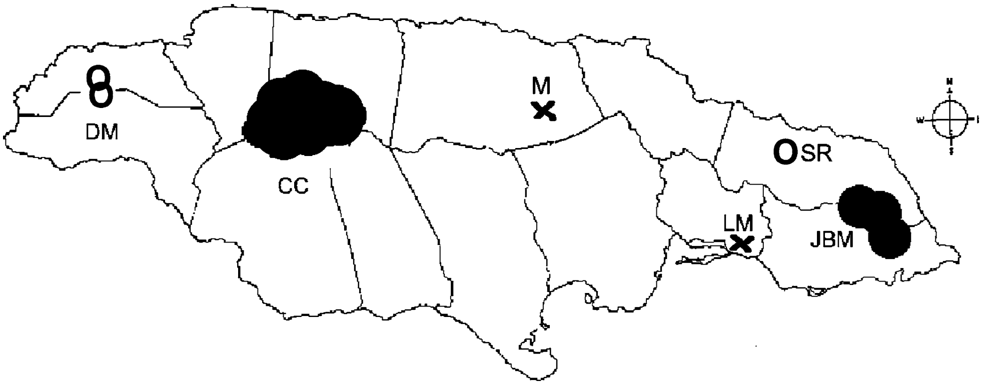

Fig. 1 Map of Jamaica showing study areas. DM, Dolphin Head Mountain; CC, Cockpit Country; M, Mt Diablo; SR, Spanish River; LM, Long Mountain; JBM, John Crow and Blue Mountains; ●, Breeding populations; ○, larval food plant only; ✗, adult sighting only from previous studies

by the eastern population is high; 30 years. annual average is 7,500 mm at Corn Puss Gap and 6,300 mm at Fishbrook.

The vegetation at the three sampling stations included trees such as *Callophylum calaba* L. (Gutterferae), *Fagara martinicensis* Lam. (Rutaceae), *Hibiscus elatus* L. (Malvaceae), *Bambusa vulgaris* Schrad. (Graminae), *Oreopanax capitatus* (Jacq.) (Araliaceae), as well as *H. catalpaefolia*; shrubs such as *Pilea* sp. (Urticaceae), *Pachystachys coccinea* Aubl. (Acanthaceae) and *Urena lobata* L. (Malvaceae); vines such as *Entada gigas* L. (Mimosaceae), and *Philodendron* sp. (Araceae) the tree ferns *Cyathea* spp. (Cyatheaceae) and herbs such as *Hedychium* spp. (Zingiberaceae). At the first two sites there had been partial clearances of the canopy and here *Colocasia esculenta* L. (Araceae) (dasheen) and *Musa* L. cultivars (Musaceae) (bananas and plantains) were grown.

In addition, 10 one-day visits were also made to the Spanish River Valley between 1991 and 2001. The Spanish River drains the north western edge of the Blue Mountain range and is 25 km west of the Rio Grande. Sampling was done along the river at in the lower part of the valley at Chepstowe (altitude 200 m) for 1.5 km and then at in the upper valley at altitude of 600 m for 1 km. There was a mixture of agricultural plots and extensive areas of natural forests. The larval food plant *H. catalpaefolia* was common. Rainfall is high, at 3,750 mm annually, but lower than in the Rio Grande Valley.

Additionally, visits were made to the western population. This was centered in the Cockpit Country. The Cockpit Country is over 500 km^2 of rugged terrain (Fig. 2). It is characteristic karst topography and consists of a jumble of steep, rocky, cone-like hills all of similar height, separated by deep depressions, often obconic, 70–200 m deep, termed ‘cockpits’ because they resemble cock-fight pits. The region as a whole ranges between 300 and 750 m in altitude. The hillsides and tops support little or no soil while the cockpits generally contain rich soil. These cockpits sustain well developed very humid forests, the canopy is generally about 30 m, but emergent trees get up to 50 m. The vegetation is very diverse, over 1,000 species of vascular plants documented (G. Proctor, personal communication). The larval food plant of *P. homerus*, *Hernandia jamaicensis* Britton and Harris, is relatively common throughout the area. Most of the Cockpit Country has been protected by its rugged terrain. However, at the periphery selected trees have been felled, while the rich soils of some cockpits have been utilized for small farming; this is particularly so in areas penetrated by roads (Proctor 1986) A total of 30 visits were made between 1984 and 2001 to the following areas: Nassua Mountains, Accompong, Crown Lands, Barbecue Bottom, Elderslie, Niagara, Troy, Windsor and Dromily, the trail between Troy and Windsor, The Land of Look Behind, and Rest And Be Thankful. Rainfall in the southern regions ranges from 2,000 to 2,500 mm while in the north it was around 1,500 mm annually and hence less wet than the east.

Two trips were made to Dolphin Head Mountain, Hanover Parish, 30 km west of the Cockpit Country, in 1995 and 2001. There has also been a very strong research and conservation presence by the Dolphin Mountain Trust

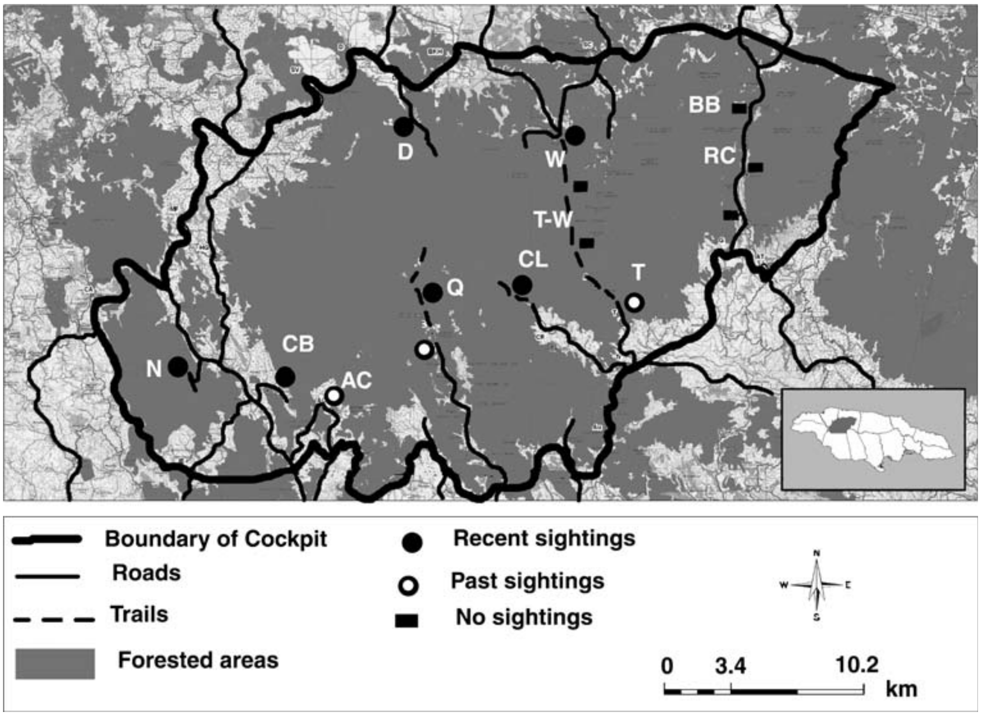

Fig. 2 Map of Cockpit Country showing study areas. AC, Acompong; BB, Barbecue Bottom; CB, Cooks Bottom; CR, Crown Lands; D, Dromilly; N, Niagra; Q, Quick Step trail; RC, Ramgoat Cave; T, Troy; W, Windsor; W/T, Windsor to Troy trail

since 1993 (Dolphin Head Trust 2007; P. Hurlock, personal communication). In this area the forest is well developed; there are over 600 species of vascular plants (Proctor 2001). There are many deep damp ravines similar to those generally used by *P. homerus*, and *Hernandia jamaicensis* is common. Rainfall is high (2,500 mm annually), but highly variable with significant dry periods.

Mt Diablo is a 70 km^2 limestone massif, with karstic summit topography, reaching an altitude of 700 m. It is located towards the middle of the island and is approximately 70 km from both the Cockpit Country in the west and the Blue and John Crow Mountains to its east. The annual rainfall of 2,000 mm is high although lower than at the John Crow Mountains and Cockpit Country and there is a significant monthly variation with marked dry seasons. The forest is well developed with 230 species of vascular plants (G. Proctor, personal communication). There has been selective logging and shifting agriculture in the area. *Hernandia* was not recorded by Proctor in his 2005 survey of the plants, or by Garraway. The only actual record of *Hernandia* in this area is a specimen from a single plant of the Cuban species which was cultivated in garden in Moneague. This specimen is part of the 'Adams Collection' at the University of the West Indies, and might be the record referred to by Turner (1991). Six 1-day field trips were made by Garraway to Mt. Diablo during the years 2006–2007.

Sampling

A total of over 2,000 man hours was spent in the field between 1984 and 2003.

At Fishbrook, monthly censuses along each of the three valleys were made from January 1991 to December 1993 for the adults and from July 1991 to June 1993 for juveniles. The latter census required 12–24 man-hours of fieldwork at each site per month. Adults were observed using 10 × 50 or 8 × 50 binoculars and, because they were relatively few, most individuals could be distinguished by their distinctive wing damage. All 205 *Hernandia* trees present 30 m on either side of the streams were marked with surveyors' tape and inspected monthly. Leaves with juveniles were marked with numbered aluminium tags. Vegetation within 10 m of each food plant was inspected for pupae if the former bore traces of late larvae. The leaves were large (25.5 ± 0.6 × 20.1 ± 0.5 cm.) and sparse, facilitating the work. Earlier sampling at Muddy Spring and observations by Turner (1991) had shown that juveniles were generally restricted to a height band of 0.5–3.0 m. and only this region was thoroughly searched during the survey, although a lookout for damaged leaves became a habit. It was essential to develop a good understanding with local farmers to preserve the study sites, a process in which social skill is at a premium.

There were 40 *H. catalpaefolia* in WR, 69 in IS and 105 in BF resulting in tree densities of 55.5/km at WR, 71.9/km at IS and 80.8/km at BF. Any tree bearing immature stages or their traces was classified as an oviposition patch. In this connection only one other lepidopterous species was found to feed on *Hernandia*; an unidentified bagworm moth (Psychidae) occasionally occurred, but the traces it left, holes made through the leaf, were quite distinct from those of *P. homerus*, which always ate from the leaf edge. *Hernandia* trees were categorised into four height classes 1–3, 3–6, 6–9 and 9–12 m. The micro-environment of five selected trees was recorded at 1.5 m between 20 May and 7 July 2000 using data loggers of the HOBO H8 Pro Series®. Data were down loaded in the field using a HOBO® Shuttle and then onto a PC. Monthly precipitation was recorded at Comfort Castle, at the edge of the study area. Ninety five percent confidence limits of the mean are given throughout this paper.

Population dynamics and mortality

The available records of *P. homerus* captures and sightings were analysed for any trends in population. Information was collected from Brown and Heineman (1972); specimens at the Carnegie Museum in Pittsburgh, Pennsylvania, and the Natural History Museum, London.

To estimate adult survival and home range, 20 males and 5 females were given black, unique marks on the lower surface of the wings and released from 7 April to 1 May 1991.

In the census all apparently healthy eggs, eggs containing parasitoids, and empty egg shells were recorded and the leaf on which they were found tagged (as above). Parasitised eggs, the development of the parasitoids and their mortality could be identified by egg colouration and subsequent dissection. All the larvae found and the traces they made were recorded. Sub-samples of larvae were reared in sleeve cages in the field to estimate the duration of the developmental instars. These cages were constructed of plastic mesh and measured about 80 by 25 cm. Juveniles were observed daily. Additional estimates of these durations were made at the field station, which was 1.5 km from Fishbrook.

The chance of observing any stage in the field depends only on its numbers there, its visibility and its duration. Because the search for eggs was exhaustive and larvae were easily found by reason of the damage they caused, we assume that these stages have equal visibility. Mature larvae normally move away from the food plant to pupate, however, so we expect that pupae were less easily found and their numbers underestimated. Adults were highly mobile and could be easily missed as numbers were so very low and activity level affected by factors such as weather conditions. We therefore relied heavily on the traces left by the eggs and the larvae. Leaves remain on the plant for a period of over three years and so larval damage represent a history for at least that time, but possibly for more than one generation. We were not able to age such traces except for those <4 months. It was possible to separate the larvae which made the traces into early (L1–L3) and late larvae (L4 and L5) by the size of the marks on the leaves.

Results

Biology

Much rather anecdotal and sometimes inaccurate information regarding *P. homerus* exists in earlier literature (Rutherford 1878; Gosse 1879; Aaron 1893; Panton 1893; Taylor 1894; Swainson 1901; Kaye 1926; Avinoff and Shoumatoff 1940; Lewis 1944a, b, 1948, 1949; Walker 1945; Brown and Heineman 1972). More rigorous studies on the biology of *P. homerus* have been undertaken only recently (Emmel and Garraway 1990; Turner 1991; Garraway and Bailey 1992; Garraway et al. 1993; Garraway and Parnell 1993; Bailey 2003), a synopsis of which is given here.

The smooth sub-spherical eggs were 1.98 ± 0.06 mm high and 1.79 ± 0.11 mm wide. They were at first pale green but quickly changed to yellow and finally dark brown just before eclosion. They took from 5 to 7 days to hatch in the field (mean 6.5 ± 0.8 days). Oviposition was mainly on two endemic species of *Hernandia* (Hernandiaceae), *H. jamaicensis* Britton and Harris in the western population and *H. catalaeifolia* Britton and Harris in the eastern population. Both plants were common in deep, narrow, humid valleys. Occasionally, eggs were laid on *Ocotea* sp., probably *leucoxylon* (Sw.) Gomez Maza (Lauraceae), (Lewis 1949; Turner 1991), which is widespread and common along streams (Adams 1972). Generally, eggs were deposited on the upper surface of young or mature leaves.

All the remaining stages of *P. homerus* showed various colours and patterns of likely survival value. There were five larval instars. The first two were dark brown with the terminal abdominal segments white, a pattern giving them close resemblance to lizard droppings, in which the white excretory material is also terminal. The third stage was similar but larger and bore a white dorsal saddle, hence more resembling a larger bird dropping, but it also had prominent black and white eyespots on the third thoracic segment.

In the final two instars the larva changed radically, with the dorsal surface becoming apple green, the thoracic segments swollen. The metathoracic segment bore a pair of blue and yellow eye-spots, joined anteriorly by a dark brown band, giving the larva when viewed from the front the appearance of a small lizard or snake with a half-opened mouth (See Emmel and Garraway 1990; Garraway and Parnell 1993). The larvae retract the head under the thorax when at rest. The mature larvae were some 70 mm long. Durations of the larval stages were: L1 5.6 ± 0.7 days, L2 6.0 ± 0.5 days, L3 9.5 ± 0.7 days, L4 11.5 ± 0.8 days and L5 19.5 ± 0.7 days. Complete larval development took about 52 days. Fourth instar larvae spun a silken mat on the upper leaf surface, which healthy fifth instar larvae augmented, and to which they returned when not feeding.

Mature larvae migrated to neighbouring plants, as far as 10 m away, to pupate. Pupation generally took place on a brown twig and occasionally on a green one. Pupae were polymorphic: either brown with variable dark brown patterning or rarely green with brown markings. Pupal development required 25.2 ± 0.5 days, making the total period for development to the emerged adult about 84 days.

P. homerus females and males have a mean forewing length of 78.2 ± 5.7 and 71.7 ± 4.0 mm respectively ($t = 4.46$, $P < 0.001$ for a difference). The span of a large female is about 160 mm. The sexes have similar patterns on the wings, which are mainly yellow on dark brown with some bluish markings on the hindwings (Brown and Heineman 1972; Emmel and Garraway 1990). From both surfaces when the wings are spread, as in flight, there is the image of a smaller, stout-bodied butterfly imprinted within the framework of the real wing margins. The small image resembles the hesperiid *Epargyreus antaeus* (Hewitson) which is also endemic to Jamaica (Brown and Heineman 1972), but several other large Jamaican hesperiids have similar colouration. When *P. homerus* is at rest with its wings open, the hesperiid image alters because the dark hind margins of the fore wings are set back. In this posture the small image acquires black tails mimicking a tailed skipper such as *Chioides catillus* Bell and Comstock, which is also found in Jamaica (Brown and Heineman 1972). There are also large eyespots on the underside of the hindwings, which are exposed when the butterfly is at rest.

The rapid fluctuations in the numbers of sightings from month to month (Table 1, Fig. 3) suggest that adults do not live more than a few weeks in the field. Adults in shade houses were kept alive for a maximum of only 6 days. Hence, the generation length would be roughly 90–100 days. In the mark/recapture study made between 7 April and 1 May 1991, 20 males and 5 females were marked and released. We recaptured only one (male) individual. This recapture was within an hour of marking and at the same location.

Phenology of the adults

Two hundred and twenty six adult sightings and captures recorded in the literature from 1901 to1986 show a high peak in July and August. Only seven sightings were recorded in the period October–March, while 219 were recorded for the April–September period. When these crude values are adjusted by dividing them by the number

Table 1 Number of adults sighted or netted at Fishbrook, 1991–1993

Months	1991	1992	1993	Total
January	6	0	0	6
February	0	1	0	1
March	14	1	0	15
April	55	1	0	56
May	13	3	0	16
June	16	23	0	39
July	23	9	0	35
August	14	5	0	29
September	5	18	2	25
October	0	11	3	14
November	0	1	0	1
December	0	1	0	2
Total	147	84	8	239

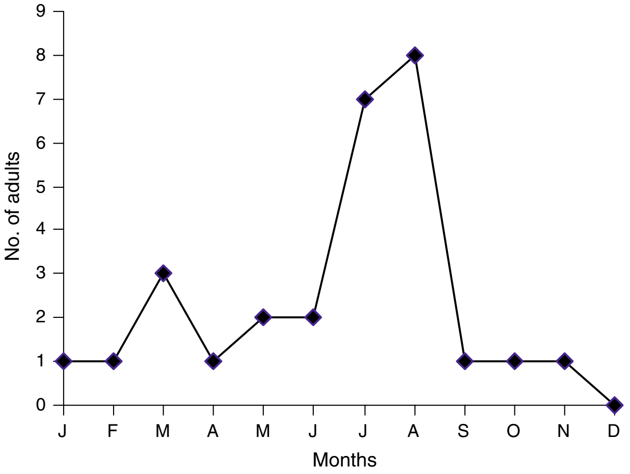

Fig. 3 Fluctuations in number of adult *P. homerus* sighted by various workers 1906–1997

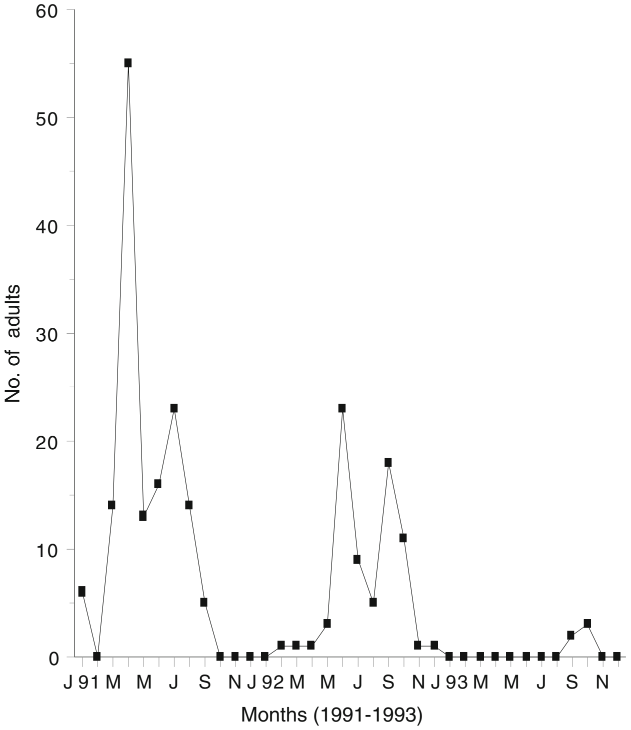

Fig. 4 Fluctuations in number of adult *P. homerus* sighted at Fishbrook, 1991–1993

of trips per month made by these authors to the field, this peak still remains although at a lower level (Fig. 4). Sightings made during the census were relatively few at 39 in the period October–March, as opposed to the 200 made in the April–September period (see Fig. 3, Table 1). The monthly sightings during the census period of 30 months were uncorrelated to monthly precipitation at Comfort Castle, ($r = 0.129$, $P > 0.05$). Two lag correlation analyses in which monthly sightings were related to precipitation in the preceding month, and in the month before that, were both insignificant ($r = 0.188$ and $r = 0.083$, $P > 0.05$).

Adult behaviour and the sex ratio

Adults normally commenced the day's activities with a period of basking on the upper surface of a large, elevated leaf, a behaviour lasting up to 35 min. Based on the number of sightings, 90.5% of the flight activity took place between 9 am and 2 pm. Both sexes were seen to feed on the flowers of a variety of plants including the food plant *H. catalpaefolia*, *Hibiscus rosasinensis* L. and *Urena lobata* (Malvaceae), *Entada gigas* (L.) *Psophocarpus palustris* Desv. (Papilionaceae), *Hedychium coronarium* Koenig, *Lantana camara* L. (Verbenaceae) and *Pachystachys cossinea* (Aubl.) (Acanthaceae). Other recorded nectar sources are *Cissus* sp**.** L. (Verbenaceae), *Mecranium* sp. Hook (Melastomataceae), *Asclepias* probably *curassavica* L. (Asclepiadaceae) and *Bidens* probably *pilosa* L. (Compositae) (Turner 1991), and *Spathodea campanulata* Beauv. (Bignoniaceae) (Lewis 1948), *Tabernaemontana achroleuca* Urb. (Apocynaceae) (Lehnert 2008).

Males made patrols in defending territory from other males. The males will patrol in a circle, in an elliptical manner or up and down streams, that is, their territories were of different shapes and sizes, defined by the topography or forest structure. Males were also seen circling high above the forest canopy. The common feature of these territories, however, is an open space in which movement of other butterflies can be readily detected. Patrolling males investigated butterflies, birds and falling objects which flew or fell nearby. Aerial battles between males were recorded several times and on one occasion at 10.30 am a group of four (probably males) were seen flying aggressively in a cluster above the canopy. Females flew through an area searching the vegetation for the appropriate foodplant; they often flew parallel to a stream or from bank to bank investigating leaves. Mating was seen only once. A pair was discovered copulating on a bamboo branch and watched for 20 min until they flew off in tandem.

The male:female ratio of adults netted in the field was 4:1 (n = 25) while that for adults reared in the laboratory was 1.5:1 (n = 19). The sex ratio of adults reared in the laboratory was not significantly different from 1:1 ($P = 0.359$), while that of adults collected in the field was significantly male-biased ($P = 0.004$).

Egg distribution

We looked at egg distribution at three spatial levels: the food item (leaf cluster), the patch (tree) and the habitat (each valley) (Hassell and Southwood 1978; Freeman and Smith 1990). During the census 1056 eggs were observed, and these occupied 940 of the 7,000 leaves inspected. In 80% of cases leaves had one egg, however, more than a single egg was occasionally found on a given leaf, with a maximum of six of different ages. The number of eggs was not dependent on the size of the leaf ($F_{0.05,2} = 2.858$, $P = 0.062$). Eggs were also found in the presence of larval instars 2–5.

Eggs were laid on the upper surfaces, never on the lower surface, of both mature as well as young and terminal leaves of *H. catalpifolia*, but rarely on very old ones. Eggs were occasionally laid on old yellowing leaves in the process of abscission (0.3%, n = 257). Two percent of the leaves used as oviposition sites at Island Spring during August 1991 had 75% or more of the leaf surface missing as a result of previous usage by *P. homerus* caterpillars.

In using of trees (patches), the total number of eggs deposited per month was correlated to the number of trees used when the effect of the varying number of adults sighted was removed by partial correlation ($r = +0.942$, $P < 0.001$, Fig. 5). The percentage of trees used for oviposition was rather constant in 1991–1992 and 1992–1993: IS 60 and 52%, WR 55 and 78, and BF 37 and 26%. The number of times a tree was used for oviposition throughout the census period varied from 0 to 9 (Fig. 6). At the disturbed sites (WR and IS combined) the percentage use during the study period was twice that at the undisturbed BF, being 60% and 31% respectively. Moreover, 66% of all the trees used were in the disturbed sites compared to 34% in the undisturbed one.

The distribution pattern of the eggs laid on trees at all sites was contagious, since the variance/mean ratio for all sites was much greater than 1(Taylor's power law, Taylor 1961; Southwood 1978). The regression of log. variance on log. mean of eggs oviposited at Island Spring resulted in a slope b of 2.2 (Fig. 7). According to Taylor's Power Law the egg distribution was aggregated. Trees were ranked in order of number of times used and egg load. At Island Spring, the distance of a tree from the stream and the amount of shading it received influenced the egg load, $F_{0.05,2} = 4.839$, $P = 0.012$ and $F_{0.05,2} = 3.669$, $P = 0.032$, respectively, i.e., the egg load was greater if a tree was close to the stream and not clustered. The top five highest ranked trees were located within 1 m from the banks of the streams.

