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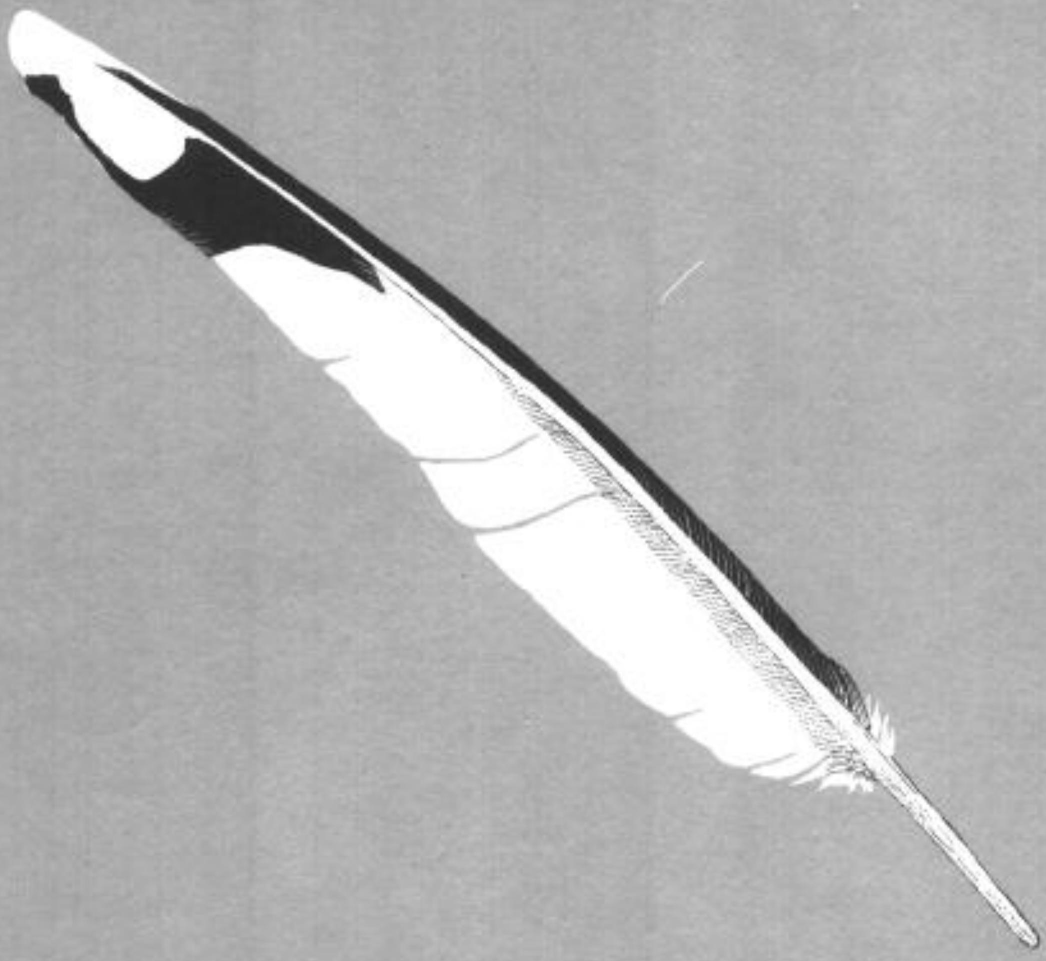

# Avian Reproductive Tactics: Female and Male Perspectives

*editors*

**Patricia G. Parker and Nancy Tyler Burley**

# AVIAN REPRODUCTIVE TACTICS: FEMALE AND MALE PERSPECTIVES

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# AVIAN REPRODUCTIVE TACTICS: FEMALE AND MALE PERSPECTIVES

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# AVIAN REPRODUCTIVE TACTICS: FEMALE AND MALE PERSPECTIVES

## PATRICIA G. PARKER AND NANCY TYLER BURLEY

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# CHAPTER 1

# EMERGING THEMES AND QUESTIONS IN THE STUDY OF AVIAN REPRODUCTIVE TACTICS

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ABSTRACT.—Many researchers have explored the ramifications of the idea that extra-pair copulation (EPC) is a male reproductive tactic to obtain parentage while avoiding parental investment since this concept was advanced by Trivers in 1972. Consortship between males and their fertile mates has been interpreted almost exclusively in terms of mate guarding by males. Females have been thought to benefit little, if at all, from extra-pair activities. This mindset has persisted and influences our interpretation of patterns of reproductive success revealed by molecular markers. Here we briefly trace the historical development of this line of reasoning and the newer, contrasting view—well represented in this volume—that females as well as males have EPC tactics. We identify specific contributions made by authors in this volume, contrast their approaches, and discuss the implications of their results for the understanding of avian mating systems and the role of sexual selection in avian social evolution. Finally, we illustrate the richness of this collection of papers by expanding on key points.

This volume had its origins in a symposium on "Avian Tactics for Extra-Pair Mating" organized by Patty Parker at the request of Thomas C. Grubb for the 1995 AOU meeting in Cincinnati, Ohio. Cognizant of the increasing number of substantial data sets showing that rates of extra-pair fertilization (EPF) are commonly much higher than was expected even a few years previously, Patty invited participants with such data sets, fully expecting to find that patterns of EPF would be interpreted in a variety of ways. What emerged in the symposium, however, was a clear and compelling empirical consensus: acquisition of multiple genetic mates is a female reproductive tactic in avian species having a diversity of social mating systems (monogamy, polygyny, promiscuity) and social organizations (cooperative breeders, territorial species, gregarious and colonial species). This consensus is reinforced by several recent papers (e.g., Gowaty and Bridges 1991; Kempenaers et al. 1992; Lifjeld and Robertson 1992; Wagner 1992; Burley et al. 1994, 1996; Lifjeld et al. 1994; Stutchbury et al. 1994). This idea provides a sharp contrast to the prevailing view, briefly discussed below as well as by several contributors to this volume (Johnson and Burley, Chapter 2; Ketterson et al., Chapter 4; Stutchbury and Neudorf, Chapter 5), that selection on males is the principal evolutionary force shaping extra-pair activities (Birkhead and Møller 1992).

Invigorated by the success and timeliness of the symposium, Patty asked Nancy Burley to join her as coeditor in developing this volume. A few of the original symposium participants have not contributed to the volume, and two new papers were solicited. We invited Frank McKinney and Susan Evarts' contribution on avian sexual coercion (Chapter 8) to provide some taxonomic balance and a complementary conceptual perspective to other papers in the collection. Also, given the historical importance of the Red-winged Blackbird in avian behavioral ecology, this volume would not have been complete without Elizabeth Gray's contribution on intraspecific variation in extra-pair mating tactics of Red-winged Blackbirds (Chapter 3).

Here we highlight some of the major findings and ideas in the volume, principal of which is the developing view that extra-pair fertilization (EPF) is not a singular consequence of selection on males (i.e., via sperm competition and male mate guarding). Rather, varying rates of EPF within and across species reflect the product of a diversity of competing reproductive tactics of females and males. We frame our discussion by posing several questions whose answers are intended to illuminate common themes and concerns of papers in this volume. Finally, we explore issues that our reading of the papers has led us to consider and that we believe are worthy of further thought and empirical inquiry.

## WHY IS THERE A SUDDEN FLOWERING OF UNDERSTANDING OF THE ROLE OF FEMALES IN EXTRA-PAIR ACTIVITIES?

Darwin (1874) noted the possibility that extra-pair copulations (EPCs) might occur in populations of "savages" and suggested that resulting EPFs would dilute the strength of sexual selection on males. Following Darwin, scattered ornithological reports were made of observations of "infidelity" and forced copulation (e.g., Huxley 1912; Christoleit 1929; Marler 1956; Weidmann 1956), but little was made of them. In the 1960s, ideas from economics, population biology, genetics, and ethology began to come together in ways that allowed scientists to think clearly about individual tactics of behavior (for a brief history, see Gross 1994). These events set the stage for Bob Trivers' (1972) articulation of the idea that EPC is a mixed male reproductive tactic in pair-bonding species, including most birds.

Trivers' (1972) suggestion proved to be very stimulating. His work and early papers by Geoff Parker (1970a, b) propelled research on sperm competition (see references in Parker 1984; Smith 1984; Birkhead and Møller 1992). Sperm competition is usually defined as the competition between spermatozoa produced by two or more males for the opportunity to fertilize ova produced by a single female (Parker 1970a), and that is the sense in which we use the term here. Recently, some authors have broadened this definition to include other aspects of sexual selection, including aspects of female mate choice (e.g., Birkhead 1995); in our view, such an approach is unfortunate in that it obfuscates rather than illuminates the various processes and the complex relationships among them. Trivers' insight also inspired research on mate guarding as a male reproductive tactic (e.g., Erickson and Zenone 1976; Hoogland and Sherman 1976; Wolf and Wolf 1976; Beecher and Beecher 1979; Birkhead 1979; Fujiyoka and Yamagishi 1981; Mc-

Kinney et al. 1983, 1984; Davies 1985; Møller 1985; Emlen and Wrege 1986). Other questions that emerged from this view included why females participate in EPCs, given that they apparently do not benefit from them (Halliday and Arnold 1987, and references therein), and queries about the causal relationship between paternal confidence and paternal investment (discussed below).

The line of reasoning initiated by Trivers remains the predominant one in behavioral ecology, as is well illustrated by the conclusions reached by Birkhead and Møller (1992) in their recent synthesis of avian extra-pair relations. In their book, they conclude not only that male mate guarding is a "widespread paternity guard in birds ... (that) is an efficient way for males to increase their certainty of paternity" (pp. 144–145) but also that

> overall, males probably stand to gain more from extra-pair copulations than females ... there are obvious benefits but few costs to males of performing extra-pair copulations .... The traditional view (e.g., Trivers 1972) that the costs of extra-pair copulations for females tend to outweigh the benefits has been given extra weight by the observation that in many species females actively resist extra-pair copulations (p. 217).

These conclusions now seem dated. Results of recent studies indicate that we need to carefully reconsider the costs and benefits of extra-pair activities to females and the tactical dynamics of extra-pair relations between the sexes.

Another significant paper of the early 1970s appears to have had somewhat less immediate impact. Bray et al. (1975) reported that female Red-winged Blackbirds socially mated to males that had been sterilized for population control nevertheless laid fertile eggs. Despite this finding, researchers studying Red-winged Blackbirds continued to assume—either explicity or implicitly—that females copulated primarily or exclusively with their social mate (e.g., Altmann et al. 1977; Searcy 1979; Weatherhead and Robertson 1979; Lenington 1980; Searcy and Yasukawa 1981).

Mike Wade and Steve Arnold (1980) were perhaps the first to point out that Bray et al.'s (1975) results might have implications for the understanding of sexual selection in Red-winged Blackbirds. In 1987, Mary Jane West Eberhard and colleagues articulated the possibility that female Red-winged Blackbirds might tactically nest on the territory of one male and copulate with other males. In 1990, Lisle Gibbs and colleagues, using DNA fingerprinting on a population of Red-winged Blackbirds, found that paternal exclusion rates averaged 45% and were highly variable. Gibbs et al. (1990) also noted that patterns of exclusion implied the possibility that females practiced mate choice of EPC partners. Researchers could no longer assume that social parentage was an accurate indicator of fitness for males of this species. The full implications for testing hypotheses emanating from research on Red-winged Blackbirds need further exploration.

Although researchers who pursued the idea that EPC is a male reproductive tactic typically assumed that EPC was neutral or deleterious to females (e.g., Gladstone 1979; Birkhead et al. 1987), possible benefits to females of engaging in EPCs also began to emerge (e.g., increased genetic variability or quality of offspring [Williams 1975], insurance against mate infertility [McKinney et al. 1984], increased protection by social mate [Lumpkin 1981]). More significantly, a few researchers began to seriously entertain the possibility that females have active EPC tactics of their own. Nancy Knowlton and Simon Greenwell (1984) observed that there should be selection on females to avoid being passive participants in sperm competition. Patty Gowaty (1985:14) noted that "EPC by females implies that the mating strategy of some females . . . is polyandrous by choice." Susan Smith (1988) suggested that female Black-capped Chickadees actively sought EPCs and argued for the importance of following females off their breeding territories to record their behavior towards males other than their social mates (see Gray, Chapter 3; Stutchbury and Neudorf, Chapter 5).

Finally, the proximate answer to the question "Why are we just now seeing that extra-pair copulation is a female reproductive tactic in birds?" is that researchers are just beginning to get good behavioral and genetic data sets that demonstrate this to be the case. Prior to the advent of appropriate molecular technologies, researchers could only speculate on what might be. Interestingly, human males and females who happen to be scientists have tended to speculate in somewhat different directions, as the above brief history suggests. Of course, this does not mean that there has been a qualitative sex difference in perspectives. Recent research shows that rates of EPF in passerines are often quite high (exclusion rates of 10–40% are typical, with extreme examples as high as 80% [see Dunn and Cockburn, Chapter 7]), higher than many, if not most, researchers have anticipated.

Most of the papers in this volume report results of molecular analyses of parentage. The molecular markers employed here are multilocus minisatellite markers (Jeffreys et al. 1985), or what has become conventional DNA fingerprinting. The power of this technique to detect nonparentage is very high (error rates are typically $10^{-20}$ or lower). It is this power, attributable to the simultaneous screening of dozens of highly mutable tandem-repetitive loci (Jeffreys et al. 1988), that has stimulated so much work in studies of parentage in bird populations in the last 10 years. A recent review reported results of molecular determination of parentage for 39 passerines and 18 nonpasserines (Gowaty 1996). Of these studies, eight represented pioneering studies in which patterns of parentage were determined using allozyme markers, despite their relatively low resolving power (e.g., Joste et al. 1985, Mumme et al. 1985).

Several papers in this volume accomplish the more difficult task of identifying the genetic parents of offspring for which one or both social parents were excluded, or are extensions of the authors' earlier work in which these assignments were made (Gray, Chapter 3; Ketterson et al., Chapter 4; Stutchbury and Neudorf, Chapter 5; Wagner, Chapter 6; Dunn and Cockburn, Chapter 7). The identification of actual parents of offspring produced through EPF or intraspecific brood parasitism (ISBP) is especially difficult in natural populations. The assignments or identifications are essentially basic exclusion analyses blown up to the largest possible scale, usually the neighborhood or subpopulation. That is, the molecular marker must be sufficiently powerful to exclude all of the parental candidates except the actual parents. If the neighborhood or subpopulation is very small, this task is not extraordinarily more difficult than a simple exclusion analysis of nest attendants. If, however, the neighborhood or subpopulation is large, the analysis becomes technically cumbersome; the polymorphism of the markers may be insufficient to exclude all possible nonparents, and it becomes increasingly unlikely as neighborhood size grows that all possible candidates would have been sampled.

This challenge has been simplified recently by the development of single-locus tandem-repetitive markers, or "microsatellites" (Litt and Luty 1989; Tautz 1989; Weber and May 1989), that have now been developed for application to birds (e.g., Ellegren 1992; Hanotte et al. 1994; McDonald and Potts 1994). Microsatellites will simplify the process of assignment by allowing the specification of the genotype of the actual parent in advance of finding the individual. Although none of the papers in this volume is based on these markers, we expect that their application will further accelerate the accumulation of studies such as those reported here.

Difficulties of parentage assignments do not apply equally to both sexes. A general conclusion across molecular studies of avian mating systems is that EPF is common among birds, but ISBP—although occurring in many avian families (Yom-Tov 1980)—appears to be (perhaps surprisingly) uncommon, which may suggest that birds generally possess a suite of behaviors adequate to limit the occurrence of ISBP (e.g., Rohwer and Freeman 1989; Fenske and Burley 1995). This means that the distribution of female reproductive success (RS) is usually well estimated by the "old-fashioned" method of simply attributing hatchlings to female nest attendants. It is the distribution of male RS that may differ markedly from estimates based on parentage inferred by nest attendance. (ISBP may, however, be an important aspect of the natural history of some species, and if so, could result in specific reproductive tactics [e.g., Vehrencamp 1977; Price et al. 1989; Gowaty and Bridges 1991].)

Even if molecular markers provided perfect knowledge of RS, the full significance of high EPF rates cannot be adequately interpreted or appreciated without detailed behavior observations. In this volume, authors demonstrate types of data needed for accurate inference of EPF patterns. Gray (Chapter 3) reports that in a Washington State population of Red-winged Blackbirds, 34% of young were produced through EPF. She has observed that females of this population actively seek EPCs and that females that engage in EPCs have higher hatchling and fledgling success. High RS accrues to females that engage in EPCs in part from the nest defense provided by EPC partners. Males also allow females that have engaged in EPCs with them onto their territories to feed. Finally, Gray also suggests that the higher hatching success of females that engage in EPCs results from greater fertilization success; apparently, significant sperm depletion occurs in this highly polygynous setting.

Stutchbury and Neudorf (Chapter 5) report that for Hooded Warblers, the EPF rate varies between 15 and 40% over the course of a breeding season. Evidence that females actively seek EPCs includes the finding that females advertise when they are fertile by making a special *chip* call, which attracts neighboring males and results in EPC attempts. Radiotelemetry shows that females make forays off their territories onto neighboring ones when they are fertile. These forays had not been previously detected using other censusing techniques.

Dunn and Cockburn (Chapter 7) also illustate the importance of behavior observations in making sense of EPF patterns. They report that in the cooperatively breeding Superb Fairy-wren, EPF rates hover around 75%. Nevertheless, only 3 of 1,930 (0.2%) elaborate extra-pair displays that were observed by the authors resulted in immediate EPCs. They also found that a few individual males had disproportionately high success in achieving EPFs. They conclude that female fairy-wrens have control over EPC; that these copulations are occurring after some delay following courtship, at sites (such as in dense vegetation) to which human observers are apparently not privy; and that females have strong preferences for particular males as EPC partners.

Extraordinarily high rates of EPF have now been documented for two species of fairy-wrens, and several potential causes of these high rates have been offered. Fairy-wrens are sedentary, territorial, and disperse over relatively short distances. These traits have led some authors to hypothesize that EPF functions to decrease inbreeding (e.g., Brooker et al. 1990) or promote high genetic diversity of young within an individual's progeny (Rowley and Russell 1990). Mulder et al. (1994) discounted the inbreeding avoidance hypothesis, partly on the basis of the observed occurrence of EPFs involving kin. Mulder et al. (1994) suggest that the high rate of EPF in fairy-wrens is driven by selection on females to produce "sexy sons" (sons good at achieving EPFs), a result that is consistent with the fact that in Superb Fairy-wrens a few individual males obtain very high rates of EPF. These authors suggest that females are able to engage in EPCs at high rates because male helpers, which are often related to the long-lived breeding females, provide additional care to young when dominant males respond to low paternity confidence by restricting their parental investment (PI). As an explanation for high EPF rates, compensatory feedings by helpers may fall into the "necessary, but not sufficient" category because the EPF rates of fairy-wrens are remarkably high even when compared to species in which male parental care is minimal (e.g., Gray, Chapter 3) or "optional" (Gowaty 1996). It would be profitable to consider evolutionary scenarios that include several factors that may have predisposed fairy-wrens to EPC at some point in their evolutionary past, as well as additional inputs that may have fuelled an "arms race" likely to lead to especially high rates of EPF.

## WHAT IMPACT WILL THE DISCOVERY OF HIGH RATES OF PASSERINE EPF HAVE ON THE CONCEPTUALIZATION OF AVIAN MATING SYSTEMS?

Traditional classifications of avian mating systems have assumed a strong correlation between social and genetic parentage. We now know that mating systems are not as straightforward as previously thought. Gowaty (1985) anticipated this outcome, and suggested parallel categories for social and genetic mating systems. For example, a species could have a mating system that is described as socially monogamous and genetically promiscuous. In this volume, Wagner (Chapter 6) adopts a variant of Gowaty's approach in his amplification of his (Wagner 1992) "hidden lek" hypothesis. The hidden lek hypothesis was originally developed for Razorbills, a socially monogamous, colonially nesting species. Razorbills aggregate away from the nesting area, apparently for the purpose of participating in EPCs. In Chapter 6, Wagner elaborates several key features of Razorbill copulatory "arenas" that make them functional parallels of leks. He extends the "hidden lek" analogy to socially monogamous and polygynous territorial species, arguing that the genetic mating systems of these species may be equivalent to those of promiscuous species. Notably, Dunn and Cockburn's (Chapter 7) findings for fairy-wrens seem most consistent with Wagner's thesis.

Although Wagner (Chapter 6) pursues the limits of a single idea—the similarity of all avian mating systems to lek promiscuity—Johnson and Burley (Chapter 2) take a complementary approach to the problem of mating system classification, arguing for a multicausal perspective. They suggest that mating system classifications should integrate social and genetic components, because genetic mating systems are products of complex social relations. The extent of the conflict between social and genetic aspects of the system reflects the extent to which individual extra-pair copulatory activity is overt or furtive. Johnson and Burley derive a scheme of seven major avian mating systems, in which the strength of mating fidelity is a central component. They identify patterns of reproductive tactics and dimorphism among these systems.

Gray (Chapter 3) establishes that the mating system dynamics of Red-winged Blackbirds vary over the species' range. Female blackbirds in Washington State benefit from EPCs and actively pursue them, whereas females in New York State do not actively pursue EPCs. Gray attributes variation in female EPC behavior to differences in social and ecological aspects of the environment. Johnson and Burley (Chapter 2) suggest that birds have considerable capacity to respond tactically to changing constraints and opportunities, implying that variation such as that discovered by Gray should be widespread. For this reason, species may "move" between mating system categories with relative ease, both in ecological and evolutionary time.

Although it is too early to anticipate the full impact of changed assumptions (that social parentage is often not good measure of genetic parentage; that EPC is neither exclusively nor primarily a male tactic) on understanding mating systems, it seems clear that the impact will be substantial. The literature on the Red-winged Blackbird is a good case in point, because this species has figured so prominently in the development of ecological models of mating systems. The polygyny threshold model hypothesized that the patchy distribution of food resources accounted for variation in size and quality of male territories, and consequent variation in male fitness. Female Red-winged Blackbirds in Washington State were thought to choose male territories on the basis of the quantity of food available for their needs, with "availability" determined by both the "intrinsic quality" of a male's territory and the number of other females nesting on it and thereby competing for the same food. Gray's findings (Chapter 3) indicate that the distribution of food resources may not be the constraint it was thought to be: females can gain access to food on other territories by engaging in EPCs with males resident on those territories.

Thus, given a certain level of food abundance (which does appear to be a constraint), the spatial distribution of food may be a less important consideration to females making nest site decisions than are social considerations, such as the abundance of available EPC partners or other females willing to contribute toward nest defense. That predation is an important variable in blackbird reproductive ecology is not a new finding (Picman et al. 1988), but the possibility that females are attracted to high-density breeding situations for access to EPC partners (e.g., Wagner, Chapter 6), rather than being constrained to accept them as a simple product of male–male competition, is inconsistent with the polygyny threshold hypothesis. From a male's point of view, the concept of territory quality may also be altered. Males may in fact benefit from the presence of neighbors by the increased vigilance toward nests that they provide; moreover, any reproductive losses the males suffer as a result of their social mates' EPCs may be balanced by their own successes in extra-pair activities (Gray 1994).

Gray's comparative perspective (Chapter 3) also illuminates a potentially incorrect assumption in the concept of operational sex ratio (OSR). OSR is measured as the relative abundance of males versus females available for breeding in a population at a given time (Emlen and Oring 1977). Variation among populations in OSR has been used to explain a range of mating system dynamics, including extra-pair behaviors (Stutchbury and Neudorf, Chapter 5). In its present form, however, OSR considers only female fertility state, not female willingness to copulate. Given the growing evidence that females have substantial control over EPF in many birds, and Gray's report (Chapter 3) that female interest in EPC varies among populations of the same species, the real OSRs of two populations having equal adult sex ratios and equal breeding synchrony might nevertheless be substantially different. In this context, the similarity of EPF rates reported for Red-winged Blackbirds in New York State (where females apparently do not initiate EPCs) and in Washington State (where they do) is perhaps surprising and deserves further inquiry.