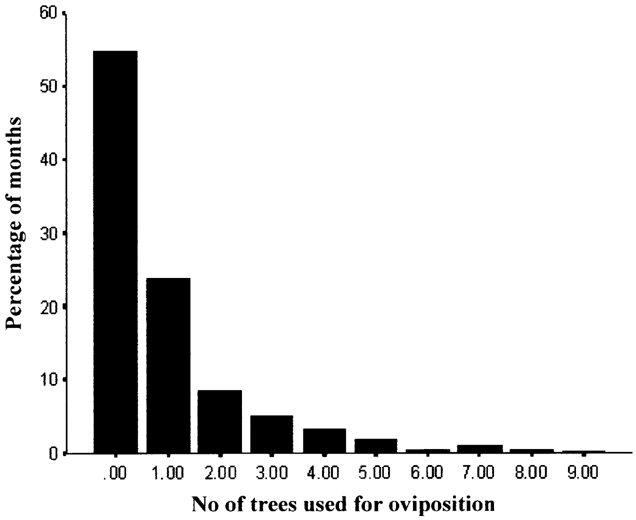

Fig. 5 Relationship between number of *P. homerus* eggs and number of trees used

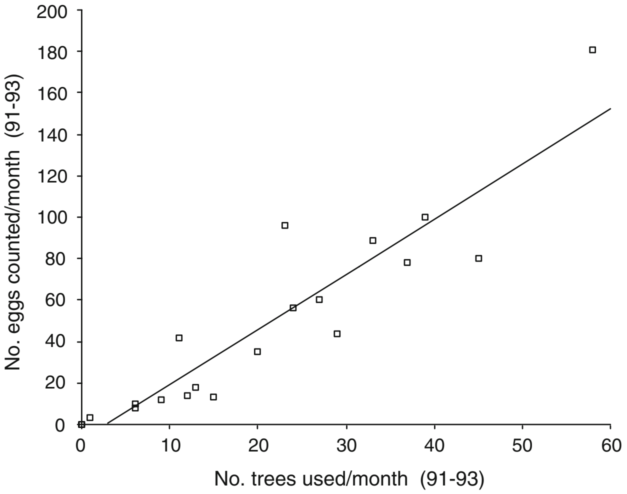

Fig. 6 Distribution of *P. homerus* eggs among trees at Fishbrook, 1991–1993

The number of eggs observed per tree varied significantly between the valleys ($F2 = 17.38$, $P < 0.001$), but not between years ($F1 = 0.23$, $P = 0.63$). The interaction between site and year had no influence on the number of eggs per tree at the three valleys ($F2 = 0.86$, $P = 0.43$). Multiple comparison showed that the mean number of eggs per tree at BF (undisturbed site) was significantly different from those

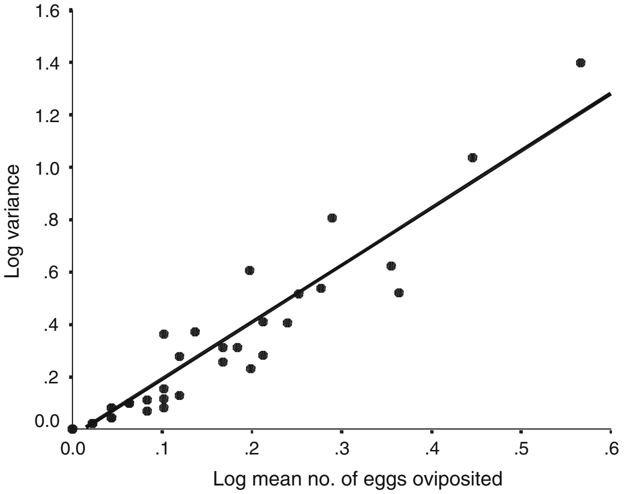

Fig. 7 Log$_{10}$ variance vs log$_{10}$ mean number of *P. homerus* eggs per tree at Island Spring, 1991–1993

at IS and WR, but there was no significant difference in these values for IS and WR (disturbed sites). For Fishbrook as a whole the number of eggs deposited per month was correlated to the number of adults sighted per month ($r = 0.714$, $P < 0.001$) while for the three valleys the monthly egg counts were all mutually correlated (Fig. 8).

Population dynamics

The adjusted historical data on adult sightings and captures were regressed on the decade in which they were made, but provided no evidence of a systematic decrease since the slope of the regression line was insignificantly different from zero ($b = 0.00$, $P > 0.05$). The status of this result will be discussed below.

Egg mortality was 74.4%, the chief factor being hymenopterous parasitoids (65.7%).Three species of hymenopterous parasitoids were recorded; *Chrysonotomyia* Ashmead sp. (Eulophidae), *Ooencyrtus* Ashmead sp. (near *submetallicus* Howard) (Encyrtidae) and an unidentified species whose pupa was recorded only once at Island Spring. *Chysonotomyia* sp. was the most important (64.1%) while *Ooencyrtus* sp. accounted for 1.6% of the egg deaths. Both the identified parasitoids only oviposited in eggs up to 3 days old. Eggs of *P. andraemon* (52), and *Battus polydamas jamaicensis* Rothschild and Jordan (8) were investigated but these were not attacked by the same parasitoids.

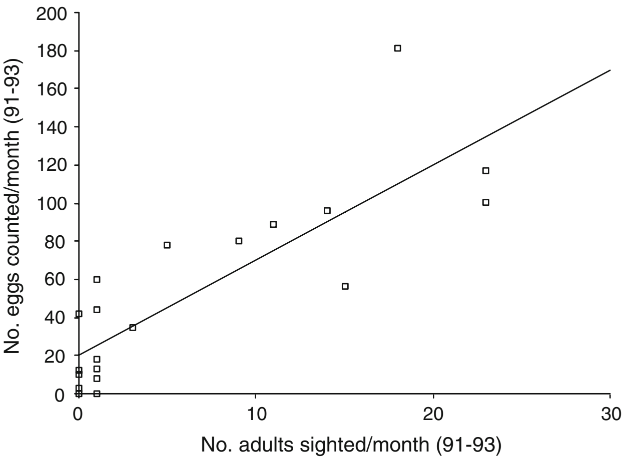

Fig. 8 Relationship between number of adult *P. homerus* sighted and number of eggs

In *Chrysonotomyia* juveniles took 8.0 ± 1.0 days for development to the emerged adult. The mean number of adult *Chrysonotomyia* sp. emerging per egg was 12.2 ± 0.5 ($n = 109$) with a maximum of 24. Males and females develop in separate hosts most of the time; 66.1% of the broods had only females, 29.4% had only males while 4.6%, ($n = 109$) had both sexes. In the single sex broods the mean number of males emerging per host was 14.7 ± 1.0 ($n = 32$) and mean number of females was 11.1 ± 0.48 ($n = 72$). In the mixed broods the mean number of parasitoids emerging was 10.6 with 6.4 females and 4.2 males. The overall proportion of females at emergence was 0.63 ± 0.04. Only 6.1 ± 0.02% developmental mortality occurred. *Ooencyrtus* adults emerged from mixed broods and the proportion of females was 0.79 ± 0.07. Generally, six adults emerged from each host.

At Island Spring and Bruck Foot, the level of parasitsation was positively correlated with the number of eggs, $r_s = 0.65$ ($P = 0.01$) and 0.48 ($P = 0.05$) respectively. However this relationship was not significant at White River, $r_s = 0.038$ ($P > 0.05$). When the data for the two disturbed areas (Island Spring and White River) were combined, the relationship was significant at the 0.01 level.

The level of parasitization at the undisturbed site, Bruck Foot (47.4%, $n = 251$) was significantly lower ($P < 0.01$) than that at the disturbed sites of Island Spring (75.6%, $n = 492$) and at White River (63.6%, $n = 313$). However, the levels at the two disturbed sites were not significantly different from each other and had a combined value of 70.9%.

More eggs were deposited in the disturbed areas compared to the undisturbed. At Island Spring and White River it was 492 and 313 respectively, while at Bruck Foot it was only 251, giving cumulative densities of IS 8542, WR 7245 and BF 3218 per km^2. When the data for the disturbed sites were combined there were 641 eggs at a density of 7970 eggs per km^2. Cumulative densities indicate that all eggs were not present at the same time but rather represent the cumulative value for the study period.

Other factors accounted for 8.3% egg mortality and might include fungi and ants. A species of fungus was observed on dead eggs but it was not clear if it affected healthy eggs; an unidentified species of ant was observed preying on a parasitized egg but there was no evidence to suggest that it is a predator of viable eggs. Mortality was also caused by a number of unknown factors which included failure of eggs to develop, as well as unexplained egg disappearance.

Larvae in any stage were killed by any of three bacteria: *Bacillus* Cohn sp., *Enterobacter* Hormaeche and Edwards sp. and *Clebsiella* sp. (Garraway et al. 1993). Laboratory analyses did not reveal any other pathogen. They were also predated by the ant *Camponotus* Mayr sp. and by birds and probably by anoline lizards, which were common in the environment.

Thirteen percent of the pupae collected (N = 15) died from symptoms related to bacterial infection in the larval stage. Mortality of adults was not observed. Of the adults captured in the field, 9% (n = 23), had bilaterally symmetrical marks which indicated that they may have been attacked by birds or lizards while resting with their wings closed. They were all males.

Spanish River Valley

In 10 one-day visits to the Spanish River Valley *P. homerus* was not recorded. The food plant *H. catalpaefolia* occurred along the banks of the river in several places which appear to the observers suitable for *P. homerus*, but there were no larval damage to the leaves. Species such as *P. pelaus* F. and *Siproeta stelenes* L., which often fly with *P. homerus*, were observed.

Mt Diablo population

In 6 one-day visits to Mt. Diablo no *P. homerus* was recorded. Proctor also made over 20 one-day trips to this area over four decades studying the plants and never recorded a sighting (G. Proctor, personal communication). Since no food plant was recorded from the area it is unlikely that a breeding population ever existed. Kaye (1926) stated that the butterfly was reported from here, these might represent transient migrants.

Western population

Comparatively little work has been done on the western population. In the literature there are records of adults at Elderslie, Accompong, Quick Step and Crown Lands (Avinoff and Shoumatof 1940; Lewis 1949; Brown and Heineman 1972; Turner 1991). In August 1986 Emmel and Garraway observed adults at Elderslie, flying 10–16 m above ground, at canopy level where sunlit openings occurred (Emmel and Garraway 1990). In another visit to the area in October 2003, Garraway, Bailey and Emmel made no sightings at Elderslie, but at Niagara 3 km northwest. Garraway and Bailey also made sightings at Niagara in 2006 and Lehnert worked on that population later that year.

No adults were recorded from the northern region of the Cockpit Country until 1997 when members of the Jamaica Parrot Project (JPP) recorded adults at Windsor. Since then, adults have been recorded with some regularity by researchers working at Windsor and Dromily. JPP personnel made the following records: 14 in 1999, 7 in 1998, and 13 in 1999. The group also recorded sightings in the traditional areas in the southern and south-eastern Cockpit Country: 1 in 1997, 4 in 1998 and 7 in 1999. Field work was carried out by the JPP 5 days per week (at least two persons each day) from March to June each year. Garraway led the Butterfly Group of the Natural History Society of Jamaica on a number of one-day trips into the area since 1999 and made the following sightings: at Dromily there were 6 in July 1999, 0 in October 1999, 0 in September 2000, 3 in May 2001, 3 in July 2003; at Windsor there was 1 in September 1999, 0 in September 2000. The Dromily site is much more remote and less disturbed compared to the Windsor area and appears to the observers more suitable for *P. homerus*. On 15 previous one-day trips to the Windsor area (1985–1995) Garraway recorded no adults.

At Dolphin Head Mountain no adult was recorded by Garraway on trips made in 1995 and 2001, or by the Dolphin Head Trust (2007). *H. jamaicensis* was common; however, there were no larval damage on the leaves. G. Proctor (personal communication) has worked in this area for over three decades and has not seen *P. homerus* there.

Discussion

The summer peak in sightings, found in the sequential studies (Figs. 3 and 4), must be a real population effect, since no diapausing stages have been found either in the field or in the laboratory (Turner 1991; Garraway et al. 1993). Several explanations are, however, possible. It could be (1) the result of increased oviposition in spring coupled with (2) high survival of the juveniles in the period immediately preceding it. Alternatively and/or additionally (3), high survivorship of the adults in the July/August period is possible. There was a close relationship between the number of eggs laid and the number of adults sighted and more eggs were observed in the warmer months of June–September. But there was no lag time between the two, which would occur if increases in adult numbers were the result of increased oviposition. Rather the eggs seem to result from increase in number of adults, the rate of oviposition/female remaining constant. This summer peak coincides with the increase in the abundance of plants flowering (Adams 1972) and hence nectar sources, which might well contribute to higher survival of adults.

Territorial behaviour is well known in the Papilionidae (Tyler et al. 1994) and found in the Jamaican species *Papilio thersites* F. and *P. pelaus* (Brown and Heineman 1972). Territories normally occupy partially enclosed areas of 50–100 m^2, often in the vicinity of hill tops, a further feature of papilionid mating behaviour (Vane-Wright and Ackery 1984). But in *P. homerus* the territories were frequently constrained by the topography, namely the steep sides of the valleys, necessarily giving them a more linear shape, the males patrolling up and down. Other territories occupied openings in the forest and hence were irregular in shape.

The restriction of *P. homerus* to a very few larval food plants is characteristic of Neotropical swallowtails (Feeny 1995). The two species of *Hernandia* are the only members of the Hernandiaceae in Jamaica. It is interesting that *Ocotea* belongs to a closely related family, Lauraceae, and the lack of larval damage on *Ocotea* strongly suggests that oviposition on this plant (Turner 1991; Lewis 1949) are oviposition mistakes (Chew and Robins 1984) rather than attempts to diversify the food resource (Larsson and Ekbom 1995).

The egg distribution per leaf was typical of swallowtails: eggs were normally deposited singly or in small groups (Brown and Heineman 1972; Tyler et al. 1994). Such a distribution is also found in the Sphingidae (South 1939; Janzen 1984), a group containing large, powerful fliers. It would seem that such a strategy is open only to species that have good powers of locating multiple larval food items, particularly when these items are spatially distant. Within those sections of the Lepidoptera that fly weakly, such as the carpet moths, eggs are typically deposited in batches (South 1939; Renwick and Chew 1994).

Egg distribution at the patch level showed a considerable degree of selection on the part of ovipositing females. Eggs were deposited non-randomly. In particular, unclustered trees were selected close to the stream within each valley. These hosts were located along the natural corridors in the forest which could be considered the edge of the habitat and probably had higher encounter rate and the increase in the area of a tree available for the female to alight on. The works of a number of authors have shown that the frequency of choice of trees at the edge of the habitat as well as unclustered and isolated trees is probably increased as a result of female movement patterns and factors such as the visibility of these plants (Gilbert and Singer 1973; Cromartie 1975; Wiklund 1977; Dempster and Hall 1980; Watanabe 1995). Since females of *P. homerus* alighted on different plants with leaves of different sizes while searching for suitable hostplants, it appears as if they are unable to recognize suitable hostplants without alighting on them. The chance of a close encounter is thus an important factor determining if a particular tree gets utilized.

Papilio homerus shows a sequential variety of colours and patterns during development that are similar to those in other congeneric and confamilial species, and presumably aid individual survival. Overall, the larval sequence is very similar to that in the Central American species *P.* (*Pterourus*) *garamas* (Geyer), to which *P. homerus* is most closely related. The excrement-like pattern of young larvae is found in several swallowtails such as *P.* (*Pt.*) *esperanza* Beutelspacher, *P. himeros* (Hopffer) and *Mimoides lysithous* (Hubner) (Tyler et al. 1994) and in *P. andraemon* (Hubner). In mature larvae a swollen thorax and eye spots are also found in *P.* (*Pt.*) *esperanza*, in which they are yellow and provided with realistic black pupils, and also in *P.* (*Pt.*) *glaucus* (L.) and P. (*Pt.*) *canadensis* (Rothschild and Jordon) (see plate 24.4 and 24.5 in Scriber et al. 1995). The actual survival value of these colours and patterns has not been tested, but the disappearance of larvae leaving body fluid behind (Garraway et al. 1993) gives an indication of predation. Turner (1991) saw bird predation, a member of the Tyrannidae eating L1–L3 larvae.

Brown/green "polymorphism" is well documented in the swallowtails (Hazel 1995), and better called "polyphenism", since it results from an environmental modification of the phenotype. Hazel noted that texture and colour are often important environmental factors in such cases. In *P. homerus*, both brown and green pupae were found on brown twigs, and occasionally on green ones. Their appearance is very cryptic, resembling dried curled leaves or small green leaves.

The "butterfly within butterfly" image may not have been described previously. We regard it as a new example of natural deception (Hinton 1973; Trivers 1985). It is also apparent in some other *Pterourus* species, for example in some sub-species of *P.* (*Pt.*) *garamus*, *P.* (*Pt.*) *hellanichus* (Hewitson) and *P.* (*Pt.*) *menatius* (Hübner) (plates 95, 98 and 99 in Tyler et al. 1994), but is not as distinctive as in the present species. Possibly the hesperiid image in *P. homerus* serves to confuse a potential predator as to either the size or the identity of the prey object, but given the rarity of this species, this would be a difficult hypothesis to test. During basking the tailed skipper image is displayed (see Emmel and Garraway 1990 Fig. 3b) but the presence of a distinct non-tailed image from the underside (Emmel and Garraway 1990 Fig. 2b) makes it likely that there is also an effect in flight. The hesperiid image might induce potential avian predators to attack less frequently, as hesperiid butterflies are relatively small and very fast and erratic fliers, and thus in optimal foraging terms "not worth the effort".

It is not clear what these new sightings in the northern Cockpit Country represent. It might be the result of (1) an expansion of geographic range, (2) an increase in population size and a corresponding increase in range or (3) a spatial shift of the population. The latter is unlikely, as adults were recorded in the traditional southern areas around the same time. The new northern population seems to represents an extension into a part of the butterfly's normal range which has recently become favourable. The entire Cockpit Country might be regarded as potential habitat changing in suitability in both space and time. This type of population expansion or spatial shift recalls the metapopulation models of Andrewartha and Birch (1954; Figs. 14.06–14.09), Levins (1969, 1970) and Hanski et al. (1993), in which changes in physical factors affect the suitability of different parts of the habitat, resulting in expansion or contraction of the sub-populations.

P. homerus require wet sites with humidities close to 100% (Parnell 1984; Emmel and Garraway 1990). The annual rainfall in the northern part of the Cockpit Country is relatively high (1,500 mm), although lower than that in southern Cockpit Country (2,000–2,500 mm). Rainfall is seasonal, with distinct dry seasons in January–April period and in July. The extensive dry season might be the critical factor limiting *P. homerus* populations in the Cockpit Country. Data from the Meteorological Office of Jamaica did not indicate any significant change in rainfall pattern during the period 1997–2000, and a complex of factors probably operates. Although Spanish River Valley and Dolphin Head Mountain are apparently suitable habitats for *P. homerus* , there were no adult sightings or larval traces. Both areas are subject to extensive dry periods and again this could be the limiting factor.

The major mortality factors for *P. homerus* eggs were hymenopterous parasitoids. A feature of their importance is the level of habitat disturbance. The butterfly laid more eggs in the disturbed areas and the level of parasitism was higher compared to that at the undisturbed site. It is not clear if the higher level of parasitism in the disturbed areas was due to the host's increased accessibility to the parasitoid or to higher density of the host. Searching parasitoids are known move though several spatial levels to find their hosts (Vinson 1976; van Alphen and Vet 1986; Roland and Taylor 1997). The parasitoids acted in a density-dependent manner at IS and BF, and while the relationship was not significant at WR, the trend was the same. This suggests that the difference in parasitism seen in disturbed and undisturbed sites is a density dependent one. It was difficult to determine the role of this mortality factor in the regulation of the population, although it is clear from the study that numbers are greatly influenced by this effect. The higher number of eggs in the disturbed sites has additional significance when the elevated levels of egg parasitism are considered. The higher levels of parasitism have the potential to make these sites into pseudosinks or even sinks (Freeman 1981; Pulliam 1988; McPeek and Holt 1992; Watkinson and Sutherland 1995; Boughton 1999). The balance between disturbed and undisturbed sites might thus be critical for the survival of the species.

The population dynamics of butterflies as a whole were poorly understood (Dempster 1983) but recent work (Hirose et al. 1980; Hanski et al. 1994; Hirose and Takagi 1995) has considerably improved the position. For the Papilionidae, however, only a few studies have been made on the dynamics of temperate and warm temperate species (Tsubaki 1973; Watanabe 1976, 1981, 1983; Matsumoto 1985).

Indications are that *P. homerus* occurs in two metapopulations (Levins1969, 1970), an eastern and a western metapopulation and to date there has been no actual estimate of the size of either of these. Work on the eastern population measured relative numbers of specific subpopulations, these showed marked fluctuations and even extinctions. Lehnert (2008) working in the west, using mark-recapture, estimated the Niagara population at 50 individuals in July–August 2004 but found it extinct in December of the same year; he surmised that this represented the entire Western Population, but the Niagara population clearly represents merely a dynamic subpopulation, and not the entire western metapopulation. The latter includes other subpopulations at Troy, Windsor and Dromily and most likely others within the uncharted areas of the Cockpit Country. Moreover, all studies in the West have been restricted to the peripheral areas, or the edges of the few roads that penetrate the Cockpit Country, and most of the 500 km^2 remain unexplored.

Although the regression analysis of the adjusted historical data provide no evidence for a decrease in the numbers of captures and sightings this is not to say that the two populations of *P. homerus* are not in decline. If it is assumed that such numbers provide an unbiased estimate of population density there is good evidence that the areas occupied by these populations have been diminishing.

Eyre (1986) estimated that the depletion of tropical rainforest in Jamaica (i.e. dry forest excluded) was 224,350 ha over the 300 years period 1491–1791. Loss of the total forestlands area was 104,530 ha between the years 1886 and 1943 (57 years) (Hooper 1886; Swabey 1945), i.e. 20% forest coverage remaining. According to Eyre (1986, 1987), there was a wave of forest clearance in the eighteenth century for plantation establishment. However, the mid to late nineteenth century seems to be the start of a period of substantial regrowth of forests mainly because of the decrease of human economic usage of land (Eyre 1987; Higman 1988; Satchell 1990). The forested area of Jamaica remained fairly constant (24–29%) for the first half of the twentieth century (Evelyn and Camirand 2003). The situation is still tenuous as was demonstrated by the impact of the Government planned program of the 1970s and 1980s to establish commercial forestry which rapidly destroyed vast acreage of natural forest. This program, however, failed and most of the introduced *Pinus caribea* L. was destroyed by hurricanes and in these areas there is presently natural regrowth and/or an active reforestation program (Headley and Evelyn 2000). Deforestation rate in Jamaica is now estimated at 0.1%, (Headley and Evelyn 2000; Evelyn and Camirand 2003) and there was clear net increase in some areas especially in the north east (Headley and Evelyn 2000). The biggest threat to the forests is probably mining (especially for bauxite, Neufville 2001) and both the western and eastern populations are in further danger as several companies have mining leases to large areas of the Cockpit Country and the Blue Mountains and there have been active explorations in recent times (Cockpit Country Stakeholders Group 2006).

Lepidopterists go only to periphery of these shrinking areas to collect and make observations. Hence, while population density in such local areas may not be diminishing, total numbers certainly have done so. Firstly, this underlines why total number and population density should not be confused in population ecology, often under the umbrella of that potentially ambiguous term “abundance”. Secondly, since the genetic diversity of a species will be related to its total numbers, some of this diversity may be lost by random genetic drift, when these numbers are in a trough, the “intermittent drift” of C.H. Waddington. Fluctuation of the numbers sighted both historically and during the census gives cause for concern.

This concern is further heightened when one takes into account that the intense human activity in the central region of the island which has produced a barrier to migration between the eastern and western populations. There is no evidence of regular migration between populations. The only record of *P. homerus* sighting outside the known population centres was in the 1940s at Long Mountain (St. Andrew Parish) 30 km to the west of the Blue Mountain population (Lewis 1944a), and Kaye’s (1926) comment that the butterfly had been reported from Mt. Diablo, near Ewarton.

A more extreme scenario, therefore, is the extinction of one or both populations as a result of a hurricane or other catastrophe. The island of Jamaica is only 230 × 80 km and so the entire island can easily be affected by a catastrophe. For example, Hurricane Gilbert, which in 1988 struck Jamaica, caused the total defoliation of trees in all but the most sheltered places, and in addition there was a shortage of nectar sources for several weeks. Populations are more buffered from catastrophes in larger habitats because these provide greater environmental diversity in which there is a greater chance of survival in a few sheltered localities.

While there has never been a comprehensive conservation programme for *P. homerus* there have been a number of advances. In 1982 *P. homerus* was listed as endangered and so protected by under the Third Schedule of the Jamaica Wild Life Protection Act of 1945. It is also protected under the Endangered Species (Protection, Conservation and Regulation of Trade) Act of 2000 (NEPA 2003). The National Environmental Protection Agency (NEPA) has developed a ‘Giant swallowtail butterfly Recovery Plan’ (NEPA 2002) which includes the following recommendations:

1. Implement and enforce management for the extant population, including protection from illegal collecting and trade.
2. Survey suitable habitat for additional populations and potential re-introduction sites; re-establish populations within the historic range of the species.
3. Monitor existing populations.
4. Conduct research on the biology of the species and on suitable management tools for maintaining its native habitat. In our view this is probably the most crucial requirement.
5. Develop techniques for captive breeding to assist in the re-establishment of populations in the wild; maintain captive populations.

While several aspects of this recovery plan are yet to be activated by NEPA, individual researchers, Government agencies, and NGOs are making their contributions, some of which are highlighted below.

The Blue and John Crow Mountains National Park in conjunction with the RARE Center for Tropical Conservation conducted an educational project in the mid 1990s (Butler 1994) and the Park Rangers have continued this programme. The establishment of the National Park has reduced, but not eliminated, intrusions into the forests by small farmers.

From1992 to 1999 Garraway and Bailey established and operated the Rio Grande Field Station in Millbank, from which they conducted a community-based environmental education programme. The Blue and John Crow Mountains National Park also established a Ranger Station. These two stations became focal points in the community as the researchers and rangers were intimately involved in community activities, increasing the effectiveness of their education program. There was a great increase in environmental awareness as the people became the ‘protectors of the environment’. This underlines the importance of direct involvement of field researchers in the lives of the people in these sensitive areas. Effective and lasting environmental education programs rely heavily on understanding the local culture and integrating the messages into this culture; too often conservation programs are developed based on spurious perceptions acquired from short visits. Additionally, NGOs such as the Natural History Society of Jamaica (NHSJ) and the Portland Environmental Protection

Agency (PEPA) have conducted education projects in these areas.

The increased awareness combined with the new legislation has greatly reduced if not eliminated organized poaching. Gone are the days when "the butterfly men", supplied with collecting and storage equipment by foreigners, openly roamed the forests with large nets. Poaching is now reduced to opportunist collection or perhaps to very highly concealed activity; the latter is unlikely given the nature of the communities, their knowledge and use of the forest. Garraway's undergraduate students have been accosted repeatedly when they visited the areas on general insect collecting trips. Garraway himself on one trip to the Spanish River Valley, an area where he is less well known, was also accosted by children and threats made to call the police; he was fortunately rescued by the adults.