## HOW TYPICAL ARE THE EPF RATES REPORTED IN THIS VOLUME FOR PASSERINES, AND FOR BIRDS IN GENERAL?

Authors of two recent overviews of avian EPF rates have come to rather different conclusions concerning the incidence of avian EPF. Fleischer (1996) concluded that, as a group, passerines have EPF rates that are much higher than those of most birds. By contrast, Gowaty (1996) did not note this dichotomy and was impressed by the absence of genetic monogamy in most socially monogamous species that have been studied. What minimal rate of EPF should be considered a significant departure from genetic monogamy is a thorny question (Johnson and Burley, Chapter 2), but we believe that EPF rates as low as 2–5% should be considered significant in that they are within the range of selection intensities that have been measured in nature (e.g., Endler 1986), as well as within the range of values historically used to assign mating system categories (e.g., the 5% criterion for polygyny).

It seems most unlikely that EPF rates have been determined for a truly random subset of all avian species, and thus any conclusion about general patterns is unwarranted at this time. Stutchbury and Neudorf (Chapter 5) illustrate this point dramatically. Their paper explores the role of breeding synchrony in determining EPF rates of New World passerines. They argue that low breeding synchrony—a trait typical of resident Neotropical passerines—favors low EPF rates, whereas high synchrony—more typical of migratory species—favors high EPF rates. Given the large number of unstudied but extant tropical songbirds, Stutchbury and Neudorf predict that genetic monogamy will be shown to be much more common among passerines than currently available evidence indicates.

Stutchbury and Neudorf's paper very effectively illustrates how changing the basic assumptions of a problem or topic can alter predicted patterns. They pinpoint basic assumptions underlying Birkhead and Biggins' (1987) prediction that EPF rates will be lower when birds breed synchronously (because males are assumed to initiate extra-pair courtship and face a major tradeoff between extra-pair courtship and guarding of their social mate). They then establish that these assumptions do not hold in their study system, the Hooded Warbler: females are not passive participants, but have EPC acquisition tactics of their own. These female tactics impede attempts of males to guard their social mates, diminishing or extinguishing the proposed relationship between extra-pair courtship and mate guarding by males. Stutchbury and Neudorf hypothesize that synchronous breeding provides all participants (females and males) with greater opportunities to pursue EPCs, and they provide convincing evidence that EPF rate is positively correlated with degree of breeding synchrony in the Hooded Warbler, a Neotropical migrant. They also present data from several other species that are consistent with their hypothesis.

## HOW COMMON ARE FORCED EPCs?

Johnson and Burley (Chapter 2) argue that EPCs should be categorized into three types, rather than the conventional two: forced EPCs (FEPCs), which are male-initiated, and to which females show active resistance; solicited EPCs (SEPCs), which females initiate; and neutral EPCs (NEPCs), which males initiate, and which females neither resist nor solicit. McKinney and Evarts (Chapter 8) review evidence that FEPC is a widespread secondary male reproductive tactic in waterfowl and that FEPCs appear to be quite costly to female waterfowl. The presence of an intromittent organ in male waterfowl (absent in most birds) may make FEPC more efficacious in this group, but McKinney and Evarts review evidence that physically coercive EPC also occurs in other groups. Of course, males are active participants in NEPCs and willing participants in SEPCs as well; the lack of an empirical category consisting of female-initiated EPCs which males refuse would seemingly substantiate the readiness of avian males to engage in extra-pair activities. But given recent evidence that males at least sometimes refuse solicited within-pair copulations (Eens and Pinxten 1995), and the possible costs of EPCs to males (e.g., Johnson and Burley, Chapter 2), we would encourage researchers to remain open-minded about this possibility. The point nevertheless remains that much of the literature to date focuses on male–male competition as the mechanism of sexual selection responsible for extra-pair activities, when in fact female choice of genetic mates through SEPC and NEPC now appears to be a highly significant force, and possibly often the driving force, in generating observed EPF patterns.

*Extra-pair displays and FEPCs:* The occurrence of a distinctive extra-pair courtship display in fairy-wrens (Dunn and Cockburn, Chapter 7) is intriguing, as is its low frequency of immediate success (0.2%). In the past, researchers observing the low apparent success rate of extra-pair courtship overtures concluded that EPCs were rare, but recently determined EPF rates show such a conclusion to be unwarranted (Dunn and Lifjeld 1994). The astonishing 75% EPF rate of fairy-wrens, combined with the huge sample of observed unsuccessful extra-pair courtships (nearly 2,000), led Dunn and Cockburn to the inescapable conclusion that responses to extra-pair courtship are delayed, and led them to query the possible duration of delayed responses. Selection on females to conceal SEPCs and NEPCs from their mates is likely to be an important force causing such delay. If so, the following scenario may result: males engage in EPC courtship opportunistically (when they encounter females), females store information about courting males' attributes, and when they choose to do so, females seek males out for "furtive" EPCs (concealed from their mates and, incidentally, from humans).

Such a scenario seems eminently reasonable for many birds, not just fairy-wrens, at least if males apportion PI in proportion to their estimation of paternity. If one function of extra-pair courtship is to make an impression to enhance future copulatory opportunities, then the frequency with which males engage in extra-pair courtship may yield little information on their success in obtaining EPCs and EPFs (e.g., Burley et al. 1996).

By accepting the possibility that the success of extra-pair courtship is often delayed (a changed assumption forced by recent evidence), it becomes important to reconsider the tactical nature of FEPC. FEPC is usually considered to be a coercive male reproductive tactic (McKinney and Evarts, Chapter 8), and occasionally a pseudocoercive female tactic to test male quality (Westneat et al. 1990). Dunn and Cockburn (Chapter 7), however, lead us to realize that forced copulation may result incidentally from errors or delays in signaling during extra-pair courtship. In such cases, it would be inappropriate to consider the behavior a reproductive tactic at all, at least in species in which NEPCs are common.

To illustrate the possibility that forced copulation may be an incidental outcome of a reproductive strategy, rather than a functional reproductive tactic, let us envision a hypothetical species typified by NEPCs and FEPCs (and in which SEPCs are uncommon). Assume that a male approaches a potential EPC partner for an uncertain mixture of immediate and future benefits. Females with the greatest interest in evaluating males for present and future mating opportunities would tend to delay departure, paying particular attention to a male's display. Apparent female interest may result in ambiguity from a male's point of view about whether a given female is interested in immediate copulation or not. If ambiguity exists, a male might proceed through his courtship sequence as he would under the assumption that the female were interested in an immediate copulation. If a female waits until the last minute (when the male attempts to mount) to decline the opportunity, she may need to employ active resistance. Human observers would likely score this as a forced copulation attempt, but this may not have been male "intent." Rather, the apparent FEPC is the product of male behavior (courtship and attempted copulation with an apparently willing female) and female behavior (failure to signal "no" until physical resistance is necessary).

How is it possible to distinguish among tactical coercion, incidental coercion, and pseudocoercion? McKinney and Evarts (Chapter 8) suggest that tactical coercion can be distinguished from pseudocoercion on the basis of the fitness consequences of EPCs to females: if there are detectable costs of female resistance, or if offspring quality suffers, for example, it seems clear that male behavior is coercive. If females demonstrably benefit from "forced" copulation, then the behavior should be classified as pseudocoercion. Because such costs and benefits are inherently difficult to measure, an absence of either cost or benefit is difficult to interpret.

Following a similar line of reasoning, it may be possible to discriminate between tactically coercive and incidentally coercive behavior in several ways. First, tactically coercive FEPC may involve unique behaviors or suites of behavior (such as abrupt copulation attempts not preceded by courtship—males pouncing on unsuspecting females—or the use of physical restraint of uncooperative females) that would not be found in incidentally coercive FEPCs. Second, we can expect that benefits to males and costs to females of tactically coercive behaviors would be greater than for incidentally coercive ones. The basis for these expectations is that incidentally coercive behaviors neither evolve nor are maintained on the basis of their fitness benefits to males, whereas tactically coercive behaviors have evolved because of their fitness benefits. The persistence of incidentally coercive behaviors despite lack of apparent benefits to males (e.g., high FEPC rates in Zebra Finches that do not result in EPF [Burley et al. 1996]) does not represent an evolutionary paradox. The persistence of tactically coercive behaviors without fitness benefits to males would pose such a paradox. Moreover, if males do benefit from tactically coercive behaviors, it is necessarily at female expense. Thus, we can expect that female resistance to tactically coercive behaviors is typically greater (unless the cost of resistance is too great) than is their resistance to incidentally coercive behaviors.

## WHAT IS THE RELATIVE INTENSITY OF SEXUAL SELECTION ON MALES VERSUS FEMALES?

The prevailing assumption, cogently summarized by Andersson (1994:143), is that "Sexual selection is usually stronger in males than in females." One of the many implications of the assumption that there is considerable disparity in intensity of sexual selection on the sexes was also expressed by Andersson (1994: 145): "Because males, but usually not females, seem able to improve reproductive success by gaining several mates, male distribution should be influenced strongly by female dispersion, which in turn should be closely related to the distribution of resources needed for breeding."

Examination of the components of this logic may be instructive. The assumption that males can improve RS by acquiring more mates, whereas females cannot, has empirical roots in Bateman's (1948) demonstration that female fruit flies allowed to mate with one male are nearly as fecund as those mating with multiple males, whereas male reproductive success continues to increase with additional mates. But what if this relationship is not always asymmetrical, or what if it is not generally asymmetrical? We have in this collection two empirical studies that show a positive relationship between a female's RS and the number of sires of her offspring (Gray, Chapter 3; Ketterson et al., Chapter 4). Ketterson et al. (Chapter 4) report the surprising result that the relationship between female RS and mating success (MS) is as strong as that for males. That is, the RS of some male juncos is enhanced significantly by fertilizing eggs laid by females other than their social mates. Female juncos, on the other hand, do not lay eggs in nests other than their own frequently enough for this event to have been sampled, but those that had multiple sires for their progeny also had higher seasonal RS. Together, these are truly exciting findings that challenge our conventional understanding of the balance of costs and benefits associated with mating behavior in female and male birds.

If there is less disparity in the intensity of sexual selection on the sexes than has been previously thought, what are the implications for the rest of the logic presented above? Are males responding to female distribution, and is female distribution determined primarily by distribution of "resources needed for breeding"? The conventional reasoning is that the resources referred to here are physical resources necessary for nesting and feeding and protecting young. But if female RS is as strongly linked to MS as is male RS, then males become as much a resource for females as females are for males. Wagner (Chapter 6) explores this logic, suggesting that female interest in multiple copulatory partners puts males in a position of conflict: although a male's reproductive interests may be best served by sequestering a social mate far from other males, advantages to females associated with acquiring multiple genetic mates will cause females to prefer to settle near aggregations of males. As long as this is the case, males in groups will benefit as long as females are able to resist male coercion to be apart from an aggregation (Gowaty 1997). But, in this scenario, breeding aggregations result not from the conventional logic (distribution of physical resources needed by females for reproduction), but rather based on sociosexual resources (potential mating partners) valued by females for reproduction.

How do females benefit from having multiple genetic mates? Gray (Chapter 3) reports for Red-winged Blackbirds in Washington State that EPC/EPF benefits females because nesting success increases in response to the enhanced nest defense that results from the participation of multiple males in this activity, and because females have enhanced access to food resources on the territories of EPC partners. The benefit(s) of multiple mating to female Carolina Dark-eyed Juncos in Ketterson et al.'s study (Chapter 4) are less clear-cut. Ketterson et al. were able to identify genetic fathers when social fathers were excluded in their junco population. In their resulting analyses they show that variance in RS of males is only slightly greater than that of females. This result is not too surprising given that this species is socially monogamous with pair-bonds that endure across seasons, and is only somewhat dimorphic and dichromatic. What is remarkable indeed is that variance in RS of both sexes, though similar, was high, and 27% of young were produced through EPF. That variances in male and female RS are high but similar suggests that female juncos obtain economic benefits from EPC such as foraging privileges, or assistance in nest defense, much as Gray (Chapter 3) reports for Washington blackbirds. Alternatively, if females sought good genes in their EPC partners, even slight agreement among females as to the male quality would seem to us to accentuate variance in male RS above that of females. Another alternative is that sperm could be limiting in the junco system, although this would not be predicted on the basis of the socially monogamous, territorial social structure.

Results such as these call into question the assumption that female birds obtain only indirect fitness benefits from EPF (e.g., improved offspring quality, which may translate into greater numbers of grandoffspring), and suggest instead that number of mates may influence female RS in ways identical to the influence on males first shown by Bateman (1948). This is an exciting possibility that greatly expands the potential force of sexual selection acting on females. This possibility therefore demands the close attention of researchers studying sexual selection in birds and other taxa.

*Sexual selection gradients and EPFs:* "Bateman's principle" was formalized by Arnold and Duvall (1994) as the "sexual selection gradient," which is defined as the slope of the partial regression between fecundity and mating success. Johnson and Burley (Chapter 2) give several reasons that ornithologists should be cautious in using sexual selection gradients to describe the intensity of sexual

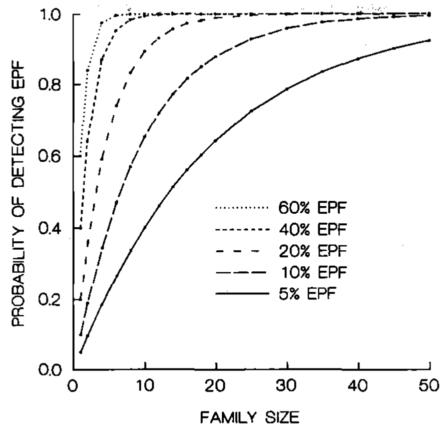

FIG. 1. The probability of detecting at least one extra-pair fertilization (EPF) as a function of family size (number of offspring produced in a season), when each female participates in extra-pair copulation (EPC) at the same rate. The curves represent different populations, each at the constant EPF rate indicated. The probability of detecting at least one EPF in a family is calculated as $(1 - w^n)$, where $w$ is the proportion of copulations that are within-pair and $n$ is family size (see text).

selection on females. We amplify briefly on one problem of statistical inference that we have encountered: given a constant rate of EPC, the probability of detecting EPF is greater for a female with higher RS than for one with lower RS. To illustrate this point, let us assume that all females of a given species engage in within-pair copulations versus EPCs at the same rate. Further assume that all copulations are equally likely to fertilize eggs. The probability, $P$, that resulting groups of offspring (e.g., broods, young of a season—referred to henceforth as families) contain only offspring sired by the social mate is $w$ where $w$ is the proportion of copulations that are within-pair, and $n$ is family size. Although $P$ decreases with family size, the probability ($q$) that families contain *one or more* extra-pair offspring $(1 - w^n)$ increases asymptotically with family size (Fig. 1). Thus, the probability of offspring produced through EPF occurring in a family increases with family size even if rates of EPC/EPF are constant. By extension, the probability of detecting any number of extra-pair copulatory partners will increase with family size.

For birds, RS values are often in the range (20 or fewer) over which family size has a large effect on the probability that a family will contain EPF offspring. In populations of small-to-moderate size, it seems likely that the relationship between family size and probability of observing EPF can be a confounding variable. Figure 2 shows the relationship between family size and the number of families in a sample that are necessary to generate a 95% probability that at least one family will contain at least one EPF offspring, given a range of EPF rates.

The clear implication from the relationships depicted in Figures 1 and 2 is that the appropriate null model for generating expected values of EPF offspring from an assumption of constant EPF rates is not independent of family size. When small families are relatively uncommon, their inclusion in regression analyses that examine the relationship between MS and RS may lead to a spurious pattern. We explore further implications, and suggest possible ways to deal with this problem, elsewhere (Parker et al., in prep.).

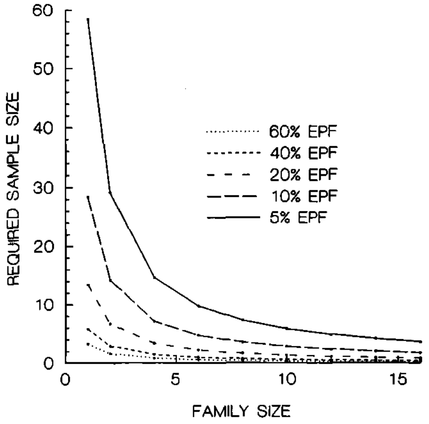

FIG. 2. The number of families that must be sampled to reach 95% confidence that at least one extra-pair fertilization (EPF) offspring will be detected. This relationship assumes that extra-pair copulation (EPC) rates are constant within populations (but vary across populations as indicated), and that all copulations are equally likely to fertilize an egg.

## HOW IMPORTANT IS SEXUAL SELECTION IN AVIAN SOCIAL EVOLUTION?

Because of widespread occurrence of social monogamy in the taxon (Lack 1968), it was historically believed that opportunites for sexual selection in birds were limited to subtle forces such as variation in the timing of onset of breeding (O'Donald 1980). Most of the papers in this volume show that this conclusion is inconsistent with current evidence. Moreover, authors here suggest either explicitly (Wagner, Chapter 6), or implicitly (Gray, Chapter 3; Stutchbury and Neudorf, Chapter 5; Dunn and Cockburn, Chapter 7), that opportunities for EPCs facilitate social evolution; this view is in marked contrast to the idea that EPC is a cost of group living (e.g., Emlen and Wrege 1986), and thereby a constraint on social evolution. Certainly the appropriate perspective on this question would depend upon whether one was considering FEPC, SEPC, or NEPC, and whether one was considering the male or female viewpoint.

Both avian sexes possess a diverse array of sexually selected reproductive tactics (Johnson and Burley, Chapter 2). It is surprising how little we know about many of them, especially given the popularity of birds as subjects of sexual selection studies. Recent research, including the papers contained herein, suggests more questions than answers. How widespread, for example, is the use of EPCs by avian females to garner economic resources? How successful are females at this tactic (i.e., how much net benefit do they accrue)? How "honest" are females in providing fitness returns for male economic contributions (e.g., Wolf 1969)? How widespread and honest is the use of behavioral fertility advertisements by female birds?

Many researchers have assumed that FEPC is not efficacious in most birds (discussed in McKinney and Evarts, Chapter 8), but what is the real relative efficacy of FEPC, NEPC, and SEPC, and how does relative efficacy vary among taxa? In some species, females typically solicit copulations (e.g., Red-winged Blackbirds [Gray, Chapter 3]); whereas in others they do so only a portion of the time (e.g., Zebra Finches [Burley et al. 1994]); and in at least one species (Purple Martin [E. S. Morton, pers. comm.]), females appear to resist most copulation attempts, even those involving their social mate. What is the significance of this variation?

It is very interesting that despite the fact that EPCs are quite furtive in fairy-wrens (Dunn and Cockburn, Chapter 7), male fairy-wrens seem able to estimate their paternity (Mulder et al. 1994). How do they do this? Can they reliably base their estimation on their own "sexiness," that is, their success in extra-pair courtship? Can they keep track of how much time their social mate spends off territory when she is fertile? What mechanisms are available for males of other species? Do females have ways of manipulating male perception of their fertility (as, for example, in lions [Bertram 1976])? How often do female birds solicit EPC or within-pair copulation when they are not fertile (e.g., Wolf 1969; Eens and Pinxten 1995)?

*Mate guarding and male retaliation:* The significance of mate guarding as a reproductive tactic to maximize paternity is reconsidered by three sets of authors in this volume. Stutchbury and Neudorf (Chapter 4) point out that few authors have investigated the efficacy of mate guarding in increasing paternity confidence. They cite several recent studies that suggest that male attempts to increase paternity by mate guarding are ineffective. In fact, the assumption that mate guarding is ineffective as a male tactic forms the basis for much of their paper. Johnson and Burley (Chapter 2) make a similar observation and suggest that a functionally neutral term, "consortship," be used to describe the close physical association between the sexes that commonly occurs between socially paired birds during the female's fertile period. They suggest that consortship evolved as an extension of courtship that occurs during pair formation, and they enumerate a number of possible functions that such consortship could have as alternatives to the mate guarding hypothesis.

If, as a growing database suggests, males are unable to prevent their social mates from seeking additional genetic mates, males might emphasize "retaliatory" tactics such as forced pair copulation and reduced paternal investment in young. Gray (Chapter 3) reports that retaliation by male Red-winged Blackbirds in Washington State is minimal: they do not force their social mates to copulate following an EPC, nor do they prevent them from nesting on their territories. Some data suggest that males may limit the time spent feeding on their territories by their social mates that engage in EPCs. What function this behavior might have is unclear. Does it increase the tendency of additional females to settle on a male's territory by increasing the apparent level of food availability? Alternatively, males may emphasize obtaining EPCs of their own, rather than retaliation against social mates. This pattern is seen in both Gray's study on Red-winged Blackbirds, as well as in Dunn and Cockburn's (Chapter 7) study of Superb Fairy-wrens.

*PI and paternity confidence:* The relationship between paternity confidence and paternal investment continues to be debated. Gray (Chapter 3) summarizes evidence that male blackbirds in New York State do not alter their tendency to feed nestlings as a result of variation in paternity, and she cites evidence from other species that also show no relationship between parental care and paternity confidence. On the other hand, Dunn and Cockburn (Chapter 7) review evidence for fairy-wrens that breeding males that have helpers do restrict parental care to nests containing extra-pair young.

Johnson and Burley (Chapter 2) suggest that apparent discrepancies among studies in the relationship between paternal confidence and investment result in part from the occurrence of conditional tactics on the part of both sexes. Thus, for example, the tactical ability of an individual to restrict its parental investment depends on its mating attractiveness (Burley 1986, 1988): males of low attractiveness may be constrained to relatively high parental investment, whereas males of higher attractiveness may inherently enjoy higher parental confidence. Consideration of the relative costs and benefits of paternal care should also affect the expected relationship between paternal care and paternal confidence. Thus, for example, where nest defense is not risky and the fate of an entire brood is at stake, males should not benefit from restricting their defense of a nest in the face of partial paternity. This is, in fact, the result that Gray (Chapter 3) found for Red-winged Blackbirds in Washington State. In Ontario, where nest defense poses significant risks to defenders, males defend less if their nests contain extra-pair young (Weatherhead et al. 1994).

## CONCLUSION

Recent discoveries of widespread active female choice of EPC partners make increasingly outdated—even ironic—the relatively recent view (e.g., Taylor and Williams 1982; Maynard Smith 1985) that female choice, by leading to the rapid fixation of traits, has a limited role as an evolutionary agent. Instead it appears that we have only achieved limited appreciation of the force of mate choice in driving sexual selection, and the force of sexual selection in mating system evolution, speciation, and other processes. Work such as that of Dunn and Cockburn (Chapter 7) indicates that exceedingly high variance in male RS that is the direct result of female choice is a reality, despite what some models may suggest. No doubt, new hypotheses for the maintenance of heritable variation in sexually selected traits, such as those of Johnson and Burley (Chapter 2), will grow in number. Work such as that of Gray (Chapter 3) and Stutchbury and Neudorf (Chapter 5) shows that females are far from passive observers of the territorial games played by male passerines. Research shows (Gray, Chapter 3) or suggests (Ketterson et al., Chapter 4) that female passerines obtain direct fitness benefits from EPCs, a possibility considered unlikely just a few years ago (Birkhead and Møller 1992). Several authors here (Johnson and Burley, Wagner, McKinney and Evarts) suggest that opportunities for the pursuit of sexually selected tactics can be the driving force behind the evolution of social organization, rather than the consequence of ecology/social organization.