There is also a much higher level of awareness among legal enforcers such as the NEPA Warders, the Custom Officers, the Police and the Judiciary; and there has been a number of educational workshops for such groups. To date there has been no prosecution for collecting *P. homerus*, although there has been for other protected species such as some birds.

The Government-planned commercial forestry project failed and the affected area allowed to return to secondary forest. The secondary forest has a different composition from the original and, consequently, the Millbank Progressive League has been actively replanting many areas with selected species including *H. catalpaefolia*, the larval food plant of *P. homerus*.

The eastern population has not been surveyed in recent times. However, Errol Francis of Millbank, formerly chief field assistant at the Rio Grande Field Station, and who helped with the previous counts, and who passes through Fishbrook on a weekly basis, informed us that there has been an increase in the number of adult sightings in recent years.

While these programs have been concentrated in the east where there has been a long history of poaching there has also been some conservation effort in the west. Organized poaching has not been reported from the west. Here the work has been spearheaded by the Windsor Research Centre which has a very strong, community-based, environmental conservation programme which has included a number of workshops on the identification as well as conservation of the butterflies of the area. The Cockpit Country Stakeholders Group had also recently emerged as an important lobbying entity, and has successfully stymied recent plans for mining in the Cockpit Country. *P. homerus* was a key species in all these efforts.

While *P. homerus* has not been declared the National Butterfly of Jamaica, it is being treated as such, and has been used extensively as a flagship species for conservation in Jamaica. It appears on many logos/emblems including the $1000.00 bank note, the logo of the Blue and John Crow Mountains National Park, T-shirts, phone cards, posters, bumper stickers, cover of school books, costumes celebrating National heritage, and a special issue of stamps. It has become an integral part of many environmental education programmes. Although much progress has been made there is still a clear need for the implementation of a comprehensive conservation programme.

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ORIGINAL PAPER

Notes on the biology, captive management and conservation status of the Lord Howe Island Stick Insect (*Dryococelus australis*) (Phasmatodea)

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Abstract The Lord Howe Island Stick Insect (*Dryococelus australis*: Phasmatodea: Phasmatidae: Eurycanthinae) is a large, flightless stick insect once thought to be extinct but rediscovered on an island (Balls Pyramid) near Lord Howe Island in 2001. A captive population at Melbourne Zoo is now in its fourth generation and aspects of the biology of the species are discussed. Observations focussed on the eggs as indicators of the health of the population and inbreeding depression, but included data on the juveniles where possible. Behavioural observations reveal that this species is very different from other Australian stick insects, but similar in many ways to overseas members of the Eurycanthinae. Veterinary interventions and post mortems have provided substantial information about the captive population and its environmental stresses, and have wider implications for captive invertebrate populations, particularly those involved in conservation programs. Evidence of inbreeding and the conservation significance of this species is discussed in context with other programs and their implications.

Keywords Inbreeding · Insect husbandry · Insect pathology · Ex situ conservation · Captive management

Introduction

The Lord Howe Island Stick Insect (LHISI) was once abundant on Lord Howe Island, 700 km off the coast of New South Wales, Australia. It apparently became extinct on Lord Howe Island within a few years of the accidental introduction of rats in 1918, following the grounding of the supply ship *Mokambo* (Gurney 1947). In 2001, a small population of the stick insects was rediscovered surviving on a rocky outcrop, called Balls Pyramid, 25 km off Lord Howe Island (Priddel et al. 2003).

The LHISI was categorised at the time as endangered under the New South Wales Threatened Species Conservation Act 1995 and presumed extinct in the IUCN Red Data List (IUCN 1983). A Draft Recovery Plan was developed by the New South Wales Department of Environment and Climate Change (NSWDECC) (Priddel et al. 2002), and in 2003 two adult pairs were removed from Balls Pyramid for captive breeding. One pair was delivered to Insektus, a private breeder in Sydney, the other pair to Melbourne Zoo. At that point almost nothing was known of their biology and ecology, other than observations made by Lea (1916). The remaining wild population is now thought to be less than 40 individuals, living on a few bushes on the side of a cliff on Balls Pyramid (Priddel et al. 2003).

Description

The LHISI is a large, flightless phasmatid, with males reaching 120 mm (more commonly 106 mm) at adulthood and females 150 mm (more commonly 120 mm) (Zompro 2001). Both sexes are uniformly black at maturity, often with a reddish-brown tinge. The body is generally smooth and shiny, and the intersegmental membranes between joints are pale grey (Fig. 1). Adult males are distinguished by two conspicuous spines on the enlarged hind femur. Females have a long, pointed sheath (the operculum or subgenital plate) underneath the last segment, with a wider and more terminally tapering abdomen.

Upon hatching, LHISI are pale to mid-green, and become darker green as they moult. Juveniles are pale

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Fig. 1 Adult female LHISI on its only recorded natural food plant, Lord Howe Island Melaleuca (*Melaleuca howeana*)

brown, becoming darker brown with age, then very dark brown to black in the final instars (Fig. 2).

Habitat

The only known population of LHISI is amongst a group of melaleucas (*Melaleuca howeana*) on the north-west face of Balls Pyramid. The melaleucas cover an area of about 30 by 10 m, and are the only vegetation on the pyramid other than groundcovers. Smaller islands around Lord Howe Island have been extensively searched for LHISI, without success.

Lord Howe Island is covered with a range of subtropical habitats, from cloud forest at the tops of the mountains to coastal vegetation on the dunes. The temperature on Lord Howe Island ranges from 15 to 25°C throughout the year, and the humidity is generally high year round. There is a great range of plant species throughout the habitats in which LHISI were once known to occur, but on much of the island the largest tree is the Lord Howe Island Fig (*Ficus macrophylla columnaris*). In the forested areas, the canopy is high and there may be little lower level vegetation or ground cover, and the soil is deep and often sandy.

Balls Pyramid is much more exposed than Lord Howe Island, with a greater range of temperatures. The humidity is also high due to its exposure to the sea, but the rock itself is very dry and there are no sources of fresh water. Consequently there is very little vegetation and almost no soil. The melaleucas on which the LHISI survive are very old and stunted, and growing very densely close to the rock. Due to the large numbers of sea birds which nest on the bushes, the foliage is covered with guano, and many of the plants are also being threatened with smothering from Morning Glory (*Ipomoea indica*). There are quantities of melaleuca leaf litter at the bases of the bushes, in some places quite deep, but this is very friable and dry.

Fig. 2 Second instar LHISI. This stage is dark green-brown, becoming brown in later instars and then black

Prior to its extinction on Lord Howe Island, the only information on LHISI was recorded by Lea (1916), but this did not include biological or dietary data. On Balls Pyramid, LHISI emerge at night to feed on the outer foliage of melaleucas and are presumed to shelter during the day at the bases of the shrubs.

Methodology

The original, wild caught pair (P1) was kept free ranging in a glasshouse at Melbourne Zoo and observations made of their behaviour nightly for the first month. This included time spent feeding, mating, exploring, egg-laying or remaining inactive. The egg-laying medium was sifted daily and eggs measured by length, width and weight. Subsequently, four egg-laying media (sand, vermiculite, peat and a 50:50 sand-peat mixture) were trialled in a glasshouse housing 130 adults. Over four generations, 3,093 eggs were set up for incubation and, of these, 2,627 were weighed, measured and their development monitored. The depth of egg deposition of the first 10 batches was measured by uncovering eggs with a fine camel hair brush.

Eggs were kept in labeled groups in sand for up to 5 months until they could be measured and weighed. They were then incubated in four different media (sand, soil, peat and vermiculite) under three moisture regimes. These included wet (media sprayed daily), moist (sprayed once a week) and dry (unsprayed). Eggs were placed 2.5 cm below the top of the media with the operculum facing upwards. Newly hatched nymphs were measured from the front of the head to the tip of the abdomen with electronic calipers on the day of emergence and a subjective assessment made of their condition (poor, good, excellent).

Nymphs were initially set up on Lord Howe Island Melaleuca, but other plant species were later included as additional choice or non-choice trials. Nymphs were kept singly or in groups of up to 40 in plastic pet paks or wooden, aluminium or plastic enclosures with mesh screening. Plants and insects were sprayed daily and a Petri dish of free water was available at all times to older juveniles and adults. Adults were kept in similar but larger enclosures to the nymphs, usually in groups of 10 females to two males. The enclosure included a wooden box (variable in size) as a daytime retreat, egg-laying media and a piece of wood or bark soaked during the day in water to increase humidity within the enclosure. Additionally, up to 200 adults were kept free-ranging in a glasshouse 5 m × 3 m × 3 m (L × W × H). Observations were variously made of feeding, moulting, intraspecific interactions and other behaviours.

Supplementary feeding trials included the young seeds and ‘cabbage palm heartwood’ of the Kentia Palm (*Howea forsteriana*), as well as Orthopteran mix. The latter is used as supplementary feed for a range of insects in captivity, particularly Orthopterans and stick insects (see Rentz 1996 for recipe).

Direct observations on LHISI feeding and indirect observations on feeding marks were used to determine the effectiveness of the Kentia Palm products. Three small Petri dishes of Orthopteran mix were weighed and changed daily and placed in three enclosures with 32 adult LHISI for 1 month, plus a control dish outside the enclosures but within the same glasshouse.

Individual nymphs and adults were tagged using queen bee markers for behavioural observations. These markers are small coloured plastic discs which are fixed to the backs of individuals using a non-toxic glue (Fig. 3). Nymphs as young as 3 months old were tagged, but tags were lost at each moult and insects required retagging. Tagged individuals were kept in groups, and every day the group checked to ensure that any individual that moulted overnight was retagged. The identity of many individuals was lost, however, as multiple insects moulted overnight and could not be individually distinguished.

Fig. 3 A pair of adult LHISIs in the daytime retreat. The male (lower) is facing the opposite way to the female (top), with two of his legs over her body. Note the yellow bee markers on the back of each thorax

The bee markers were fixed to the dorsal surface of the thorax, slightly to one side for nymphs so it did not interfere when the thorax split down the middle during moulting. LHISI have a tendency to choose to spend the day in damp, mouldy conditions and the tags quickly became covered in frass and dirt which was removed by gentle scrubbing. The bee markers lasted several months on the back of adults.

LHISI deaths were recorded and selected specimens were post mortemed by Melbourne Zoo veterinarians.

Biology and life history

Eggs

The gestation period, the ability of females to store sperm and the influence on the eggs of multiple matings with different males is not known. Males of this species do not transfer an obvious spermatophore as do other stick insect species.

Females begin laying eggs about a fortnight after reaching adulthood, whether a male is present or not. Whether this species is able to reproduce pathenogenetically is not yet known. A number of adult females have begun producing eggs before being given access to a male, but none of these eggs has hatched. The number of these eggs produced (42) is not sufficient to adequately determine viability, as any group of 42 eggs may or may not produce any offspring, particularly at the beginning of a female’s egg-laying period. Female *Extatosoma tiaratum* will mate if given access to males but produce eggs parthenogenetically if no male is available within 33 days of maturity (Carlberg 1981, 1982). Whether a similar process occurs with LHISI is not known and requires further research.

The first several batches of eggs produced by each female tend to be smaller than those produced later on, and the very first eggs may be slightly misshapen, particularly the micropylar plate. The eggs produced at the end of a female's life may also be smaller than those produced previously, and females will continue producing eggs until death, although the rate of egg production declines dramatically towards the end.

The eggs (Fig. 4) are relatively large, whitish to pale cream and covered with a fine, raised, net-like structure (Hennemann and Conle 2006). On contact with moisture, eggs become very dark in colour, ranging from dark grey-brown to black, and if sitting on a moist surface the egg may be black on the lower side and white on the dry side. The dark colour fades as the egg dries out, suggesting the egg wall is very porous and/or absorbent. Unviable eggs also become very dark as they age, and this has led to erroneous descriptions based on old museum specimens.

The average length of an egg is 6.36 mm (range 3.6–7.1 mm, $n = 2627$) and the width 3.95 mm (range 2.1–4.45 mm, $n = 2627$). Most specimens are about 6.2 mm long and 3.6 mm wide. The average weight of an egg is 0.058 g (range 0.005–0.08 g, $n = 2627$). At the top is a flat operculum through which the nymph emerges, and on the side towards the opposite end is a tear-shaped micropylar plate, about 2.4 mm long. One specimen, which subsequently hatched successfully, possessed one micropylar plate on each side of the egg, a state that has not been previously recorded for Phasmatodea (Clark Sellick 1998).

Females generally produce eggs in batches of 9–10, about a week to 10 days apart. Smaller batches are commonly produced, and single eggs may be deposited in the intervening periods. The sex ratio of successfully hatched young appears to be about 50:50 overall. There is some evidence that the early eggs from any individual female will produce female offspring, and later eggs tend to be male, although this requires further confirmation. This situation leads to dramatic changes over time in the sex ratio of the entire population, with the adult population at Melbourne Zoo varying between 10% female in one period and 98% female in another. Eggs are deposited in the egg laying medium at an average depth of 2.5 cm (not including those deposited on the surface of the medium) (range 0–3.8 cm, $n = 48$).

Fig. 4 LHISI eggs. Most are laid subterraneously but some are deposited on the soil surface

The average number of eggs produced per female was 149.1 (range 52–257, $n = 28$ females studied). The number of eggs produced by P1, the wild-caught female, was 257 and was the highest number produced by any female so far. The average number of eggs produced per female from subsequent generations was 161.58, the difference possibly due to inbreeding issues (see below).

The average incubation time for LHISI in captivity was 209.1 days (range 175–241 days, $n = 624$). There was no significant difference between the incubation media trialled, and the moisture regimes ($P < 0.05$). Vermiculite was the most successful incubation media and has been used continuously since the completion of the trial.

Just under half (47%) of the eggs so far analysed have hatched. The hatch rate depends strongly on an egg's parentage (and generation number—see below). The percentage hatch rate of eggs produced by individual females over all generations varied from 5% to more than 70%. For all 22 females from F2, for example, the percentage varied from 22.2 to 73.6%.

There was little difference in volume, weight or morphology between eggs that hatched and those that did not, and there was no significant difference between the two groups ($P < 0.05$). However, more of the smaller and lighter eggs did not hatch than hatched. For eggs that hatched, only 32.92% were 0.05 g or less ($n = 404$ eggs). For eggs that did not hatch, 50.67% were 0.05 g or less ($n = 1{,}115$ eggs) (1,519 eggs total).

Conversely, more of the larger and heavier eggs hatched than did not hatch. For eggs that emerged, 67.08% were 0.06 g or greater ($n = 404$ eggs). For eggs that did not emerge, only 49.33% were 0.06 g or greater ($n = 1115$ eggs) (1,519 eggs total) (Fig. 5).

Similar results were obtained when eggs were analysed by weight (Fig. 6).

Eggs which did not hatch within the above incubation period can be classified into four states:

(1) those that remain intact and appear to be still viable;

(2) those with an intact operculum but with a thick yellow exudate around the operculum to which the incubation media adheres;

(3) those that have lost the operculum and contain, within the body of the egg, a thick yellow fluid; and

(4) those that have lost the operculum and are completely empty.

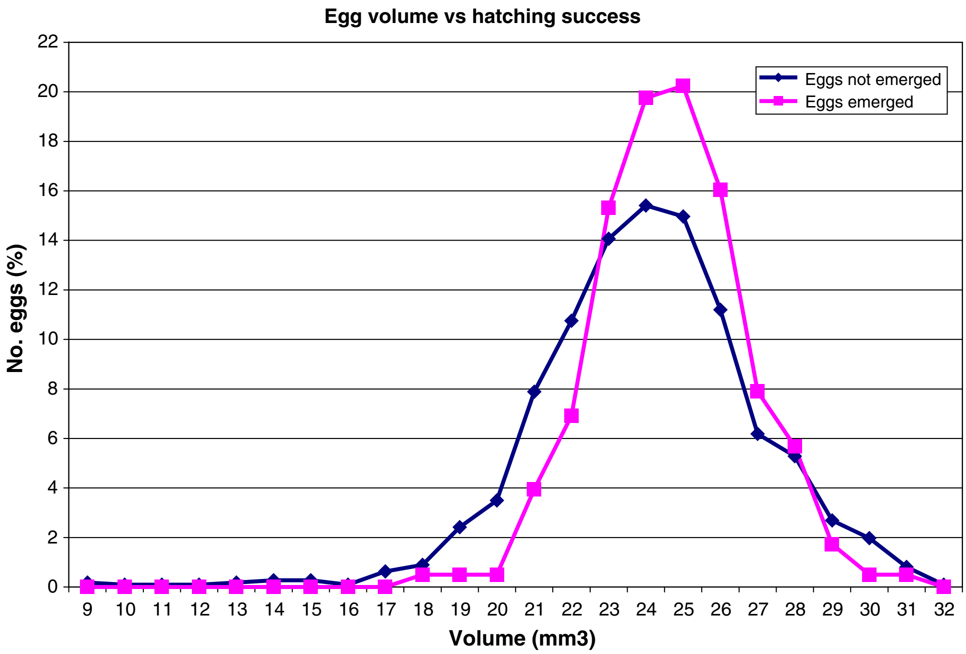

Fig. 5 Percentage eggs which hatched or did not hatch in relation to egg volume

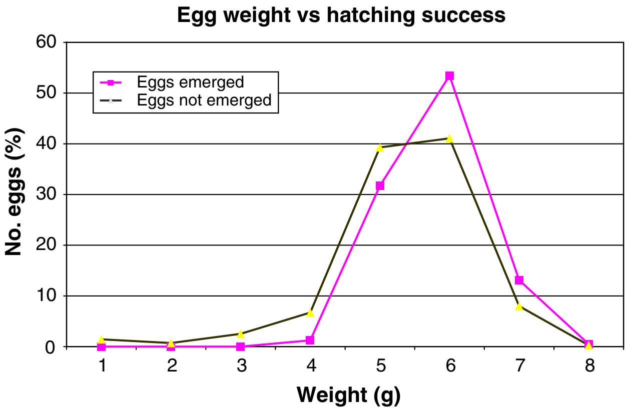

Fig. 6 Percentage eggs which hatched or did not hatch in relation to egg weight

LHISI's closest relative, *Eurycantha calcarata* from Papua New Guinea, is known to deposit its eggs subterraneously and in captivity the most successful egg-laying media is peat. For LHISI the best egg-laying media (in order of success) are peat (26.2%), sand (23.5%), peat-sand mixture (14.2%) and vermiculite (3%) ($n = 1{,}250$). However, the largest proportion of eggs (28.1%) were produced within the daytime retreats, deposited amongst frass. It is not known whether these eggs were produced during the day, or in the evening before the females left the retreat to feed etc. In addition, 5% of eggs were collected from the floor of the enclosure, presumably produced during nightly activities.

Juveniles

The average body length of newly hatched LHISI was 19.73 mm (range 13.61–23.57, $n = 1{,}235$). Hatchlings usually emerge from the egg underground, and burrow to the surface to climb the nearest large object. Most individuals appear to hatch during the night, but will also hatch throughout the day, including the afternoon.

There are five instars between egg and adult, but the length of the each instar can vary significantly between individuals. Moulting takes place at night and is generally completed by 5 am. The process takes approximately 25 min, with the juvenile hanging from a branch of the food plant or from the top of the enclosure. Occasionally an individual may become caught in the skin and is unable to successfully complete ecdysis, which results in the death of the individual. More commonly, the forelegs of an individual may become caught in the old skin and either be lost or slightly deformed. This may be rectified during subsequent moults.

Nymphs may moult within a fortnight of emerging from the egg, but there is overlap between different stages of different individuals throughout the rest of the instars. The intermoult period in the later instars may be as little as 10 days. LHISI reach maturity at between 201 and 224 days, averaging 210 days ($n = 32$). Adults may live for up to 18 months after maturing.

Behaviour

LHISI appear to be a particularly gregarious species. Lea (1916) reported that 68 nymphs were collected from a single tree hollow on Lord Howe Island, and there are also reports that large numbers sheltered within the roof spaces of houses on the island. When given the option of several daytime nesting boxes in captivity, groups of insects tend to crowd into a single nesting box rather than spread out into smaller groups. Both adults and nymphs shelter together during the day in groups of mixed age.

Adult males are endowed with large spines on the hind femora, the exact purpose for which is unclear. They sometimes use these to squeeze a finger when handled by humans, and they may be used against other males (Bedford 1975, Minott 2006). In captivity, males are not kept with other males in the presence of females, following the death of a female which may have been caused by one of several males sharing her enclosure. Adult female Eastern Goliath Stick Insects (*Eurycnema goliath*) have twice been observed to fatally injure other adult females by (inadvertently) squeezing the victim's body in the crook of the well-spined hind legs (unpubl. obs.). Male LHISI have been kept together in groups without females and without incident, and single males have been kept successfully with groups of up to 10 adult females.

Feeding behaviour

LHISI feeding on *Melaleuca howeana* will consume leaves of all ages, from those at the base of the plant to the tips of the stems. LHISI will methodically consume every leaf on a branchlet, moving from the tip to the base, so extended bare patches are left after feeding. The leaves are consumed right down to the petiole and the insect will often continue on to chew the bark, leaving small raised scars in the stem. Small branchlets may be chewed through as the insect pushes the stem right into the base of the mandibles. Feeding appears to be in sessions of about 1–1.5 h (although they may extend up to 260 min), followed by extended periods of inactivity.

LHISI will also chew non-plant material, such as plastic. Despite vigorous and audible chewing, the material is usually left unmarked, so the significance of this behaviour is unknown. They will chew bark of other trees and plants such as tree ferns, but again it appears that little or no material is actually consumed.

Mating behaviour

Mating takes place usually with the female horizontal on the ground and the male above her, but it will sometimes occur with both hanging vertically on a plant or at an angle of 45° (Fig. 7). If mating vertically, the male may lose his grip on the female and hang downwards by the abdomen until he is able to gain a footing and return to the upright position, still attached to the female (Honan 2007b).

Mating episodes take between 14 and 25 min, and there may be up to three episodes per night, usually with one to two nights in between episodes. The female may continue to feed during mating, but generally both sexes remain completely immobile, with not even the antennae moving. The male may remain on the back of the female for some time following cessation of mating.

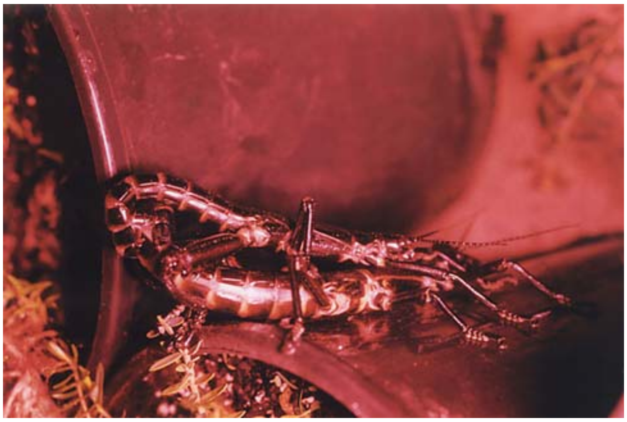

Fig. 7 A pair of LHISI mating on the side of a plant pot (photo turned sideways for clarity). The male (top), identifiable by his thickened hind femora, is curling his abdomen over and then underneath that of the female (bottom)

Egg-laying behaviour

When about to lay an egg, a female moves her body backwards slightly and immediately probes with the tip of her abdomen into the soil. She arches her body as she pushes the tip down into the soil and after a period of usually only a couple of seconds, begins to grind her entire abdomen back and forth sideways. This continues for a variable period until she moves her body forward slightly and removes her abdomen from the soil, leaving behind an egg.

She will then pat down the soil with her abdomen. Every time the abdomen touches the soil it moves to one side slightly to smooth the soil, and the end also curls under the abdomen towards the front slightly, further smoothing the soil. This is repeated a variable number of times, sometimes with pauses in between. She then remains immobile for a couple of minutes, during which time another egg will appear at the tip of her abdomen. The process is then repeated.

Pair bonding

'Pair bonding' is unusual in insects and not clearly defined, but there are reports that adult males and females of *Eurycantha horrida* form bonds if kept together for a period.

The behaviour of individual pairs of LHISI that have been kept together for a long period suggests a bond between some pairs. When a male and female are kept together in the same enclosure, the pair characteristically spends the day in the retreat with the male alongside the female and two or three of his legs over the top of her body (Fig. 3). Nine pairs kept together as individual pairs at Melbourne Zoo for several months were observed daily over a month to investigate the relationship between male and female, determined by the location of each in relation to the daytime nesting box. There were four possible combinations:

- male inside nesting box and female outside;
- female inside nesting box and male outside;
- both sexes within nesting box; and
- both sexes outside nesting box.

Behaviour differed markedly between pairs, but remarkably consistent within each pair over time. In one pair, both sexes were found together in the nesting box every day of observation, with the male's body lined up beside that of the female and with three of his legs stretched over her; in other pairs both were outside the nesting box on most occasions, or the male outside the box and the female inside. Of the total 270 observations, never once was the male found inside the nesting box and the female outside.

Diet

The diet of the stick insects on Lord Howe Island is not known, as no records were kept before they became extinct there. The only related published information is that juvenile LHISI were found in large numbers during the day in hollows of tree trunks, presumably of the dominant Lord Howe Island Figs (*Ficus macrophylla columnaris*) (Lea 1916). On Balls Pyramid, they are known to feed on Lord Howe Island Melaleuca (*Melaleuca howeana*), but they may have other additional plant sources there.

In captivity, LHISI have largely been fed on Lord Howe Island Melaleuca (*Melaleuca howeana*). They have also been successfully reared on Tree Lucerne (*Chamaecytisus prolifer*), Blackberry (Bramble) (*Rubus fruticosa*) and Moreton Bay Fig (*Ficus macrophylla*) (Table 1). They show signs of being adaptable to a range of food plants. All stages have done particularly well on Tree Lucerne, with several generations now having been reared on it.