We cannot assume, of course, that avian patterns are typical of those occurring at a broader scale (e.g., in vertebrates). Gowaty (1996b), for example, has recently suggested that female choice has had a more important role in avian evolution compared to mammalian evolution because female birds are more successful at resisting male attempts at coercion than are female mammals. To examine the broader implications of this idea, it is important to compare the consequences of variable opportunities for coercion within and across avian taxa (McKinney and Evarts, Chapter 8). Although the idea that male control of resources is an important force in structuring mating systems is not new (e.g., Thornhill and Alcock

1983), for many birds, at least, it seems we have underestimated female autonomy in mate choice even when males do have substantial control over resources.

Avian mating systems do not appear as uniform and monotonous as has sometimes been suggested. In particular, they show a great deal of variation in male parental care. Although the importance of male parental care in the evolution of reproductive tactics discussed in this volume is currently debated, we expect that it will be shown to be a key variable in future studies of avian mating tactics, and a very useful one for intertaxon comparisons. Above all, we hope that the questions posed and the ideas and perspectives taken by the authors of this volume will invigorate the study of avian reproductive tactics.

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# CHAPTER 2

# MATING TACTICS AND MATING SYSTEMS OF BIRDS

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ABSTRACT.—In light of current knowledge of the behavioral and genetic complexity of avian mating systems, both conventional classifications of mating systems and traditional models for their evolution are inadequate. In this paper we attempt to provide a synthetic view of the major avian mating systems, recognizing common aspects without imposing arbitrarily rigid categories. Our scheme incorporates both genetic and social aspects of mating systems and focuses on individual mating tactics. Although classification tends to imply stasis, we suggest that mating systems may be quite fluid in both ecological and evolutionary time. Flow is possible because the range of mating tactics available to both male and female birds is not limited by the mating system. Thus, individuals may respond quickly to the opportunities and constraints of changing circumstances. The movement of populations or species between mating system types may also be closely related to the fluctuating heritability of traits used in mate choice. We suggest that conditional mating tactics and female mating (as opposed to parental) tactics are key mating system parameters. Predictions (such as the expected relationship between paternity and male parental investment) that ignore conditional mating tactics, or explanations (such as for consortship patterns) that ignore conditional or female mating tactics are likely to be simplistic or erroneous. Future understanding of avian mating systems will be most enhanced by close analysis of the opportunities and activities of all phenotypic classes within a population, and by experimental manipulation of those opportunities. Genetic, developmental, and historical constraints that may affect the expression of mating tactics should also receive more attention. As this kind of information becomes available, a more complete, accurate, and integrated understanding of avian mating systems will be possible.

Over the past 20 years, students of avian mating systems have gone from the conviction that more than 90% of all bird species are faithfully monogamous (Lack 1968) to an awareness that bird mating systems are not so straightforward as they might appear on the surface. This realization began with the discovery that female Red-winged Blackbirds (*Agelaius phoeniceus*) mated to vasectomized males laid fertile eggs (Bray et al. 1975). When allozyme markers later allowed exclusion of some putative parents, the idea of widespread copulation outside the pair-bond became plausible (Gowaty and Karlin 1984; Gavin and Bollinger 1985; Joste et al. 1985; see Birkhead and Møller 1992 for other references). The introduction of DNA fingerprints further demonstrated that the social or "sociographic" (Gowaty 1981; Wickler and Seibt 1983; Gowaty and Bridges 1991) mating system assigned to a species was not necessarily compatible with the genetic relationships observed (Westneat et al. 1987; Westneat 1990). Concurrently, careful studies of color-banded birds revealed complex social mating systems such as polygynandry in the Dunnock (*Prunella modularis* [Davies 1985, 1992]) and ambisexual polygamy in the Penduline Tit (*Remiz pendulinus* [Persson and Öhrström 1989]). Studies such as these indicated conflict between the sexes over the optimal mating system and demonstrated that even social mating systems cannot always be neatly categorized.

In the face of the current knowledge of social and genetic relationships, traditional definitions of avian mating systems are inadequate. Most importantly, they are population-level generalizations that do not take individual strategies into account. Monogamy, for example, implies faithful pair-bonds among some unspecified majority of the individuals in a population, ignoring the possible existence of a minority of polygynous individuals that could account for a substantial share of the reproductive success in the population. The opposite extreme is exemplified by the 5% criterion for polygyny, in which a polygyny level of 5% in an otherwise socially monogamous population is sufficient reason to classify the population as polygynous, ignoring 95% of the population (Verner and Willson 1966; Møller 1986). Both approaches are good examples of how adhering to rigid classifications can result in overlooking mating system complexity (Ostfeld 1987; Oring et al. 1994).

Traditional labels such as "monogamy" say nothing about the existence of mating tactics such as extra-pair copulation (EPC) among monogamously bonded individuals. Even before molecular parentage analysis, studies of the behavior of individually color-banded birds suggested that within a particular mating system, population, or sex, the costs and benefits of engaging in EPCs may vary among individuals (Ford 1983; Mock 1983; Birkhead et al. 1987; Westneat 1987b; Sherman and Morton 1988; Smith 1988). Molecular data resoundingly confirm the necessity of looking beyond population generalizations to the behaviors of individuals.

One of the most obvious failures of the old definitions is that they were formulated without knowledge of genetic parentage. Estimates of extra-pair paternity in wild populations now exist for more than 70 bird species (Gowaty 1996b). So far, however, most studies have not specified the range of individual strategies or variation among individuals in genetic reproductive success. For example, the percent of extra-pair offspring in a population says nothing about how those young came about: did one particularly attractive male account for all of the extra-pair paternity or did every male receive an equal share? Although DNA fingerprinting works well for paternity exclusion, its ability to assign genetic parents is limited, partly due to the difficulty in comparing bands across gels (Queller et al. 1993; Burley and Parker, Chapter 1). New genetic markers such as DNA microsatellites offer potential for identification of genetic parents, even in fairly large populations (Queller et al. 1993). The ability to make assignments will allow quantitative, as opposed to qualitative, descriptions of mating systems, taking individual variation into account. Although it is encouraging that accurate descriptions of genetic mating systems are now becoming possible, strictly genetic definitions fail also, because it is possible for the genetic relationships to be similar in two very different social mating systems. For example, socially monogamous and socially polygynous species may be characterized by similar gametic contribution ratios (Gowaty and Bridges 1991). The availability of powerful molecular analyses does not obviate the need for careful behavioral observations; indeed, the readiness to pigeonhole rather than observe acutely may be responsible for some misclassification of mating systems.

Finally, the terminology of "social" versus "genetic" mating systems (Gowaty 1981; Wickler and Seibt 1983; Gowaty and Bridges 1991) implies that two separate entities exist, when in fact they are two incomplete descriptions of the same system. The genetic mating system is a description of genetic relationships, which result from social behavior. In the current state of knowledge, there may appear to be discrepancies between the social and genetic mating systems, as for example when socially monogamous species engage in extra-pair relations. This sort of apparent discrepancy between a species' social and genetic mating systems actually indicates that important behavior has been overlooked, and not that there are two conflicting mating systems. A fully characterized mating system, in which all genetic parentage could be assigned and all social behaviors were observed, should show no discrepancy between behavioral and genetic information.

Although researchers understand the complexity of avian mating behavior much more clearly now than 10 years ago, large empirical and conceptual gaps remain. One colleague summarized the state of affairs bluntly, "The study of mating systems is a mess." We agree that things are a bit muddy, but we are optimistic that a clearer view is possible. Here we discuss the diversity of avian reproductive tactics across major mating systems and propose a new classification of avian mating systems.

## PERSPECTIVE

Since the 1960s, influential authors have emphasized the perspective that mating systems of birds and mammals are structured by ecological opportunities (e.g., for male control of resources) and constraints (e.g., the time available for breeding) (Lack 1968; Orians 1969; Jarman 1974; Emlen and Oring 1977; Rubenstein and Wrangham 1986 and references therein). More recently, researchers have explored the role of other potentially important considerations, especially phylogeny (Ligon 1993) and demography (Murray 1984). We believe that numerous variables must be considered to provide a good explanation for evolution of a particular social organization in a particular taxon. Our approach here is more limited, however; we seek to describe basic patterns of avian mating and the forces of sexual selection that shape them.

When Darwin (1871) originated the concept of sexual selection, he thought in terms of male–male competition and female choice of mates, and a majority of authors since have adopted this view. Following Trivers' (1972) articulation of the concept and significance of parental investment (PI), it should be clear that male choice of mates and female–female competition may frequently contribute to the sexual selection dynamic, but these forces have received little empirical consideration. From a scope of inquiry restricted to female choice and male–male competition, it is an easy step to a common oversimplification: which sex is in control? Although in any given social mating system one sex may appear to have a clear advantage (e.g., males in female defense polygyny; females in simultaneous polyandry), we suspect that upon careful examination, only in parthenogenetic and possibly haplodiploid species will one sex receive a disproportionate share of the reproductive success. Nevertheless, it is difficult to do justice to male choice and female competition, because so much less is known about these processes (Johnson 1988).

We propose a unitary view of mating systems that goes beyond a description of pair-bonds or detection of extra-pair relations. The whole mating system can be seen as a suite of interrelated aspects of a species' reproductive biology that evolved together: copulation behavior of males and females, pair-bonds, fecundity, parentage, parental care patterns, mating tactics such as EPC, mate guarding, competition for mates, mate choice, and others. Our classification is based on a combination of genetic and social criteria.

Certain predictable relationships are expected among the various mating system features, such that it is possible to characterize, classify, and name a limited number of the most common or likely mating system types. The seven mating system types we discuss can be viewed as suites of polygenic characters. Although this classification is not meant to be all-inclusive, and in theory there could be a continuum of intermediates, certain combinations of traits are more likely to occur than others. For example, sexual size dimorphism generally increases with the degree of polygyny, at least when male–male combat plays a major role (Payne 1984). In species where choice predominates, size and ornament dimorphism may be poor predictors of degree of polygyny (Trail 1990). In addition, species may move among categories in ecological or evolutionary time as selection pressures change (see Discussion).

An important component of this classification is the strength of mating fidelity, which we define as the tendency to produce offspring with a single mate. High fidelity could occur via mate choice or as a result of mate control (Gowaty 1996a, 1997). Gowaty (1996a) defines "helpfully coercive" males as those who manipulate females into mating with them by helping. In addition, males theoretically can control female fidelity via aggressive coercion (mate guarding or forced copulation) or resource brokering (Gowaty 1996a). However, there are several reasons to believe female birds are able to resist male control over their fidelity. (1) Compared to mammals, there is a paucity of evidence for female-defense polygyny in birds, because female birds are highly mobile and cannot be confined by males to a spatially fixed territory, although some species in which females cluster in colonies may provide exceptions (Webster 1994). (2) Males of most bird species lack intromittent organs, such that forced copulation is probably not an efficient means of effecting genetic fidelity and does not necessarily enhance male reproductive success (Burley et al. 1996; but see McKinney and Evarts, Chapter 8). (3) Females that pay for male assistance by being faithful may practice serial fidelity, in which they vary their partners by switching mates between clutches or years (Johnson, unpubl. data).

A perspective based on balancing the various costs and benefits of fidelity may explain much of mating system diversity. Costs of EPCs may include predation risk, avoidance of enforcement by members of the social group (Florida Scrub Jays, *Aphelocoma coerulescens* [D. McDonald, pers. comm.]), physical injury incurred by copulating with a large male, disease, time, or lost parental effort (PE) from the social mate. Benefits may include differing mate choice criteria for social mates (perhaps chosen for their territories) and genetic mates (possibly chosen for aesthetics or good genes), bet-hedging, avoidance of harassment or injury, access to resources, or PE from EPC partners. To allow for rigorous testing of evolutionary hypotheses, empirical studies of mating systems need to become much more quantitative. It is essential to specify the proportion of a population that maintains pair bonds, what percent engages in extra-pair fertilizations, the relative variance in male versus female genetic mating success, the success rate of conditional mating tactics, and so on. Beginnings in this direction are exemplified by Petrie et al. (1992) and Oring et al. (1994).

## CONCEPTUAL FRAMEWORK: THE ARRAY OF MATING TACTICS

In this section we discuss key concepts that form the basis for our mating system classification and allow us to specify the mating tactics that we expect to see in each mating system. We attempt to use descriptive, existing terminology and avoid jargon whenever possible, but some new terms are necessary, and we use a slightly different focus with some existing terms.

A **pair-bond** is a social and copulatory relationship between two individuals, in which members of the pair (**social mates**) share some aspect of rearing offspring. This may be as little as sharing the same space, as when a female nests in a male's territory with no male PE (see below) beyond nest site defense or exclusion of other individuals from a feeding territory; or as great as sharing nest building, incubation, and feeding of nestlings and fledglings. **Genetic mates** are individuals who share parentage, and may or may not also be social mates. **Copulatory partners** are individuals that copulate together but may or may not also be social mates and/or genetic mates. **EPCs** are copulations with individuals other than the social mate. EPCs may be **forced** (**FEPC**; i.e., the female resists), **solicited** (**SEPC**; i.e., the female initiates the copulation), or **neutral** (**NEPC**; i.e., the female displays neither resistance nor solicitation). EPC may or may not result in **extra-pair fertilization (EPF)**.

**Parentage** is the proportion of juveniles in a brood that are actually offspring of a social parent (Westneat and Sherman 1993). Males have reason to doubt their parentage more often than females, and because so few data exist on intraspecific nest parasitism (Gowaty and Karlin 1984; Brown and Brown 1989; Rohwer and Freeman 1989), we focus here on male parentage, or **paternity**. For mating systems in which no social partnerships are formed, paternity as defined here does not occur. In some such cases females nevertheless choose to mate with a single male and thus show high **mating fidelity**. Within populations, both paternity and mating fidelity could theoretically vary from 0 to 1.0. Lacking sufficient quantitative information, we use qualitative categories (low, moderate, high) for these variables.

**Reproductive effort** (**RE** [Williams 1966]) is the proportion of an individual's time/energy budget that is allocated to reproduction, as opposed to maintenance or growth. RE is composed of **mating effort** (ME), plus in many cases **PE**, and in some cases **nepotistic effort** (NE), effort expended in assisting the reproduction of nondescendent kin. We focus here on ME and PE, assuming that NE is constant or absent (see Discussion). PE is the proportion of an individual's total RE budget that comprises **diffuse** and **focused PE** (**PEd** and **PEf**, respectively). PEf is the investment, contributed to an individual offspring by a parent, that increases the offspring's chances of surviving and reproducing but also decreases the parent's ability to invest in additional offspring (equivalent to PI [Trivers 1972]). Likely examples of PE that may be partitionable enough to be considered to be PEf include feeding and defense of offspring. PEd includes morphological, behavioral, and physiological modifications that enhance parental function in ways that cannot be partitioned among individual offspring or broods. Examples include energy expended in learning parental skills, modifications for the production of crop milk, and development of a brood patch. Note that the inclusion of PEd broadens Triver's original (1972) definition of PI. For example, learning parental skills, a type of PEd, actually increases ability to invest in subsequent offspring, and thus would not qualify for inclusion as PI by Trivers' definition (or PEf by our definition). **Mean male PE** is the average amount of PE of males in a population, and **PE variance** is the variance in PE among males in a population. Reference to PE below denotes PEf unless otherwise indicated.

Trivers (1972) argued that, within a species or population, the relative selectivity of males and females in mate choice should be directly proportional to their relative PI (PEf), and the results of a number of studies appear consistent with this expectation (references in Andersson 1994). In some species, it has been relatively easy to establish a cost of parental care (e.g., Røskaft 1985; Nur 1988 and references therein), but in other species, parents appear to suffer little or no long-term consequences of naturally occurring levels of parental care (e.g., Murphy and Haukioja 1986; Wolf et al. 1988), suggesting that significant variation exists in the expense of parental care. It follows that individuals may put much more RE into ME in species in which care of individual young has little cost, especially if fecundity is constrained by ecological, historical, or physiological considerations.

The **sexual selection gradient** is the partial regression slope of the relationship between fecundity and mating success (Arnold and Duval 1994). This quantity expresses the influence of mating success on total fecundity, thus approximating the strength of sexual selection. Mating success is the number of mates that bear the progeny of an individual male or sire the progeny of an individual female and so is equivalent to genetic mating success. The male and female sexual selection gradients have predictable relationships to key behavioral aspects of the mating system, such as PE, ME, and conditional mating tactics.

The sexual selection gradient is a very useful concept, at least in making broad-scale comparisons across mating systems. However, a particular difference between the sexes in sexual selection gradients does not necessarily mean a corresponding difference in the influence of sexual selection. There are several reasons why we use sexual selection gradients as defined by Arnold and Duval (1994) with caution.

First, for females but also for males in some mating systems, the relationship between fecundity and number of mates may not be a causal one. For example, females with larger clutches may have higher numbers of EPCs than females with smaller clutches, simply by virtue of the length of the fertile period. That is, even if EPC rate remained constant, a female that produced more young could also produce more EPC young. Whether or not the actual EPC rates of the two groups can be detected is a problem of statistical inference, discussed by Burley and Parker (Chapter 1).

Alternatively, older or larger females could be more fecund, by virtue of their age, size, or experience, and also have more mates than other females. This relationship could occur if older or larger females are more attractive mating partners and therefore have more success in obtaining multiple partners. Perhaps males mated to older or larger females are constrained to accept their mates' tendencies to seek additional partners, because such females are more valued as mates. This possibility is suggested by Gray (Chapter 3). If older female Red-winged Blackbirds settle on territories earlier than younger ones, perhaps they monopolize the sites to which they can attract, through EPC, the greatest numbers of males to assist in nest defense.

In the same vein, a female that produced two clutches and copulated with two males would have twice the fecundity of a female that produced one clutch and copulated with one male, but in this case the correlation between fecundity and number of mates does not necessarily imply strong sexual selection. Rather, the fecundity of either female is much more strongly influenced by her ability to produce larger clutches or more clutches than by the number of mates she acquires. In the above examples, fecundity is correlated with mate number, but increasing mate number does not cause increased fecundity, and the sexual selection gradient would thus overestimate the strength of sexual selection on females.

Second, fecundity may not always approximate fitness. Mate quality may influence the fecundity of a female's offspring (Weatherhead and Robertson 1979). If so, and if female quality influences access to mates of high quality, fecundity is an insufficient measure of fitness. In this case, the sexual selection gradient would underestimate the strength of sexual selection on males.

Finally, preferences for mate quality over quantity may constitute substantial sexual selection that is unaccounted for by the sexual selection gradient. For example, attractive individuals may benefit by obtaining mates of superior quality rather than obtaining larger numbers of mates. Low-quality or inexperienced individuals may have trouble holding social mates or may display low fecundity despite having several mates. In both situations the sexual selection gradient would underestimate the actual strength of selection for mating attractiveness.

Thus, the sexual selection gradient may ignore significant sources of sexual selection (mate quality) or attribute to mating success aspects of fecundity that rightfully belong under natural selection (clutch size or number). Unless variation in mate number is caused by variation in mating attractiveness or intrasexual competitive ability, and unless fecundity closely approximates reproductive success (RS), a relationship between mate number and fecundity is not a sexual selection gradient.

## PATERNITY, PE, AND CONDITIONAL PE TACTICS

Authors have repeatedly suggested that some confidence of paternity is a precondition to the evolution, maintenance, or expression of male parental care (Trivers 1972; Gladstone 1979; Zenone et al. 1979; Westneat 1987a; but see Knowlton and Greenwell 1984 for a reversed interpretation of the causal relationship). Others, however, have argued that low paternity does not affect the evolution of male PE, or vice versa (Maynard Smith 1977; Grafen 1980; Wittenberger 1981), an expectation that appears most plausible if all males in a population have equal/constant expectation of paternity (May and Robertson 1980; Westneat 1987a), if males cannot assess their relative paternity, and/or if there is no tradeoff in effort devoted to EPC versus PE (May and Robertson 1980; Werren et al. 1980; Westneat 1987a). Recent modeling does indicate that when paternity of a particular brood is predictable relative to that of other broods, males may profit from facultatively adjusting PE (Whittingham et al. 1992; Xia 1992; Westneat and Sherman 1993; but see Houston 1995). Growing evidence suggests that males can assess paternity (Burke et al. 1989; Dixon et al. 1994; Burley et al. 1996). Some studies show a positive relationship between male PE and paternity (e.g., Vehrencamp 1977; Joste et al. 1982, 1985; Craig and Jamieson 1985; Davies 1985; Houston and Davies 1985; Westneat 1987a, b; Møller 1988; Dixon et al. 1994), whereas others show a negative or no relationship (Craig and Jamieson 1985; Frederick 1987a, b; Lifjeld et al. 1993; Whittingham et al. 1993; Westneat 1995).

Some of the variation in the relationship between paternity and parental care may be explained by variation in the cost (to males) and benefit (to females) of male parental care. Generally, we would expect lower rates of EPF in species in which the cost of male parental care is substantial versus those in which male parental care is quite expendable. Additionally, complex relationships between paternity and PE are likely because of the occurrence of conditional reproductive tactics that involve a reallocation of ME and PE based on individual chance of success. **Conditional tactics** are not fixed according to genotype or phenotype, as are alternative tactics (see p. 32), and the particular conditional tactic adopted by an individual is subject to change with changing circumstances. Specifically, males with high mate-getting ability ("attractive" males) may lower PE and increase extra-pair courtship to gain fitness through EPF; males that are not attractive to females may allocate more reproductive effort to PE to retain their mate and/or to increase paternity (differential allocation [Burley 1981, 1988; Møller 1994; Burley et al. 1996]). The success of the attractive male's tactic naturally hinges on female willingness to accept lowered PE in return for "good genes," to produce "sexy sons" (Weatherhead and Robertson 1979) and/or high-quality daughters (Trivers 1985). Thus, for any given level of PE contributed, attractive males may enjoy higher paternity (Burley et al. 1996).

Very unattractive males may have so few mating opportunities that they become willing to adopt low-payoff tactics, such as contributing low- or medium-cost caretaking activities to broods in which their paternity is quite low, rather than abandoning their philandering mates and producing no offspring. Where such unattractive phenotypes persist in evolutionary time because of genetic and/or developmental constraints (e.g., delayed plumage maturation [Enstrom 1993]; testosterone titers [Hill 1988]), females may evolve tactics to exploit the parental willingness of unattractive males.

Implicit in the idea that males have conditional tactics is the concomitant occurrence of female conditional tactics. Females mated to males of high genetic quality may be willing to accept reduced PE, whereas females of high genetic quality may be able to demand greater male PE (Burley 1988). Differential allocation is thus a mechanism by which an individual's high mating attractiveness could enhance fecundity, through the greater economic contributions provided by a mate, without an increase in number of mates. Thus, sexual selection cannot be tied exclusively to mate number. For attractive individuals of both sexes, however, the opportunity to restrict PE could lead to increased lifespan and thus greater number of social mates secured over the course of a lifetime. If so, sexual selection gradients derived from data on lifetime RS and mating success should be increased for both sexes.

In summary, we predict that there are at least two conditions under which exceptions to the predicted correspondence between paternity and PE will occur: the occurrence of conditional tactics that cause males to alter allocation to PE will generate complex patterns, and males whose access to mates is very limited due to low attractiveness may adopt low-payoff tactics that include substantial parental care in the face of low paternity. These expectations in no way invalidate the underlying reasoning predicting a correspondence—everything else being equal—between paternity and PE, but do lead us to suggest that ceteris paribus often is not an appropriate assumption. Finally, we should note that in comparative studies of the relationship between paternity and PE, inclusion of species in which males are not social parents (e.g., Møller and Birkhead 1993) is not legitimate (see also above, p. 25).