As they may have had other food sources on Lord Howe Island or even Balls Pyramid that are not yet known, a supplementary diet of Orthopteran mix was offered to LHISI in captivity at Melbourne Zoo. Of the 90 replicates, there was no evidence of feeding by any stick insects.

In his 1852–1855 journal of the voyage of the HMS Herald which berthed at Lord Howe Island in 1853, John MacGillivray noted "colonies of a singular cricket-looking wingless insect between 4 and 5 inches in length which the people on the island have designated the 'land lobster'" and which "feeds on rotten wood" (Etheridge 1889). Local sources suggested this was the 'heartwood' of the Kentia Palm. Consequently, pieces of Kentia Palm trunk and heartwood were offered to LHISI in captivity. Up to 10 pieces of wood, either dry or soaked in tap water, were placed in enclosures for 2 years, but there was no direct or indirect evidence of feeding. Following observations of the P1 female chewing fibres of Tree Fern trunks (*Cyathea australis* and *Dicksonia antarctica*), 5 cm long pieces of tree fern trunk were offered for 2 years, also with no evidence of feeding.

Discussions with several locals on Lord Howe Island revealed that their parents had observed LHISI feeding on young seeds of the Kentia Palm. Seeds of all ages (including unripe specimens) were subsequently collected and 50 were offered on dishes to free ranging LHISI in captivity. After 2 months there was again no evidence of feeding.

Clinical cases

Due to the conservation value of LHISI specimens held in captivity and the difficulty in obtaining further specimens, veterinary interventions have been undertaken on a number of ailing and dead specimens to determine the cause of morbidity or death.

The first case occurred within 2 weeks of the P1 female being collected from the wild. The female ceased feeding and started to become inactive about a week after being in captivity, following her first episode of egg laying. Over several days her activity, particularly feeding activity, was notably reduced and for 5 days she ceased feeding altogether (Fig. 8). During this period she was x-rayed to determine if she was egg bound due to a possibly inappropriate egg-laying substrate, and six eggs were clearly seen inside her abdomen (Fig. 9). These eggs were subsequently deposited by the female and later developed very thin, brittle shells, and eventually disintegrated entirely, presumably due to the effects of the x-ray, but all further eggs appeared undamaged. Other analogous stick insects (*Eurycnema goliath* and *Extatosoma tiaratum*) x-rayed at the same time showed dozens of eggs in the abdomen, so the LHISI female was apparently not egg bound. Her foregut was also seen in the x-ray to be full of air, suggesting aerophagy, a sign of distress in vertebrates, particularly birds (H. McCracken Dr, Senior Veterinary Surgeon, Melbourne Zoo, personal communication).

After 5 days she became completely immobile and did not react to touch or light, and a solution of melaleuca leaves (mashed with a mortar and pestle), glucose and calcium in distilled water was administered to her with an

Table 1 Plant species offered to LHISIs in captivity

Scientific name	Common name	Comments
Melaleuca howeana	Lord Howe Island Melaleuca	Reared several complete generations through egg to adult and egg again. Can be fed long term on this species alone
Chamaecytisus prolifer	Tree Lucerne	
Rubus fruticosus	Blackberry	Reared one generation through egg to adult and egg again
Ficus macrophylla	Moreton Bay Fig	
Rubus species	Native Blackberry	Hatchlings did not feed at all (in non-choice tests)
Coprosma repens	Mirror Bush	
Nerium oleander	Oleander	
Lantana montevidensis	Lantana	
Tagetes lemonii	Mexican Marigold	
Abelia grandiflora	Glossy Abelia	
Pipturis argentius	No common name	
Ligustrum vulgare	Privet	
Gardenia angusta	Gardenia	Hatchlings fed initially but did not survive past second instar (in non-choice tests)
Pollia crispata	Rainforest Spinach	
Asystasia bella	River Bell	
Clutia pulchilla	No common name	
Alnus jorullensis	Evergreen Alder	Hatchlings fed well but did not survive to adulthood (in non-choice tests)
Acacia iteaphylla	Flinders Ranges Wattle	Hatchlings fed well and are still surviving provided very soft tips are used (in non-choice tests)
Photinia robusta	Red Tip	
Rubus laudatus	North American Blackberry	
Sida rhombifolia	Paddy's Lucerne	Adults did not feed at all (in the presence of other plant species)
Prostanthera lasianthos	Mint Bush	
Prostanthera rotundifolia	Australian Mint Bush	
Westringia fruticosa (wynyabbie gem)	Native Rosemary	
Mellicope elleryana	Pink Euodia	
Kunzea erycoides	Burgan	
Rubus parvifolius	Native Raspberry	
Alpinia caerulea	Native Ginger	
Alocasia species	Cunjevoi	
Howea forsteriana	Kentia Palm	Adults fed to some degree (in the presence of other plant species)
Hibiscus tiliaceus	Sandalwood	
Correa laurenciana	Mountain Correa	
Allocasuarina species	Casuarina	
Bougainvillea species	Bougainvillea cultivar	
Ficus longifolia (sabre)	Long Leafed Fig	
Ficus benjamina	Small Leafed Fig	

Table 1 continued

Scientific name	Common name	Comments
Callistemon viminalis	Callistemon Hanna Ray	Adults fed extremely well (in the presence of other plant species)
Leptospermum lanigerum	Woody Tea Tree	
Rosa species	Domestic Rose	
Ficus benjamina	Weeping Fig	
Schefflera actinophylla	Umbrella Tree	
Alphitonia excelsa	Red Ash	
Cullen adscendens	Mountain Psoralea	
Omalanthus populifolius	Queensland Poplar	Hatchlings did not feed at all (in non-choice tests) and adults did not feed at all (in the presence of other plant species)
Citrus limon	Lemon Tree	Hatchlings fed well and are still surviving provided very soft tips are used (in non-choice tests) and adults fed extremely well (in the presence of other plant species)

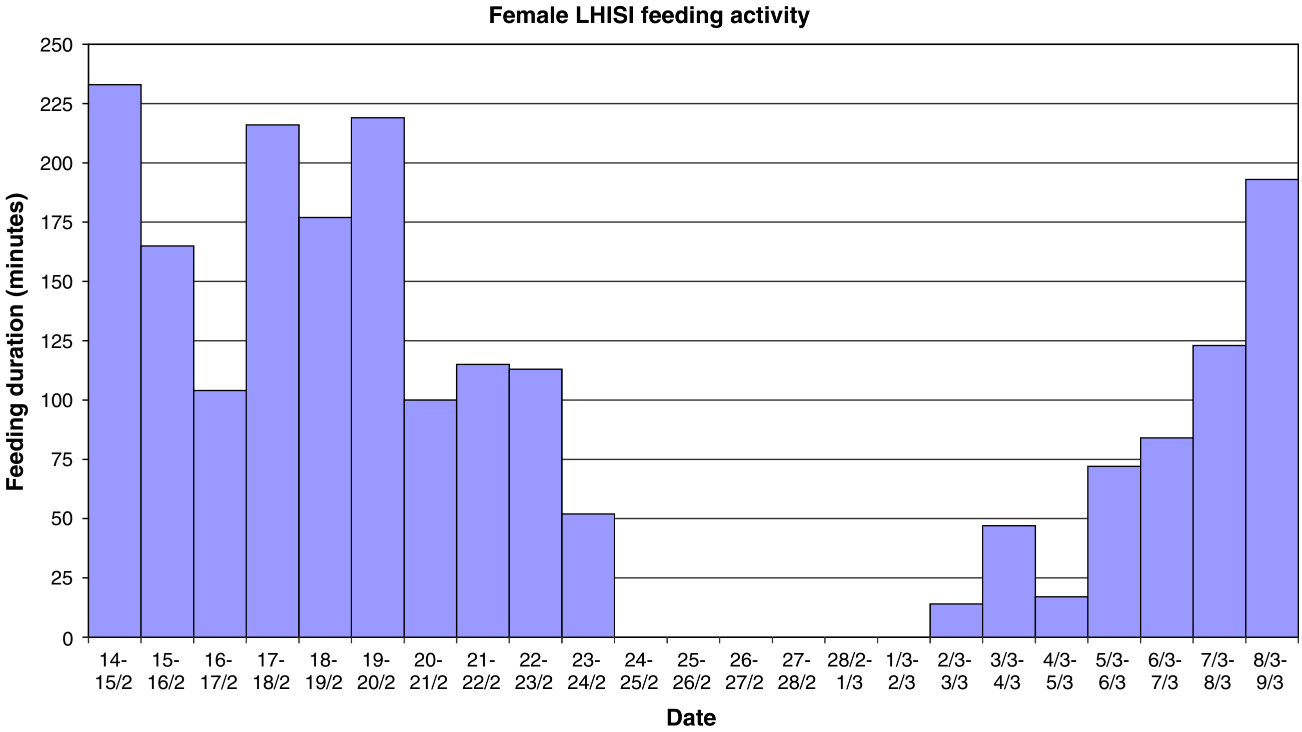

Fig. 8 Time spent feeding by the P1 female collected from Balls Pyramid for the first month in captivity. Note the cessation of feeding for 5 days before treatment

eyedropper on her mouthparts. Within a few hours, she became active again and resumed normal activity, subsequently living for another year. The cause of her morbidity and the reasons for the success of the treatment are still unknown.

A number of other specimens, both those that have died of apparently old age and those that have died unexpectedly, have been subsequently post mortemed. Post mortem examinations included gross necropsy, histological examination of tissues by veterinary pathologists and scanning electron microscopy. The gross necropsy was particularly useful, despite the fact that the Melbourne Zoo veterinary practitioners were not at the time well acquainted with the internal anatomy of invertebrates. Normal anatomic structures are easily identifiable and gross changes in the gastrointestinal tract, body condition and exoskeleton of

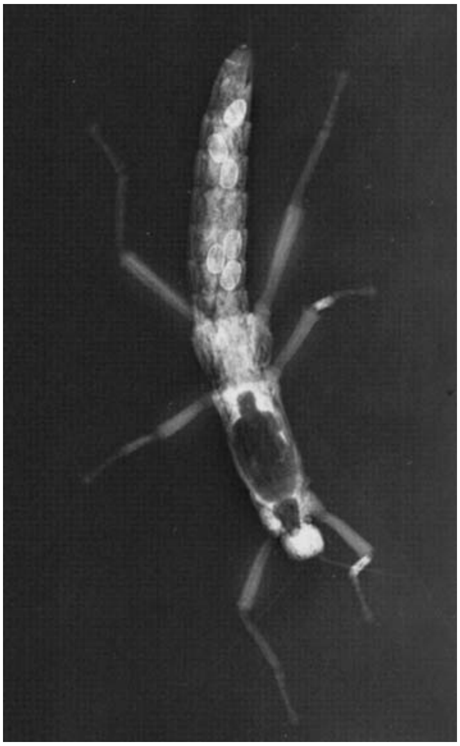

Fig. 9 X-ray of the P1 female collected from Balls Pyramid. Note the black area within the thorax (a symptom of aerophagy) and the six white eggs in the abdomen

healthy specimens which have died of old age are readily comparable to subadult or adult specimens which have died unexpectedly.

For example, the location and quality of food in the gut gives an indication of when the insect last fed. Watery and/or foul-smelling gastrointestinal contents are suggestive of possible infection or other pathology. Dull, slightly discoloured body fluids and intracoelomic fat indicate an aged specimen, whereas a smaller than usual quantity of fat indicates illness. The complete absence of intracoelomic fat in the abdomen indicates an extended period of illness preceding death. The size and condition of the ovaries or testes also gives an idea of the overall health of adults.

These factors help determine whether the cause of death is acute or chronic. A chronic illness may indicate immunosuppression as a result of exposure to environmental stress, toxins or disease. Environmental stress was indicated in one adult male that died prematurely. Upon dissection, his foregut was full of newly chewed leaves, his hindgut full of well-processed leaf material, his testes well-developed and plenty of fat throughout the body, suggesting a healthy condition and that he was feeding well right up to the point of death. However, his internal organs appeared very dry, with almost no free fluid in the body cavity, suggesting general desiccation. The enclosure in which he was being kept was moved off the floor to an area in the glasshouse where humidity was higher, the mesh of the enclosure was changed for a smaller mesh size, and humidity was increased in the glasshouse throughout the night. There have been no subsequent deaths attributable to desiccation.

On another occasion, an adult female was discovered near death and attempts were made to revive her using the treatment administered to the P1 female during her period of morbidity, without success. The Melbourne Zoo veterinarians also administered a modified form of Ringer's solution (Schultz and Schultz 1998), also without success. An x-ray revealed nine well-developed eggs in her abdomen and signs of aerophagy. Upon dissection, the foregut was found to be stretched like a balloon, and the foregut was almost empty, suggesting she had not eaten for some time. There was a reasonable spread of fat throughout her body, but not as much as seen in previously dissected specimens. On the inside of the gut, at the junction of the fore- and hindgut was a small area of green pigment, which appeared to be part of, or embedded in, the gut wall. This was analysed by pathologists without result. The pigment may have come from a pelletised fertilizer used on the potted melaleuca plants, as the colour was identical to that of Greenjacket Osmocote, perhaps consumed inadvertently by the female. Greenjacket Osmocote has been removed from the potting mix and there have been no subsequent cases attributable to this.

Multiple deaths occurred during two incidents in small LHISI enclosures without obvious cause and without stick insects in nearby enclosures being affected. The food plants were tested for insecticide and herbicide but none was found. There were less than usual fat bodies spread throughout the abdomen, air in the foregut without any leaf material and only brown fluid with air bubbles in the hindgut. The brown fluid was also found on the floor of the enclosure. Under histological examination, a number of LHISI specimens had multifocal cuticular lesions (including pallor and erosion) apparently associated with a fungus or unusually large bacterium (spirochaete), but scanning electron microscopy and culture failed to identify them further. The overgrowth of fungi (or bacteria) in dead specimens in part occurred after death, but the location and extent of the growth within the body cavity but outside the gastrointestinal tract suggested that it occurred because the animals were immunocompromised before death.

Several individual deaths also subsequently appeared to be caused by a fractured cuticle (supported by a strong epithelial and hypercellular reaction at the site(s) observable only with high powered microscopy) and ulceration in the midgut, both associated with bacterial growth. These fractures were found all over the body, including on whole mounts of the head. The cuticular fractures had a yellow, serous fluid with a superficial cap of protein and bacterial colonies, again with cuticular widening and pallor. Due to the internal scarring, this was interpreted as an old fracture that had allowed access of fungi or bacteria (possibly *Klebsiella pneumonia*) into the coelomic cavity, resulting in subacute ulceration around the gastrointestinal tract leading to terminal sepsis. Coupled with evidence of recent feeding, this suggested mechanical damage and/or acute stresses caused by other insects (possibly due to overcrowding), transport or handling.

Although only a small proportion of deceased LHISI have been analysed by post mortem, five separate pathology reports from specimens collected at Melbourne Zoo and Healesville Sanctuary have reported or inferred that the direct or indirect cause of death was cuticular fractures which allowed bacterial infection and, subsequently, terminal sepsis. This is a condition not reported previously in the limited but growing literature on invertebrate medicine (Lewbart 2006). Given the gregarious nature of LHISI and their habit of clinging to each other tightly with their exceptionally strong tarsi within their daytime retreats, this is an area that requires further investigation.

One of the most important features of veterinary interventions of endangered invertebrates is that practitioners and pathologists have access to, and become familiar with, healthy specimens. This enables identification of normal versus abnormal tissues and recognition of pathological changes, and builds up a bank of detailed digital images from necropsies that can be used for referral.

Genetic management

The original population of LHISI on Lord Howe Island, anecdotally comprising many thousands of individuals, was significantly larger than the surviving population on Balls Pyramid, which is estimated to be less than 40 individuals. The captive population is founded on two pairs, one taken to Melbourne Zoo and the other to Insektus in Sydney.

Population fragmentation

There is some evidence that fragmented insect populations are able to adapt to reduced variation in the long term and that even rapid fragmentation can evoke evolutionary change in less than 100 years (Hanski and Poyry 2007). LHISI have been present on Balls Pyramid for at least 80 years, since the founder population became extinct on Lord Howe Island, probably in the early 1920s. Given that LHISI are flightless, that Balls Pyramid has never been connected by land to Lord Howe Island, and that the two are separated by 23 km of open ocean, how the population came to establish there is not known. However, there are three known possibilities:

(1) floating across on vegetation. The sea is generally treacherous between Lord Howe Island and Balls Pyramid, and there are no sloping shores on Balls Pyramid for vegetation to wash up, only sheer cliff faces. This may have occurred any time over the last several thousand years;

(2) carried across by seabirds. Thousands of seabirds nest on Balls Pyramid but, as there is no vegetation there, nesting material must be carried across from Lord Howe Island. In the 1960s, a dead LHISI was found incorporated into a seabird nest (McAlpine 1967; Smithers 1966). If a moribund or dead female was taken across by a bird, viable eggs in her abdomen in theory may be able to hatch. At Melbourne Zoo, 40 eggs in total have been collected from the abdomens of dead females but none of these have hatched. Once again, this method of establishment on Balls Pyramid may have occurred any time over the last several thousand years.

(3) carried across by fisherman. Lord Howe Island was officially discovered in 1788 but not settled until about 1834 (Etheridge 1889). Since then, fishermen have been travelling from Lord Howe Island to the rich fishing grounds around Balls Pyramid (Nicholls 1952) and, anecdotally, used LHISI for bait before they became extinct. Transfer by fishermen may therefore have occurred between 80 and 170 years ago.

Under the latter scenario, the LHISI population on Balls Pyramid would be relatively young and, because of the lack of host plants there, must have remained small during its entire history. Whether this population is like some studied, that have adapted readily to rapid fragmentation or like others, that have shown no evolution or microevolution whatsoever (Hanski and Poyry 2007), requires further study.

LHISI were collected for museums in large numbers before becoming extinct on Lord Howe Island. One notable difference between the museum specimens and the current captive population is the size of the hind femora of the adult males. In the museum specimens, the femora are often at least as wide as the abdomen and the femoral spines are stout and elongated, whereas the captive males have femora half the width of the abdomen or smaller, with significantly smaller and narrower spines.

There are two possible explanations for this situation:

(1) as LHISI were very common on Lord Howe Island, collectors were able to freely choose the largest, most impressive specimens for their collections, strongly biasing the sample;

(2) wide femora and long spines in adult males are traits that positively select for their survival and

reproduction, useful either in defending themselves against predators or fighting off other males.

If the first explanation is true, enlarged femora may be a rare trait which nevertheless should, over time, appear in captive populations. If the second explanation is true, enlarged femora are no longer useful in a captive, predator-free environment, but may appear more frequently in the population if those that bear them are afforded access to more females.

Interestingly, the P1 male collected from the wild on Balls Pyramid had large femora and femoral spines (once again attributed to collector bias) but almost all of its descendants have notably smaller femora.

Inbreeding depression

Various authorities on conservation genetics state that a viable population must contain between 50 and 1,000 individuals to prevent inbreeding (Thompson et al. 2007; Nunney and Campbell 1993) and up to 5,000 individuals to preserve genetic variation and avoid the expression of deleterious genes (Lande 1995). Inbreeding depression operates on small populations in two ways: by lowering overall fitness through increased homozygosity and by reducing adaptive variation and therefore the animals' ability to deal with environmental stresses, exposure to toxins and disease (Thompson et al. 2007). LHISI in captivity have demonstrated both increased homozygosity and lowered fitness, and are exposed to environmental stresses and other factors, such as occasional overcrowding.

Attempts have been made previously to measure inbreeding in insect populations in captivity. Saccheri et al. (1996) measured fecundity, egg weight, hatching rate, adult emergence rate, adult size and frequency of morphological deformities in the Bush Brown butterfly (*Bicyclus anynana*) in the laboratory, and found evidence of inbreeding at surprisingly high levels in just a few generations. There has long been evidence of inbreeding in vertebrates in captivity, but it has been assumed by many that insect populations contain sufficient inherent variation and other traits that help them avoid inbreeding depression, although there have been few practical studies (Thompson et al. 2007).

For LHISI in captivity, fecundity, egg size and weight, hatching rate and nymphal size were measured over four generations (P1 + F1 − F3). Morphological deformities and nymphal survival rate were also noted but not rigorously measured. The size of the eggs produced by F1 females was dramatically smaller than those produced by the P1 female (Fig. 10). This was true even when adjusted for hatched versus unhatched eggs.

The adult fecundity, egg weight, hatching rate and nymphal body length also decreased from the P1 to F1. There was also evidence of morphological abnormalities, particularly to the abdomens of adult males, and dramatically lower survival rate of newly hatched nymphs.

In June 2004, four adult males from F1 were sent to Insektus in Sydney and four adult males from Insektus were incorporated into the Melbourne Zoo population. After the new males were introduced, no further abnormalities were observed, the size of the eggs and nymphs increased, the hatching rate increased from less than 20% to about 80%, and the survival rate of nymphs and adults rose to almost 100%. Consequently the population at Melbourne Zoo, which had been around 20 surviving adult individuals at any time during the first 3 years of captive

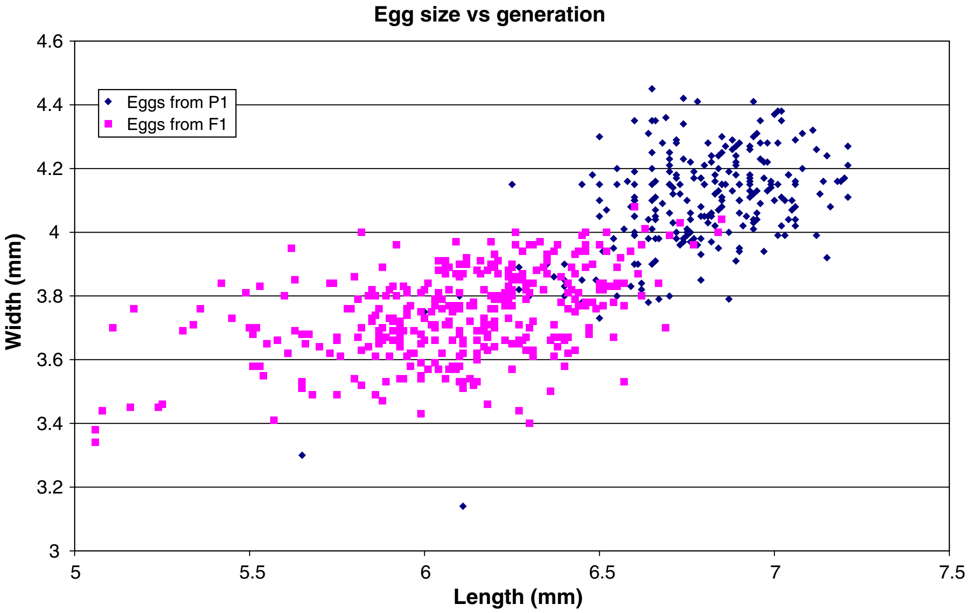

Fig. 10 Comparison of egg sizes produced by P1 and F1 females

management, rose to 600 within 12 months of the males' genes taking effect (Honan 2007a).

Following this apparent inbreeding depression, F2 individuals at Melbourne Zoo were kept separated into 18 genetic lines which have been maintained in the intervening period. Adult females are kept in groups of 10, to which two adult males from other genetic lines are added and rotated at irregular intervals. Given that the detailed reproductive biology and behaviour of this species is not known, the effect of this rotation and potential alleviation of inbreeding is also unknown. Despite these attempts at genetic management, there is currently evidence of further inbreeding and, as the captive population at Insektus in Sydney no longer exists, in the long term the only viable solution may be the introduction of new genetic material from the remaining wild population.

Conservation significance

The LHISI provides a significant example of the benefits, as well as the tribulations of captive breeding in invertebrate conservation. On the negative side, conservation workers are often forced to deal with species about which there is no background biological information, and in addition there is often no biological information from related or analogous species as there might be for vertebrates. If a threatened invertebrate species is to be taken into captivity, there is also usually no husbandry information, which can make rearing and breeding more difficult.

There is also very little funding available for zoo-based invertebrate conservation projects, particularly in comparison to programs focussing on threatened vertebrate species. Apart from labour by zookeepers, the funds required by the LHISI project were minimal and most of the funds provided were as charitable donations. Three small glasshouses currently house more than 10 times the known wild population of LHISI, with room to grow the collection. This is the case for most invertebrate conservation programs (Pearce-Kelly et al. 2007), for which the requirements for space, finances and other resources are low, but where skills and labour are at a shortage, particularly due to the labour-intensive nature of invertebrate husbandry.

Consequently, although there are sufficient resources at Melbourne Zoo to maintain a population of LHISI in captivity, these are not adequate to effectively study the species' biology and genetics. This is the case for many invertebrate conservation breeding projects and has consequences for the long term management of each species, leading to suboptimal husbandry and genetic management. Post mortems of unexpectedly deceased specimens, for example, are worth little unless the results can be analysed and used to improve husbandry techniques. Although results are currently gained from post mortems and pathology analyses, the significance of most of them are still completely unknown. On the positive side, some invertebrate conservation programs genuinely do require almost no funding and, due to the ability of many invertebrate species to recover from threatening processes and population fragmentation, they can be returned to the wild as soon as the threats have been removed.

In some cases, a conservation program based on a single species of invertebrate can act as a taxonomic surrogate for a range of both vertebrate and invertebrate species within the same habitat, as demonstrated by LHISI. Up to 15 species or subspecies of vertebrates (and untold numbers of invertebrates) have become extinct on Lord Howe Island since rats were accidentally introduced in 1918. Some of these vertebrates still survive on tiny islets around Lord Howe Island or on other islands in the Pacific and are themselves endangered to varying degrees.

Planning for a rodent eradication project is currently underway on Lord Howe Island, and in this case invertebrates (LHISI) rather than the vertebrates are the impetus for the project. Rodent baiting trials were successfully conducted on islands analogous to Lord Howe Island in early 2007, and trials using non-toxic, dye-laced baits were undertaken on Lord Howe Island in August 2007. The full baiting program is scheduled for 2010, after which LHISI eggs, juveniles and adults will be returned to the island, followed by other vertebrate species in the longer term.