### MATING EFFORT

Mating effort is the proportion of RE that is devoted to focused plus diffuse mating effort. **Focused ME (MEf)** is any investment of time/energy spent to secure or sustain a particular mate that decreases an individual's chances of securing additional mates (after Low 1978). **Diffuse ME (MEd)** is investment that cannot be partitioned among individual mates. **Mean male ME** and **variance** are the mean and variance of male mating effort in a given population. Types of ME typically thought to be incurred by males in the pursuit of social and genetic mates include courtship displays; calling or singing; ornamentation; and display of artifacts such as grass or flowers, or structures, as shown by bowerbirds (Table 1). Whether a particular activity or display should be considered MEf or MEd depends on whether its cost can be reasonably partitioned among potential mates. If an individual attempts to mate with multiple individuals during a breeding season, for example, then the cost (including the risk of predation) of producing and maintaining a bright nuptial plumage is diffuse, whereas the cost of displaying it to a particular potential mate is focused. When individuals incur substantial focused ME, they should show mate selectivity; more precisely, mate selectivity should be proportional to the sum of PEf and MEf.

Frequent copulation with social mates has been thought to dilute the effects of a mate's extra-pair activities. Alternatively, however, frequent copulation could function as a demonstration of male quality and thus be a component of consortship (Briskie 1992; and see consortship, below). FEPC behaviors and other male activities (e.g., enhanced territorial defense [Møller 1990]) that either force or persuade females not to mate with alternative mates are types of focused ME.

Diffuse male ME includes all the morphological, behavioral, and physiological accouterments that may confer advantage in male–male competition (Table 1). Of course, if males compete for access to a particular female, the expense constitutes focused ME. In species in which females regularly copulate with more than one

TABLE 1. Examples of diffuse versus focused mating effort made primarily by males, primarily by females, and by both sexes of birds.*

| Diffuse | Focused |
|---|---|
| **Male and female** | |
| Courtship display, especially on leks; dance, song, bowers | Courtship display; including dance, song, artifacts |
| Ornaments | Mate choice, including time spent evaluating particular mates |
| Time spent searching for mates | PE that prolongs mate's survival |
| Seasonal increase in testis/ovary size | Frequent pair copulation |
| Seasonal testosterone/estrogen surge | Sneaking behaviors associated with EPC |
| Early arrival at breeding grounds to secure mate/territory, travel to lek | Fighting over mate |
| Defense against venereal disease | Consortship |
| Dominance behaviors, breeding and sometimes nonbreeding season territory defense | Vocal communication with mate |
| **Mainly male** | |
| Territorial song | Postpairing song to stimulate female to breed |
| Large body size and weapons | Courtship feeding |
| Structures aiding sperm competition: sperm morphology, large testes, cloacal protuberances | Cloaca pecking |
| Male–male cooperation, queuing, multiple lek attendance | FEPC |
| Badges | Infanticide—mainly male? |
| | Low-payoff "PE" |
| **Mainly female** | |
| Sperm storage structures | Avoidance of male coercion and unwanted EPC attempts |
| Structures/physiology associated with sperm expulsion | Expulsion of unwanted sperm |
| Inciting male–male competition | Nest and egg destruction |
| | Inciting male–male competition |
| | SEPC |

* EPC = extra-pair copulation, FEPC = forced extra-pair copulation, PE = parental effort, SEPC = solicited extra-pair copulation.

male, **sperm competition** (by which we mean competition among spermatozoa within the female reproductive tract, rather than the broader meaning attributed to the term by Birkhead and Møller 1992) may result in evolution of greater testes volume and modifications of sperm, including morphology, motility, longevity, or quantity. These and the costs of testosterone production (Zuk 1990, 1994) constitute diffuse male ME.

Females as well as males of many species of birds, including socially monogamous birds, may incur substantial ME (Table 1). In many species, females have colorful plumage and participate in courtship activities including displays, dances, and vocal exchanges. Female–female competition for access to mates is an additional form of female ME; for example, cost of early arrival at breeding grounds to secure a superior mate (MEd) and attempts to limit copulatory access of other females to superior males (MEd or MEf [Petrie et al. 1992]). Mate choice is also a component of female (and sometimes male) MEf, including efforts to incite male–male competition (Thornhill 1988; Montgomerie and Thornhill 1989) and time and effort spent evaluating potential mates. Efforts to reduce forms of male coercion and male–male competition that are not advantageous to the female are

TABLE 2. Hypotheses that have been proposed for the functions of consortship in birds.

| Hypothesis | Reference |
|---|---|
| Surveillance, mate guarding | Trivers 1972; Birkhead 1979 |
| Protection from unwanted suitors | Parker 1974; Lumpkin 1983 |
| Copulation access | Gowaty and Plissner 1987 |
| Strength of pair-bond | Lumpkin et al. 1982 |
| Predation protection | Lumpkin 1983; Martin 1984; Gowaty and Plissner 1987 |
| Courtship feeding | Birkhead and Møller 1992 |
| Passive presence | Björklund and Westman 1986 |
| Demonstration of mate quality | Briskie 1992; Johnson and Burley, Chapter 2 |
| Determination/demonstration of fidelity | Johnson and Burley, Chapter 2 |
| Demonstration of parental ability, willingness | Johnson and Burley, Chapter 2 |

also MEf (e.g., FEPC or NEPC when FEPC might cause injury). Covert activities by socially mated females to obtain additional genetic mates are likely to be MEf. Diffuse female ME also includes the cost of activities and structures (e.g., sperm storage organs) that facilitate sperm competition as well as those that eliminate or inactivate unwanted sperm (as, for example, following FEPC).

An implicit expectation in much of the relevant literature is that male birds allocate a much greater share of RE to ME than do females. Consideration of the above list of activities constituting ME leads us to conclude that the discrepancy may not be so great as sometimes implied. Indeed, it would seem that in a population in which there is a substantial increase in male ME to extra-pair activities, female ME is likely to increase in response.

**Consortships** between socially mated individuals that involve close physical association commonly occur prior to and/or during the interval during which females are fertile, that is, during the period over which sperm may be stored and function in fertilization. The most commonly invoked functional explanation for consortship is that it enables males to limit female access to alternative mates ("mate guarding" [Birkhead 1979; Birkhead and Møller 1992 and references therein]). Several recent studies, however, have shown a lack of correspondence between the strength of guarding and resulting paternity of broods within populations (Westneat et al. 1990; Kempenaers et al. 1995; Enstrom and Burley, unpubl. ms.). Moreover, in many instances such associations may not be sufficiently intense or continuous to preclude all female contact with EPC partners, and guarding mechanisms may be ineffective if females are able to engage in furtive EPCs and have mechanisms for selective use of sperm.

Lumpkin (1981, 1983) suggested that females of some species have capitalized on male guarding tendencies, receiving protection from predators or avoiding harassment by unwanted suitors. She suggested females prolong the interval of guarding by deceptive signaling of fertility during infertile periods. Since that time, several additional hypotheses for the function of consortships have been proposed (Table 2). We suggest that consortship may have evolved as an extension of courtship that occurs during pair formation, and that consortship may have different functions in different species. In addition to previous hypotheses, we suggest that consortship might function to demonstrate or determine the following attributes.

*Mate quality:* Individuals of one or both sexes indicate their vigor and stamina and hence their suitability as genetic and social mates. In this view, males seek to discourage partners from seeking EPCs by "proving" their superior quality. Males and females could use consortship to discourage their social mates from abandoning them for new social mates or to test the quality of their mates (Briskie 1992).

*Mate fidelity:* If males have little control over their mate's EPC behavior, they may nonetheless seek to ascertain their mate's intentions immediately prior to and during the fertile period, and thereby gauge paternity. Females might use consortship to convince social mates of their paternity in order to obtain maximal PE from them.

*Parental ability or willingness:* Males and/or females might use consortship to convince social mates that they will invest substantial PE. Alternatively, males and females may use consortship to work out a social contract of mutually agreeable PE for an impending clutch (Burley 1988); females might adjust clutch size depending on their expectation of male assistance, based on information acquired during consortship.

Thus, consortship may serve several possible functions, some of which are not mutually exclusive. We cannot provide a complete list of predictions stemming from all alternatives here. Instead we suggest that what is needed most is detailed examination of the behavior of consorting birds, combined with paternity analyses of resulting clutches, in order to specify function in particular cases. Information is needed on questions such as what fertile females do when not consorting, what males do when they observe their mates engaging in EPCs, and what the consequences are of experimentally altered consortship rates. (Is paternity affected, do PE patterns change? Do only males attempt to maintain close contact during their mate's fertile period, or do females also show this tendency?) Guarding of mates against EPCs is only one possible function of consortship, and so we typically use the broader term here to refer to this aspect of focused ME.

*Alternative mating tactics and conditional ME allocation:* Alternative (phenotype-dependent) mating tactics appear to be very rare among male birds, unlike the situation in some other taxa (e.g., Thornhill and Alcock 1983; Gross 1982, 1985). The rarity of this phenomenon may be explained by a low success rate of FEPC in most birds, which limits its utility as a primary reproductive tactic. Another possible contributing factor may be the widespread adoption of PE by male birds, which makes the use of conditional, as opposed to alternative, ME tactics possible and potentially profitable. If so, we would expect to see greater occurrence of alternative male ME tactics in species with no paternal care. The one obvious example in birds, Ruffs (*Philomachus pugnax*), fits this expectation (Lank et al. 1995). The long life span and high mobility of birds may be other reasons for the prevalence of conditional as opposed to alternative mating tactics: both may allow males to experience increased mating opportunities at another time or place.

Conditional mating tactics may involve FEPC (as opposed to reallocation of PE, above). In many birds, FEPC may be inefficient and be adopted more often by males whose mate-getting abilities are relatively low. Where the cost to males of forcing copulation is low, however, FEPC may be adopted as a secondary reproductive tactic by a majority of males, both mated and unmated (McKinney

1985). Due to a low cost–benefit ratio it would seem likely that rates of FEPC would be higher in colonial/gregarious species than in solitary/territorial species (Beecher and Beecher 1979; Emlen and Wrege 1986; Morton et al. 1990). Mated males at risk of low paternity may increase allocation to mate guarding, determination of their paternity, and territory defense against male intruders.

Females are also expected to have conditional ME tactics. Specifically, they are more likely to seek additional genetic mates when the quality of current social/genetic mates is low or in doubt. Thus, for example, females mated to low-ranking or unattractive males may seek EPCs more often and/or avoid FEPCs to a lesser extent than females mated to more attractive males (Smith 1988; Burley and Price 1991; Smith et al. 1991; Burley et al. 1996). The mate choice criteria for social mates are likely to differ from the criteria for genetic mates. Particularly females mated to low-genetic-quality males on poor territories may choose social mates for potentially high PE, while looking to EPC partners for good genes or aesthetic traits. Where males provide PE and female availability is limiting, males may tolerate lower paternity in exchange for access to superior mates; in this case, for females socially mated to males of a given quality, more attractive females may have higher EPF rates than less attractive ones. Thus, for females as well as males, more attractive individuals may have greater access to both social and EPC partners than do less attractive individuals (Burley 1981, 1986). If female PE limits female fecundity, differential access may still allow females to increase offspring quality, but the fitness consequences of differential access may be more apparent by counting grandoffspring than offspring. This sort of selection for attractiveness would not be apparent from sexual selection gradients. On the other hand, if differential access results in increased offspring number, this will be reflected in sexual selection gradients.

Sometimes the distinction between ME and PE is blurred. For example, in long-lived species with typically enduring pair-bonds, individuals might increase parental care (apparent PE) with a resultant increase in the life span of the current mate (functional ME [Oring 1982; Bart and Tornes 1989; Breitwisch 1989]). Females may engage in activities that appear to be ME, but that function to increase male PE. Female Willow Warblers (*Phylloscopus trochilus*) that participate in EPCs obtain PE from copulation partners that later usurp the territory (Arvidsson 1992). A female might encourage consortship (apparent ME) in order to increase her social mate's estimation of paternity, and hence his PE to her offspring. In western populations of Red-winged Blackbirds, females obtain material benefits from EPC partners in the form of increased nest defense (Gray, Chapter 3). Economic contributions to females by their EPC partners are a major way in which positive sexual selection gradients can be generated for females.

Given that males and females have different interests and mating tactics, **manipulation behavior** is common. For example, females may copulate multiply with their mates to deceive them regarding paternity (for the purpose of gaining increased PE) or to prevent their mates from engaging in EPCs with other females (Petrie 1992). A male may consort closely with his mate during her fertile period to demonstrate his fidelity, then engage in EPCs after she has completed her clutch. In complex mating systems such as in polygynandrous Dunnocks and Alpine Accentors (*Prunella collaris*), the clash of individual interests can result in suites of tactics and countertactics (Davies et al. 1996). Differential allocation

TABLE 3. The major avian mating systems. **ME** is the proportion of reproductive effort devoted to mating. **Primary ME** indicates the primary type of mating effort, with examples. **Conditional ME** indicates the type of conditional mating effort adopted by individuals unsuccessful with the primary form of ME, with examples. **ME/PE tactics** indicate ways individuals may allocate mating effort and parental effort to increase options for reproduction.* All entries are for a specified sex and mating system. Although true monogamy is considered to be a single mating system, two variants are compared.

| Mating system | ME | Primary ME | Conditional ME | ME/PE tactics |
|---|---|---|---|---|
| Promiscuity I | | | | |
| Male | Approaches 1 | MEd: ornaments, calls, displays, size, mating site competition | MEf: especially forced copulation, sperm competition; cooperation, queuing | None |
| Female | Low | MEf: female choice for heritable traits, avoidance of forced copulation | MEf: young subordinate females must wait for alpha males, possible copying | Mechanisms to neutralize forced copulation; sperm expulsion; egg abandoning |
| Promiscuity II | | | | |
| Male | Approaches 1 | MEd: as in promiscuity I | More MEf: as above, plus alternative behavior tactics and plumage morphs | None |
| Female | Low | MEf: female choice for heritable traits, genetic diversity, complementarity | Females unable to mate with preferred males mate with less preferred males | As in promiscuity I |
| Frank polygyny I | | | | |
| Male | Moderate to high, high variance | More MEf: attraction of multiple females to territory<br>MEd: male–male territory competition | Queuing on empty territory to increase future access to quality territory | Less attractive males give more PE |
| Female | Low to moderate | MEf: choice for heritable traits, resources, male PE, female–female competition | Mate-switching between clutches | Late arriving females may accept lower/no male PE |

TABLE 3. Continued.

| Mating system | ME | Primary ME | Conditional ME | ME/PE tactics |
|---|---|---|---|---|
| Frank polygyny II | | | | |
| Male | Moderate to high, high variance | MEf/MEd higher than above, due to paternity-enhancing behaviors | MEf: sperm competition, FEPC, SEPC | Less attractive males more PE, risk-prone PE by unattractive males |
| Female | Low to moderate | MEf: choice for resources, heritable traits, genetic diversity, complementarity, PE | EPC by females mated to low-quality males | Females likely to exploit willingness of parental males |
| Cryptic polygamy | | | | |
| Male | Moderate, high variance | MEf/MEd higher than in frank polygyny, males less ornamented | As in polygyny II | As in polygyny II, male PE higher than polygyny |
| Female | Moderate | As in polygyny II | As in polygyny II | As in polygyny II |
| Monogamy by coercion | | | | |
| Male | Low to moderate | MEf: mate guarding, frequent pair copulation | FEPC, sperm competition, SEPC very low | High male PE |
| Female | Low to moderate | MEf: females attempt to avoid male coercion | Females mated to unattractive males attempt to avoid male control | High female PE |
| Monogamy by choice | | | | |
| Male | Low | MEf/MEd very high: consortship, male mate choice, low ornamentation | "PE" that prolongs mate's survival | High male PE |
| Female | Low | MEf/MEd very high: consortship, female mate choice, low ornamentation | "PE" that prolongs mate's survival | High female PE |
| Polyandry | | | | |
| Male | Low to moderate | MEf: male choice for female heritable traits, resources; consortship | Low incidence of EPC, sperm competition | More attractive males may have lower PE and be monogamous |
| Female | Moderate to high | Female MEf highest of any system: mate attraction, territory defense, consortship | Low EPC for heritable male traits, social mating for male PE | Unattractive females or those with low resource-holding power increase PE |

EPC = extra-pair copulation, FEPC = forced EPC, ME = mating effort, MEd = diffuse ME, MEf = focused ME, PE = parental effort, SEPC = solicited EPC.

also can be viewed as mate manipulation. An unattractive mate can be manipulated into increasing PE if its relatively attractive mate decreases PE, because reduced, but still nonzero genetic RS is preferable to finding itself unmated or mated to a lower quality individual. We discuss other examples of manipulation behavior throughout the manuscript. Given current definitions of communication (e.g., Krebs and Dawkins 1984), many if not most sociosexual behaviors could be considered manipulative.

**Mate choice criteria** refer to the traits on which individuals may base mating decisions (Trivers 1972). Heritable traits include those for which there is sufficient genetic variation in a population that the quality of the offspring genome can be enhanced through nonrandom mate choice. The two main classes of heritable traits are indicator traits, which serve as markers of high vigor or viability (Zahavi 1977; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984), and aesthetic traits (Darwin 1871), those whose benefits are based on a strong consensus among choosing individuals that those traits are attractive (Burley 1985). Attractiveness of aesthetic traits is arbitrary in the sense that they are not preferred because of their value as indicator traits. Multiple routes to the evolution of aesthetic traits are possible (Fisher 1930; Burley 1985, 1986; Ryan 1990; Endler 1992; Enquist and Arak 1993). It is possible that a particular trait may have been influenced by more than one of the above processes. For example, it is possible that only relatively viable males are able to develop aesthetic traits (Balmford and Read 1991).

**Genetic diversity** implies selection for mating with multiple mates having unlike genotypes. The degree of genetic diversity within a brood may influence the degree of sibling competition within a brood (Willson and Burley 1983) and may reflect a bet-hedging strategy on the part of the mother, given uncertainty of genetic quality of potential mates and/or the environment. Individuals may also choose mates on the basis of **genetic complementarity** (Potts et al. 1991), the quality/quantity of reproductive resources controlled by potential mates, or ability and willingness of potential mates to incur focused PE and ME (Trivers 1972; Maynard Smith 1977; Low 1978; Andersson 1994). **Parental** and **mate willingness** reflect the amount of ME or PE likely to be provided by the potential mate, and therefore his/her likelihood of seeking additional social mates (social polygamy), as well as the probability that the potential mate will seek other genetic mates or abandon the choosing individual altogether.

Other criteria of mate choice are possible, but most can be classified into the above categories. Mate preferences for kin, for example, may reflect genetic complementarity (coadapted genomes) or preferences for high ME, PE, or NE. The costs of choosing mates may constrain mate choice or result in conditional tactics such as copying the choices of other individuals (e.g., Gibson et al. 1991).

## SEXUAL DIMORPHISM

Strictly speaking, since dimorphism refers to morphological differences, **sexual dimorphism** in birds consists of size dimorphism, dichromatism (coloration patterns), and the occurrence of secondary sexual traits such as spurs and wattles. Typically, however, authors include sex differences in behavior or song production under the dimorphism umbrella. **Ornaments** are traits that have no direct survival function (although they may be indicator traits), but function instead in mate attraction. Ornaments include feather traits, soft parts, and vocalizations, as well as inanimate display objects (e.g., bowers). **Weapons** (e.g., spurs) function in intrasexual combat. (A particular trait could function as both an ornament and a weapon [Darwin 1871].) Several studies have shown relationships between size dimorphism/ornamentation and mating system (Payne 1984; Møller 1986; Höglund 1989; Björklund 1990, 1991; Webster 1992; but see Shutler and Weatherhead 1990). Male–male competition for defendable reproductive resources or display sites is thought to favor large male body size and thereby increase size dimorphism (Payne 1984; Andersson 1994).

Forms of avian ornamentation are so varied that quantitative objective comparisons across major taxa are difficult, if not impossible, to make. Males of a dully plumaged species may have elaborate songs, and those of an ostentatiously dichromatic one may have a simple song: which species is more dimorphic (Höglund 1989)? Then again, a brightly colored forest dweller may not appear as colorful in its natural habitat as does a moderately colorful prairie species: is it appropriate to score its coloration level based on its relative appearance in a museum collection (Endler 1993; Bennett et al. 1994)? In general, tests of predictions regarding the significance of patterns of dimorphism should involve species that are carefully selected on the basis of taxonomic affinities, ecological considerations, and social organizations.

It is also important to make a distinction between the degree of dimorphism of ornamentation and the flashiness of ornamentation. Some socially monogamous species (e.g., macaws, woodpeckers, jays, crested pigeons, toucans, puffins) are quite ornamented and monomorphic, with males and females both being colorful. Females of these species may derive benefits from bright plumage that are not directly associated with mating; for example, bright females may have an advantage in social competition, especially joint territory defense (Wolf 1969; Burley 1981; West Eberhard 1983). Thus, these species may not necessarily constitute an exception to the general pattern of increased ornamentation and apparent polygyny. On the other hand, bright female coloration patterns could reflect strong male mate preferences in taxa with little sex difference in sexual selection intensity. If this is the case, a lack of dimorphism in ornamentation could be consistent with mating system patterns. Data on the genetic and social aspects of the mating system, as well as direct measurements of mate preferences of monomorphic bright birds, are needed to address this question.

Given the above caveats, in a comparison of species with biparental care and having similar social mating systems, species with greater sexual dimorphism or greater sex differences in ornamentation or courtship display would be expected to have greater discrepancies between the social and genetic aspects of their mating systems. Moreover, when aesthetic mate choice is operating, we would expect EPF patterns to reflect female mate preferences for heritable ornaments, thus increasing male variance in RS and the resulting male sexual selection gradient. A test of this prediction would require knowledge of the ornamental value of traits; that is, establishing that females indeed have mate preferences for traits that human observers think may function as ornaments. This is important, in part, because past selection events may have reduced heritability of ornamental traits to near zero; if so, and if females routinely experience costs of extra-pair activities, then selection would also favor a reduction in female mate preference for the now nonheritable ornament. In fact, it appears that heritability of secondary sexual plumage traits is low in at least two dichromatic species studied (Red Junglefowl, *Gallus gallus* [Johnson et al. 1993]; Zebra Finches, *Taeniopygia guttata* [Burley and Bartels 1990; Price 1991; Burley, unpubl.]) and that females of these species pay more attention to soft-part coloration (which has been shown to be heritable in both species) than they do to plumage patterns (Burley and Coopersmith 1987, unpubl.; Zuk et al. 1990; Burley and Price 1991; Price and Burley 1993, 1994; Ligon and Zwartjes 1995). The implications of heritability reduction of ornamental traits are discussed further below.

## CAUSES OF NONFIDELITY

The underlying causes of nonfidelity have important implications for the intensity of sexual selection. If nonfidelity is caused by limited access to preferred social mates with superior heritable traits, EPF will increase the intensity of sexual selection on males. Evidence to date suggests that females of two species seek EPF partners with superior heritable qualities (Zebra Finches [Burley and Price 1991; Burley et al. 1996]; Purple Martins, *Progne subis* [Morton et al. 1990]). At the 1995 AOU symposium in Cincinnati, Ohio, Ellen Ketterson employed an apt sports metaphor in discussing components of the fitness of male Dark-eyed Juncos (*Junco hyemalis*): "To be a top ranked basketball team, it is necessary to win at home and win away." Based on DNA fingerprinting evidence, Ketterson et al. (Chapter 4) found that tendency for male juncos to win at home (achieve high paternity) correlates positively with tendency to win away (achieve EPFs), creating distinct classes of winners and losers. Wagner (1993, Chapter 6) has gone so far as to suggest that coloniality has evolved repeatedly among socially monogamous birds due to female tendency to aggregate in leklike arenas for the purpose of evaluating and choosing EPC partners.