Another positive element to the LHISI project is its high profile, similar in Australia to that of the Eltham Copper Butterfly (*Paralucia pyrodiscus lucida*) and Richmond Birdwing (*Ornithoptera richmondia*), and similar in many ways to the profile generated by vertebrate conservation programs. This is in part due to the unusual appearance and biology of the stick insects, their apparent extinction for several decades and the story surrounding their rediscovery and collection from the wild. Due to media coverage in Australia and particularly overseas, the LHISI project has high recognition amongst the general public and this has contributed in some degree to raising the profile of invertebrate conservation in Australia.

One of the most useful roles of zoos in invertebrate conservation is to raise the profile of a range of insects and other species, highlight their positive contribution to humans and the ecology, and destigmatise them as a group (Lewis et al. 2007). Zoos are also able to undertake formal and informal education programs and involve the public directly in community action, which can be one of the most effective means of preserving species and habitats (Sands and New 2002). In addition, zoos have some role to play in direct conservation of invertebrates, particularly single species conservation (Honan 2007a; Pearce-Kelly et al. 2007), despite assertions by some authorities that captive breeding has little or no role in effective conservation programs (Collins 1990). This is evidenced by the fact that some invertebrate species would no longer exist in the wild or would not survive long term in their natural habitat but for ongoing conservation programs (New 1995).

With the rodent eradication program in process, the LHISI recovery program utilises both in situ and ex situ conservation measures, the captive management component being particularly important due to the perilous state of the wild population. Although invertebrate conservation programs are now tending away from the single species approach to a more holistic habitat approach (Yen and Butcher 1997), there is merit in attacking the problem at both levels (Clarke 2001). Apart from current issues surrounding inbreeding depression, the LHISI project has served as insurance for the wild population, with currently more than 400 adults and juveniles spread across seven captive populations in Australia and overseas, and more than 13,000 eggs under incubation. With the rodents removed from Lord Howe Island, a viable population should be returned to their original habitat within the next few years to colonise the island in a threat-free environment.

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ORIGINAL PAPER

Invasive species threats to native aquatic insect biodiversity and conservation measures in Hawai'i and French Polynesia

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Abstract Impacts of invasive species, and of attempts to control them, on the aquatic invertebrate fauna of Hawaii and French Polynesia are reviewed and discussed, as a foundation for determining conservation need. Aquatic insects are poorly documented in the region, with many species undescribed, so that practical conservation must be pursued with highly incomplete basic taxonomic knowledge. The establishment of at least one dedicated reserve for aquatic invertebrates is recommended for each high island in an archipelago, as an aid to safeguarding local endemic species, and other recommendations include increased monitoring for new alien species (particularly of fish), planning for removal of alien species from selected water bodies where alien species are less likely to recolonize, effective protection of key sites with high biodiversity value, and securing sites for future restoration and translocation or rare and endangered species.

Keywords Simuliidae · Feral ungulates · Introduced fish · Zygoptera · Austral Islands · Rapa · Tropical streams · Marquesas

Introduction

The conservation status of native aquatic insect faunas found in tropical insular regions, especially highly diverse groups such as Odonata, Diptera, and Heteroptera, is poorly known. A notable exception is Hawai'i, where extinctions in some groups have been well documented (Liebherr and Polhemus 1997; Englund 1999). Restricted habitats, small population sizes, and a lack of defenses against invasive species make tropical insular species especially vulnerable to disturbance and extinction (Simberloff 1986, 1995; Paulay 1994). Conservation biologists working on isolated oceanic islands such as Hawai'i and other areas of Polynesia have long recognized that introduced species represent the most pervasive and persistent threat to the survival of these insular biotas (Vitousek 1988; Meyer and Florence 1997; Loope et al. 2001 Staples and Cowie 2001). Within the Pacific region, the Hawaiian Islands have again received the greatest amount of attention related to the spread of invasive species and their impacts on native aquatic biota (Eldredge 1994). Several other tropical regions including Fiji (Andrews 1985), French Polynesia (Polhemus et al. 2000; Keith et al. 2002; Englund 2003) and New Caledonia (Gargominy et al. 1996; Marquet et al. 2003) have had limited research devoted to this problem.

In Hawai'i, the first published record of any aquatic insect species is of the 1826 introduction of the invasive mosquito *Culex quinquefasciatus* Say (Hardy 1960). The introduction of this mosquito and its subsequent vectoring of avian malaria have resulted in catastrophic impacts on the Hawaiian forest bird fauna (Van Riper et al. 1986, Van Riper and Scott 2001). While extinctions among Hawaiian forest birds and the current restriction of their remaining populations to elevations above the range of mosquitoes has received considerable worldwide attention, a less publicized but nevertheless ongoing pattern of species extirpation has also been occurring among native Hawaiian insects, both terrestrial and aquatic. In both cases invasive species are implicated strongly.

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In addition to the problems caused by invasive species, lack of taxonomic resolution remains one of the greatest problems related to assessing needs for arthropod conservation on oceanic islands (Gillespie 1999). Particularly for aquatic insects, relatively few species have been collected or described from insular tropical Pacific, and this lack of basic knowledge prevents effective conservation measures from being established. The remote nature and consequent difficulty in accessing these areas has also been a major obstacle in providing basic taxonomic assessments for many islands. Outside of Hawai'i, only the most economically important aquatic insects such as the biting blackflies and sand flies (Simuliidae and Ceratopogonidae respectively) and mosquitoes (Culicidae) have received any great amount of ecological or taxonomic treatment. For example, other than the extensive research conducted on the anthropophilic black flies of French Polynesia by Craig (1997, 2001, 2003, Craig and Currie 1999; Craig and Joy 2000; Craig et al. 1995, 2001), biting Ceratopogonidae (Macfie 1935), and Dolichopodidae (Bickel 1994; Evenhuis 1999), little is known about the aquatic insect fauna of the Society Islands or French Polynesia (e.g., Paulian 1998; Séchan 1998).

The lack of attention to aquatic systems throughout the insular Pacific region may have resulted from the fact that initial biological assessments of freshwater ecosystems were generally haphazard and secondary to terrestrial arthropod assessments. Although thousands of new terrestrial arthropod species were collected during the Pacific Entomological Surveys of French Polynesia and elsewhere by Bishop Museum and Hawaii Sugar Planters' Association staff during the late 1920s and 1930s (Zimmerman 1935; Adamson 1936, 1939) only a small portion of these were aquatic insects, consisting mostly of a few aquatic species of Tipulidae (Alexander 1932; 1933, 1935), Dolichopodidae (Lamb 1933), and Odonata (Mumford 1935, 1936; Needham 1932). Additionally, the biting flies that created an obvious nuisance to researchers (Simuliidae and Ceratopogonidae) (Edwards 1932; 1933a, b) and a few shore fly species (Ephydridae) (Malloch 1935) were also described from these early surveys.

The overall dearth of Pacific aquatic insect collections in general contrasts greatly with the treatment of Hawaiian Odonata, which attracted the attention of both professional and amateur naturalists from the first stages of European exploration, probably due to their large size and stunning appearance. The first native aquatic insect described from Hawai'i was *Anax strenuus* (Hagen 1867), collected during the expedition of the Danish corvette *Galathea* in 1846 (Bille 1851). The first native damselfly collected and described from Hawai'i was *Megalagrion xanthomelas* taken by G.F. Matthew of the Royal Navy some time prior to 1876, although the specimens were apparently only labeled "Sandwich Islands" (Polhemus 1996). A few years later, McLachlan (1883) described five endemic damselfly and one dragonfly species from specimens collected in Hawai'i by Reverend Blackburn. In the 1880s, Blackburn made further collections of native aquatic insects in Hawai'i, describing three *Megalagrion* damselflies from O'ahu, Läna'i and Maui (Blackburn 1884).

The most comprehensive historical collections of Hawaiian aquatic insects began in 1892 with the formation of Cambridge University's Sandwich Islands Committee, which sent R.C.L. Perkins to Hawai'i to collect and catalog the islands fauna (Juvik 2001). Perkins' work led to the subsequent publication of the *Fauna Hawaiiensis*, which included descriptions of many new aquatic insect species (Perkins 1913). The aquatic insect specimens collected by Perkins and later collectors such as Williams (1936) provided a wealth of historical information on aquatic insect distributions prior to large-scale perturbations from urbanization and the introduction of the majority of non-native species into Hawai'i.

By contrast, relatively few aquatic insect species were described or documented from the Pacific Entomological Surveys of the 1920s and 1930s, or surveys such as the St. George Expedition to Tahiti in the 1920s. These included two new species of Veliidae (Cheesman 1926) and a few widespread dragonfly species collected by Evelyn Cheesman during the St. George Expedition (Cheesman 1927). The historical record of Hawaiian aquatic insects largely provided by Perkins and Williams is thus lacking from most other Pacific island areas. The Hawaiian record also provides a revealing indication of how much has been lost from Hawaiian streams and wetlands, especially in the lowlands (Englund 2002).

Invasive species impacts on Pacific islands aquatic insects outside Hawai'i

Because early collections of insects in Hawai'i were made subsequent to Polynesian disturbances but prior to the more devastating urbanization and large-scale invasive species introductions that accompanied European contacts, there has been a thorough documentation of species impacts in the Hawaiian Archipelago. However, in many other parts of the tropics it is much more difficult to document extinctions or even invasive species impacts on native arthropods. The Hawaiian Islands occupy a relatively small and discrete area, so changes over time are easier to document than in continental areas or large islands such as New Guinea. However, there are interesting parallels between the well-documented extinctions and negative impacts resulting from invasive species introductions in Hawai'i and those on other Pacific islands.

Because invasive ungulates such as feral pigs or goats directly modify large areas of native habitat, and other invasives prey upon or parasitize native species, their impacts on Hawaiian arthropods are likely much greater than those of direct anthropogenic habitat modification such as urban or agricultural developments. O'ahu exemplifies the impacts of invasives because although large portions of the island are now devoted to housing, agriculture, or commercial developments, numerous undeveloped low-elevation areas still remain, although these are dominated by invasive plants and insects. For example, surveys of Pearl Harbor wetland areas showed that only 25% of identified taxa were native aquatic insect species (Englund et al. 2000), and terrestrial insect surveys in the undeveloped Wa'ahila Ridge area of the O'ahu lowlands yielded only 16% native species (Cowie et al. 1999). Of arthropods collected during similar surveys around the Kahului, Maui Airport area only 11% were natives (Howarth and Preston 2002). On Kaua'i, only 24 of 283 (<10%) identified insect species from surveys of a mixed 900 ha lowland mixed agricultural and undeveloped area were native species (Asquith and Messing 1993). These results show clearly that invasive insect species now dominate the Hawaiian lowlands.

A suite of invasive plant and animal species often work in combination to eliminate native species by changing and eliminating native species habitat (Vitousek 1988). For example, feral pigs accelerate the spread of strawberry guava (*Psidium cattleianum*) into native wet *Metrosideros* forests above Hilo, on the island of Hawai'i, leading to a strawberry guava monoculture with virtually no native plant species (Englund et al. 2002). This same pattern of susceptible populations being displaced by invasive species has been repeatedly observed not only in Hawai'i, but also in other vulnerable areas of high endemism.

Although generally little work has been done on the impacts of invasive species on aquatic insect populations, the South African Odonata are an exception (Samways 1999). With 155 species of Odonata of which 6.5% are threatened, and a moderately high endemism rate of nearly 19%, South Africa contains a rich fauna, including species with narrow habitat ranges making them vulnerable to extinction (Samways 1999). Of the 29 endemic South African Odonata taxa, the most restricted species are mainly from the Eastern and Western Cape Provinces. Threats to the South African endemics include habitat disturbance and invasive species.

Overall, impacts of invasive species on the South African Odonata appear to be relatively small, with only 1.3% of the fauna known to be suffering negative effects (Samways 1999). The situation of introduced rainbow trout impacting native Odonata species in South Africa contrasts with that of Hawai'i, where neither extinctions nor range contractions were found in trout streams containing endemic damselflies (Englund and Polhemus 2001). This is hypothesized to result from the restricted range of trout in Hawai'i because of thermal limitations, and also possibly habitat segregation, given that trout and Hawaiian damselfly larvae occur in different habitats. Trout were mainly found in deeper pools while damselfly larvae inhabit waterfall faces and cascades and appear to rarely enter into the stream drift (Englund and Polhemus 2001). By contrast, other species of invasive fish in Hawai'i such as mosquitofish (Poeciliidae) have been found to be much more serious threats to Hawaiian damselflies (Englund 1999).

Success and failure in controlling harmful aquatic insects and invasive species in Hawaii and French Polynesia

The potential difficulty in eliminating established invasive species is well illustrated by programs aimed at controlling species affecting human health, particularly blackflies and mosquitoes, and for which effects on non-target species have not been described. In French Polynesia, attempted control programs have been mostly unsuccessful in reducing native biting aquatic fly populations of such problematic species as *nono noir* (Simuliidae) and *nono blanc* (Ceratopogonidae). By far the most serious of these biting flies is *Simulium buissoni* Roubaud, a species endemic to Nuku Hiva and Eiao Islands in the Marquesas (Craig et al. 2001). *Simulium buissoni* bites any endothermic animal and makes life virtually unbearable for humans living near stream and wetland areas.

Unsuccessful control of disease vectoring species such as the mosquito *Aedes polynesiensis* Marks and other nuisance native aquatic insects found in French Polynesia began in 1970. The first recorded effort involved a native carnivorous fish, *Kuhlia rupestris*, in attempts to eliminate filariasis from the Marquesas Islands (Séchan et al. 1998). Efforts were then made in Nuku Hiva to unsuccessfully replace the anthropophilic *S. buissoni* with non-biting simuliid species (Séchan et al. 1998), although the identity and original location of the replacement black fly specie(s) was not mentioned. After these fruitless attempts at biological control, a shift to insecticides was made to eradicate *S. buissoni* in the Marquesas, and trials of different insecticides showed that temephos (Abate™) exhibited the greatest promise (Séchan et al. 1998). In 1986, the entire Taiohae watershed of Nuku Hiva was treated with temephos with "excellent results" (Séchan et al. 1998). By 1993 the government of French Polynesia sponsored a black fly eradication project for *S. buissoni* on the entire island of Nuku Hiva (Craig et al. 1995; Séchan et al. 1998). From January to April 1993, temephos was added to all flowing rivers on Nuku Hiva on a bi-weekly basis. Populations of biting female *S. buissoni* were reduced to 4% of previous levels after the first two applications of insecticides (Craig et al. 1995). However, the eradication plan was cut short by heavy rains in March 1993. By October 1993, *S. buissoni* populations had increased to pretreatment levels (Craig et al. 1995). This failed effort cost nearly US $200,000 and has not been repeated on Nuku Hiva or elsewhere.

The Hawaiian Islands provide one of the few examples of a successfully controlled and eradicated invasive aquatic insect species, the mosquito *Aedes aegypti* (Linnaeus), responsible for the great dengue fever epidemics in Hawai'i during World War II and earlier, as documented by Hardy (1960). *Aedes aegypti* is a domestic species and preferentially breeds in artificial containers holding clean water, such as old tires, flower vases, beverage containers and other urban debris, and was formerly found in great numbers in urban Honolulu. However, the yellow fever outbreak of 1911 in the crew of a visiting vessel from Mexico led to drastic mosquito control measures around the city. Starting in 1911, banana plants within the city were eradicated as possible breeding sites, and other strict control measures by the State Board of Health were implemented that eventually led to the last *A. aegypti* being collected on O'ahu in 1957. It is probable the control efforts in the 1950s were successful while earlier efforts were not, because of the diligent and continuous long-term cleanup operations conducted by the State Board of Health. The last statewide collection of *Aedes aegypti* was in 1971 based on BPBM collection data and subsequent surveys in the 1970s and 1980s (Evenhuis in litt.). Although *Aedes albopictus* (Skuse) was responsible for the 2002 dengue fever outbreak on Maui and O'ahu, *A. aegypti* is a far more efficient dengue vector than *A. albopictus*. It is quite likely the recent dengue fever outbreak would have been much worse if *A. aegypti* had not been eliminated from the Hawaiian Islands.

Discussion

Lessons learned from successful eradication programs

As stated earlier, successful eradication of invasive species has been decidedly erratic in the Pacific, with small islands being the one habitat category with notable cases of success. Few insects have been eradicated in the Pacific region. They include the Oriental fruit fly (*Bactrocera dorsalis* (Hendel)) from Rota (Steiner et al. 1965), Guam, Tinian and Saipan (Steiner et al. 1970), and also from Okinawa (Tsubaki 1998).

An ongoing monitoring program is critically important for successful eradication of incipient populations of invasives. This is because newly introduced species are found in localized areas and this limited distribution greatly increases the chances of eradication (Myers et al. 2000).

The failed blackfly control effort on Nuku Hiva also provides additional perspective on eradication issues. For instance, prior to launching any eradication project it is important that the biology of the target species be well-known and that potential non-target impacts are evaluated. On Nuku Hiva, temephos was considered target-specific to black flies because Odonata and chironomid larvae were reportedly found alive both before and after treatments of streams. Séchan (1993) did not "notice mortality of other invertebrates associated with *S. buissoni*", in spite of the fact that quantitative toxicity tests were conducted only on freshwater prawns; these studies found that native prawns (*Macrobrachium* spp.) were not harmed by concentrations of temephos used during field treatments (Séchan 1993). The authors of this black fly eradication project stated that "the taxa [in Nuku Hiva streams] have been identified which do not differ from that reported in Moorea, in the Society Archipelago" (Séchan et al. 1998). However, the freshwater fauna found in Moorea, Society Islands and in Nuku Hiva, Marquesas Islands are dissimilar (Keith et al. 2002) as each French Polynesian island, similar to the Hawaiian Islands, has its own suite of endemic aquatic insects (Polhemus et al. 2000; Englund 2003). Recent joint Smithsonian/Bishop Museum expeditions to Nuku Hiva in 1999 and 2001 have found many undescribed species of native aquatic insects, with descriptions of these new species just beginning (Evenhuis 2003, Englund and Polhemus ms). For example, a radiation of at least 5 undescribed, large, endemic damselfly species on Nuku Hiva was recently recorded (Polhemus et al. 2000) along with two new species of large, endemic aquatic flies (Dolichopodidae) from that island (Evenhuis 1999). Evenhuis (2003) also described an additional three new species of aquatic Dolichopodidae from elsewhere in the Marquesas. Because of a lack of biodiversity surveys and toxicity data on aquatic organisms other than *Macrobrachium* prawns before the implementation of the control program for *S. buissoni*, there might have been serious negative impacts on the endemic aquatic fauna in Nuku Hiva streams. Further toxicity tests on non-target organisms other than crustaceans are clearly warranted.

Other efforts to control biting flies such as the introduced *nono blanc* (ceratopogonids) in the Marquesas have been more environmentally benign, and involve the construction of seawalls in populated areas such as Atuona on Hiva Oa, and Taiohae on Nuku Hiva. These seawalls reduce the amount of available brackish water habitat favored as breeding sites for the *nono blanc* along beach areas by holding back the freshwater lens. Although there are no published accounts or studies on the efficacy of these freshwater retaining seawalls, many local residents claim they do work, and anecdotal observations of biting *nono blanc* in the areas where the seawalls have been installed indicate relatively low-levels of these ceratopogonids (Englund, pers. observ). Impacts on estuarine organisms from seawall construction are unknown.

Threats and opportunities in conserving native aquatic species

Freshwater species and their habitats are currently suffering severe negative impacts worldwide (Saunders et al. 2002), with invasive species and water diversions being the primary threats to such systems on tropical Pacific islands. Most water diversions in island groups other than Hawai'i, such as those in French Polynesia, are in the lower stream reaches and thus cause relatively minimal impacts. While little can be done in the long-term to reduce water diversions for municipal and agricultural uses on these islands, the threat of invasive species can still be addressed. An optimal conservation plan for freshwater organisms therefore needs to not only discourage the spread of invasive species, but also to target watershed protection and include freshwater protected areas to provide whole-catchment integrity (Saunders et al. 2002). Although reserve designation does not automatically guarantee protection, it does at least provide legal and political recognition regarding the importance of watersheds and some regulatory mechanisms to deal with current and future threats.

In some respects, the conservation of tropical Pacific island streams such as those found in tropical Polynesia will be simpler than trying to protect and conserve much larger continental systems. Because of the relatively recent volcanic origin of these islands, these Polynesian watersheds are much shorter in length, less integrated and have steeper topographic profiles (Craig 2003), allowing for an easier delineation of specific watersheds. Conversely, although these watersheds may be easier to protect because of their small size, they are also more vulnerable to disturbance because of this same compact nature. In islands throughout tropical Polynesia the entire watershed from the ocean to its headwaters in the mountains is only a few kilometers long, and can be quickly colonized by invasives. At the same time, streams separated by steep topography often contain a different suite of specialized and endemic aquatic insect species (Englund and Polhemus 2001). Thus each must be viewed as a separate ecological and conservation unit.

As stated earlier, major gaps exist in our knowledge of the local composition of aquatic insect faunas throughout the tropical insular Pacific, even for the intensively studied Hawaiian Archipelago. For example, eight undescribed native aquatic insect species were found during relatively recent helicopter-accessed surveys of 14 remote stream areas on three Hawaiian islands (Englund et al. 2003). These findings were noteworthy in the context of a literature review from the period 1990 to 2003 which revealed an average of only 0.9 new aquatic insect species described per year from the Hawaiian Islands (Englund et al. 2003), despite the fact that aquatic insect collection efforts had been unusually high throughout that period. Additionally, this example illustrates how little basic information is known regarding the numbers and types of aquatic insect species in Hawaiian inland waters, let alone their basic ecological, evolutionary, or life history parameters; this problem is even more acute in the remainder of the Pacific. In the best-case scenario of planning ecological reserves to preserve native biodiversity, a systematic inventory of the aquatic insect fauna for all major Pacific high islands would occur first, with conservation priorities and candidate reserve areas subsequently delineated for highly diverse, sensitive, and intact watersheds.

Conservation of aquatic biodiversity through invasive species prevention and watershed preservation

A prudent recommendation would be that at a minimum, one relatively intact watershed from each island in an archipelago be selected as a biodiversity reservoir for aquatic species. Specialized habitats in island areas are of particular concern as they may be considered islands within islands, and many have restricted populations of endemic biota. It is important to have one reserve on each island within a given archipelago, because numerous single island endemics have been found during surveys of the few island groups so far examined in detail, such as Hawai'i, the Marquesas (Evenhuis 1999, 2003; Polhemus et al. 2000), and the Australs (Englund 2003, 2004). Such reserves would also be beneficial by providing baseline sites as control areas for assessing changes in other watersheds within an island or island group. Realistically, funding for surveys and taxonomic expertise will remain limited for the foreseeable future, so that efforts to preserve native species by providing a reserve protection framework may of necessity be implemented in the absence of such baseline information.

Because of the severity of the invasive species threats, it is urgent that conservation actions occur immediately even if comprehensive taxonomic treatments of the fauna found on each archipelago or individual island within an island group are unavailable. Limited knowledge of Pacific island biotas is usual, and there are presently few taxonomists available to describe the many new species found within each archipelago. Because ever-increasing global trade is leading to the rapid spread of invasive species, and human population increases are leading to greater resource demands, it is necessary to protect the relatively intact watersheds in the tropical Pacific as soon as possible. Hawai'i clearly demonstrates that even in a relatively well-studied tropical island system, new taxa are constantly being discovered. The preservation of aquatic ecosystems prior to the full or even partial delineation of all their component taxa will become increasingly necessary to avoid future large-scale biodiversity losses. However, even if only limited funds are available, then brief biodiversity surveys targeting a select number of indicator species from each proposed area (Howarth 1990) would have great value in prioritizing conservation agendas. In the tropical insular Pacific damselflies (Zygoptera) (Polhemus and Asquith 1996) and certain aquatic Heteroptera such as Veliidae (Polhemus and Polhemus 2004) or Saldidae (Cobben 1980) are obvious indicator groups sensitive to disturbance and are found in a wide of range aquatic habitats. Damselflies are also charismatic enough to be easily observed and collected by amateurs, and are often known and appreciated by indigenous peoples, making these insects good "flagship species".

Such an approach could be compellingly argued in the Marquesas archipelago, which is exceptional in Polynesia for lacking introduced fish (Polhemus et al. 2000; Keith and Marquet 2002), therefore providing a unique opportunity to preserve native aquatic biodiversity. The easiest and most cost-effective way to preserve this Marquesan aquatic biota would be to maintain a strict prohibition on the importation of any non-native freshwater or estuarine fish species. Because fresh water is limited and the Marquesas Islands undergo frequent severe droughts, it is doubtful that aquaculture, a worldwide primary source of invasives, would ever be promoted. Direct jet service from Papeete, Tahiti provides a four-hour link between the island groups, and has the potential to facilitate importation of aquarium fish, which can be found for sale in Papeete. To enhance public awareness in French Polynesia, educational materials on the potential impacts of releasing aquarium fish into streams should be prepared and distributed to pet stores and governmental agencies. This material would explain the nature of the threat, and advocate the preservation and protection of native aquatic fauna, since most island residents are not aware of the unique biota found in Marquesan streams and elsewhere in French Polynesia. Educational information in the form of color posters and brochures could also inform the public as to why freshwater stream animals are an important part of their cultural heritage, and explain the steps that they can take to preserve this patrimony. Educational fact sheets stressing the importance of native aquatic life can be prepared and handed out with every aquarium-related purchase. These fact sheets can discuss how to properly dispose of freshwater aquarium plants and animals, and the implications of improper disposal, including potential cleanup costs to stakeholders (e.g., the case of *Salvinia molesta* in Hawai'i).

Conclusions

Recommendations for successful invasive species removal

Attempts to remove invasive aquatic species need to be well planned, and a thorough understanding of their ecology and life history is necessary to ensure success. For example, treatment of lower Käne'ohe Bay streams in O'ahu, Hawai'i, with a piscicide such as rotenone to eliminate invasive fishes would ultimately be unsuccessful because low salinity estuarine regions provide refugia for several species of salinity-tolerant poeciliids and tilapia that are currently harming native aquatic life. The large size of Käne'ohe Bay and public outcry over treating the entire bay would certainly preclude the effective use of rotenone in this region.

Conversely, isolated and unconnected stream habitats are common on geologically younger islands in volcanic archipelagoes such as Hawai'i or the Society Islands. Because many aquatic habitats such as high gradient stream areas entering the ocean as terminal waterfalls (Fig. 1) include little to no estuarine habitat, there would be a higher probability for aquatic ecosystem restoration once detrimental alien species such as poeciliid fish were removed.

Recommendations for the conservation and restoration of insular Pacific aquatic insects

In addition, constant vigilance is needed to effectively keep invasive species from becoming established. Snake interceptions and captures in Hawai'i from 1990 to 2000 (Kraus and Cravalho 2001) are a good example of the concerted efforts required to keep out undesirable species entering as smuggled pets or via commerce. Even though in theory it may be easiest to control incipient invasions of highly vocal animals, such as the coqui frog (*Eleutherodactylus coqui*) in Hawai'i, because they are simpler to detect than usually more cryptic invaders, a political and regulatory framework still needs to be in place at the time of invasion to allow eradication at an early stage. New freshwater fish invasions may be more difficult to detect than the more visible animals such as reptiles because of the great number of established alien tropical aquarium fish throughout Hawai'i (Englund and Eldredge 2001), combined with relatively few competent observers monitoring the wide range of Hawaiian freshwater habitats. Terrestrial and

Fig. 1 Waterfalls at Taipi Stream, Nuku Hiva, Marquesas, French Polynesia, where new species and genera of aquatic insects were found in surveys from 1999 to 2001

aquatic insect invasions are even more difficult to detect and manage because of the small and inconspicuous nature of larval and adult stages. Because of these factors, insects have the greatest rate of yearly establishment of all animal or plant groups in Hawai'i (Staples and Cowie 2001), with 2,782 established nonindigenous insects occurring in Hawai'i (Eldredge and Evenhuis 2003) and others becoming established at an alarming yearly rate of 20–30 species (Howarth et al. 2001). Eradication efforts for invasive insects are also problematic because after their initial detection they have usually already undergone a population explosion and often are found in high densities across a wide range of habitats.

Howarth and Ramsay (1991) offered a set of recommendations and solutions regarding the conservation of island insects and the habitats upon which they depend. The guidelines included a comprehensive and integrated program of research and monitoring, education, reserve management, legal and legislative actions, controlling the introduction of alien species, and pest control programs. While these suggestions provided a solid framework, many of the recommendations have unfortunately not been implemented, mainly resulting from a lack of funding attributable to a lack of political support. The recent publication of the State of Hawai'i Aquatic Invasive Species Management Plan (Shluker 2003) provides a much-needed comprehensive framework to prevent or at least reduce future problems caused by invasive aquatic plant species, such as the *Salvinia molesta* infestation in Hawai'i that cost US $1.25 million to remove in 2003 (Gima 2003). Because this plan involved all interested stakeholders from the very beginning, including aquarium, aquaculture, and shipping industries, and resource managers on each island it has a reasonable chance of success. Other recent developments, such as the formation of the various Invasive Species Councils for each main Hawaiian Island (e.g., BISC or Big Island Invasive Species Council, etc.), have shown that grass-roots efforts at controlling invasive species can be successful if invasions are detected at an early phase. Examples of this include the nearly complete eradication of the invasive tree *Miconia calvescens* on O'ahu and the eradication of many other incipient alien plant invasions on Maui Nui (F. Starr, pers. com.). Of course, interception and early detection of invaders is by far the most-cost effective manner to deal with invasive species, but even if enforcement and quarantine resources were unlimited there would still remain a need for the capacity to eradicate incipient invasions, given the daily volume of commerce and visitor arrivals to Hawai'i.

Because so many indigenous aquatic insect taxa, particularly in Hawai'i but also elsewhere in the Pacific, now have significantly reduced ranges (Englund 1999, 2001, 2003), the ultimate goal of biodiversity preservation should be to restore populations to a level robust enough to allow species to withstand major environmental disturbances such as hurricanes or droughts. Population restoration should at first involve small, discrete habitat units that can be permanently cleared of the invasive species identified to have caused declines. Native species should then be translocated and reintroduced to areas having either natural or constructed dispersal barriers to prevent re-invasion by the problematic alien species, but this should only be done within the same island or nearby islands that have identical or very similar taxa. For example, even though the Hawaiian damselfly *Megalagrion xanthomelas* has long been considered a single species found on multiple islands (Polhemus and Asquith 1996). Jordan et al. (2005) found this species exhibited different mtDNA haplotypes between Maui Nui and Hawai'i Island. As *M. xanthomelas* has been extirpated from many of its original habitats (Englund 1999, 2001a) restoration efforts should focus on using nearby populations instead of potentially genetically different ones from more distant locations. Additionally, in some cases active management to protect aquatic insects may be required, such as ant monitoring and control for the protection of terrestrially breeding damselfly species such as *Megalagrion nesiotes* or *M. williamsoni*.

Such measures could be instituted throughout tropical Polynesia in areas such as Hawai'i, the Marquesas, and the Austral Islands where there are currently sizable uninhabited valleys containing significant streams. These valleys historically supported large Polynesian populations that intensively cultivated taro (Kirch 1985) but today are nearly or completely uninhabited. Notable examples in Hawai'i would include virtually all north shore Moloka'i streams and Hanakoa, Nualolo, and Kalalau Valleys on Kaua'i; the Hakaui Valley on Nuku Hiva in the Marquesas; and virtually the entire island of Rapa in the Austral chain. The native aquatic fauna of these areas remains largely intact because it sustained no measurable long-term impacts from historical Polynesian taro cultivation and settlement, and these areas were subsequently depopulated and neglected after European colonization. For example, the north shore Moloka'i streams, intensively utilized by ancient Polynesians, now contain some of the rarest aquatic species in Hawai'i because they lack invasive species (Englund and Arakaki 2003) that arrived after European contact. These areas present opportunities for the creation of freshwater reserves in lightly populated regions with little corresponding human conflict. The Pelekunu Nature Conservancy Preserve on Moloka'i provides the best example in tropical Polynesia of an intact, pristine watershed formerly heavily cultivated for taro that is now abandoned yet highly protected. In order to preserve the rare native aquatic species found there, Pelekunu is now intensively protected from feral ungulates with the assistance of local Moloka'i hunters and has recently been monitored for invasive aquatic species (Englund and Arakaki 2003).

Challenges in Preserving Rapa Island habitats

While the formation of the 'grass roots' Invasive Species Councils in the Hawaiian Islands has proven to be an effective action for the early detection and eradication of invasive species, particularly plants, different conservation actions are being proposed elsewhere in Polynesia to preserve native biodiversity. Rapa, in the Austral Islands of French Polynesia is a small (40 km^2), 650 m high island lying at 27°S, with a climate more temperate than Kaua'i, Hawai'i. Despite its small size, Rapa has a highly diverse flora and fauna, including many island terrestrial endemics having large radiations, such as the *Miocalles* weevils (Paulay 1994) and certain Lepidoptera (Clark 1971), a remarkably species-rich land snail fauna (Solem 1982; Fontaine and Gargominy 2003), and a highly diverse endemic flora (Florence 1997; Meyer 2003; Meyer et al. 2003). Working with the people of Rapa, the Gouvernement de la Polynésie française is willing to take conservation steps to protect its most valuable biological and cultural assets: the cloud forests and dry forests. Recent biodiversity surveys on Rapa (Englund 2003; Fontaine and Gargominy 2003; Meyer 2003) funded by Gouvernement de la Polynésie française provided insights into potential conservation measures to help ensure that the unique biodiversity of this small, remote island is not lost.

The central volcanic mass on Rapa is Mt. Perau, containing the last area of middle-elevation moist forest and cloud forest that is important from a global biodiversity perspective (Paulay 1994, Clarke 1971). The native vegetation on Mt. Perau remains extant mainly because the slopes of Mt. Perau are generally steep, up to 80° (Paulay 1994), making sampling and conservation efforts in this area quite difficult, but also limiting access by ungulates to many areas around the summit. Current efforts are focused on saving this globally important and biologically valuable high cloud forest. In addition, Rapa contains remnants of some of the best preserved dry and mesic forest habitats in southern Polynesia, and in 1982 was estimated to have 20% of its original native forest cover (Paulay 1982), although this figure is now undoubtedly significantly reduced because of the continued proliferation of ungulates which threaten both the terrestrial and freshwater ecosystems.

Rapa receives an average of 2500–3000 mm of rain at sea level per year but undoubtedly is much wetter in the cloud-covered mountains (Paulay 1985). Rapa has many relatively large stream systems for an island of its size, and these streams are still completely free of any introduced aquatic species (Englund 2003). Despite its small size, Rapa has an endemic aquatic fauna of great worldwide interest. For example, the endemic damselfly *Ischnura thelmae* is the world's largest (up to 34 mm in length) in the cosmopolitan genus *Ischnura* (Lieftinck 1966). Although common in the 1960s (Lieftinck 1966), *I. thelmae* now appears to be seriously threatened not by introduced alien fish species, such as what has occurred in Hawai'i (Englund 1999), but because of riparian forest losses. This species seems to be an obligate forest-dweller; it was never observed during thorough surveys along riparian habitats on Rapa in overgrazed stream and open pasture areas and only found in heavily forested areas (Englund 2003). A significant observation was that *Ischnura thelmae* forages long distances away from streams in areas of native forest. Thus, there was a clear link between the condition of the native forest and the health of the native damselfly populations (Fig. 2).

Most of the native terrestrial insect biodiversity remaining on Rapa is found in a narrow zone of native

Fig. 2 *Ischnura cardinalis* from the island of Raiatea, one of the many island endemic damselflies from Polynesia

forest between 500 and 650 m at the summit of Mt. Perau (Englund 2003) that is estimated now to be no more than 20 ha in size (J.Y. Meyer, pers. comm). The collection of many undescribed species from Mt. Perau in December 2002 by Englund (2003) illustrates that much remains to be discovered about the insect fauna from this mostly intact native forest area. The cattle grazing line at the summit of Mt. Perau starts at about 370–400 m elevation, and cattle were visibly trampling down *Freycinetia* sp. to gain further access up into the summit areas, with evidence of goats found near the very summit. In 2002, goat damage was observed as high as the 550 m elevation on the ridgelines of Mt. Perau.

The primary invasive species problem on Rapa is the presence of feral cows, goats, and horses that have denuded and destroyed all but a small portion of the high elevation cloud forest. The ungulate problem has significantly worsened since the 1980s, with the horse population apparently increasing from one in 1980 (Paulay 1985) to a substantial herd of more than 50 that were observed only in the lower Agairao Valley alone in December 2003 (Englund 2003). Only a few high summit areas containing the original undisturbed cloud forest and middle elevation moist forest area survive (Meyer 2003). Because of the habitat loss caused by feral ungulates (Fig. 3), immediate actions are clearly required to preserve the cloud forest of Mt. Perau. On Rapa, knives are still used to hunt cattle and goats. As authorities have strictly controlled firearms and ammunition, hunting will not be a short- or long-term answer to control the large ungulate populations, which were estimated to number 500 cattle and 5,000 goats in 1984 (Paulay 1994). The permanent population of Rapa was 497 people in 1996 (Recensement Général de la Population website) thus the amount of livestock present on the island far exceeds what could be consumed internally. The current remaining option is to fence ungulates out of the Mt. Perau summit area, and to work with and employ local residents to implement this plan.

Dry forest areas are even more imperiled than cloud forests on Rapa, and a small patch (1–2 ha) containing rare plant species at Pariati Bay was proposed to be fenced to exclude livestock as soon as funding becomes available. Plans were also made to put in place to start a fencing project for the Mt. Perau area sometime after the Pariati dry forest is fenced (J.Y. Meyer, pers. comm.), which will be the major step in protecting the high cloud forest region. Because relatively few invasive plant species are found in Rapa, fenced off areas should regenerate quickly with native species. The protection of this terrestrial ecosystem will have the added benefit of protecting streams flowing off Mt. Perau. Saving this unique terrestrial ecosystem will

Fig. 3 Cattle and horse overgrazing and fire damage affecting the entire watershed in 2002 on Rapa, French Polynesia

Fig. 4 A new species of water skater, *Campsicnemus* sp., found in pristine stream habitats on the island of Rapa, Austral Islands, French Polynesia

thus lead to the preservation of aquatic habitats and their associated aquatic insects (Fig. 4), including the endemic *Ischnura thelmae*.

Recommendations for regular monitoring to detect new invasions

For Hawaiian aquatic systems there is currently no regular monitoring program in place to detect new invasions of aquatic biota. Although staff of both the Hawaii Division of Aquatic Resources and the Hawaii Biological Survey of the Bishop Museum conduct numerous surveys throughout the year, these are mainly on a contract, project, or as-needed basis. A monitoring program to detect early invasions of aquatic species initiated in the year 2000 at Pelekunu Stream could serve as a statewide model. The Pelekunu Nature Preserve, Moloka'i contains large, free-flowing streams, is a refuge for some of the rarest aquatic animals in Hawai'i and the world, and is one of the last areas in Hawai'i lacking alien aquatic vertebrates of any kind, including frogs. The Nature Conservancy Hawai'i, Moloka'i, office along with cooperating scientists from the Bishop Museum and Hawaii Division of Aquatic Resources, conducted surveys from 2000 to 2002 to monitor the status of certain native aquatic species in this system. This monitoring of aquatic invertebrates was conducted in conjunction with endemic freshwater fish monitoring to help effectively manage and preserve native aquatic biodiversity. The initial monitoring of Pelekunu Stream provided extremely valuable information (Englund 2000, 2001b; Englund and Arakaki 2003), but because of lack of funding was not been conducted in either 2003 or 2004. Because alien fish and other invasive aquatic species continue to spread rapidly throughout the Hawaiian Islands, this monitoring program should be reinstated as a matter of priority.

In addition, a contingency or rapid-response plan should be drawn up that would immediately eliminate any alien aquatic vertebrate species accidentally or intentionally introduced into Pelekunu Stream. For example, immediate chemical treatment of the stream with rotenone should occur if any introduced fish species were detected during monitoring. Although this would also eliminate most native aquatic invertebrates in the treated areas, recolonization from nearby areas would be immediate, and harm would be short-term and inconsequential compared to the much longer-term threat of alien fish. By contrast, lack of action when fish or other major alien species introductions occur into Pelekunu watershed would deal a severe blow to the preservation of native Hawaiian aquatic fauna biodiversity. Currently, high mountain ridges keep introduced amphibians out of Pelekunu Stream, even though bullfrogs (*Rana catesbeiana* Shaw) are found in the adjacent Wailau Stream watershed. Bullfrog control at Pelekunu Stream would be much more difficult than eliminating invasive fish species, and research into controlling and reducing frog numbers in neighboring Wailau Stream should be undertaken to alleviate this threat. The necessity of detecting invasive aquatic species early on underscores the importance of periodic aquatic monitoring in the Pelekunu watershed. Similarly, regular monitoring of a select number of water bodies on each main Hawaiian island could have been accomplished for a small fraction of the cost required to remove invasive *Salvinia molesta* from Lake Wilson, O'ahu in 2003.

As the above example of Pelekunu Valley demonstrates, in tropical insular Polynesian streams even small areas devoid of alien species currently provide a last refuge for native aquatic species, and are of great conservation value. For instance, a 95 m section of an unnamed tributary at Tripler Army Medical Center contains the last O'ahu population of *Megalagrion xanthomelas* and its continued precarious existence there provides the potential for translocating and restoring this formerly common damselfly species (Englund 2001a). The case of *M. xanthomelas* on O'ahu indicates endemic aquatic biota can survive in extremely restricted habitats for up to 90+ years after the introduction of poeciliid fish to an area (Englund 1999). Although this is not an optimal situation for long-term survival of this species, it does provide an indication of the resilience of island species when even small amounts of habitat not containing invasive species are available. The Tripler habitat is relatively secure because of its location inside a US military facility, but other similarly restricted habitats for endangered aquatic organisms are in need of similar protections, such as the small reach of East Wailua Iki Stream on Maui next to a major highway containing the last known *Megalagrion nesiotes* population.

Future challenges in aquatic insect conservation

Conservation of aquatic ecosystems in Hawai'i and French Polynesia has come a long way in the past century, from advocacy of large-scale introductions of invasive species to a current recognition that many, if not most, species of aquatic invasives introduced into insular environments have had long-term, deleterious consequences. The earliest introductions of fish in the mosquitofish family started in Hawai'i in 1905 (Van Dine 1907) and slightly later in Tahiti in 1920 (Keith et al. 2002), and proved to have deadly consequences for native aquatic biota. A pattern of state-sponsored early biological control introductions of fish shifted after World War II to sportfish introductions (Maciolek 1984; Polhemus and Englund 2003). Some of these sportfish species, such as smallmouth bass, have had negative consequences for stream biota, while others like trout have either not become established in the case of Tahiti (Keith et al. 2002), or are so thermally restricted (as in Hawai'i) that they exhibit few measurable impacts (Englund and Polhemus 2001). Most introductions of aquatic biota into insular Pacific environments since the 1980s have been from aquarium releases or as intentional food releases by migrant populations. For example, several species of armored catfish common in the aquarium trade have been introduced into Hawai'i (Sabaj and Englund 1999) and appear to be anthropogenically spreading to new watersheds; in Tahiti, green swordtails, *Xiphophorus helleri* (Heckel), were first observed in 2003 in the Papeno'o River (Englund, unpubl. data) and are also probably spreading. Intentional food releases are a continuing problem and are exemplified by the apple snail, *Pomacea canaliculata* (Lamarck). Apple snails were first introduced to Hawai'i in 1989 and greatly harm the culturally important wetland taro crop and are now widely distributed throughout the archipelago (Lach and Cowie 1999).

Wherever they have been introduced, fish and other harmful aquatic species introductions have eliminated key elements of the native aquatic insect fauna such as damselflies and had other unintended side effects. These negative impacts include native fish predation, spreading new parasites to which the native aquatic biota has not been previously exposed, and competition for food resources. Research is now beginning to reveal why certain native aquatic insect taxa have declined in tropical Pacific stream areas such as Hawai'i and French Polynesia, but arresting this decline and beginning the process of restoration will require the concerted efforts of a variety of governmental agencies, nongovernmental organizations, and private citizens.

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ORIGINAL PAPER

Philosophical justifications for the extirpation of non-indigenous species: the case of the grasshopper *Schistocerca nitens* (Orthoptera) on the Island of Nihoa, Hawaii

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Abstract The case of *Schistocerca nitens*' establishment on the island of Nihoa presents a challenging case for conservation biologists with respect to the justification for human efforts to extirpate the insect. In justifying our actions we seek reasons that are ecologically plausible (i.e., consistent with empirical and theoretical understandings of science), ethically compelling (i.e., based on sound reasoning from well-established moral principles), and logically consistent (i.e., avoiding fallacies and contradictions). Our analysis shows that the conventional arguments for conservation programs do not meet these criteria in the case of *S. nitens*. The following reasons fail on the basis of ecological, ethical, or logical standards: the protection of biodiversity, avoidance of ecological harm, biological qualities of the invasive species (herbivory, fecundity, mobility, recency, and functional integration), anthropogenic basis of arrival, harmfulness or unnaturalness of human agency, the interference with ecological processes, or disturbance of equilibria. Rather, we suggest that an aesthetic argument provides an ecologically, ethically, and logically sound basis for conservation biologists to justify taking action against the grasshopper. The aesthetic concept of a "thick sense" of beauty gives rise to a compelling moral case for extirpation based on virtue ethics in a manner similar to the argument against tolerating roadside litter.

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Introduction

Scientists often learn important lessons in the most unexpected ways, such as Alexander Fleming's accidental discovery of penicillin, Charles Darwin's serendipitous experiences on the Galapagos Islands, and Barbara McClintock's fortuitous encounters with corn. And in 1964, an unplanned incident began a series of events that have forced us to reconsider conservation biology's widely accepted practice of extirpating non-indigenous species. In that year, the Grey bird grasshopper, *S. nitens*, arrived on Sand Island off the coast of Oahu (Anonymous 1965a, b; Fig. 1). Its introduction could have been facilitated by inadvertent human activity, although we know that the insect can fly at least 300 miles over open ocean (Song et al. 2006); in 1988 the Desert locust, *Schistocerca gregaria*, crossed the Atlantic Ocean from West Africa to the Caribbean and South America (Kevan 1989; Ritchie and Pedgley 1989). The Grey bird grasshopper's remarkable capacity for flight probably accounts for its inexorable spread until finally reaching Nihoa, one of Hawaii's largest uninhabited islands.

After arriving in 1977 (Beardsley 1980), the grasshopper (which has locust-like qualities in terms of its adult swarming behavior) flourished on Nihoa's 63 ha of crumbling rock and tropical flora (Fig. 2), with as many as 400,000 individuals occupying the island in 2004 (derived from Gilmartin 2005). Conservation biologists were alarmed when *S. nitens* stripped 90% of the vegetation on the island in 2004, including denuding endemic, endangered, and locally rare plants (Gilmartin 2005). The

Fig. 1 *Schistocerca nitens* adult (photo P. Oboyski)

Fig. 2 Panorama of Nihoa Island in October 2006. (Photo A. Latchininsky)

grasshopper population crashed the following year and then built back up to perhaps 20,000 individuals in 2006 (Latchininsky 2008). Because of the remoteness and difficult accessibility of Nihoa, we do not know the current status of the population. We do know, however, that the agencies (US Fish & Wildlife Service, the National Oceanic and Atmospheric Administration and the Hawaii's Department of Land and Natural Resources) administering the Papah~naumoku~kea Marine National Monument to which Nihoa belongs are extremely concerned with this grasshopper.

The Nihoa population of *S. nitens* appears to be quite healthy. The notable fluctuations in numbers in 2004–2006 were typical of the "boom-and-bust" population dynamics associated with locusts and grasshoppers. The insect develops continuously and produces more than one generation per year on Nihoa. Insufficient soil moisture during the drier, spring–summer–autumn period of the island's climate, appears to be the limiting ecological factor responsible for egg desiccation. Natural enemies are limited to Millerbirds and predatory arthropods, and they do not seem to significantly reduce of *S. nitens* populations. The Gray bird grasshopper readily feeds on most of the island's 26 plant species although grasses like *Eragrostis variabilis* appear less appetizing than other plants. Since its first appearance on Nihoa and Necker Island in 1977, the insect has colonized most of the Northwestern Hawaiian Islands: French Frigate Shoals, Laysan and Lisianski (Latchininsky 2008).

A workshop hosted by state and federal agencies in 2005 was premised on the idea that the Grey bird grasshopper did not belong on Nihoa (Gilmartin 2005). The ideal outcome was seen to be the eradication of the insect, if this could be accomplished without undue risk to the rest of the species on the island. Given that the assembled experts could not conceive of any method to accomplish this goal, the agencies were left with a watch-and-worry response along with the possibility of rescuing rare and endangered species from the island for ex situ propagation if the grasshopper populations once again irrupted. Amidst the intense discussion and debate concerning how best to eradicate, or at least suppress, the Grey bird grasshopper, the fundamental premise of conservation biology—that the insect should not be allowed to exist or flourish on Nihoa—was never explicitly raised.

What is it that we value about Nihoa such that *S. nitens* is perceived as a dire threat that should be eliminated or managed as an invasive pest? Conversely, we could frame the question as: What is it about the Grey bird grasshopper that has so agitated conservation biologists? Although grasshoppers and locusts are typically viewed as agricultural threats, in a rather unexpected way *S. nitens* has forced us not only to explore new approaches to pest management but to confront the values that lie at the core of conservation biology.

Probing deeply into the qualities of the grasshopper (and its new home) that engender such antipathy is not merely an academic exercise. Rather, we are seeking a clarity of environmental and ethical motives that is essential to credible policies and practices. If biologists are incoherent in their accounts of why *S. nitens* ought to be extirpated, then social and political support for conservation programs will likely be (and perhaps ought to be) called into question. We have what seems to be an archetypical case in conservation biology: a remote, uninhabited island being colonized by a non-indigenous species. Without being able to give ecologically plausible (i.e., consistent with empirical and theoretical understandings within science), ethically compelling (i.e., based on sound reasoning from well-established moral principles), and logically consistent (i.e., avoiding fallacies and contradictions) reasons for taking action in this seemingly clear-cut scenario, the credibility of conservationists will be eroded. If we are not sure as to why the Grey bird grasshopper warrants eradication, then more ambiguous and complicated cases (e.g., removing feral goats from Pacific Islands or eradicating pigs from Santa Cruz Island) likely will be intractable.

We propose that two major lines of thought have the potential to capture the core rationale for extirpating the Grey bird grasshopper: the newcomer adversely alters the ecological state (static features, such as species richness) or the alien species interferes with ecological processes (dynamic qualities, such as energy flow). As will be seen, the arguments supporting these central concepts fail for a variety of reasons in the case of *S. nitens*. Given the inadequacy of the traditional explanations for conservation biology's management actions, we propose an alternative philosophical structure derived from the concept of human virtues rather than natural values.

Conservation of ecological states

The contention that ecological states are the source of value driving conservation biology can be analyzed in terms of the island and the insect. In the former context of the island, one might argue that *S. nitens* changes Nihoa from its present condition (an ecological claim). One might also contend that the current, largely natural state of the island's biota approximates an ideal instantiation. That is to say, the geological features, climatic conditions, and geographic aspects of this island could take innumerable forms (e.g., a remote amusement park for the wealthy, a guano mine, a historical recreation of Polynesian life, or a wildlife sanctuary), but the set of conditions that comes closest to those which would obtain in the absence of humans are the most desirable. If so, then substantial changes caused by human action, even if indirect, are wrong (an ethical claim). In the latter context of the insect, one can contend that the Grey bird grasshopper has particular qualities that make its presence on Nihoa adverse to the existing conditions (an ecological claim) which represent a good or valuable state of affairs (an ethical claim).

Before entering into our analysis, we need to explicitly note that those who would base conservation biology on the protection of ecological processes (e.g., evolution, succession, competition) rather than static considerations will likely object to our characterization of policies and practices. We begin with a critique of ecological states because this framing of conservation is historically primary and remains seriously considered. For example, the Endangered Species Act is concerned with fixed entities rather than dynamic processes; within the time-frame of national politics evolutionary change is moot. With the development of ecology from static terms to notions of flux, new conceptualizations of conservation biology have emerged. These will be analyzed in the second, major section of the paper.