Other causes of nonfidelity may decrease the intensity of sexual selection. These include female bet-hedging due to uncertainty of mate quality, selection favoring genetic diversity of progeny, and selection for genetic complementarity of mates. Another explanation for multiple mating by females is that it may reduce the advantage of segregation distorter genes. A gene that gains an advantage over other sperm genotypes (segregation distorter) within an ejaculate may be associated with reduced organismal fitness. By copulating with multiple males, females reduce the relative advantage of a segregation distorter that impairs the competitiveness of the ejaculate in which it occurs (Haig and Bergstrom 1995). Of course, increasing and decreasing factors operating in the same system may result in a net effect of no change in sexual selection intensity. It is possible to make predictions about the relative strength of these forces in various mating systems (see below).

High mating fidelity should occur whenever one has the best social mate possible, although most individuals are not expected to accomplish this ideal. Another reason for maintaining fidelity is the increased ME required for locating better genetic mates. Costs here include risk of parasite or venereal disease infection, search time, and predation risk. Finally, mates may control crucial resources such as safe or proven nest sites, or high fidelity may function in acquiring ME from one's mate and PE for one's offspring. We tend to think males experience very few costs associated with pursuit of EPFs, but if males do experience significant costs, males as well as females may show high fidelity.

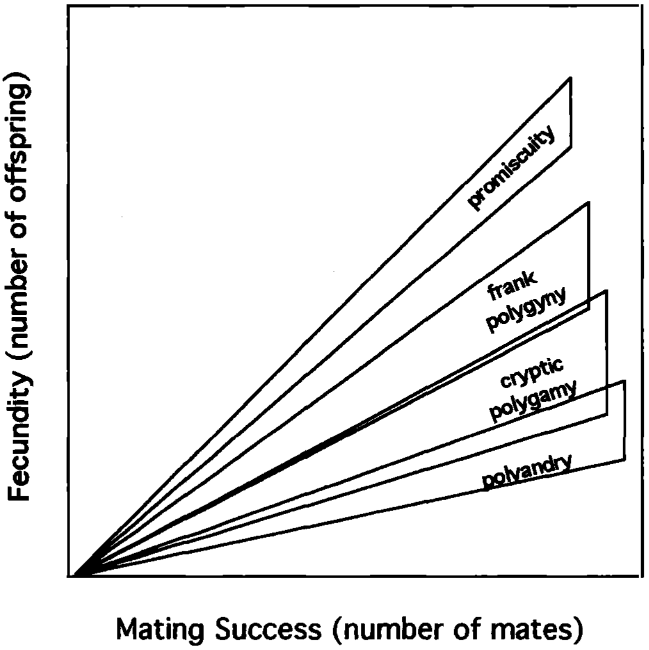

FIG. 1. Range of sexual selection gradients (after Arnold and Duval 1994) expected for major mating systems. Polyandry gradients are represented for females, all others are for males. Within each mating system, the steepest gradients are expected for species in which mating effort (ME) is highest, for the sex represented. True monogamy is not included because it is defined by very low variance in mating success for both sexes. See text for discussion of expected between-sex differences in sexual selection gradients.

## SEVEN MAJOR AVIAN MATING SYSTEMS

Summaries of characteristic allocations of each sex to ME and typical forms of ME for each mating system are provided in Table 3. The ranges of sexual selection gradients in each mating system are provided in Figure 1.

### PROMISCUITY

Promiscuity is characterized by the absence of pair-bonds and the absence of male PE. Promiscuous males put all of their RE into mating, giving a mean ME equal to 1 and a variance of 0 (ME refers to proportion of RE; the absolute amount of energy put into mating is expected to vary among individuals). The primary form of mating investment is mate attraction, which may include competition among males for display sites. Conditional ME tactics may be present; in particular, unattractive males may attempt forced or sneaky copulation. We consider two major forms of avian promiscuity.

*Alpha-male promiscuity (promiscuity I):* In this mating system a strong consensus exists among females about male attractiveness, and most, if not all, females have mating access to males with preferred phenotypes. It is ironic that a Gray, tsystem typified by high female mating fidelity should be labeled "promiscuous." However, we see no use in adding jargon when the above definition, based on lack of male PE, is widely used. A well-documented example of alpha-male promiscuity is the Long-tailed Manakin (*Chiroxiphia linearis* [McDonald 1989a, b; McDonald and Potts 1994]). In this species, males use traditional display perches that females attend for mating, and mating success is highly skewed: four males accounted for 86% of the copulations seen during an 8-yr period (McDonald 1993). Mating fidelity is high (McDonald and Potts 1994). Other apparent examples of this mating system include Sage Grouse (*Centrocercus urophasianus* [Gibson and Bradbury 1985, 1991]) and Black Grouse (*Tetrao tetrix* [Alatalo et al. 1991]), although genetic mating patterns have not been established in these species. These examples suggest that promiscuity I includes mostly lekking species. In this system, the variance in male reproductive success is very high, because a few males sire all of the offspring in the population and many males fail to mate at all, at least in a given season. Alpha males achieve reproductive success through female choice, rather than mechanisms such as mate guarding or male PE that are often associated with increased male fitness in pair-bonding species. Female variance in both mate number and RS is expected to be low, because no female is prevented from mating, either through male mate choice or female–female competition. The sexual selection gradient for males should therefore be much higher than for females.

In this system, strong female consensus/preference for alpha males severely limits mating opportunities for unattractive or younger males. Males in species with extremely high variance in male mating success may respond by adopting unusual conditional tactics. Long-tailed Manakins, for example, engage in cooperative display, which occasionally nets copulation opportunities for subordinate males; form queues, which allow subordinates to inherit dance perches; and attend more than one display site, which may also increase opportunities for inheriting a display site (McDonald 1989a, b; McDonald and Potts 1994).

With an extremely high sexual selection gradient (Fig. 1a), exaggerated male ornamentation, courtship display, and/or size dimorphism is expected. Competition for display sites may favor size dimorphism as well. Demographic divergence between the sexes (e.g., in age of first reproduction) is another consequence of sexual selection expected in this mating system (McDonald 1993). Females choose males bearing elaborate traits for their values as indicators of good genes or for their aesthetic appeal. A recurring question of central importance is whether the heritability of preferred traits persists in populations with this mating system, and if it does, how heritability is sustained (see Discussion).

*Male–female promiscuity (promiscuity II):* This mating system differs from promiscuity I in that much less consensus exists among females regarding the best mate, and individual females may mate with several males, perhaps to gain genetic diversity among offspring, insure fertility (although data are scant or nonexistent [Birkhead et al. 1987]), or as a result of limited access to the most preferred males. Females may also mate multiply for reasons not directly related to fertilization (e.g., as a trade-off for reduced harassment). Possible examples of this mating system are the Common Peafowl (*Pavo cristatus* [Petrie et al. 1992]), the Ruff (van Rhijn 1983, 1991; Lank et al. 1995), and the Village Indigobird (*Vidua chalybeata* [Payne and Payne 1977]). Again, genetic mating systems remain to be determined. It is possible that females have several copulatory partners but select genetic mates through postcopulatory female choice (active selection of sperm by females within the female reproductive tract). Alternatively, sperm competition may determine paternity. If either process results in strong mating skew in favor of one male, the result could be yet another variant of promiscuity, in which females copulate multiply but fertility is alpha-male biased.

The major difference between promiscuity I and II is decreased variance in male RS in promiscuity II, due primarily to the fact that a larger variety of males has mating opportunities in promiscuity II. As a result, the difference between the sexes in sexual selection gradients should be less striking. Nevertheless, the degree of sexual dichromatism and male ornamentation should remain great. Females choose mates on the basis of indicator traits, aesthetic traits, and/or possibly genetic complementarity. Choice for complementarity might reduce the number of mates taken by individual females, but this reduction in number of matings would be offset by a lack of consensus among females regarding complementarity of males.

As in promiscuity I, absence of male PE means that conditional mating tactics are limited to forms of ME. In promiscuity II, however, female consensus is much weaker, allowing the possibility of alternative behavioral tactics and plumage morphs, as occur in Ruffs. Lower female consensus may increase male mating opportunities enough that extreme measures such as cooperation or queuing do not occur in these species. So far cooperation and queuing have not been reported; however, very few well-documented examples of this mating system are known. Given the extreme mating skew in both forms of promiscuity, but particularly in promiscuity I, diverse and creative alternative male mating tactics should be selected.

### FRANK POLYGYNY

In frank polygyny, an appreciable fraction of the mated males in a population typically has more than one social mate simultaneously. Another fraction has a single mate, and some fraction will likely be unmated. Each female has a pair-bond with an individual male and uses reproductive resources (e.g., nest site, feeding territory) contributed at least partly by that male. Males have low-to-moderate PE and moderate-to-high ME. Numerous historical and ecological variables should influence the form of frank polygyny seen in a population.

In frank polygyny, female mate choice is constrained to varying degrees by the inability of all females to mate with males having highly preferred phenotypes; this constraint is lower in species in which males typically have low PE, and in which maximum harem size is correspondingly large. Thus, availability of preferred mates may sometimes result in high female fidelity in species with low male PE. This would not be a general expectation, however, for several reasons. First is the possibility of conditional male ME tactics. If these are present, less attractive males may attempt to increase mate-getting ability through increased PE, whereas females may maneuver to have more attractive males as genetic mates, at the same time retaining less attractive males as social mates. Second, if male PE is quite low, then selection on males to assure paternity may also be low, and female opportunity for multiple mating may be high. We suspect that, to the extent that female-defense polygyny occurs in birds (e.g., McKinney 1985; Webster 1994), it will not be characterized by high female fidelity to the social mate; accordingly, this variant is included in frank polygyny II, below.

Varying degrees of female fidelity may also reflect varying costs of fidelity or nonfidelity. One potential cost of nonfidelity is the risk of rejection by males that hold high-quality territories or safe nest sites, if such resources are rare. Female–female competition for nest sites may be appreciable if females nest colonially and synchronously, especially if the sex ratio is female-biased, allowing resource-holding males to discriminate against nonfaithful mates. Females may become increasingly vulnerable to male control as sexual size dimorphism increases. Gowaty (1996a) has suggested that females may be less prone to engage in EPCs if their mates are much larger and more powerful; when copulation is especially risky (due to injury by larger males, male attempts to displace other copulating males, or predation risk), females may minimize the number of copulations per clutch. Conversely, it may pay to engage in NEPC with a large male to avoid the risk of injury via FEPC. Other factors besides large male body size may influence male control, including sex differences in patterns of philopatry, differences in tendency to live near kin, and sex differences in time of arrival at the breeding grounds (Gowaty 1996a).

Even where male PE is seemingly small, it could be critical for female RS. In Great-tailed Grackles (*Quiscalus mexicanus*), for example, males have an apparently high ME, but their PE occurs as defense of nests in apparent proportion to their paternity (Johnson, unpubl.). A low-risk, low-cost strategy for females of multibrooded and/or long-lived species might be to pay for male PE with fidelity on a per-nest basis, because females of such species can change mates between clutches or between years. This strategy might also be employed by females of some monogamous species (see below).

For both frankly polygynous systems described below, as the degree of frank polygyny (the number of social mates per mated male) increases, we expect male and female age of first reproduction to diverge. The demographic divergence that results from increased sexual selection may result in delayed plumage maturation in dichromatic species, as well as in increases in size and plumage dimorphism, and the adoption by unmated males of alternative tactics such as FEPC. Increased population variation in ME should also occur as the degree of frank polygyny increases, because attractive/dominant males will allocate more RE into ME, whereas lower quality males will allocate more to PE. Size dimorphism and ornamentation are expected to be high, although not as striking as under promiscuity.

*Faithful-female frank polygyny (frank polygyny I):* In this mating system, females show high fidelity to their social mate, engaging in a low incidence of NEPC. If FEPC does occur, it typically does not result in production of offspring, because females have considerable control over fertilization events. Accordingly, FEPC is not likely to be an important conditional male ME tactic. Examples of high-fidelity frank polygyny include the Ring-necked Pheasant (*Phasianus colchicus* [von Schantz et al. 1989]) and Wood Warbler (*Phylloscopus sibialatrix* [Gyllensten et al. 1990]). One study of the Wood Warbler estimated the fraction of polygynous males in the population at 23% (Gyllensten et al. 1990); in this same study, molecular analysis of blood from 13 families uncovered no incidence of paternity exclusion.

In frank polygyny I, the sexual selection gradient of males is expected to be much higher than that of females, but the male gradient will be relatively lower than in promiscuous systems. This occurs because male fecundity depends not only on the number of mates but to a limited extent on the quality of resources or parental care males provide, which effectively lowers the male sexual selection gradient (Fig. 1a). Males in this mating system are expected to exert some degree of direct or indirect (via female–female competition) mate choice (Trivers 1972; Burley 1977). The ratio of male to female sexual selection gradients should therefore be moderate to high, but lower than under promiscuity, and generally speaking, sexual dichromatism should be lower than in promiscuous systems. Size dimorphism, however, may vary among species depending on the relative importance of male ME allocated to male–male competition.

Although low-to-moderate mean male PE is expected, there is potential for high variance in male PE as a result of conditional ME tactics. Mean ME will therefore be moderate to high, and there will be potential for substantial ME variance.

*Non-faithful-female frank polygyny (frank polygyny II):* In this mating system, males have multiple mates and females have only one social mate at a time, but confer paternity to additional males. Lower female fidelity could result from more constrained female mate choice (e.g., greater male control over female use of reproductive resources; active male defense of females that constrains their access to alternative social mates) and/or a lower cost–benefit ratio of seeking EPFs. Examples of frank polygyny II include the Red-winged Blackbird (EPFs = 28% [Gibbs et al. 1990]; EPFs = 23% [Westneat 1993]) and Bobolink (*Dolichonyx oryzivorous*; EPFs approximately 15% [Wittenberger 1978; Gavin and Bollinger 1985; Bollinger and Gavin 1991]).

Differences in sexual selection gradients between frank polygyny I and II are not immediately predictable, because they depend on variables such as the differences in harem sizes in the two systems and the effect of EPFs in polygyny II on the variance in male reproductive success. Overall, given the large number of criteria available to females for mate choice in polygyny II (resources, good genes, aesthetics, parental care, genetic complementarity, and genetic diversity), female choice may tend to equilibrate male RS in this system, thus contributing to a lowering of the male sexual selection gradient. On the other hand, a relatively low male sexual selection gradient would also be expected in those polygyny I species in which females pay for PE on a per-clutch basis and switch mates between clutches. Lower paternity in polygyny II should lead to higher levels of MEf invested in a social mate and lower or more variable PE.

### Cryptic Polygamy

Recent research has revealed EPFs in species that have been traditionally defined as socially monogamous; moreover, the rate of EPF among these species appears to be remarkably variable. As more data become available, it is apparent that some species/populations form a gradual continuum of varying EPC rates. There is no entirely satisfying way to subdivide this array of mating systems, because to do so is to make categorical variables out of a suite of continuous ones. Until more information becomes available, we think it unwise to create categories that would be arbitrary, and so we consider as one category socially monogamous species in which EPF is a recurrent phenomenon.

Cryptic polygamy has received attention because of its cryptic nature: an apparently monogamous mating system turns out to have relatively high potential for sexual selection. In this mating system, potential exists for both males and females to increase their RS by increasing mate number. Overall, we expect the ratios of the male–female sexual selection gradients to be lower than in frank polygyny and higher than in true monogamy, but the magnitudes of sexual selection gradients and their ratios are likely to be highly variable among species.

Females may be able to enhance fecundity if their EPC partners provide sufficient aid to enhance offspring survivorship, particularly if the types of male parental care are of low cost relative to the benefit to offspring. Under these conditions, there may be no profit for social mates in restricting parental care, whereas EPC partners may provide care in the face of modest paternity (e.g., low-risk nest and fledgling defense [Gray, Chapter 3]). Genetic benefits to females of EPC include those mentioned previously: reduction of meiotic drive, good genes, or genetic diversity. For variance to exist among females in the ability to acquire the benefits of EPCs, there must be variation in female quality that affects the willingness of social or EPC partners to contribute PE in the face of uncertain paternity.

The range of male mating tactics found in cryptic polygamy is likely to be similar to that found in frank polygyny II (Table 3). Very attractive males may gain fitness through EPCs as well as having high paternity "at home." Less attractive males may adopt the low-payoff tactic of investing wholly in the social mate (lower ME), whereas females may be selected to capitalize on their willingness to contribute PE. Unmated males may adopt forced copulation (ME only).

Male tendency to adopt low-payoff parental behaviors could increase if females choose social mates based on parenting skills; thus, males could increase future mate-getting opportunities by learning parenting skills (e.g., Burley 1981), which would effectively decrease the cost of low paternity. Another factor favoring low-payoff tactics is low or highly unpredictable survivorship across breeding seasons, implying no benefit to waiting to breed. However, males with high PE and high rates of nesting success (more "*K*-selected") should be less likely to adopt low-payoff tactics; females needing high male PE should show higher fidelity because the costs of mate abandonment associated with decline of paternity confidence should be high for any one egg or clutch.

Sperm competition should be intense when paternity is low to moderate or highly variable. If mate consortship lowers EPC/EPF rates, a reallocation of male ME from ornamentation to increased body or testis size may occur. As always, the benefits females gain from EPFs will affect the distribution of EPFs among males and have consequences for predicted levels of ornamentation.

An interesting feature of this mating system is that, although males and females have the same social mating system (monogamy) and a similar genetic mating system (they both participate in EPCs), potential still exists for sexual selection to be stronger on males than females. The ratio of male to female sexual selection gradients in this mating system will depend on two factors. The first is the degree to which female fecundity responds to an increase in mate number. For example, in socially monogamous females, parental care from the EPC partner is one way increased mating success can increase female fecundity, resulting in a higher female sexual selection gradient and a lower ratio of male to female gradients (for others ways, see above). The second factor is the degree of consensus among females. If all females mate with one EPC partner but consensus exists among females as to the best male EPC partner, variance in male mating success could be much higher than that of females. In this case, most females probably would not have access to appreciable PE provided by the attractive male EPC partner, and female sexual selection gradients should therefore be limited at the same time male sexual selection gradients were enhanced. In the second scenario, the ratio of male to female sexual selection gradients will thus be greater than in the first. The relative ornamentation of the sexes should conform to the differences in sexual selection gradients.

Currently, more instances of cryptic polygamy are reported than any of the other mating systems in which genetic aspects are known (references in Gowaty 1996b). Examples of cryptic polygamy with low incidence of EPF include Field Sparrows (*Spizella pusilla*; up to 12% [Petter et al. 1990]), Zebra Finches (2.4% [Birkhead et al. 1990]), and Eastern Bluebirds (*Sialia sialis*; 20% [Gowaty 1996b]). Higher EPF rates are exemplified by Purple Martins (32% [Morton et al. 1990]), Tree Swallows (*Tachycineta bicolor*; 38% [Lifjeld et al. 1993]; 53% [Dunn et al. 1994]), Dark-eyed Juncos (*Junco hyemalis*; 28% [Ketterson et al., Chapter 4]), and White-crowned Sparrows (*Zonotrichia leucophrys*; 34% [Sherman and Morton 1988]). Purple Martins exemplify a cryptically polygamous species in which young males appear to be forced to adopt low-payoff reproductive tactics. Second-year males have paternity rates of only 24%, whereas older males have paternity rates averaging 96% (Morton et al. 1990).

### TRUE MONOGAMY

In true monogamy most males and females are singly bonded, and paternity is very high. Conceptually, one can envision monogamy as achieved through mate choice (by one or both sexes) or through enforcement of fidelity through physical coercion by males or by other costs that make EPC an untenable option.

In monogamy by choice, the benefits of fidelity to females outweigh the benefits to seeking EPFs. Because so many potential benefits to seeking EPFs exist, monogamy by choice is most likely to occur in conjunction with high PE by both sexes, and thus females need to be able to rely on substantial male parental care in order to reproduce successfully. Young are thus likely to be very altricial and have long dependency periods, perhaps having specialized diets that are difficult for parents to supply, requiring a great deal of defense, or having other special requirements. The need for parental cooperation is high, which favors long-term (greater than one breeding season) pair-bonding in long-lived species. Pair-bonds may break in such species primarily in response to nonfidelity, and the threat of abandonment may be a reinforcement to fidelity. Circumstances that favor very strong female fidelity will also favor very high male allocation to PE, and, with exceedingly low profit to extra-pair courtship, low effort in seeking such matings. Thus, selection pressures act in a positive-feedback fashion, and fidelity is reinforced. Nevertheless, mated males and females may consort together continually to assess condition and parental willingness, and they may copulate frequently to minimize parental uncertainty and maximize parental willingness, behavior which has sometimes been viewed as male (Birkhead and Møller 1992) and female (Petrie 1992) mate guarding. In this mating system, selection for purely ornamental traits should be relatively weak, but to the extent they occur they should occur in both sexes. Sexual dimorphism should primarily reflect differences in parental roles of territory defense, food finding, and the like. Slight differences in sexual selection gradients should occur, and sperm competition mechanisms should be minimal, unless there is a class of unmated males that attempt FEPC.

In monogamy through coercion, males enforce female fidelity through consortship that functions as mate guarding, and through frequent male-initiated copulation. Low rates of FEPC and NEPC, very low rates of EPF, and sperm competition mechanisms should be present. Males of these species should have a higher ME than in monogamy through choice, and the ratio of sexual selection gradients may be higher. Size dimorphism is likely to be present, with males larger than females. We predict that paternity will be lower in coercive monogamy, because the conflict of interest between the sexes is greater.

Likely examples of true monogamy maintained by choice are the Black Vulture (*Coragyps atratus* [Decker et al. 1993]) and Lesser Kestrel (*Falco naumanni* [Negro et al. 1992]); a possible example is the Red-cockaded Woodpecker (*Picoides borealis* [Haig et al. 1994]). Monomorphically bright species, such as toucans, puffins, and some woodpeckers, are most likely to display monogamy by choice or cryptic polygamy. Possible examples of male-enforced monogamy include the Northern Fulmar (*Fulmaris glacialis* [Hunter et al. 1992]), the Willow Warbler (Gyllensten et al. 1990; Arvidsson 1992), and the African Marsh Harrier (*Circus ranivorus* [Simmons 1990]). Leach's Storm Petrel (*Oceanodroma leucorhoa* [Mauck et al. 1995]) also shows true monogamy. It is unclear in this case if monogamy is maintained by female choice or male enforcement. We place species in categories based on available evidence of male control; more data could prove that these examples belong in another category.

Gowaty (1996a) has proposed that male coercion is the major factor determining variation among mating systems. In her view, mate guarding is seen not as simply a mechanism to protect a fertile mate from other males, but as an intimidation tactic, and males use "resource brokering" to control female behavior. Likewise, male assistance is termed "helpful coercion," emphasizing that females may be coerced into fidelity in order to gain male help. We prefer to limit the term "coercion" to apply to cases in which physical control is present. In other cases, it is difficult to determine which sex is more coercive. If, as we suggest elsewhere (Burley and Johnson, in prep.), male birds have been manipulated into increasing parental roles through female choice, it seems inaccurate to label female preferences for paternity-investing males as male "coercion."

### POLYANDRY

Polyandry is characterized by females mating with several males (either simultaneously or sequentially), male PE higher than that of females, and steeper sexual selection gradients for females. True, role-reversed polyandry is the rarest of the major avian mating systems, and even in populations that show this mating system, most females are monogamous. However, this system has attracted attention as much for its role reversal and reverse sexual dichromatism as for its pairing patterns and therefore we include it. Although there may be more than one form of true polyandry, because so few examples of true polyandry exist in nature, we discuss these variations under a single category of this mating system.