Threats to the ecological *status quo* of Nihoa

Risks to biodiversity Nihoa supports a unique fauna that includes 243 arthropod species (184 of these are insects) and 27 species of birds (Evenhuis and Eldredge 2004). Several of the arthropods are extremely rare, including three species of orthopterans found nowhere else on earth. Two of the bird species are also endemic to the island. The population of Nihoa Millerbird (*Acrocephalus familiaris kingi*) has ranged from as few as 31 individuals to more than 700 (Morin et al. 1997). The Nihoa Finch (*Telespiza ultima*) appears to have a more stable population, ranging from 900 to 4,000 individuals over the last 30 years (Rowland et al. 2007). Some ecologists postulate that entire assemblages of detritivorous arthropods (including crickets, earwigs, and mites) and their predators (such as spiders) depend on organic material provided by the seabirds (Conant et al. 1983).

The island also hosts 26 species of vascular plants, 12 of which are endemic to the Hawaiian Islands and three of which are found only on Nihoa: *Pritchardia remota* (there were 1,042 mature specimens of the Nihoa fan palm in 2006 [Kropidlowski 2006]), *Schiedea verticillata* (a member of the carnation family), and *Amaranthus brownii* (which hasn't been seen since 1983, when there were fewer than 35 specimens [Conant 1985]).

A conservationist might contend that the Grey bird grasshopper threatens the integrity of Nihoa's biodiversity. At the very least, *S. nitens* quantitatively alters the richness and evenness of species (i.e., richness is increased and given the abundance of the grasshopper, evenness is likely decreased). In qualitative terms, *S. nitens* might be perceived as an "out of place" organism that does not belong on the island because Nihoa has, to our knowledge, never supported an acridid species. But these objections would apply to any of the resident species when they first arrived, or at least those species which were the initial representatives of their taxa. Moreover, there are dozens of other alien insect species (Evenhuis and Eldredge 2004) and given that nothing is being done about these, it is evident that merely being "out of place" is not a sufficient condition for triggering extirpation if we are also seeking logical consistency in our management practices.

We would hasten to point out, however, that one could make a distinction between what is sufficient to "motivate" us to action and what is sufficient to *prima facie* "warrant" action if we were so motivated. This distinction is important because the demands of consistency are presumably far stronger concerning the ethically warranted basis than the practically motivated basis. So, the conservationist holding the "out of place" view could conceivably argue that we are *prima facie* warranted in extirpating all non-indigenous species from an ethical perspective, but practical considerations only motivate us in the case of the *S. nitens*. However, as we shall see, there does not appear to be a compelling practical basis for picking out the grasshopper as a species that might be readily extirpated.

In addition to the inherent desirability of consistency for rational action, it can be argued that if species, like individual animals, are moral patients (i.e., entities deserving of moral consideration without being moral agents themselves, as we do not blame or praise species or individual animals for their actions), then considerations of justice would compel us to treat equals equally and unequals unequally (Hull 1977; Goodpaster 1978; Johnson 1991; Singer 2003). As such, if we act so as to extirpate *S. nitens* and fail to act in an equivalent manner for other species that are equal in relevant ways to the grasshopper, then we have been unjust. Of course, one could question whether particular individuals, populations or species can be harmed or benefited such that they count morally so that it would be wrong to extirpate the grasshopper but to ignore other alien species. Various arguments have been made that would endorse this view, including the contention that living beings have intrinsic value (Callicott 1986; Rolston 2001; O'Neill 2003), that insect sentience is sufficient to warrant moral consideration (Lockwood 1988), that ecological wholes are morally relevant (Leopold 1968; Warren 2000; Devall and Sessions 2001), and that to be morally considerable is to have a condition that can be better or worse insofar as that entity (individual, population, or species) is concerned (Johnson 1991).

Although the harm to Nihoa's biodiversity by *S. nitens* may not be unique, a differential response to a new species by conservation biologists might be justified if economic analysis revealed unequal costs of eradication. That is, even if the grasshopper is just another species in a long series of colonists, it may be acceptable to target a species that is no worse than its predecessors (equal benefit of eradication) if it can be eliminated with the expenditure of fewer resources (lower cost of eradication). However, the 2005 panel concluded that the grasshopper was extraordinarily difficult, if not impossible, to eliminate from the island (Gilmartin 2005), and other alien species would seemingly be much better targets for control efforts (e.g., bait stations for ants).

Moreover, in light of the mobility of *S. nitens*, eradication can be viewed as only a temporary accomplishment given that the island likely would be reinfested. In ethical terms, "ought implies can"—we cannot be morally obligated to do that which is beyond our ability. And the eradication of *S. nitens* from Nihoa is arguably impossible without eliminating the insect from all of the eastward islands, a task that would be impossible without enormous costs to other species and competing human interests (there are many higher demands on the limited funds available for conservation).

Likelihood of harm Another possibility for the differential response could be that conservation biologists believe that the grasshopper has a much greater capacity to alter the abundances of indigenous species and to drive these species to extinction. After all, *S. nitens* has occasionally all but stripped Nihoa of its vegetation during outbreaks and the other 88 alien insect species known from the island (Evenhuis and Eldredge 2004) have not caused such obvious harm. So, is this concern about the state of biodiversity on Nihoa sufficient to justify the eradication of *S. nitens*?

The possibility that a new arrival will threaten existing species does not seem to be an adequate rationale. Nihoa has experienced numerous invasions in the past. When the island emerged through volcanic processes 7.2 million years ago, it was a lifeless mass of rock (Clague 1996). The initial, pioneer species were surely displaced by later arrivals such that the flora and fauna have been undergoing replacement and turnover for millennia. If an organism's capacity to alter the *status quo* constitutes the basis for eradication, then it follows that we ought to do our best to determine what species were the initial pioneers (only these first aliens arrived without disturbing the pre-existing biodiversity) and then systematically eliminate all other species. Of course this position would require us to provide a reason for privileging earlier floristic and faunistic conditions on the island. Before tackling this issue, however, there is another question that we must consider.

Why should we favor a biological community at all? We could also argue that the geological state of the island was the original condition and that we ought to value and protect this pre-biotic state. If this is taken to be the natural or ideal condition toward which conservation efforts should aspire, then we are obligated to assure that Nihoa persists as a lifeless mass of rock. Surely plants have altered the rate of erosion and changed the island from the way it would be had these organisms not been allowed to flourish.

This line of argument gives rise to the difficulty of selecting any particular ecological state on the island to be worthy of conserving. One might object that this sort of slippery slope argument is unconvincing, that no conservation biologist actually ends up with this conclusion. Presumably we don't arrive at bare rock as our conservation goal because we favor life over non-life for good reasons. But the concern of how we go about selecting the favored biotic community that lies somewhere between molten lava and the current set of living organisms is valid for two reasons. First, this line of argument is particularly relevant with regard to conservation biology in which we look back in time to identify a particular objective but there is no obvious stopping point in this retrogression. Second, this concern (even if one takes it to be something of a strawman) highlights a pressing need on the part of conservationists to be clear and explicit about their motives.

Identifying a non-arbitrary conservation goal The Grey bird grasshopper undoubtedly constitutes a recent change to the biodiversity of Nihoa. But the same could be said about newly arrived species at any previous period of the island's history. Why should conservation biologists privilege the contemporary *status quo*? There does not seem to be a convincing basis in terms of intrinsic value for selecting the recent past as the Golden Age—the set of ecological conditions that serve as the ethical basis for conservation. Rather, we can infer that our interests—and hence, extrinsic values—are intractably a part of conservation goals (Minteer and Manning 2003; Weston 2003; Cittadino 2006). Ever since David Hume raised the problem of deriving a moral position from empirical facts (Norton and Norton 2007), philosophers have struggled with this issue (Fleming 2006). Using a statement of how something "is" as the basis for how a situation "ought" to be has been called the naturalistic fallacy. However, in terms of conservation biology, the risk is one of constructing a new twist on this old problem. That is, we may be guilty of using how an ecological situation used to be in order to assert how it should be. But we can no more derive "ought" from "is" than we can legitimately deduce "ought" from "was"—the latter perhaps should be called the conservationist fallacy. As such, there must be some additional and compelling reason, other than mere ecological history, to ground our environmental ethics.

Rather than 1976 (the year before *S. nitens* arrived on Nihoa [Beardsley 1980]), we could just as well choose the period between 1,000 and 1,700 CE—the time in which humans occupied the island. If this was our conservation standard, we'd have 25 people living on Nihoa year round and another 150 seasonal inhabitants. These native Hawaiians would hunt seabirds and fish the waters, along with constructing stone houses, water diversions, shrines, and agricultural terraces for planting sweet potato and other crops (Emory 1928). To be true to history, they might even repeat the wildfire that was accidentally started in 1885 by Princess's Lili'uokalani entourage (Clapp et al. 1977), but this time perhaps none of the Nihoa fan palms would survive the conflagration.

Is logically possible for conservationists to take a dynamic, rather than static, view of ecology and object to the presence of *S. nitens* on the basis that this insect and its consequent effects are non-natural without worrying about the species having disrupted some previous ecological state on Nihoa. That is, one could be unconcerned about the changing conditions of a natural system such that there is no fixed Golden Age to serve as a goal and focus instead on the nature of the change (i.e., accepting natural changes and rejecting anthropogenic changes). This position will be addressed subsequently, but insofar as ecological states might serve as a basis for ethical action, conservationists implicitly favor some unspecified time prior to the arrival of *S. nitens*. However, there does not appear to be any logically consistent, ethically compelling and ecologically plausible basis for identifying any particular period. Evidently, the agencies currently managing the island would exclude the seven centuries of human occupation, given the extreme measures that are taken to protect the island from people (USFWS 2001). Perhaps two dozen living humans have set foot on Nihoa and these individuals were subjected to extraordinarily intense cleansing procedures (e.g., clothing, supplies and equipment had to be sealed and frozen for 48 h before being allowed on the island).

Why the desired ecological state of Nihoa encompasses a time-frame in which humans and grasshoppers are excluded but other colonists are included may be simply a matter of expediency. That is, we arguably know more about the state of the island in 1976 than in 1876, 1776 or any other earlier time. From an ethical perspective, such a justification is consistent with the notion that "ought implies can" (i.e., we cannot be morally required to do that which is not possible). This rationale makes conservation efforts simpler for biologists, but it is a rather weak argument in terms of ecology. It is not clear that we cannot reasonably know about earlier states of the island. Indeed, the surest conditions allowing the simplest management would be the original, lifeless version of Nihoa.

In light of the strong aversion to anthropogenic disturbances, it would seem that the Golden Age was a time in which human effects were non-existent. As such, conservationists would have to target a period prior to 1,000 CE. This is because it appears that the absence of trees (other than the fan palm) is a result of native Hawaiians having deforested the island to supply themselves with firewood and building materials (Emory 1928). But others might argue that these early people were a natural part of Nihoa and the proper ecological target is the island's state between the loss of the ancient people and the arrival of Europeans (i.e., the window of time between 1,700 and 1,822 CE). If so, then we must make sense out of what is meant by the property of being natural (or indigenous) and whether this constitutes a suitable basis for conservation—an issue that we address in the next section.

Undesirable qualities of the target, *S. nitens*

There are several features of *S. nitens* that conservation biologists might use to justify the extirpation of this species. Although some of these properties are particularly applicable to the Grey bird grasshopper (i.e., it is herbivorous and extremely numerous), others appear to be more universal but are well exemplified by *S. nitens* (i.e., it can be characterized as an adventive visitor, a recent immigrant, and alien or non-indigenous species). We analyze each of these qualities in an effort to determine if they provide a logically consistent, ethically compelling, and ecologically plausible basis for deciding which species are to be protected (or at least tolerated) and which are to be exterminated.

Undesirable qualities of S. nitens We might justify our intolerance of *S. nitens* based on its feeding habits (Fig. 3). Conservation biologists could maintain that in ecosystems with endangered plants, newly arrived herbivores should be considered imminent threats. Moreover, the grasshopper has demonstrated its capacity to decimate Nihoa's vegetation (Fig. 4), notwithstanding the fact that the island's flora appears to have fully recovered (Latchininsky 2008). But future insect outbreaks could conceivably drive one or more of the rare plant species to extinction. So, if we consider the intrinsic value of species to be ethically compelling and the loss of endangered plants via grasshopper herbivory to be ecologically plausible, we have two of the desired elements of a justifiable rationale for extirpating the insect.

We also seek logical consistency with regard to a credible account of why *S. nitens* should be eliminated, to the extent possible, from Nihoa. However, it appears that such coherence is lacking. The island also harbors non-indigenous, herbivorous coleopterans (ant-like leaf beetles, weevils, sap beetles, bark beetles, and flea beetles), heteropterans (seed bugs and plant bugs), dipterans (leafminers), homopterans (including scales, delphacids, leafhoppers, mealybugs and aphids), lepidopterans (noctuids, leafminers, plume moths, and grass moths), orthopterans (long-horned grasshoppers) and thrips. Yet, there are no plans to extirpate these insects to protect the plants. It is entirely possible that the chronic feeding by other alien herbivores does as much or more damage to the survival of Nihoa's plants as the grasshopper does in its boom-and-bust feeding.

Fig. 4 Grasshopper *S. nitens* damage to Nihoa fan palms *P. remota* combined with drought in 2004 (photo J. Culliney)

Heavy feeding by *Schiedea nitens* on the rare plant, *Schiedea verticillata*, was reported during the 2002 and 2004 outbreaks. Observers described a scene of nearly complete defoliation resembling "a temperate-zone winter landscape," with leafless twigs girdled and bark chewed from woody plants (Culliney 2004), but there is no evidence that this plant, or other species on the island, was permanently damaged. Nor does it seem that *S. nitens* has diminished the prevalence of native herbivores, including endemic species of concern such as the Nihoa long-horned woodborer, click beetles, seed bugs, leafminers, and various weevils. In fact, a survey in 2006 found an abundance of *Rhyncogonus exsul* at the same time that island was supporting about 20,000 grasshoppers (Latchininsky 2008; Fig. 5).

Fig. 3 Damage to *Sida fallax* by young nymphs of *S. nitens* (photo A. Latchininsky)

Fig. 5 Damage to *Sesbania tomentosa* by *R. exsul* weevil (photo A. Latchininsky)

If being an herbivore is not sufficient grounds for extirpation, perhaps the criterion for extirpation is quantitative. Abundant and prolific organisms might qualify as legitimate targets. But sheer numbers alone would not seem to be an ecologically plausible justification. And even if we accept this as a reason, the conservationists have failed with respect to logical consistency. Several other non-indigenous species (including some herbivores as well as predators of endemic species) are much more prevalent that *S. nitens*. Cockroaches, ants (there are no native ants on Hawaii, and there are nine ant species on Nihoa), and aphids are certainly more numerous, and they likely comprise a greater biomass than the grasshoppers, at least in some years. If the biomass or number of scavengers, herbivores, or predators that have recently arrived on the island is the rationale for extermination efforts, then *S. nitens* should not be the primary (or only) species of concern to conservationists. However, there are no systematic efforts or plans to extirpate these other insects.

Finally, the modes of invasion by some insects may be different than that of *S. nitens*, but this does not seem to be relevant. That is, *S. nitens* (and presumably the aphids) arrived to the Hawaiian Islands with human assistance and then hopscotched on their own from one island to another until arriving at Nihoa. Other insects (e.g., cockroaches) were likely transported to Nihoa by humans. If anything, the latter mode of arrival would seem to provide a more compelling basis for eradication in light of there being no intermediate steps having been taken by the insect of its own accord to invade Nihoa. However, the relevant concern seems to be element of human agency in the invasion, whether or not the insect was delivered directly to an ecosystem.

Justifiable eradication of non-indigenous species The Grey bird grasshopper can be considered an adventive visitor, a species that comes and goes from the island. Given the paucity of annual data (there are no reports of *S. nitens* from Nihoa between 1983 and 1997), it is possible that the grasshopper has periodically disappeared from, and then recolonized, Nihoa. If so, then a conservation biologist might contend that such a species is not an integral part of the ecosystem and that it may bring with it undesirable pathogens and parasites (there are three endemic orthopterans on the island). But if this is the basis for extirpation, then we once again encounter a most troublesome inconsistency. Eight species of birds on Nihoa—which was earlier known as “Bird Island”—are visitors (Evenhuis and Eldredge 2004) including the bristle-thighed curlew, the ruddy turnstone and the Pacific golden plover. There is no effort to eliminate these animals, presumably because they have been using the island as a stopover for many years. However, this may also have been the case for nearly 40 years with *S. nitens* (and perhaps painted lady butterflies and dragonflies, as we shall see) and may continue to be the case for centuries if no action is taken. But it seems more likely that the grasshopper has become continuously established on the island, and perhaps this is a sufficient basis for extirpation.

Schistocerca nitens is a relatively recent immigrant to Nihoa. It was first seen on the island in 1977, but given its mobility (Song et al. [2006] reported that individuals flew 300 miles from Baja California to Socorro Island) and its presence on Kauai since at least 1970 (which is just 150 miles from Nihoa), it is quite possible that the grasshopper was on Nihoa well before the first sighting. Conservationists could argue that new arrivals to largely intact ecosystems are justifiable targets of extermination. Based on the precautionary principle, recent immigrants might be presumed guilty of harm. But again, the federal and state agencies are inconsistent in the application of this criterion, undermining the credibility of the principle.

During the 2006 expedition, a team of scientists made the first sighting of a painted lady butterfly (*Vanessa cardui*) and only the second observation of a dragonfly (species unknown) on Nihoa (Latchininsky 2008). However, there was no policy requiring that these newest arrivals be summarily exterminated. In addition, a pintail duck, another visitor, was seen for the first time on the island. Given the damage that has been done by non-indigenous vertebrates on other tropical islands (Ely and Clapp 1973), it would seem logically consistent to have attempted to kill this bird if being a recent immigrant is the quality that motivates the extirpation of *S. nitens*. One might contend that the failure to eliminate a single bird is a rather weak argument for inconsistency, but had the scientists encountered a rat, pig, or goat (any of which could have been pregnant) it seems certain that the individual would have been summarily removed. But perhaps the basis for eliminating a non-indigenous species is better framed in other terms.

Conservation biologists have variously described species using a panoply of overlapping terms and concepts, including: alien, exotic, adventive, invasive, naturalized, indigenous, and native. Finding crisp, unambiguous boundaries between these categories is difficult. However, the key difference appears to be that of becoming a component in biotic interdependencies. Being a component of a functioning ecosystem appeals to both ecological and ethical considerations, as circumscribed by Aldo Leopold’s land ethic (1968). That is, an action is right when it fosters stability, integrity, and beauty of a biotic community. By extension, a species becomes tolerable or valued when it “fits in”—when its ecological functions (e.g., feeding) are harmonized with the rest of the community.

As such, species would not need to be native—which we take to mean having evolved in situ, as would be the case

Fig. 6 Nihoa Millerbird *Acrocephalus familiaris kingi* on *Sesbania tomentosa* (photo A. Latchininsky)

with only a few endemics—to warrant our protection, but they must be naturalized. For example, the swordfern *Nephorolepis mulitflora* is considered to be a naturalized species which probably arrived via wind dispersal (Conant 1985). Why it is considered to be naturalized or functionally indigenous is not entirely clear, although it appears that it is not overwhelming other plants but "fitting into" the community without displacing competitors. And if insects or birds use the plant for food or shelter, then one might contend that it has become integrated into the ecological state of the island.

If we adopt this version of Leopold's ecological ethic, then does *S. nitens* pass the test? There is evidence that *S. nitens* has already become a stabilizing force in the Nihoa ecosystem (Latchininsky 2008). In the years prior to the arrival of the grasshopper, the Millerbird population was hovering below 200 individuals (Morin et al. 1997; Fig. 6). With the outbreak of the Grey bird grasshopper, the insectivorous birds flourished, with 450 reported in 2002. Their numbers dropped to fewer than 200 when the grasshopper population subsequently crashed. Although the evidence is circumstantial, one might contend that *S. nitens* is a buffer against food shortages that could threaten the rare, endemic bird. Current, albeit limited, evidence suggests that the when dry conditions prevail, the grasshopper population decline lags behind that of insects less well-adapted to drought, thereby providing the Millerbird with a nutritional "bridge" in an otherwise adverse period.

There is also intriguing evidence that *S. nitens* is evolving an island race. Easily flushed from the vegetation, a typical Grey bird grasshopper normally flies a long distance from the point of disturbance. However, the grasshoppers on Nihoa are notably reluctant to take wing, and they dramatically truncate their evasive flights, landing just 3–10 m away from the point of disturbance (Latchininsky 2008; although others have not noted this tendency [M. MacDonald, pers. comm.]). The diminishment of flight is a well-known adaptation on small islands (long flights being fatal if the organism cannot readily make its way back to land). Perhaps *S. nitens* is on its way to becoming *S. nihoensis*.

Whether or not *S. nitens* is part of the ecosystem, the quality of "fitting in" has problematical elements as a standard for tolerating species. Such an approach places a conservation premium on whatever species happened to arrive first to a place. Given the random nature of wind dispersal, favoring the earliest species would privilege winged insects. One might argue that such r-selected species are more natural colonists than other kinds of animals, but then *S. nitens* would qualify in this regard. As for plants, if New Zealand spinach (a newly arrived species that is ripped up when found on Nihoa) had managed to colonize during an earlier wave of colonization, it might now warrant protection. To stretch this line of argument further, all of the endemics on Nihoa evolved from an earlier species that upon its arrival probably diminished the stability and integrity of the biotic community. Had the first orthopterans to reach the island been extirpated as being threats to the existing order, we would not have the endemic katydids or crickets that are now regarded as extremely valuable.

What is not clear is why being the first to arrive at a newly formed island is a justifiable basis for warranting protection. Even if we favor the "first species" (or "first people") to an area, few—or perhaps, none—of the species that initially settled on Nihoa still live there. So what we're conserving today is a set of species that represents the most recent iteration of a long series of displacements. There appears to be no compelling rationale for favoring the residents that just happened to comprise an ecologically stable biotic community when the Papah ~ naumoku ~ kea Marine National Monument (or its predecessor, the Hawaiian Northwest Islands National Wildlife Refuge) was formed. Had the Grey bird grasshopper arrived before the first biological surveys of the island in 1885 (Clapp et al. 1977), the species would have been perceived as being part of the ecosystem with its periodic irruptions being no less an element of the island's integrity than the outbreaks of locusts elsewhere in the world.

The rationales for seeking the extirpation of *S. nitens* from Nihoa based on more-or-less static qualities of the insect and the island do not appear to be ecologically plausible, ethically compelling or a logically consistent. However, organisms and ecosystems are dynamic entities, so perhaps conservation biologists can justify their intolerance of the Grey bird grasshopper in terms of processes rather than states.

Conservation of ecological processes

There are several lines of argument pertaining to ecological dynamics that might explain why *S. nitens* is a valid target for suppression or extirpation. The rationales include: the process by which the grasshopper arrived on Nihoa, the changes in the island's ecological workings that have followed the insect's colonization, the erratic nature of the grasshopper's population dynamics, and the potential permanence of the Grey bird grasshopper (and its effects) on the island. Once again, these candidate justifications should meet the standards of being ecologically plausible, ethically compelling and logically consistent with respect to the practices of conservation biology.

Anthropogenic introductions

The arrival of *S. nitens* on Sand Island at the entrance of Honolulu harbor in 1964 triggered eradication efforts. The presumption was that the insect had been accidentally introduced through (unintentional) human assistance (Anonymous 1965a, b). However, based on the distances the grasshopper subsequently moved between islands and the track of hurricanes from Mexico, today's entomologists cannot fully discount the possibility that the species arrived on its own (G. Nishida, pers. comm.). At least six aerial applications of malathion were used to eliminate the grasshopper, but within 5 years it had made the short, 3 km crossing to Oahu. This dispersal and the subsequent spread of *S. nitens* from island to island were most likely accomplished by the insect of its own accord. So, the justification for seeking to eradicate the grasshopper from Nihoa (and anywhere else in the Hawaiian Islands) might be derived from the anthropogenic nature of its original colonization. Setting aside the possibility that the Grey bird grasshopper arrived on its own, we must account for why a human-facilitated introduction legitimizes eradication.

The conservation biologist could appeal to the unique or higher value of natural processes. Of course, the contention that natural processes are good does not imply that anthropogenic processes are bad; we would certainly not want to argue that creating art, writing essays, or conducting science are unethical for being particularly human activities. To address this issue, we must first determine whether the conceptual divide between humans and nature is valid. A tremendous amount of intellectual capital in environmental philosophy has been focused on whether this dichotomy is real and useful (Mill 1874; Taylor 1981; Devall and Sessions 2001; Rolston 2001; Singer 2003; Fleming 2006). Even if we accept that there is a meaningful difference, we must then make the case that the metaphysical distinction has ethical relevance. So not only should the relocations of species by human agency be essentially different than natural movements of organisms into new places, but the anthropogenic introductions must have some quality that makes them unacceptable or at least of diminished value.

In conservation biology, human changes to the environment are taken to be inherently harmful. Extending the concerns regarding ecological restoration raised by Elliot (2003) and Katz (2003), Moffett (2007) has recently made what might be the most compelling argument for the differentiation and preservation of what is natural (i.e., not of human artiface). His argument pertains to wild lands, but the implications for anthropogenic changes to the natural world are clear. In brief, he contends that wilderness (spatially expansive natural settings that are minimally altered by humans, recognizing that there are degrees of naturalness) have a kind of authenticity insofar as they have come into being in a manner that cannot be duplicated by humans. Our efforts in restoration ecology, no matter how similar to natural processes, yield a result that is at best an artful counterfeit (even a perfect copy of the *Mona Lisa* would be devalued by not having been authentically painted by the hand of Leonardo da Vinci).