In birds, the female sexual selection gradient is typically weak (Fig. 1b). The only way fecundity of female birds can respond strongly to increased mating success is if females mate with multiple, high-PE males, such that females can allocate substantial energy away from parental care and into multiple clutching (but see above, p. 33). With low male PE, multiple mating could result in small increases in female fecundity if genetic diversity among offspring improves survivorship. Generally, though, fecundity is limited by PE demands on avian females, except under role reversal and polyandry.

At least two variations on the polyandry theme exist. In one, females attract and defend males sequentially, leaving each with his clutch to mate with the next male. Confirmed examples (albeit with low incidence) include the Red-necked Phalarope (*Phalaropus lobatus* [Hildén and Vuolanto 1972; Reynolds et al. 1986; Reynolds 1987]) and Red Phalarope (*Phalaropus fulicarius* [Schamel and Tracy 1977]). This variation of polyandry is characterized by weak reversed sexual dichromatism; females are more ornamented than males. Female sexual selection gradients of these species should be steeper than those of males. Paternity confidence is expected to be moderate. Females may have the opportunity for EPCs, but they must provide at least moderate paternity certainty in return for high male PE. PE and ME variance should be low under mate-attraction polyandry. Female ME will be in the form of mate attraction and mate consortship, and males will invest in mate consortship and possibly sperm competition. In this variation of polyandry, unattractive females are expected to provide greater PE to retain more attractive males. Male mate choice for indicator or aesthetic traits should act to increase female ornamentation or display. Females should choose male primarily for specific indicators of PE, with lesser emphasis on aesthetic traits. The role-reversed Eurasion Dotterel (*Charadrius morinellus*), in which male mate choice is not readily apparent, provides an apparent exception to this prediction (Owens et al. 1994). However, it is possible that male choice is passive and is mediated by female–female competition (Johnson 1988). In addition, it is unclear to what extent this species represents an example of true polyandry.

In resource-defense polyandry (after Emlen and Oring 1977), females defend a territory on which they lay several clutches, each incubated simultaneously by a different male. Examples include the Spotted Sandpiper (*Actitis macularia* [Oring et al. 1983, 1994]) and Northern Jacana (*Jacana spinosa* [Jenni and Collier 1972]). The mating system is characterized by reversed sexual size dimorphism, which presumably evolved through intrasexual competition for territories. We suggest that the sexual selection gradient of resource-defense polyandrous females will be similar to that of cryptically polygamous males with high PE (Fig. 1). In both systems RS is limited by the need to allocate resources to PE. In cryptic polygamy, males can theoretically gain large numbers of EPCs but must provide appreciable PE; polyandrous females are limited by the number of clutches they can produce and by availability of males to rear their clutches.

Male PE is very high, due to largely male incubation, but because polyandrous species are frequently precocial, male PE may not be as high as in true monogamy with altricial young. Parentage should be moderate to high. Male ME and ME variance are very low, because most male RE is allocated to PE. Female ME is the highest of any mating system. Female ME is allocated to resource defense, mate consortship, and male attraction. Females with only moderate resource-holding power may be expected to increase PE to retain their mates. Females exercise choice for high male PE and good genes, whereas males choose females based on resources, ornaments, and good genes.

## DISCUSSION

We suggest viewing the mating system as a suite of coevolved traits, including not only social pairings, but also individual mating strategies and genetic relationships. In this view of mating systems, some aspects of mating systems seem sufficiently interrelated to allow for clear predictions, whereas many are not. Thus, for example, we do not expect mating fidelity to be a good predictor of male PE across mating systems, in part because parentage is a prerequisite for high PE, but PE is not a prerequisite for high mating fidelity in mating systems such as alpha-male promiscuity. We do expect that the relative sexual selection gradients of males versus females are causally related to sexual divergence in ornamentation, size (see below), or courtship display, although this relationship can be very difficult to quantify objectively.

The mating systems we have described fall into four natural clusters. (1) Promiscuity is defined by a lack of male PE. Lack of male PE limits the mating tactics of unattractive males to conditional ones such as forced copulation, deceit, and (less commonly) to queuing behaviors (McDonald 1989a, b), or even genetically determined alternative mating tactics (Lank et al. 1995). Lacking PE, a large allocation of RE goes to diffuse rather than focused ME, which should result in very high levels of male ornamentation or extravagant courtship display. (2) In true monogamy, with high female fidelity, both males and females have high PE. The ME allocation of both sexes emphasizes focused ME. We expect sexual dimorphisms in these species to reflect parental role specializations, including resource defense and possibly feeding specializations. (3) In polygyny (polygyny I, polygyny II, and cryptic polygyny), great variation potentially exists in the relative sexual selection gradients of the two sexes, although the male gradient should always be steeper. Nevertheless, throughout this range, the kinds of conditional strategies available to males and females remain relatively uniform, especially for polygyny II and cryptic polygyny. Moreover, at this time we lack any clear indication that the vast majority of species can be neatly and unambiguously assigned to one of these three mating systems. Much research will be needed before we can ascertain just how useful these categories are. (4) Polyandry is the only mating system in which female sexual selection gradients are steeper than those of males. We expect low-to-moderate EPF rates in polyandrous species, and thus a ratio of sexual selection gradients that is similar in magnitude (but sexually reversed) to those of cryptically polygamous species with substantial male PE.

A number of avian species do not conform closely to our classification of seven mating systems. In some cases, species have complex mating systems that combine elements of several of the mating system categories. Polygynandry in the Dunnock (Davies 1992), ambisexual polygamy in the Penduline Tit (Perrson and Öhrström 1989), and simultaneous polygyny/sequential polyandry in the Rhea (*Rhea americana*) and tinamou species (references in Oring 1986) are examples of mating systems that cannot be neatly categorized.

Up to this point, we have omitted discussion of NE and cooperative breeding. We prefer to categorize cooperative breeding as a form of social organization, rather than a mating system per se. In theory, cooperative breeders could be truly monogamous (with helpers receiving only indirect fitness benefits, or perhaps waiting in queues for their turn to breed), to cryptically polyandrous (females engaging in NEPCs or SEPCs with helpers on their breeding territory), to frankly polyandrous (as in fraternal polyandry), to cryptically polygynous (males obtaining EPFs with females from other territories), to frankly polygynous (multiple females breeding per territory). "Classically" cooperative breeders have traditionally been assumed to be truly monogamous; recent data suggest that they are sometimes cryptically polygamous (Dunn and Cockburn, Chapter 7). In fact, cooperative breeding is not a unitary phenomenon and spans surprisingly diverse forms of social organization (Brown 1987; Stacey and Koenig 1990 and references therein). What is important to point out here is that the presence of NE tends to weaken the force of sexual selection (Michod 1993). Thus, for example, intrasexual competition within a breeding group is weakened by relatedness of same-sex individuals (Bertram 1976). If substantial NE is present in a species/population, our expectations regarding sexual selection gradients and mating tactics must take this into account.

The ecological pressures that shape cooperative breeding systems may have substantial effects on the dynamics of sexual selection in these systems. In classical cooperative breeding, where suitable habitat is saturated and females must disperse early in life (e.g., Pruett-Jones and Lewis 1990), females must settle on any territory, thus greatly constraining female mate choice. Male mate choice may be similarly restricted in such species. The high rate of EPF observed in socially monogamous, cooperatively breeding malurid wrens, for example (Mulder et al. 1994; Dunn and Cockburn, Chapter 7), may have evolved in response to lack of opportunity for choice of social mates by females, leading them to seek EPC partners with aesthetic traits or good/complementary genes. Twenty percent of Splendid Fairy-wren (*Malurus splendens*) pairings involve close relatives; thus, EPCs may function to increase genetic diversity (Rowley and Russell 1990). The resulting high EPF rates may lead to lower rates of paternal care by social mates, but evidence suggests that in such cases, male helpers compensate completely for the decline of paternal care, resulting in no net cost of lost care to females that seek EPCs (Mulder et al. 1994; Dunn and Cockburn, Chapter 7). Another factor that may contribute to high EPF rates in these species is that adult sex ratios are highly biased toward males, apparently as a result of female mortality during dispersal (Pruett-Jones and Lewis 1990). The limited availability of females may constrain males to accept their mates' EPCs, at least to some degree, because alternative social mates are not readily available to males, whereas alternative genetic mates are highly available to females. Males may make high ME, in the form of high sperm production (S. Pruett-Jones, pers. comm.), both to increase paternity "at home" and to capitalize on the tendency of breeding females to engage in EPCs. The general point here is that we expect that ecological and life history constraints on social mate choice will promote the tendency of avian females to seek EPCs, with multiple ramifications for mating tactics.

Our categories are sufficiently broad that some authors may want to subdivide them. We have paid minimal attention to spatiotemporal patterning of mating systems; for example, comparison of sequential and simultaneous bonding patterns, or within-species variation over time and in space. One category in particular, cryptic polygamy, is likely to contain many species with a large range of variation in the average number of genetic mates per individual, thus perhaps justifying more than one category of this particular type. At this time, however, it seems pointless to adopt a criterion that distinguishes among cryptically polygamous species on the basis of an arbitrary EPF rate.

This classification scheme is not intended to be definitive. As more data on various species accumulate, we may discover that most species are exceptions, in some way or another. Yet we do suspect that, from the perspective of mating tactics, the commonalities among species and mating systems will prove to be as striking as their differences. Below we pose two queries that this scheme suggests and attempt to suggest research and/or provide preliminary answers that follow from them.

*(1) The heritability conundrum: How are very steep sexual selection gradients maintained over evolutionary time?* This question has been raised, in various forms, repeatedly over the past two decades (Maynard Smith 1978, 1985; Taylor and Williams 1982; and see in this paragraph, below). The behavior of females of alpha-male promiscuous species, in particular, is relevant. It seems logical to expect that, given enough time, intense sexual selection for ornamental traits reduces heritability of those traits to a point that it is no longer in the best interest of the females to choose as a mate a male that is the mate of most of other females in the population. Compelling mechanisms have been proposed for the relatively long-term maintenance of heritability in highly preferred ornamental traits: the occurrence of biotic factors (especially parasitism) that cause viability selection (in host populations) to vary greatly between generations and result in coevolutionary races between hosts and parasites (Hamilton 1982; Hamilton and Zuk 1982), spontaneous recurrence of deleterious mutations (Rice 1988), and the occurrence of positive genetic correlations between the sexes for traits on which selection acts in different directions in males and females (Lande and Arnold 1985; Lande 1987). (For discussion of these and related ideas, see Andersson [1994].)

We suggest that, in addition to the above possibilities, within certain taxa, sexual selection will result in a positive feedback process that favors amplification of sensory drive processes (Burley 1985, 1986; Ryan 1990; Enquist and Arak 1993). That is, if females of a given species have latent preferences for a wide variety of evolutionarily novel ornaments or displays (Burley 1986; Burley, in prep.), then there may be selection to enhance mutation rate in regions of the genome that affect male secondary sexual traits. An enhanced mutation rate would produce numerous offspring with low attractiveness, but in environments in which very few individual males sire most of the offspring, the cost of producing such unattractive offspring is low relative to the potential benefit of producing a few highly attractive offspring. In a species with very high variance of male RS resulting from female preference, a female with suppressed aesthetic preferences that was inattentive to the nuances of male ornamentation could make a very poor mate choice, whereas a female with finely tuned sensitivities could make a very strategic mate choice. Thus, sensory drive processes and increased mutation rates for novel mutants reinforce one another. (If, however, females assess and copy the mate preferences of others, heritable variation in the sensitivity of female aesthetic mate preference may be functionally insignificant.) The cost of this strategy would be reduced if such mutations were concentrated in displays or ornamental structures such as feathers. This mechanism is most likely to occur in taxa in which few males may commonly sire most of the young of a generation; that is, in which male PE is absent or low. Similarly, variation may occur in the extent to which the aesthetic mate preferences that derive from sensory drive processes are suppressed through selection (as in truly monogamous species, pp. 45–46) or "encouraged" to thrive. Birds of paradise, galliforms, and hummingbirds appear to be avian groups in which the proliferation of sensory drive processes seems especially likely, because these taxa show extreme diversity of highly modified plumage, in conjunction with elaborate displays. One test of this hypothesis would be to compare mutation rates of ornamental feathers to those of other structures. In the galliforms, many plumage mutations have occurred in domesticated and captive populations (Delacour 1977), and the large numbers of captive individuals would allow a test of this prediction.

Our hypothesis differs from that of Pomiankowsky and Møller (1995), who suggest that greater than linear directional selection results in higher mutation rates for trait values, and thus maintains genetic variance for ornamental traits. In the hypothesis we present above, increased mutation rates are driven by the interaction between aesthetic preferences and novel traits rather than by directional selection, and the phenotypic result is novel ornaments or display, rather than simply exaggeration of an existing ornament.

*(2) Spatiotemporal stability of mating systems: To what extent do populations/species move between system categories?* Mating systems of a given species often vary in time or space. Pied Flycatchers (*Ficedula hypoleuca*) in Sweden show relatively high rates of EPCs and mate consortship (Gelter and Tegelstrom 1992), whereas those in Norway show very low EPC rates (Lifjeld et al. 1991). The incidence of polyandry in Red Phalaropes and Red-necked Phalaropes varies from nonexistent to low, apparently varying with the adult sex ratio (Hildén and Vuolanto 1972; Schamel and Tracy 1977; Reynolds 1987). Eastern Bluebirds show variation in percent of nondescendent nestlings with nestbox availability (Gowaty and Bridges 1991). Variation in habitat quality affects harem size and amount of male parental care in Red-winged Blackbirds (Searcy 1979; Yasukawa and Searcy 1982; Muldal et al. 1985). Thus, mating systems are dynamic, rather than static, and numerous life history (e.g., age of first reproduction, population sex ratio), and ecological variables (e.g., breeding synchrony [Stutchbury and Neudorf, Chapter 5]; habitat quality; resource distribution) may contribute to spatiotemporal variability. Just how much variation a given species shows can only be determined by a great amount of work; researchers should accordingly be cautious in inferring species-typical patterns from a single study or field season.

We expect that many populations may move reasonably freely in ecological time along the cryptic polygamy continuum, and possibly into frank polygyny, depending on local circumstances. In addition to life history and ecological variables, heritability of ornamental traits could contribute substantially to mating system changes. As mentioned above, as heritability of such traits declines in polygynous populations, rates of EPF are expected to decline as well. Should a new ornamental trait arise, its heritability may be very high, and rates of EPF, and possibly the degree of frank polygyny, might increase rapidly. For Zebra Finches, a socially monogamous estrildine with a typical EPF rate around 2.5–

5% in both free-living and captive populations (Birkhead et al. 1990; Burley and Price, unpubl. data), experiments that increased discrepancies in male attractiveness by the application of color bands resulted in an overall EPF rate of 28% (Burley et al. 1996) and an increase in the degree of frank polygyny by attractive males (Burley 1988). Results were consistent with the hypothesis that the primary function of females' seeking EPFs is to obtain mates with superior heritable qualities: unattractive males had much lower paternity, and attractive males had both higher paternity and greater success in obtaining EPFs (Burley et al. 1996). In a long-term experiment, some attractive males became simultaneous bigamists (Burley 1988). Color bands are not, of course, heritable, but results of a number of experiments (references in Burley et al. 1996) indicate that Zebra Finches respond to them as if they were. One would expect that, in a population composed only of males with bands of the attractive color (mimicking fixation of an attractive allele), EPF rates would return to "baseline" levels for Zebra Finches, but this experiment has not been performed.

Changes in the heritability of ornamental traits could also cause populations to move between promiscuity II (lower heritability of male ornamentation) and alpha-male promiscuity (higher heritability), and between monogamy (lower heritability) and cryptic polygamy (higher heritability), and between monogamy (lower heritability) and polyandry (higher heritability of female ornamentation). The emergence of a new heritable ornament in a frankly polygynous population might allow highly attractive males (of some taxa) to forego PE altogether (and less attractive males to increase PE), thus spanning the bridge between promiscuity and polygyny, at least for some interval. Conversely, the adoption of PE by males of low attractiveness in a promiscuous species could be a means of obtaining offspring in an otherwise hopeless situation. Other evolutionary avenues to further mating system evolution would depend upon a host of ecological and historical constraints and opportunities that are beyond the scope of this paper (Burley and Johnson, in prep.).

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# CHAPTER 3

# INTRASPECIFIC VARIATION IN EXTRA-PAIR BEHAVIOR OF RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*)

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ABSTRACT.—Extra-pair behavior differs among populations of Red-winged Blackbirds (*Agelaius phoeniceus*). In the population that I studied in Washington State, female redwings actively seek extra-pair copulations (EPCs), whereas female redwings in a New York population do not. Females in my study population benefited from copulating with extra-pair males by increasing the proportion of young they fledged; females in other redwing populations may either gain or lose from extra-pair activity. In Washington, increased fledging success resulted from significantly lower depredation rates of clutches laid by females that copulated with multiple males. In addition, a lower proportion of nestlings tended to starve in broods containing extra-pair young. Females that engaged in EPCs improved their reproductive success by gaining additional nest defense from extra-pair males and access to additional food resources on extra-pair territories. Variation in female extra-pair behavior among redwing populations can be attributed both to differences in male behavior towards social mates that have engaged in EPCs and to differences in social and ecological factors that enhance the incentive for females to seek EPCs. Female incentive to initiate copulations with multiple males is considerable in my study population due to a large number of adjacent male neighbors that can potentially contribute to extra-pair nest defense, an increased risk of sperm depletion because of a high degree of polygyny, and a limited food supply that can be augmented by foraging on extra-pair territories. Further evaluation of the importance of these factors in shaping female extra-pair behavior will require additional observations of female behavior in other redwing populations and experimental tests in which breeding conditions are manipulated and their effect on female extra-pair mating patterns assessed.

Research during the past decade has revolutionized the way biologists view and define mating systems. The observation by Bray et al. (1975) that mates of vasectomized Red-winged Blackbirds (*Agelaius phoeniceus*) laid fertile eggs bolstered the newly emerging notion that social mates also copulated with individuals outside of their social bond (Marler 1956; Robinson 1956; Smith 1984). These extra-pair copulations (EPCs) now are well documented in the literature for many avian species (for a review see Birkhead and Møller 1992). Despite numerous accounts of extra-pair copulations and extra-pair fertilizations (EPFs) in birds, however, there is no general framework that can be applied to predict reliably the frequency of EPF, the identity of the individuals involved, or which sex will seek and initiate EPCs.

The occurrence of extra-pair behavior is highly variable, both within and among avian species (Johnson and Burley, Chapter 2). In some species EPCs and EPFs are more common than within-pair copulations or paternity (Splendid Fairy-wren [*Malurus splendens*] [Brooker et al. 1990]), whereas extra-pair activity is reportedly absent in others (Ring-necked Pheasant [*Phasianus colchicus*] [von Schantz et al. 1989], Willow Warbler [*Phylloscopus trochilus*] [Gyllensten et al. 1990], Field Sparrow [*Spizella pusilla*] [Petter et al. 1990]. Male success in gaining EPCs may vary according to age (Rook [*Corvus frugilegus*] [Røskaft 1983], Purple Martin [*Progne subis*] [Morton et al. 1990], Bobolink [*Dolichonyx oryzivorus*] [Bollinger and Gavin 1991], rank (Black-capped Chickadee [*Parus atricapillus*] [Smith 1988; Otter et al. 1994]), fighting ability (White Ibis [*Eudocimus albus*] [Frederick 1987]), and secondary sexual characteristics (Zebra Finch [*Taeniopygia guttata*] [Burley and Price 1991], Barn Swallow [*Hirundo rustica*] [Møller 1991]). When first documented, EPCs were regarded as a mixed reproductive strategy pursued primarily by males (Pied Flycatcher [*Ficedula hypoleuca*] [Björklund and Westman 1983], Black-billed Magpie [*Pica pica*] [Buitron 1983], Indigo Bunting [*Passerina cyanea*] [Westneat 1987], Northern Oriole [*Icterus galbula*] [Edinger 1988]). More recent evidence demonstrates that females of many species seek EPCs as well (Razorbill [*Alca torda*] [Wagner 1991], Blue Tit [*Parus caeruleus*] [Kempenaers et al. 1992], Eurasian Oystercatcher [*Haematopus ostralegus*] [Heg et al. 1993], Chaffinch [*Fringilla coelebs*] [Sheldon 1994; also see Stutchbury and Neudorf, Chapter 5]). In general, the relative costs and benefits of extra-pair behavior to males and females differ both intra- and interspecifically (Buitron 1983; Birkhead 1991; Lifjeld et al. 1991; Wetton and Parkin 1991; Davies et al. 1992; Westneat 1992a; Gray 1994; Weatherhead et al. 1994). Such widespread variation has made it difficult to identify the factors that cause different patterns of extra-pair behavior in birds.

Red-winged Blackbirds are excellent subjects for comparative studies of extra-pair behavior because their breeding biology is well documented and their social systems differ geographically (Verner and Willson 1966; Orians 1969; Weatherhead and Robertson 1979; Lenington 1980; Orians 1980; Searcy and Yasukawa 1995; Beletsky and Orians 1996). Redwings typically breed in marshes and wetlands, where males establish territories that are defended vigorously throughout the breeding season. Males are primarily polygynous, although the degree of polygyny varies between populations, being generally higher in the western United States, where males mate socially with 2 to 20 females per breeding season (Beletsky and Orians 1989). In populations in eastern North America, males typically mate socially with one to four females per breeding season (Westneat 1993a; Weatherhead 1995). Females are socially paired to the male defending the territory on which they are nesting and are responsible for building nests, incubating eggs, and feeding nestlings. Males in western populations seldom feed nestlings but males in eastern populations often do (Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990; Beletsky and Orians 1991; Westneat 1995).

Several recent studies have documented the frequency of EPF in redwing populations in eastern Canada and the eastern United States (Gibbs et al. 1990; Westneat 1993a, b). These studies have shown that the relative costs and benefits of extra-pair behavior to males and females may differ between populations (Westneat 1992a; Weatherhead et al. 1994; Westneat 1994; Weatherhead and Boag 1995). An investigation of redwing extra-pair behavior in the western United States has revealed that interpopulational variation in mating tactics occurs throughout the redwing's range (Gray 1994).

My purpose here is to use comparative data to begin to identify the functional basis of variation in extra-pair behavior and to make predictions regarding the conditions that favor the pursuit of EPCs by both females and males in different avian populations. Specifically, I will review evidence for female control of EPC and EPF in a population of redwings in the western United States and discuss how differences in parental behavior, social organization, and environmental factors among redwing populations may lead to different female and male reproductive strategies.

## EXTRA-PAIR ACTIVITY IN A WESTERN RED-WINGED BLACKBIRD POPULATION

I studied the reproductive behavior of a western population of Red-winged Blackbirds on the Columbia National Wildlife Refuge in central Washington State from 1990 to 1992. The population in this general area has been studied for the past 15 years (for a detailed description of the study site see Orians 1980; Beletsky and Orians 1996). I observed courtship and copulatory behavior of individually banded birds on three main study marshes using both scanning and focal methods (Altmann 1974; Gray 1996). To analyze paternity, I collected blood samples from breeding adults and offspring surviving 4–5 days for genetic analysis using multilocus DNA fingerprinting. Details of these methods are found in Gray (1997a).

*Copulation and fertilization patterns:* In this population females initiate both within-pair copulations and EPCs. Females begin solicitation for copulation with a precopulatory display consisting of an easily recognized high-pitched chitter and wing flutter. After this initial display females crouch with their head and their tail raised. A female then may be approached by a displaying male (see Orians and Christman 1968). If a female remains crouched the male will mount. Copulation lasts a few seconds, during which time the male presses his cloaca against the female's cloaca. Female cooperation appears to be necessary for successful sperm transfer (Fitch and Shugart 1984; Burley et al. 1996; McKinney and Evarts, Chapter 8).