From this philosophical perspective one might infer that we are obligated to minimize anthropogenic changes to natural systems, such as Nihoa (let us set aside, for the moment, the contention that the island is not wilderness insofar as non-indigenous insect species are nearly as abundant as indigenous species—and likely more prevalent in terms of population and biomass), and to act quickly and decisively to reverse human impacts. Presumably, the rapid extirpation of alien species would protect the authenticity of an ecosystem, much like a conservator's quick action to remove a vandal's paint splatter from the *Mona Lisa* would maintain the integrity of the artwork. So, if we stipulate that Nihoa is wilderness (a questionable claim in light of the current species' composition) and that Moffett's argument is ethically sound and reflects some ecologically plausible concerns with regard to alien species vis-a-vis invasion biology (Sax et al. 2005), then it follows that natural processes are particularly valuable and that we ought to do whatever is practically reasonable to erase the evidence of anthropogenic introductions from nature preserves. The question then becomes one of whether our efforts to quash the Grey bird grasshopper on Nihoa are coherent. And given the moral status of natural systems, it would seem that inconsistency would not be only irrational but unjust (i.e., failing to treat equals equally and unequals unequally).

At this point one might argue from the perspective of ecological processes that unequal treatment of species with respect to extirpation may be just. Perhaps the cumulative effects of exterminating all of the non-indigenous species might be harmful, even devastating, in that Nihoa has such a substantial proportion of these organisms. If so, then selectively eliminating particular non-indigenous species would be ethically defensible. However, such a contention concerning the dependence of Nihoa raises the question of whether there is, in any meaningful sense, an indigenous and functional community of organisms. Even setting aside this concern, there appears to be no ecological evidence that any of the indigenous species or processes would be at dire risk from the elimination of all aliens. There might well be some adjustments in plant and animal abundances but the Nihoa ecosystem does not appear dependent on these organisms. Moreover, even if there was such concern, the available, albeit limited, evidence is that *S. nitens* might be one of the few non-indigenous species providing a benefit to a Nihoa native (i.e., the Millerbird). So even if prudential considerations were to yield unequal treatment, it is not evident that *S. nitens* should be the first non-indigenous species slated for elimination.

With further regard to consistency, let's consider what would seem to be a case of ecological (and moral) equals. The painted lady butterfly most likely arrived in Hawaii via human agency (as presumably did *S. nitens*), so the federally-funded Hawaiian Ecosystems at Risk Project considers *V. cardui* to be a non-native species (HEAR 2008). In addition, Hawaii's Office of Environmental Quality Control lists this butterfly as a pest of native plants. However, the agencies responsible for the protection of Nihoa have not sounded the alarm concerning the recent discovery of the painted lady butterfly on the island and there appears to be no plan for monitoring and eradicating the insect if (or more likely, when) it becomes established.

Another instance of functional equals (at least with respect to human effects) being treated unequally on Nihoa pertains to archeological remains which are unambiguously anthropogenic in origin. If humans and the consequences of their actions are unnatural, then traces of early Hawaiian settlement—at least some of which continue to alter the ecological processes (e.g., terraces and water courses)—should be removed along with *S. nitens*. However, the archeological sites are being protected (US NPS 2007).

More general problems also arise if we justify extirpation of alien species by appeal to their having arrived in an ecosystem—whether wilderness or otherwise—through either intentional (e.g., pigs and goats on Pacific Islands) or inadvertent (e.g., the Grey bird grasshopper on Hawaii) human assistance. By this line of argument, we ought to extirpate wolves from Yellowstone National Park. Of course, a conservation biologist might contend that such anthropogenic re-introductions are allowable in cases in which humans were the cause of the species having been lost from an area. But if we accept this caveat, we end up with seemingly absurd proposals such as Pleistocene re-wilding (Donlan et al. 2005), in which we are compelled to move African elephants and lions to North America in an effort to compensate for the role of humans in the loss of the continent's megafauna.

One might object that we've provided a rather unsympathetic reading of conservation biology. To the extent that early humans had a role in the extinction of megafauna (most ecologists would agree that hunting was a significant factor [Martin 1967, 1984; Alroy 2001]) or alterations in the ecology of Nihoa, perhaps these effects were natural. If ancient humans behaved in natural ways, perhaps modern people have no obligation to mitigate the consequences of primitive societies. But we then need to make sense of what is (un)natural about humans. Why stone spear points were natural and firearms are not, is unclear. If the latter technology is natural then we need not worry about trying to restore the Moa to New Zealand (if such was possible), but we'd want to pursue the restoration of passenger pigeons to North America. As with the search for the Golden Age, there does not appear to be a compelling time in human history before which we were natural and after which we were capable of unnatural acts.

Returning the matter of anthropogenically introduced species, to be consistent we should extirpate brown trout, brook trout, and wild horses from the western United States. Wheat, rice, soybeans, and dozens of other non-indigenous agricultural plants also would be slated for elimination, unless their contribution to human well-being was a sufficient good to offset their deleterious effects (and this argument would probably not hold for many minor crops). These latter cases are neatly avoided by Moffett, given that the North American continent, the western region of the United States, and the farmlands of the Midwest could hardly constitute wilderness.

There is a final, rather sticky problem with regard to mitigating anthropogenic changes in ecosystems of any sort. In coming years, we will encounter the apparent necessity of extirpating species that invade new habitats in response to anthropogenic climate change, given that human agency played an indirect but essential role in their movement. With Moffett's allowance for degrees of wilderness, one might contend that the climatic refugees might make an area less natural but not unnatural. But the erosion of value would seem to be as concerning than its sudden elimination. The former process allows us to constantly renormalize our perceptions such that there may well come a time in which a scenario that would seem utterly unnatural to us would be perceived as unproblematical to future humans. Of course, one must be careful about what we *prima facie* ought to do and what we ought to do "all things considered." Perhaps if we could magically exclude climatic refugees from invading new habitats we should do so, but in light of all relevant considerations we are not ethically compelled to expend the resources needed to do so. However, one of the things to consider in this broader context is that the economically cost-free exclusion of species that are driven into new habitats by anthropogenic climate change might well condemn these species to extinction. As such, even the "all things considered" provision does not necessarily mitigate—and may well heighten—what we took to be our *prima facie* moral duties.

Interference with ecological processes

We turn now to the possibility that a disruption of ongoing interactions among biotic and abiotic components of an ecosystem is sufficient grounds for eradication. There can be little doubt that the Grey bird grasshopper has, at least periodically, altered the energy and nutrient flows on Nihoa. For example, heavy feeding by *S. nitens* during outbreaks (Centre for Overseas Pest Research, COPR 1982) has surely reduced energy capture and changed the carbon flux. However, the same could likely be said of earlier insect herbivores to arrive on the island, and there has been no effort to exterminate these species. And the situation becomes even more muddled with respect to predatory insects.

Conservation biologists explicitly approve of the presence of an introduced, seven-spotted lady beetle (*Coccinella septempunctata*) because this insect may be protecting rare and endangered plants by suppressing the non-indigenous aphids on Nihoa (Evenhuis and Eldredge 2004). But if protecting indigenous species is grounds for tolerating an alien organism, then there is arguably as much or more circumstantial evidence that *S. nitens* is a benefit to Millerbirds as there is for ladybird beetles protecting indigenous flora (there appear to be no data supporting the contention that the beetle is having a positive effect on indigenous plants). Another non-indigenous predator, *Trox suberosus*, did not trigger an eradication effort even though there seems to have been no indigenous ecological processes facilitated by this insect. At least there were no known benefits until *S. nitens* arrived, and it is now possible that *T. suberosus* feeds on the grasshoppers' eggs and suppresses population growth—at least there is as much evidence of this, as there is for the benefits provided by *C. septempunctata*. If so, then we are left to wonder whether the *Trox* beetle is an ecological asset in the same sense as the ladybird beetle (i.e., controlling a non-indigenous herbivore population) or an ecological liability if the grasshopper has become a stabilizing food reserve for Millerbirds.

The "unnatural" nature of non-equilibria

We next turn to the erratic nature of *S. nitens'* population dynamics as a reason for targeting this species for eradication. The traditional view of ecological entities (e.g., populations, communities, and ecosystems) is one of equilibrium dynamics (Keller and Golley 2000; White 2006). This perception may be historically grounded in the Greek ideal of the Golden Mean from which eventually followed the Darwinian attraction to uniformitarianism and the Victorian and Protestant virtues of moderation (Stoll 2006). Twentieth century ecologists inherited the notion, accepting that a healthy, functional population should be not exhibit erratic changes in abundance, and if a disturbance does occur then the population is expected to reliably return to a steady state via dampened oscillations.

As such, the instability of *S. nitens* could be taken as evidence that the species is exhibiting unnatural population dynamics which constitutes evidence that the grasshopper is maladapted to Nihoa. However, this interpretation is not ecologically plausible in light of modern science, nor is it logically consistent. We now know that native acridid species (and other organisms) can exhibit non-equilibrium dynamics such that population outbreaks and crashes are a normal aspect of their natural history (Lockwood and Lockwood 1991, 1997). And if boom-and-bust changes were evidence that a population was not well adapted to a particular locale, then the Millerbird's fluctuations between 31 and >700 individuals over the last 30 years would indicate that this species was no better fit to life on Nihoa than is the Grey bird grasshopper.

We would further note that even if equilibrial dynamics (or any other feature contrary to the biology and ecology of *S. nitens*) was an adequate description of the natural world, we cannot conclude that this is the way the world ought to be. Deriving a moral position from empirical facts is the naturalistic fallacy. At least such a deductive move is enthymematic (i.e., missing a premise); in the case of conservation biology the argument is missing a sound reason as to why natural entities, systems, or processes ought to be preserved. Moffett's (2007) reliance on authenticity might be sufficient with further explication of why we should value that which came into being in a manner that cannot be duplicated by humans. The central concern with respect to the naturalist fallacy is that descriptive and prescriptive assertions are qualitatively different kinds of statements such that neither can be logically reduced to the other (hence the missing propositional bridge). As such, an accurate description of how much of Nihoa's plant biomass <u>is</u> consumed by *S. nitens* (up to 90% during an outbreak) does not necessarily lead to any ethical judgment regarding whether this is bad or whether we should intervene.

Process without end? The final consideration with respect to ecological processes serving as the basis for eradication of *S. nitens* pertains to the apparent permanence of the grasshopper (if we take sustained existence to be a kind of process). Perhaps conservation biologists are incensed by this insect because its presence, and hence the changes that it imposes to the island, appear to be irreversible. The inexorable process of colonization is a threat to our presumed superiority and our standing as the most effective colonists on earth. In effect, the grasshopper is beating us at our own game.

The Grey bird grasshopper provides a stark reminder of the limitations of our scientific and technological prowess. When challenged to propose a method of extirpation with absolutely no economic constraints, the participants in the 2005 workshop failed to generate a single method for exterminating this insect while protecting the non-target organisms (Gilmartin 2005). Every method that was deemed capable of eliminating *S. nitens* was almost certain to inflict greater collateral harm to the flora and fauna than the grasshopper was causing. In effect, the process of restoring the biotic community to its pre-grasshopper condition is impossible because whatever method is used to extirpate *S. nitens* (e.g., chemical control with various insecticides and formulations, biological control with predators, parasites, or pathogens, or cultural control with traps or other devices) would likely yield ecological processes and states less—rather than more—like the those prior to the alien introduction.

But if *S. nitens* has wounded our pride and incited our ire, then why isn't the same reaction elicited by the irreversible colonizations by ants, aphids, beetles, cockroaches, flies and other insects on Nihoa? There is an important difference that sheds light on what might be the most plausible justification for eradicating *S. nitens*. The grasshopper—in terms of both the size of the individuals and the magnitude of their ecological effects—is impossible to overlook. Like a kind of environmental graffiti, *S. nitens* is impossible to ignore. One could easily boat past or walk across Nihoa without noticing the presence of the other 88 species of non-indigenous insects. But it would be quite impossible to miss from the deck of passing ship a 90% loss of vegetation during a grasshopper outbreak or to overlook during a hike the 4 cm long locust-like insects flushing from the foliage. Although such emotional and psychological reactions to *S. nitens* might not seem to constitute an ecologically plausible or ethically compelling rationale at first glance, these concerns are relevant to a philosophical theory that has not been previously applied to conservation biology. The conspicuousness of *S. nitens* and the reaction this evokes may provide a plausible rationale and defensible motive for conservation biologists to pursue the elimination, or at least the suppression, of this species.

Conservation of beauty and virtue

In his seminal book, *Aesthetics and the Environment*: *The Appreciation of Nature, Art and Architecture*, Allen Carlson (2000) addresses a wide range of theoretical accounts for an aesthetic of natural objects. Others have previously considered the aesthetic value of species and while finding this axiology compelling in particular cases, philosophers have seemingly been dissatisfied with the anthropogenic roots—although not necessarily anthropocentric, as one can be a subjectivist without being egocentric—of this perspective (Russow 1981; Singer 2003). But those seeking an intrinsic value in species may be doomed to frustration as the search for an objective value of nature is based on the metaphysical presumption that human perceptions, interests, and needs can somehow be isolated from our knowledge of the world (Weston 2003).

A concern worth addressing, albeit too briefly, is the subjectivity of aesthetics. Although one could maintain the nihilistic or solipsistic position that beauty (as with reality, truth, knowledge, and morality) is radically relativistic such that anyone's claim is as valid as anyone else's, few—if any—philosophers would accede to such a stance (Zangwill 2007). Although there are many conceptual models for aesthetic appreciation which apply to the natural world with greater or lesser success (Carlson 2000), aestheticians are unwilling to simply throw up their hands and declare that anything goes. Rather, a normative element seems valid with respect to the judgment of taste; one can be mistaken about aesthetic claims. There is not sufficient space for us to explore the philosophy of aesthetics, but we would appeal to the commonsensical observation that it is not the case that if I think something is beautiful then it is beautiful. If such were the case for beauty (or metaphysics, epistemology, or ethics), there is simply no point in exploring, analyzing, or discussing the matters of beauty (let alone refining, cultivating, or educating people in making aesthetic judgments or in creating works of art).

Carlson's aesthetic argument represents a compelling philosophical account with regard to its descriptive power (i.e., it seems to account for how we value species) and its prescriptive features (i.e., it provides a morally defensible consideration, if not the entire rationale, in our valuing of species). The most relevant analysis with respect to justifying the extirpation of *S. nitens* from Nihoa (and eliminating non-indigenous species in general) is his "eyesore" argument. We contend that this aesthetic basis for human action is ecologically plausible, ethically compelling, and logically consistent.

The eyesore argument makes an explicit appeal to aesthetic values, rather than ecological or ethical considerations (except insofar as there is an implicit and seemingly non-controversial claim that we ought not to destroy what is beautiful or we at least ought to prefer or privilege that which conserves beauty all other things being equal). However, we'll argue that these latter aspects are entirely consistent with the aesthetic position and that differential treatment of *S. nitens* and other alien species on Nihoa is coherent in light of aesthetic value. Carlson's argument shifts the issue from being centered on nature (and whatever ecological and ethical factors might underpin the eradication of non-indigenous species) to an anthropocentric foundation which appears to be far less likely to overreach or generate problems of consistency.

Carlson develops his argument from two premises. He maintains that we should prefer aesthetically pleasing environments over displeasing ones and that human-generated junk, trash, and debris is not aesthetically pleasing. Although he does not allude to non-indigenous species, the extrapolation from physical litter (e.g., empty bottles, candy wrappers, and styrofoam cups) to biological litter (e.g., non-indigenous species, invasive weeds, and anthropogenically introduced organisms) is entirely consistent with his line of argument.

Preference for aesthetically pleasing environments

The most obvious reason for preferring beauty is that it satisfies a justifiable interest, one that is consistent with human virtue. That is, we might contend that we ought to prefer aesthetically pleasing environments because beauty is both valuable (in an axiological sense) and good (in a moral sense). As such, during a fire in the Louvre it would be wrong to choose to save a soiled napkin in preference to the Mona Lisa. The beauty of the painting is sufficient to justify our choice of rescuing it.

Carlson notes that in the context of environmental aesthetics, however, there is the further temptation to posit a correlation between something being natural and its being beautiful. This association might be defensible for pristine natural places and objects, but problems arise when considering altered sites and things that are not completely natural. Carlson focuses on roadsides and why litter is undesirable, but the same considerations would hold for Nihoa (which is not pristine given that almost 50% of the insect species on the island are non-indigenous) and *S. nitens* (which might be thought of as biological litter in this context). The most serious problem is that artists and craftsmen are demonstrably capable of making some objects more aesthetically pleasing by making them less natural. The cabinetmaker or the sculptor is capable of altering wood and stone in ways that make the resulting objects more beautiful than the raw materials. Of course this contention depends on the origin and nature of the wood or stone, but surely beautification is possible in at least some circumstances (e.g., carving from scrap lumber scavenged from a dump or the sculpting from stones found in the slag heap of a mine site).

Recall also the earlier concerns with regard to the contention that natural states or processes have greater value than those of human creation. This position was found to be weak, although Moffett proposed a possible defense with respect to wilderness (which he took to be large, complex systems with nominal human disturbance). In effect, these places are the sorts of pristine locations in which Carlson finds the possibility of a correlation between the natural and the beautiful. If we appeal to naturalness as the justification for preferring a site or object, then we've shifted to a new argument. That is, we'd be contending that we ought to clean up our mess—be it physical trash or biological litter—not because it is ugly but because it is not natural. So, let us set aside the notion that natural things are beautiful (recognizing that if this is true, then perhaps the case for extirpating *S. nitens* is stronger) and address the central aesthetic premise of the eyesore argument.

(Biological) trash is not aesthetically pleasing

The rationale for removing roadside litter hinges on successfully arguing that trash is ugly, a position that Carlson shows to have important ethical ramifications. Likewise, to make a case that the extirpation of *S. nitens* from Nihoa can be justified in aesthetic (and eventually moral) terms, we must understand what makes something aesthetically pleasing and why the grasshopper fails in this regard. Hospers (1946) makes a powerful and vital distinction between two senses of beauty: thin and thick. The thin sense of beauty pertains to our sensual enjoyment of a place or object by virtue of its physical appearance. A thick sense of beauty involves an engagement with the qualities and values that the appearance conveys to the viewer. This form of beauty is "expressive" insofar as it is evokes an experience beyond the sensory phenomenon. Such a distinction is similar to Leopold's (1968) differentiation of the pretty from the beautiful in the context of environmental aesthetics.

Carlson uses the example of an old house. With a thin sense of beauty, the observer sees and appreciates the elaborate woodwork, stained glass windows, elegant architectural lines, etc. But a thick sense of beauty evokes a sense of profound craftsmanship, attention to detail, concern for quality, and more genteel times. The house's aesthetic qualities become linked to human values and elements of a virtuous life. Likewise, a thin sense of beauty regarding Nihoa would involve an appreciation of the island's soaring cliffs, luxuriant vegetation, and graceful birds. A thick sense of beauty might involve a sense of the rich interdependencies among the organisms, the fortitude of species living in such a difficult location, and the capacity of life to convert bare rock into a vibrant biotic community.

With respect to the thick sense of aesthetics pertaining to the Grey bird grasshopper, it is important to note that the insect is much like a locust in its natural history. Although the species does not aggregate in nymphal bands, the adults form swarms and may undergo morphological changes consistent with phase variation and certainly exhibit the long-distance flights of locusts (Song et al. 2006). Indeed, *S. nitens* has been called a locust by various authors (e.g., Heitler and Burrows 1977; Mizisin and Ready 1986; Harrison 1989; Song et al. 2006), a term that produces a strong, adverse response in Judeo-Christian cultures (Lockwood 2004). The literary thread that weaves from the Biblical story of the plagues of Egypt (Exodus 10:1–20) through Laura Ingalls Wilder's account of locusts in *On the Banks of Plum Creek* may be useful in an effort to *describe* why we react negatively to the presence of *S. nitens*.

Of course, it is possible that people could come to view insects (including locusts) as a valuable and tasty food source, in which case the thick sense of beauty via this association could be positive. Indeed, one could posit almost any sort of cultural linkage to an element of nature. Our effort, however, is to provide a plausible account for contemporary conservation biologists' response to *S. nitens* in light of the actual, not merely the possible, associations between humans and acridids that have developed in western societies.

From the concept of a thick sense of beauty, Carlson contends that litter is unsightly not because of any intrinsic property of trash such as its physical appearance but because of what the litter implies about us. It is offensive because its presence means that humans are litter-makers. That is, the expressive qualities of a hamburger container alongside the road include the implication that we are the sort of people who endorse "waste, disregard, carelessness, and exploitation." Likewise, *S. nitens* is aesthetically displeasing not because of any aspect of the insect (in fact, one might contend that the grasshopper is quite beautiful in some regards) but because its presence on Nihoa expresses our being an arrogant people who care only about ourselves, lack sensitivity to the needs of others, and leave our mark by changing the world however we please. A society that does not clean up its biological trash would be the sort of people one might expect to dam the Grand Canyon, pave Old Faithful, shoot the last condor for sport, serve dolphin for dinner, and crush the weak and vulnerable among our own ranks.

Along with this, one might contend that our concern is, at least in part, driven by a sense of guilt. As such, we pick up trash or extirpate species to undo or correct an earlier wrong and thereby relieve our sense of shame. Such a possibility would point toward a metaethical theory of psychological egoism (Sober 2000) or at least a kind of emotivism (Gensler 1998). Given that Carlson is already committed to a form of aesthetic subjectivism, it would not seem to be a serious problem if ethical discernment is also based on one's mental experiences. We would note, however, that such a possibility does not commit us to a degenerate kind of moral relativism.

Carlson also makes the more controversial argument that if we find a place or object aesthetically offensive in a thick sense, then it will be much more difficult to appreciate it in a thin sense. For example, until World War II it seems that people in various cultures found the swastika to be aesthetically pleasing. Its clean lines, sense of movement, and balanced form were appealing. However, with the adoption of this object as a symbol of the Nazis, it took on a thick sense, evoking the horrors of war and genocide. So a psychological contamination of this sort can preclude one's ability to find something pleasing in a purely sensual manner. In a parallel manner, it seems plausible that conservation biologists' knowledge of the presence of *S. nitens* on Nihoa—and the thick sense in which the island has come to represent the capacity humans to spoil even remote places of no economic value—means that a thin appreciation of this place is no longer possible. For those who are aware of *S. nitens* (and the grasshopper and its effects are difficult to ignore), Nihoa is a less beautiful place.

From the aesthetic to the moral, ecological and rational

Trash is a statement of who we are. In effect, litter expresses the values and attitudes of those who are responsible for litter. By accepting the presence of garbage in public places, we tacitly condone (even approve of) values and attitudes consistent with waste, disregard, carelessness, and exploitation. And it is here that Carlson makes the turn from aesthetics to ethics.

The human qualities implicit in roadside trash are not morally acceptable to us. We do not approve of behaviors that are wasteful, careless, and exploitative. Likewise, we see little or no virtue in arrogant people who care only about themselves, lack sensitivity to the needs of others, and change the environment however they please—all of which are apparently endorsed by our tolerance for the presence of biological litter (e.g., *S. nitens* on Nihoa). Rather than a utilitarian or deontological (rights/duties based) ethic, conservation biology may be rooted in virtue ethics (Hursthouse 1999; Swanton 2003). As such, it is our moral character rather than our intentions or the consequences of our actions that is to be judged as praiseworthy or blameworthy. To be ethical is to be the sort of person who has learned how to make rational decisions in light of the richness of circumstances and in so doing leads a life that is worthy of imitation and admiration. And littering—whether physical or biological—would not be consistent with a person who is living a good life. As such, efforts to eliminate *S. nitens* from Nihoa (i.e., to clean up our mess) would be ethically virtuous.

The virtuous person must be, at least for the Greeks, rational as this is an essential and distinguishing quality of being human. So, is the extirpation of the Grey bird grasshopper logically consistent with the other actions (and inactions) of conservation biologists? One can argue that *S. nitens* is aesthetically offensive, particularly in the thick sense of ugliness, in a way that the other non-indigenous species on the island lack. Moreover, a species that could not readily be seen during a hike or a species whose ecological effects could not be seen from a passing ship would not have the same potential for being considered biological litter. A minimum condition of being ugly in the thin sense would be to be visible, and the other alien insects (and most of the non-indigenous plants) are simply not apparent. As such, singling out *S. nitens* for extirpation—a sort of biological litter control campaign—is a logical policy from an aesthetic perspective.

Finally, conservation biologists are often limited in terms of the resources that can be committed to pursuing the protection of a species, habitat, community, or ecosystem. As such, the concept of "triage" is commonly applied as an approach to addressing the multifarious challenges of selecting which species to add or subtract from a locale. Although *S. nitens* is clearly not the easiest or least expensive alien to extirpate from Nihoa, nor is there good evidence that it is the most damaging non-native species on the island, we might frame the decision to target this species for extermination as a form of aesthetic triage. That is, the *S. nitens* could be understood as the organism with the greatest capacity to offend our thick sense of beauty.

All that remains of our original criteria for a justification of conservation biologists' efforts to eliminate *S. nitens* is ecological plausibility. Our earlier dismissal of naturalness as a foundation of beauty would seem to undermine any appeal to the ecological effects of the grasshopper. By making the move to aesthetics, the justification becomes about us and our virtues rather than about the object or place of concern. However, recall that a thick sense of aesthetics depends on the capacity of something to evoke associated values. The reason that we find *S. nitens* aesthetically offensive is precisely because of what the insect represents in ecological terms. If it did not in any way alter the existing relationships and processes or if it actually enhanced these in some unambiguous way (its effects on the Millerbird being countered in an aesthetic sense by its rather more evident capacity for denuding the vegetation) we would be much less inclined to be put off by its presence. In this regard, its being a locust—a property that seemed culturally interesting but otherwise irrelevant earlier—becomes germane. A locust is an invasive, dominating, pestiferous, overwhelming creature. Borrowing Carlson's description of what is implied by litter, we even perceive that these insects represent a sort of biological endorsement of waste, disregard, carelessness, and exploitation.

In summary, the eyesore argument of environmental aesthetics of Carlson seems to have the greatest potential for providing a justification for conservation biologists' efforts to extirpate *S. nitens* from Nihoa. And perhaps this argument represents the strongest philosophical foundation for our general approach to tolerating or trying to eliminate non-indigenous species. The interpretation of such organisms as biological litter understood in terms of a thick sense aesthetics provides an ethically compelling, ecologically plausible, and logically consistent explanation for our actions.

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