During my study, I observed 404 redwing copulations. Seventy-two (18%) of these were EPCs. The majority of copulations, both within- and extra-pair, occurred during a female's fertile period. EPCs, however, peaked 1 day closer to egg-laying than within-pair copulations (Gray 1996). The precopulatory and copulatory behavior of females appeared to be the same during within-pair copulations and EPCs; the same was true of male behavior. Occasionally males attempted to copulate forcibly with a social mate ($n = 15$), but I never observed a male attempting to force an EPC (Gray 1996).

DNA fingerprinting analyses revealed that 34% (136 out of 403) of the nestlings sampled were sired by an extra-pair male. More than one-half (54%) of all fingerprinted broods ($n = 134$) contained at least one offspring sired through EPF. I determined the genetic paternity of offspring sired through EPF by fingerprinting each excluded offspring a second time on a new gel with potential genetic fathers,

TABLE 1. The location of within-pair and extra-pair copulations in a Washington population of Red-winged Blackbirds observed from 1990 through 1992.

| | Location of copulation | | |
|---|---|---|---|
| | Territory of social mate | Territory of extra-pair male | Off marsh |
| Within-pair copulations | 246 (74%) | — | 86 (26%) |
| Extra-pair copulations | 16 (22%) | 28 (39%) | 28 (39%) |

defined as other males defending a territory on the same breeding marsh (Gibbs et al. 1990; Westneat 1993a).

*Female control of offspring paternity:* In this population, females behaviorally controlled paternity of their offspring (Gray 1996). Females typically copulated with their social mate on his territory, although occasionally socially paired individuals copulated off the marsh (Table 1). In contrast, the majority of EPCs occurred away from a female's nesting territory. On those occasions when females solicited EPCs on their nesting territory, they did so only when their social mate was absent.

The ability of males to prevent social mates from engaging in EPCs was limited because they could not leave their territories to follow fertile females on forays for any length of time without risking territory loss (Orians 1961; Rohwer 1982; Beletsky and Orians 1987a, b). The only successful male tactic for protecting paternity that I observed involved males preventing copulation between a social mate and an extra-pair male by actively attacking them during courtship ($n = 9$). In all but one instance, the intervening male was forced to leave his territory briefly to interrupt extra-pair courtship off the marsh. Only once did I observe courtship interrupted between a socially mated pair (Gray 1996).

In contrast, females were not constrained to remain on their nesting territory. Daily 1-hr focal observations of female behavior ($n = 119$ focal hours; $n = 22$ females) revealed that on average, females spent more than 50% of their time away from their nesting territory, regardless of whether they engaged in EPCs ($\bar{x}_{\text{EPC}} = 40.52 \pm 12.00$ min/hr, $n = 9$; $\bar{x}_{\text{no EPC}} = 37.57 \pm 11.50$ min/hr, $n = 13$; $t = 0.58$, d.f. $= 20$, $P = 0.57$). Although frequent forays off territory were common for all females regardless of their copulatory status, long foray times during peak fertilization (2 days before the first egg was laid [Westneat 1993b]) were correlated with a female's success of producing extra-pair young. I found a significant positive correlation between the average number of minutes a female spent foraying off territory during peak fertilization and the EPF rate of the subsequent brood (Kendall's tau = 0.4271, $n = 14$, $P = 0.02$). Thus, females engaged successfully in EPCs by soliciting them mainly away from their nesting territory, and they appeared to improve their chance of producing extra-pair young by increasing the amount of time they spent off territory immediately before egg-laying began.

*Female choice of extra-pair partner:* Females engaged in EPCs primarily with adjacent neighbors, although occasionally they copulated with a nonadjacent territory holder from the same marsh (Table 2). Adjacent neighboring males sired the majority of extra-pair young; nonadjacent neighboring males sired a small proportion of extra-pair young. I was unable to determine the genetic parentage

TABLE 2. The number of males with which females engaged in extra-pair copulations (EPCs) and with which females produced extra-pair fertilized (EPF) offspring according to male territory status.

| | Male status | | | |
|---|---|---|---|---|
| | No. adjacent territory holders | No. nonadjacent territory holders | No. floaters | No. unknown fathers |
| No. EPCs = 72 | 59 (82%) | 12 (17%) | 1 (1%) | — |
| No. EPF young = 136 | 111 (82%) | 6 (4%) | — | 19 (14%) |

of 19 extra-pair offspring, so it is possible that floater males, defined as males not known to defend a territory in the study area, sired them. However, I observed only one copulation involving a female and a floater male; therefore, these offspring probably were sired by territorial males that I was unable to include on the second set of gels with extra-pair young and potential sires.

I found no evidence that females had organized mate preferences for extra-pair partners. No correlation occurred between the proportion of offspring reared on a male's territory that he sired and his success in obtaining EPFs (Kendall's tau $= 0.0564$, $n = 46$, $P = 0.71$). The total number of offspring a male sired each year (social progeny and extra-pair young) was highly correlated with the number of nestlings fledged from his territory (Gray, unpubl. data). For all three breeding seasons, there was no correlation between the number of offspring a male fledged in a previous year and his success in achieving EPCs or EPFs in a future year (Gray 1997a). In addition, the rates at which males produced extra-pair young were not correlated across years (Gray, unpubl. data). Thus there were no "supermales" that significantly increased their reproductive success in any one breeding season by siring a large number of extra-pair young off territory and simultaneously preventing many EPFs on territory. In other words, reproductive gains through EPF off territory were approximately equal to reproductive losses on territory.

***Benefits to females of copulating with multiple males:*** Engaging in EPCs did not significantly increase a female's clutch size; females that did and that did not engage in EPCs laid a similar number of eggs ($P = 0.10$ [Gray 1997a]). However, females that engaged in EPCs hatched a significantly greater proportion of eggs and fledged a significantly greater proportion of young compared to females that did not engage in EPCs (Table 3). Improved hatching success may be due to female avoidance of temporary male sperm depletion, which could result from elevated daily rates of copulation in such a highly polygynous population. Improved fledging success resulted from significantly lower depredation rates in

TABLE 3. Mean hatching success and mean fledging success for females that engaged and did not engage in extra-pair copulations (EPCs), 1990–1992.†

| | Mean hatching success (no. eggs hatched/ no. eggs laid) | Mean fledging success (no. young fledged/ no. eggs hatched) | $n$ |
|---|---|---|---|
| Females that engaged in EPCs | 0.81 ± 0.30* | 0.49 ± 0.40** | 88 |
| Females that did not engage in EPCs | 0.55 ± 0.43 | 0.35 ± 0.42 | 92 |

† Mann–Whitney $U$-test, two-tailed, corrected for ties; * $U = 2{,}770.5$, $P < 0.0001$; ** $U = 3{,}266.0$, $P < 0.02$.

TABLE 4. Mean principal component (PC) scores reflecting active male aggression towards a mounted nest predator, a Black-billed Magpie (*Pica pica*), for adjacent male neighbors that copulated and that did not copulate with the nesting female. Larger positive PCI scores reflect a more aggressive response to the mount.*

| Male copulatory status | Mean PCI score: male aggression towards a nest predator |
|---|---|
| Engaged in extra-pair copulation (EPC) with the nesting female | 0.81 ± 1.14 |
| Not known to have engaged in EPC with the nesting female | −0.17 ± 0.54 |

* Unpaired *t*-tests; $t = -2.632$, df = 10.2; one-tailed $P = 0.01$.

clutches laid by females that copulated with multiple males and a tendency for a lower proportion of nestlings to starve in broods containing extra-pair young (Gray 1997a).

*Additional nest defense.*—Because more vigorous defense of a nest may reduce the probability of nest predation (Blancher and Robertson 1982; Montgomery and Weatherhead 1988), I hypothesized that clutches laid by females that had engaged in EPCs may have been depredated significantly less often than clutches laid by females that did not engage in EPCs because extra-pair male(s) joined social mates in defense of a nest.

To test this possibility, I presented a mounted nest predator, the Black-billed Magpie, to 46 nests with 3–7-day-old nestlings and recorded responses of neighboring males (details in Gray 1997b). The response of each male neighbor was recorded by a single observer during a 10-min presentation period. Each observer recorded the number of strikes to the mount, the number of flights at least 2 m above and directly over the mount, time(s) within striking distance of the mount giving shrill warning calls, time within 1 m of the mount, time within 1–3 of the mount, time within 3–10 m of the mount, and the total amount of time that the male focused on the mount during the presentation, which was calculated at the end of each session.

I analyzed these data using a principal components analysis. Results yielded two significant principal components, which accounted for 75% of the variation observed. I interpreted the first principal component as an index of active male aggression towards the mount and the second principal component as a measure of passive interest in the mount (for a complete discussion see Gray 1997b). I used loading scores for each principal component to calculate a score reflecting active male aggression towards the mount (PCI) and a score reflecting passive interest in the mount (PCII) for each neighboring male.

Male neighbors differed significantly in their active aggression towards the mount, depending on their copulatory history with the nesting female. A comparison of mean PCI scores revealed that males were significantly more aggressive towards a predator at a nest on a neighboring territory if they had copulated with the breeding female than if they had not (Table 4). In contrast, neighbors that copulated or that did not copulate with the nesting female did not differ significantly in their passive interest, or mean PCII, scores ($t = -0.228$, d.f. = 10.7, $P = 0.82$). Most neighbors, regardless of whether or not they had engaged in EPCs with a neighboring female, were inquisitive about a predator's movement and behavior on an adjacent territory.

These results demonstrate that male redwings will actively defend nests in which they have a potential genetic investment, even if they are not socially paired to the breeding female. As a result, female redwings in this population may seek copulations with multiple males to improve their chances of gaining additional nest defense, which in turn decreases predation.

*Access to additional food resources.*—To test whether lower starvation rates in broods containing EPF offspring might result from females gaining access to food resources on extra-pair territories, I experimentally manipulated food resources on male territories and quantified male responses to each foraging female (details in Gray 1997b). I increased female incentive to feed on a neighboring territory by placing a feeder baited with sunflower seeds and millet on male territories ($n = 12$) for a 2-hr observation period. During this time, I recorded the number and type of interactions between the territorial male and each female attempting to forage on his territory. Interactions ranged from the male permitting a female to feed on the feeder, to the male chasing a female off the feeder or off the territory, to the male aggressively attacking a female. I defined a successful feeding bout as one in which a female remained on the feeder undisturbed for at least 5 s. I repeated this procedure twice for each male.

Data were analyzed using a principal components analysis. Two significant principal components accounted for 58% of the variation observed. I interpreted the first principal component as a measure of intermale variation in male–female interactions, which reflected a male's propensity to respond to all foraging females. The second principal component represented differential male tolerance towards foraging females (for a complete discussion see Gray 1997b). I used loading scores for each principal component to calculate a score reflecting the degree of male–female interaction (PCI) and a score reflecting male intolerance towards a foraging female (PCII) for each territorial male–female pair.

Mean PCI scores did not differ significantly between females according to their social or copulatory status with the territorial male ($F_{3,290} = 0.77$, $P = 0.51$). Thus, the degree with which males interacted with foraging females during the feeder experiment was not influenced significantly by a female's relationship with that male. The *type* of interaction between the territorial male and each foraging female, however, did differ significantly depending on the pair's social and copulatory status. Foraging females that were socially paired to the territorial male were tolerated more often on territory and on the feeder than foraging females that were not socially paired to him (Table 5). However, among females that were not socially paired to the territorial male, females that had engaged in EPCs with that male were significantly more likely to be permitted to forage on his territory compared to females that had not engaged in EPCs with him. Thus, engaging in EPCs significantly improved a female's chance of gaining access to food resources on extra-pair territories.

*Costs to females of copulating with multiple males:* I found very little evidence that the pursuit of EPCs was costly to females (Gray 1997a). During behavioral observations, male aggression towards females was rare and was seldom directed towards unfaithful social mates. I never saw males retaliate against unfaithful mates with chases or forced copulations, and I never observed a forced copulation

TABLE 5. Mean principal component (PC) scores reflecting male intolerance towards females attempting to forage at a feeder placed on his territory for a 2-hr period. High positive PCII scores indicate that the territorial male prevented the female from foraging on his territory, and high negative PCII scores indicate that the territorial male tolerated a foraging female. Females are categorized according to their pairing status and copulatory history with the territorial male.† All pairwise comparisons of categories are significantly different ($P < 0.05$) except those indicated, based on a protected least-significant difference test (SPSS, Inc. 1993).

| Pair status | Female copulatory history | Mean PCII score: male intolerance towards a foraging female |
|---|---|---|
| Socially paired | No known extra-pair copulations (EPCs) | $-1.362 \pm 1.283$ |
| Socially paired | Female engaged in EPCs | $-0.552 \pm 1.262$]ns |
| Not socially paired | Female engaged in EPC with the territorial male | $-0.001 \pm 0.329$]ns |
| Not socially paired | No known EPC with the territorial male | $0.052 \pm 1.048$ |

† ANOVA, $F = 7.93$, total df = 293, $P < 0.001$.

immediately following an EPC. Males did not desert or prevent females that participated in EPCs from nesting on their territories. I found no evidence of sexually transmitted diseases or parasites (Gray 1997a).

Male retaliation against social mates that have copulated with extra-pair males may be more subtle, however. During the feeder experiment, females that engaged in EPCs were prevented from foraging on their social mate's territory significantly more often than females that did not copulate with extra-pair males (Table 5). I was unable to determine, however, the extent to which engaging in EPCs affected a female's ability to forage on her social mate's territory when feeding conditions were not manipulated. Females that engaged in EPCs may have been trading opportunities to forage on their nesting territory for opportunities to forage on an adjacent territory. If so, the cost of a social mate's resistance to foraging on his territory would depend in large part on the differences in territory quality across the breeding marsh. Although males may retaliate against social mates that have engaged in EPCs in other subtle ways that I have not yet detected, it appears that in this population the benefits of EPC to females outweigh any measurable costs.

## CONTRASTING FEMALE REPRODUCTIVE STRATEGIES

Evidence from my study population demonstrates that female redwings frequently take an active role in pursuing copulations with extra-pair males, which often significantly increases their reproductive success. Detailed observations of female extra-pair behavior in another redwing population, located in New York State, have revealed that female behavior varies substantially across populations.

*A comparison of female extra-pair behavior between two redwing populations:* In the Washington population that I studied, females controlled paternity by pursuing EPCs off their nesting territory. In contrast, in a New York population males, not females, are reported to initiate and pursue EPCs (Westneat 1992a). Unlike their western counterparts, female redwings in New York have been observed only resisting or passively accepting the advances of extra-pair males (Table 6). In addition, female behavior in this population is noticeably different during extra-pair courtship; females crouch less and resist more than during with-

TABLE 6. Differences in female extra-pair behavior between two populations of Red-winged Blackbirds.

| | Washington State | New York State† |
|---|---|---|
| Courtship | No difference in female behavior during extra-pair and within-pair courtship | Females crouch less and resist more in extra-pair than in within-pair courtship |
| Extra-pair copulation (EPC) | Females solicit | Females tolerate |
| Location of EPC | Off nesting territory | On nesting territory |
| Time spent by female on territory | 50% | 95% |

† Westneat 1992a.

in-pair courtship. Females do not visit neighboring territories to engage in extra-pair courtship with the resident male, even when their social mate is temporarily removed (Westneat 1992a). In fact, females that intrude onto neighboring territories are not courted but are reported to be chased away by the defending male. All extra-pair interactions and copulations occur when neighboring males intrude onto another male's territory (Westneat 1992a). The fact that females in this population spend 95% of their time (compared to 50% of their time in Washington) on their own territories when they are fertile and do not leave their territory to solicit copulations from extra-pair males when their social mate is temporarily removed is consistent with the view that these females rarely, if ever, initiate extra-pair courtship or copulation either on or off the breeding marsh. This conclusion also is supported by the absence of a correlation between the frequency or duration of female forays off a nesting territory and the proportion of a female's brood that is sired by extra-pair males (Westneat 1992a).

*Differences in male paternity protection strategies:* The strategy that a male adopts to maximize paternity will depend on both the reproductive behavior of his social mates and the behavior of extra-pair males. In Washington State a male's presence on territory does not prevent his social mates from engaging in EPCs. In addition, the need to constantly defend territorial boundaries prevents males from closely following fertile mates on lengthy forays away from the breeding territory, where females primarily solicit EPCs. Rather, males in this population are restricted to using strategies such as opportunistically encountering a social mate courting an extra-pair male during a foray off the marsh to intervene in extra-pair courtship and to prevent EPFs (Gray 1996).

Male strategies to prevent social mates from engaging in EPCs are different in the New York population. In this case, males spend most of their time repelling intruding extra-pair males rather than attempting to prevent initiation of extra-pair courtship by their social mates. Because extra-pair courtship in this population occurs on a female's nesting territory and is not initiated by the female, a male's intervention in EPCs occurs primarily *on* his territory, unlike the Washington population where most intervention occurs *away* from the breeding territory. Thus, in New York, male tactics for maximizing paternity depend on males remaining on territory, whereas in Washington they depend on males leaving their territories.

As a result, to reduce the number of extra-pair offspring sired on their territories most effectively, males in the Washington population should increase the amount of time they spend away from their territory during a social mate's fertile period, whereas males in the New York population should decrease the amount of time they spend away from their territory during a social mate's fertile period. Unfortunately, I do not have these data for the Washington population. Westneat (1993b), however, found that in his study population males forayed for distinctly shorter periods of time several days before a social mate laid her first egg compared to foray times during the rest of her reproductive cycle. Male presence on territory reduced the occurrence of extra-pair male intrusions; during temporary removals of territorial males, the rate at which extra-pair males intruded onto a female's nesting territory and courted her were 100 times greater than on control territories (Westneat 1994). This paternity protection strategy was not always effective, however, because males were required leave their territories daily to forage, and it is during this time that extra-pair males intruded onto their territory and copulated with their social mates (Westneat 1993b).

*A comparison of data collection methods among studies:* Methodological differences in behavioral observations are unlikely to explain the differences in female redwing extra-pair behavior reported for these two populations. Differences in methodology may, however, partly explain differences in the number of copulations observed for each population. In my study, I observed female and male reproductive behavior from a 7-m-high cliff bordering one edge of my main study marsh. This vantage point enabled me to observe individuals on the breeding marsh and in the surrounding uplands, where many EPCs took place. From 1990 through 1992, I scanned daily (2 hr after sunrise and 2 hr before sunset) for courtship and copulatory behavior over the entire marsh, including the area immediately bordering it ($n$ = 402 observation hours). During this time, I observed 309 within-pair copulations and 66 EPCs. I supplemented these observations in 1992 with daily 1-hr focal samples (Altmann 1974) on 26 randomly selected females as each female began to line her nest cup, which was typically several days before she laid her first egg. During focal observations, I recorded all within-pair and extra-pair events, including courtship, chases, attempted mounts, and copulation. Data were collected in the same manner as those collected for the New York population, on a slightly modified version of Westneat's data sheets. I spent 119 hr observing focal females; during this time I observed 23 within-pair copulations and 6 EPCs. Thus the focal procedure yielded fewer copulations per unit time compared to the scanning procedure, but it allowed me to quantify female time budgets and to observe a relatively greater number of extra-pair events that did not result in copulation (Gray, unpubl. data).

All observations of female reproductive behavior in the New York population were collected using focal procedures (Westneat 1992a, 1993a). During 318 female focal hours, 71 copulations were observed, 4 of which were EPCs. Observers also recorded the behavioral sequence of events for 58 cases of extra-pair courtship that did not result in copulation. Females were visible nearly continuously during each focal hour, during which time they almost never forayed into a neighboring territory (Westneat 1992a). When females did foray off the study area ($n$ = 84), they often remained visible ($n$ = 25). Occasionally ($n$ = 10), extra-pair activity was observed during forays off the marsh, but during this time females never responded to male extra-pair courtship with a precopulatory display or crouch nor did they initiate extra-pair courtship with another male.

TABLE 7. The proportion of total copulations observed that occurred between non-socially paired individuals, the proportion of offspring sired through extra-pair fertilization (EPF), and the proportion of broods containing extra-pair fertilized (EPF) young in three populations of Red-winged Blackbirds.

| | Proportion of observed copulations that were EPCs | Proportion of offspring sired through EPF | Proportion of broods with EPF offspring |
|---|---|---|---|
| Washington* | 18% (72/404) | 34% (136/403) | 54% (72/134) |
| New York† | 6% (4/71) | 25% (122/497) | 43% (63/147) |
| Ontario | — | 25% (137/546)‡ | 39% (67/174)‡ |
| | — | 28% (31/111)§ | 47% (17/36)§ |

* Gray 1994.
† Westneat 1995.
‡ Weatherhead et al. 1994.
§ Gibbs et al. 1990.

The fact that only focal procedures were used to observe female behavior in the New York population probably explains why proportionately fewer EPCs were observed there compared to the population in Washington State. Even within the Washington population, scanning techniques yielded more copulation observations per hour (1.01 copulations/hr) compared to focal observations (0.24 copulations/hr). This disparity does not, however, account for differences reported in female extra-pair behavior. In both populations, female behavior was observed both on and off the nesting territory. Despite the few successful EPCs detected in New York, many interactions between potential extra-pair partners were observed, none of which suggested that females in this population actively pursue EPCs. Although it is possible that females in New York occasionally pursue EPCs during forays off the breeding marsh, when they are hidden from both their social mate and the observer recording their behavior, the relatively short amount of time they spend off their nesting territory each day and the lack of extra-pair behavior observed during many of these forays makes it unlikely that female pursuit of EPCs in this population is a common occurrence.

## WHY MIGHT FEMALE REPRODUCTIVE STRATEGIES DIFFER?

Why do females in various redwing populations adopt different reproductive strategies? A female's decision to initiate EPCs and her response to extra-pair courtship should depend on the relative costs and benefits she obtains from copulating with extra-pair males. To date, the fitness costs and benefits to female redwings of engaging in EPCs and producing extra-pair young have been studied in three redwing populations: Washington State in the western United States, New York State in the eastern United States, and the province of Ontario in eastern Canada. The relative rates of extra-pair copulation and fertilization in each of these populations varies somewhat, although extra-pair activity is common within each population (Table 7). However, as I have pointed out, female and male reproductive behavior among populations is not uniform. In addition, the effect of extra-pair behavior on female reproductive success reportedly differs among populations (Westneat 1992a; Gray 1994; Weatherhead et al. 1994).

In some populations, female solicitation of EPCs may be inhibited by the threat of male retaliation towards social mates that copulate with extra-pair males. Studies to date present no evidence showing that males retaliate against unfaithful social mates by attacking, chasing, or copulating forcibly with them (Westneat 1992a; Gray 1997a). However male retaliation may be more subtle. Males may retaliate indirectly against EPFs on their territories by reducing parental care at nests likely to contain extra-pair offspring, either by decreasing nestling provisioning or by reducing nest defense against predators.

In addition, female incentive to solicit EPCs will depend on how much a female can potentially gain from copulating with multiple males, which in turn will depend on social and environmental variables such as the number of potential extra-pair partners, the degree of polygyny, and the availability of food resources on the breeding marsh. The extent to which female sexual behavior is influenced by each of these factors will depend on their relative importance in each population.

I now consider how four of these factors, retaliation by social mates, the density of breeding males, the degree of polygyny, and the availability of food resources, affect the relative costs and benefits to female redwings of engaging in EPCs. My goal is to assess the relative strength of each of these factors in shaping different female reproductive strategies among redwing populations.

*Retaliation by a social mate:* Male provisioning of young.—In eastern populations, most male redwings feed nestlings on their territory, whereas in western populations most males do not (Verner and Willson 1969; Yasukawa and Searcy 1982; Beletsky and Orians 1990, 1991; Yasukawa et al. 1990; Westneat 1995). Male feeding of redwing nestlings significantly increases a brood's fledging success (Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990; Patterson 1991). In fact, male provisioning can compensate entirely for the loss of female care when breeding females are permanently removed, so that broods raised by a single redwing male can fledge an equivalent number of young as broods with biparental care (Whittingham 1994). Thus, in populations such as New York, where males can retaliate against the threat of EPF by withholding nestling feeding and potentially reducing a social mate's fledging success, the costs to females of engaging in EPCs may be higher than in populations such as Washington, where males rarely feed nestlings and thus have a more limited means of retaliation.

In several species males adjust their investment in social progeny according to the likelihood that a proportion of their offspring have been sired by extra-pair males (Joste et al. 1982; Houston and Davies 1985; Møller 1988; Westneat 1988; Koenig 1990; Nakamura 1990; Davies et al. 1992; Dunn and Cockburn, Chapter 7). For example, male swallows that were experimentally removed for several hours during their social mate's fertile period fed their offspring significantly less than did control males (Møller 1988). There is no evidence, however, that male redwings that typically feed nestlings adjust their relative level of provisioning according to the proportion of their brood that is sired by extra-pair males (Westneat 1995). In New York, male redwings provision broods equally regardless of their paternity in each brood, and males with low average paternity feed nestlings at the same rate as males with high average paternity. A similar lack of adjustment in male parental care relative to the proportion of his social progeny sired by extra-pair males has been reported in Indigo Buntings (Westneat 1988), Purple Martins (Morton et al. 1990), and Tree Swallows (*Tachycineta bicolor* [Whittingham et al. 1993]). Thus, no evidence supports the hypothesis that female redwings in New York avoid the pursuit of EPCs because their social mates retaliate by reducing offspring provisioning.

*Male nest defense.*—In redwing populations, approximately 80% of all nests that fail are destroyed by predators (Westneat 1992b; Beletsky and Orians 1996). Nest predators have a large impact on redwing reproductive success because a single predator usually consumes the entire contents of a nest (Ricklefs 1969; Lenington 1979; Weatherhead 1995).

Territorial male redwings typically defend nests by mobbing predators, either individually or in groups (Searcy and Yasukawa 1995). Group mobbing often is more effective than an individual attack in deterring a potential nest predator because it increases the aggressiveness of the defensive response (Andersson 1976; Bildstein 1982; Shields 1984). Even when nests are defended by a single individual, however, increased intensity of defense often decreases the likelihood of predation. In a study of redwing nest defense in Ontario, nests that successfully fledged offspring were defended significantly more vigorously by the territorial male compared to nests that failed ($P = 0.015$ [Weatherhead 1990]).

As a result, territorial males may retaliate against social mates that have engaged in EPCs by defending their broods less aggressively compared to broods that are unlikely to contain extra-pair young, making EPCs very costly for females. On the other hand, extra-pair males may contribute to predator defense at nests where they have copulated with the breeding female and perhaps sired offspring. If so, copulating with multiple males may benefit a female by increasing the number of individuals defending her nest.

Both territorial and extra-pair male redwings have been reported to adjust their level of defense against nest predators according to their perceived certainty of paternity within a brood. Measurements of territorial male responses to a potential nest predator (human [*Homo sapiens*]) revealed that males sometimes defend broods of social mates containing extra-pair young less vigorously than broods containing no extra-pair young (Weatherhead et al. 1994). Studies also have demonstrated that extra-pair males will defend nests on neighboring territories if they have copulated with the breeding female (Gray 1997b). Whether a female redwing accrues a net gain or a net loss in nest defense from copulating with an extra-pair male will depend on the relative strength of each of these male responses in a population.

In my study population, females that engaged in EPCs fledged a significantly greater proportion of offspring than females that did not engage in EPCs (Table 3). Multiply-sired broods were depredated significantly less often than broods sired solely by the social mate (Gray 1997a), and extra-pair males that copulated with a breeding female were significantly more aggressive towards a mounted nest predator on a neighboring territory if they had copulated with that female than if they had not (Table 4). I did not measure whether territorial males decreased their intensity of nest defense if their social mate had copulated with an extra-pair male; however, it appears that the increased nest defense provided by an additional extra-pair male far outweighed any cost of reduced defense by the social mate.

In a redwing population in Ontario, on the other hand, additional nest defense by an extra-pair male did not compensate for reduced defense by a female's social mate. Extra-pair mating lowered a female's probability of nest success in large part because her social mate defended her nest less vigorously if extra-pair young were present. Broods containing no extra-pair offspring were the most likely to fledge young, broods with offspring sired solely by extra-pair male(s) were the least likely to fledge young, and broods with mixed paternity had intermediate fledging success (Weatherhead et al. 1994). These results suggest that nest defense is relatively more costly for males in the Ontario population compared to males in Washington. If nest defense posed no risk to defending adults, males would benefit from defending all nests on their territory vigorously against predators regardless of the threat of EPF because males, on average, sire the majority of social progeny in each brood even when extra-pair young are present. In Ontario, however, nest defense increases the likelihood of predation on a defending male (Weatherhead, pers. comm.). More vigorous nest defense attracts predators such as hawks, which have been observed killing adult redwings. As a result, there is no evidence of cooperative male nest defense in this population (Weatherhead 1995). In contrast, in Washington I have never observed mobbing males attract additional predators. Even if mobbing occasionally attracts adult predators to the breeding marsh, the relative infrequency of danger to defending males may explain why, despite the high frequency of EPFs in this population, territorial males do not recognizably reduce defense of their social mates' nests, and territorial and extra-pair males cooperatively defend broods.

Results from Ontario also differ from a study of redwings in New York in which females that copulated with extra-pair males fledged significantly more offspring compared to females that did not engage in EPCs (Westneat 1992a). These data were inconclusive regarding the relative costs and benefits to females of engaging in EPCs, however. Westneat (1992a) could not determine reliably whether predation rates in New York were affected by the presence of extra-pair young. In addition, he did not measure territorial and neighboring male responses to predators at nests of females that had copulated with extra-pair males. Because females that accepted EPCs in this population experienced a net gain in reproductive success, it is possible that in New York, as in Washington, extra-pair males contributed to nest defense, and males did not partially restrict their defense of nests on their territory that contained extra-pair offspring because nest defense was relatively inexpensive to defending adults.

*Density effects:* Even when a female experiences a net reproductive gain from copulating with extra-pair males, her decision to seek, rather than merely to accept, EPCs will be determined primarily by the incentive provided by her social and her physical environment. If a female can increase her probability of successfully fledging a brood by enlisting additional nest defense from neighboring males, she should be more prone to seek EPCs when there is a large number of potential extra-pair partners nearby.

Studies from a number of avian species have revealed a positive correlation between the density of individuals breeding in an area and the frequency of EPF (reviewed in Wagner, Chapter 6). In several redwing populations the density of males on a breeding marsh is positively correlated with the proportion of offspring sired through EPF (Gibbs et al. 1990; Gray 1996). In the population that I studied in Washington State there is a significant positive correlation between the number of contiguous male neighbors per female and the proportion of a female's brood that is sired by extra-pair males (Gray 1996). Because female redwings mainly initiate EPCs with males that are neighboring residents, and it is these adjacent neighbors that provide the benefit of additional nest defense, the greater the number of contiguous male neighbors the greater a female's potential to increase the vigor of defense of her nest.

In Washington, where densities of breeding males are high (2.15 males/10 $m^2$), the opportunity for group mobbing and therefore the effectiveness of cooperative nest defense should be greater than in populations such as New York (0.25 males/10 $m^2$) and Ontario (0.23 males/10$m^2$) where the density of breeding males is much lower. In addition, the possibility of larger mobbing groups in Washington may reduce any risks that typically confront defending adults. As a result, females in populations such as Washington that have many potential extra-pair partners in close proximity should have more incentive to seek EPCs than females in populations with only one or two adjacent male neighbors.

*Degree of polygyny:* Socially mated redwings copulate frequently throughout a female's fertile period (0.26 ± 0.11 copulations/hr [Westneat 1993b]; 0.25 ± 0.66 copulations/hr [Gray 1997a]). Males do not, however, have an inexhaustible sperm supply, and recent experiments suggest that males cannot control the number of sperm they release per ejaculate in order to compensate for sperm depletion (Birkhead and Fletcher 1995). Although less is known about sperm depletion in wild bird populations, studies of domestic birds have shown that the number of sperm per ejaculate decreases by approximately 50% after each copulation (McDaniel and Sexton 1977; Tan 1980; Ansah et al. 1984; Birkhead 1991). These sperm stores are typically replenished overnight (Birkhead et al. 1994). Thus, frequent copulation has the potential to lead to low sperm counts and possible temporary male infertility on a daily basis.

As a result, males that are mated socially to a large number of synchronously fertile females may become sperm limited, and females that are mated socially to these males may be more likely to seek EPCs to counter the possibility of producing an inviable egg. In Great Reed Warblers (*Acrocephalus arundinaceus*), the proportion of infertile eggs per territory increases with an increasing degree of male polygyny, suggesting that a positive relationship exists between copulation frequency and temporary sperm depletion (Urano 1990). If females use EPCs as a mechanism to ensure higher rates of fertilization, females socially paired to highly polygynous males should seek EPCs more often than females socially paired to slightly polygynous or monogamous males. In addition, multiply-sired broods should contain fewer unhatched eggs than clutches sired solely by the social father (Wetton and Parkin 1991; Gray 1997a).

Redwings are particularly useful for studying the relationship between degree of polygyny and the likelihood of producing inviable eggs because the degree of polygyny varies widely both within and between populations. Male redwings in Washington are highly polygynous; they mate socially with up to 20 females during a breeding season. These females breed both synchronously and asynchronously, and 15% of all clutches contain at least one unhatched egg (Gray 1997a). In Washington, the number of females socially paired to a male is significantly and positively correlated with the proportion of unhatched eggs laid on his territory. In addition, broods with EPFs contain significantly fewer unhatched eggs compared to broods with no extra-pair offspring (Gray 1997a). In contrast, redwing males in New York are slightly polygynous or monogamous, and fewer than 4% of all clutches contain an infertile egg (Westneat 1992a). Thus, a higher degree of polygyny appears to be correlated with a female's probability of producing an inviable egg. As a result, females in highly polygynous populations such as Washington should have greater incentive to seek copulations with multiple males to ensure fertilization compared to females in populations such as New York, where males typically have only one or two social mates.

*Availability of food resources:* A female's incentive to seek EPCs also may be influenced by the availability of food resources on her nesting territory. An insufficient food supply on a nesting territory may motivate females to initiate copulations with extra-pair males if they are rewarded by access to additional foraging areas on the breeding marsh. Despite relatively high marsh productivity in Washington, the local resource base cannot support all breeding adults, and therefore individuals forage both on and away from their breeding territory (Orians 1980). If a female could spend more time foraging near her nest, she would benefit by reducing her energetic costs of searching for food. Thus, females in Washington may seek EPCs in an attempt to increase the amount of time they spend foraging on the breeding marsh.

In New York redwings gather a higher percentage of food on their breeding territory than redwings in my study population, and therefore adults spend less time off their territory looking for food (Westneat 1994). If one reason females seek EPCs is to access food resources on extra-pair territories, females in New York may have less incentive to solicit EPCs compared to the more food-limited females in Washington. At present it is difficult to assess the relative importance of food resource availability to female pursuit of EPCs without experimental tests. An experiment that might shed light on this question would involve artificial supplementation of the food supply in the Washington population to determine whether there is a corresponding decrease in the proportion of females that seek EPCs and a reduction of food supply on breeding territories in the New York population to determine whether females begin seeking copulations with extra-pair males.

## CONCLUSIONS

In this paper I have explored several possible reasons why female redwings in my study population actively seek EPCs, whereas female redwings in another population do not. A female's decision to initiate copulations with multiple males will depend both on the fitness consequences of her extra-pair behavior, as well as on the social and environmental conditions that provide her with an incentive to seek EPCs. I found no evidence suggesting that males retaliate against social mates that have copulated with extra-pair males by reducing nestling feeding of social progeny. Males may, however, decrease the intensity of defense at a social mate's nest if she has copulated with extra-pair males. Whether this reduction is compensated for by an increase in extra-pair male defense will depend on the cost of defending nests, as well as the frequency of cooperative mobbing within a population.

Social and environmental factors also are important determinants of female extra-pair behavior. Female redwings in Washington may have more incentive to seek EPCs compared to females in New York due to a greater number of adjacent male neighbors that can contribute to extra-pair nest defense; a greater risk of sperm depletion due to a high degree of polygyny, which can be countered by copulating with multiple males; and a relatively larger gain from foraging on extra-pair territories due to limited food resources on nesting territories. To test how reliably these conditions can predict reproductive strategies in other populations, we need observations of female extra-pair behavior in redwing populations such as Ontario, where the fitness consequences to females of engaging in EPCs differ. Although it is still unclear how female redwings decide with which males to socially pair and to copulate, it is evident that a female's reproductive decision is based on a suite of characteristics unique to each breeding situation.

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# CHAPTER 4

# THE RELATIVE IMPACT OF EXTRA-PAIR FERTILIZATIONS ON VARIATION IN MALE AND FEMALE REPRODUCTIVE SUCCESS IN DARK-EYED JUNCOS (*JUNCO HYEMALIS*)

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ABSTRACT.—Differences among species in breeding system and degree of sexual dimorphism are thought to be mirrored by species-level differences in past or present sexual selection. The greater the deviation from monogamy, the greater the potential influence of sexual selection on the sex that is more variable in reproductive success (RS). The recent discovery of extra-pair fertilizations (EPFs) in apparently (i.e., socially) monogamous bird species, and the fact that EPFs have the potential to increase variance in RS of such species, led us to quantify EPFs in Dark-eyed Juncos and to explore the relative impact of EPFs on male and female variation in RS. We obtained season-long measures of frequency of EPFs, numbers of mates acquired, and apparent RS (young produced in nests of social mates) and genetic RS for 50 male and 45 female juncos studied during two breeding seasons in Virginia, USA. Forty-two of the 50 males produced offspring and 19 of these 42 (45.2%) lost paternity to EPFs. Thirty-eight of the 45 females produced offspring, and 13 of the 38 (34.2%) had at least one young sired by EPFs. There were no cases of conspecific brood parasitism. Of 187 young, 53 (28%) were sired by EPFs. Males that gained EPFs rarely suffered losses, and males that were victims of EPFs rarely gained by them. The result was that some males were more successful than others. We calculated variance in male and female apparent and genetic RS and mating success (MS, number of mates per season). We also calculated statistical dependence of RS on mating success. Among males, apparent reproductive success was less variable (standardized variance [SV] = 0.55) than genetic success (SV = 0.72), indicating that EPFs increased variance in male RS. The sex difference in variance in genetic success (male SV = 0.72, female SV = 0.51) was considerably less than the sex difference in variance in mating success (male SV = 0.65, female SV = 0.37). Interestingly, in both males and females, genetic RS increased with number of mates, suggesting that sexual selection, when defined as the statistical dependence of RS on MS, was acting on both sexes. To our knowledge this is the first study to report EPF-based sexual selection in a socially monogamous female songbird. Although an increase in RS with MS will clearly cause selection to favor attributes of individ-

uals that mate multiply, some would argue that selection should be called sexual only in situations in which access to additional mates is necessary to increased RS. Others see value in the statistical definition employed here. Regardless of the definition, more interspecific comparisons of males and females with respect to variance in apparent RS, genetic RS, MS, and the relative degree of dependence of RS on MS, should prove useful in determining whether and how these measures relate to degree of sexual dimorphism.

Many species-level differences in degree of sexual dimorphism, broadly defined to include sexual dichromatism and sex differences in physiology and behavior, are thought to result from differences between the sexes in the intensity of sexual selection (Darwin 1871; Selander 1972; Emlen and Oring 1977; Payne 1984; Gowaty 1985; Andersson 1994). Among bird species that are sexually monomorphic and monogamous and in which both parents care for young, the relationship between mating success (MS, number of mates) and fecundity or reproductive success (RS) is expected to be similar in males and females. As a consequence, variances in male and female MS and RS are also expected to be similar, as is the intensity of sexual selection acting on traits that affect mating success. At the other extreme, in highly dimorphic species with polygynous mating systems and little male parental care, fecundity is thought to depend more strongly on mating success in males than in females. As a consequence, variances in male mating success and RS are expected to be greater, and traits that enhance male mating success are expected to be under stronger selection.

Comparative and experimental tests of these generalizations require accurate measures of both MS and RS, and this was once thought to be a straightforward proposition (Clutton-Brock 1988). MS was determined by counting the number of pair bonds formed by individually marked birds, and to determine RS one needed only to find nests, associate them with a marked pair, quantify their contents, and observe their success or failure in producing fledglings or independent young. The success that was apparent to the field observer was believed to be true RS. Newly developed methods to determine genetic relatedness now allow more accurate measures of RS, and in many species the results have revealed discrepancies between apparent and actual mating systems and between apparent and genetic RS (e.g., Gowaty and Karlin 1984; Gowaty 1985; Westneat 1987; Gibbs et al. 1990; Rabenold et al. 1990; for summaries see Westneat et al. 1990; Birkhead and Møller 1992; Westneat and Webster 1994).

As a consequence, we must reassess old generalizations and confront the paradoxes that new information has revealed. If extra-pair copulations (EPCs) are common in what are now called socially monogamous species and if these frequently result in extra-pair fertilizations (EPFs), we must ask whether males of such species are actually less subject to sexual selection than males of socially polygynous species. If not, why do we find greater phenotypic differences between the sexes in socially polygynous species? Similarly, if EPFs are common in monogamous species, then why is male parental care also so common, given that it is frequently directed toward unrelated young (Whittingham et al. 1992; Westneat and Sherman 1993; Møller and Birkhead 1993; Ketterson and Nolan 1994)? Do certain forms of male parental care (e.g., incubation) appear only in truly monogamous species whereas other forms (e.g., feeding offspring) evolve despite deviations from true monogamy (Ketterson and Nolan 1994)? Before we can give satisfactory answers to these questions, we need more information on the frequency of EPFs and their relative impact on variation in male and female RS from a wide variety of species.

A primary objective of this paper is to make such comparisons using genetic data from the Dark-eyed Junco (*Junco hyemalis*). Juncos are socially monogamous, weakly dimorphic songbirds in which both males and females care for young. In asking whether sexual selection is acting on this species, and, if so, whether it is acting more strongly on males or females, we employ the approach of Arnold (1994; after Bateman 1948) and Arnold and Duvall (1994). The approach distinguishes between selection and response to selection, and it asserts, like Bateman (1948), that the cause of sexual selection is the dependence of fecundity on MS. To characterize sexual selection, the argument reads, comparisons of males to females must be made along three key parameters: (1) variance in RS, (2) variance in MS, and, most fundamentally, (3) the relationship between MS and RS (Arnold 1994; Arnold and Duvall 1994).

When such comparisons are made on a socially monogamous bird such as the junco, three outcomes are possible (Fig. 1). First, if a species is truly monogamous, we would expect all males and females either to be unmated or to have only one mate. If the sexes are equally likely to acquire mates, they would be equally dependent on MS for RS and would exhibit equal variance in RS (Fig. 1a). Sexual selection on both sexes would be weak. Second, if EPFs occur, and if multiple mating is beneficial only to males, RS in males should increase with number of mates. If female reproductive potential is saturated by a single mate, female RS would level off with MS (Fig. 1b). Variance in MS and RS would be greater in males than females, and male RS would be more dependent on MS than female RS would be, with the result that sexual selection would act more strongly on males than females. Third, if both males and females benefit from multiple mating via EPFs, then RS in both sexes would increase with MS. As with true monogamy, variance in MS and RS would again be similar for males and females (Fig. 1c). However, in this case, instead of the relatively low magnitudes of variance in MS and RS that are associated with true monogamy, the small intersexual differences in variance in MS and RS could be accompanied by relatively large within-sex variation. Sexual selection would be acting strongly on both sexes in the sense that individuals that acquired more mates would produce a disproportionately larger number of the next generation's offspring.

If EPFs enhance variation in RS of one sex more than the other, it is likely over evolutionary time that EPFs will have a greater impact on the phenotype of the more affected sex, leading to greater sexual dimorphism (Møller and Birkhead 1994). To determine whether EPFs differentially affect variance in RS of male and female juncos, we measured apparent and actual genetic success in a free-living population studied for 2 years and for which we determined both the frequency of EPFs and the identities of the sires of EPF young. We then compared means, variances, and standardized variances of male and female RS and MS. To investigate the existence of sexual selection, sensu Arnold (1994) and Arnold and Duvall (1994), we used regression analysis to determine and compare the extent to which RS is affected by number of mates in both males and females.

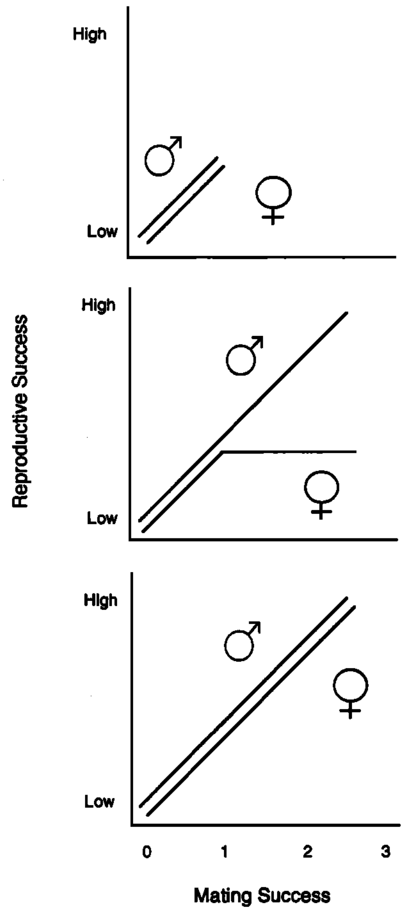

FIG. 1. Three possible relationships between mating success (number of mates) and reproductive success (RS, number of offspring) in males and females: implications for the relative intensity of sexual selection on the sexes. Top panel depicts true monogamy; middle panel depicts situation in which male RS but not female RS is enhanced by an increase in the number of mates; bottom panel depicts situation in which both male RS and female RS increase with mating success.

## SPECIFIC OBJECTIVES

(1) How frequently do EPFs occur in juncos? What proportion of males loses paternity to EPFs? What proportion of offspring is produced by EPFs? Is the number of individuals acquiring parentage as the result of EPFs equal to the number losing parentage in this way?

(2) Are EPFs important to males? Is male RS enhanced by an increase in number of mates, defined as the number of females successfully inseminated? Does RS achieved by EPFs come instead of, or in addition to, apparent RS with social mates? Are EPFs important to females? Is female RS enhanced by an increase in the number of mates, defined as the number of males that fertilizes a female's eggs? Does the proportion of young sired by EPFs increase as an individual's RS increases, as would be expected if females with greater success attracted more mates?

(3) When males and females are compared, what are the relative magnitudes of variance in RS, variance in number of mates, and degree of dependence of RS on number of mates?

## THE SYSTEM

*Background:* We studied a population of Carolina Dark-eyed Juncos (*J. h. carolinensis*) that breeds at or near Mountain Lake Biological Station, Pembroke, Giles County, Virginia, USA (see Chandler et al. [1994] for description of the study area) and that has been under study since 1983 (e.g., Wolf et al. 1988, 1991; Ketterson et al. 1991b, 1996). Juncos are widely distributed, abundant, and geographically variable; the Carolina race breeds at higher elevations (~1,000 m and above) in the mountains of southeastern North America.

Males and females exhibit moderate dimorphism (Fretwell 1972). They differ slightly in body mass (e.g., at the time young leave the nest, breeding males average 21.0 g, breeding females 20.0 g [Wolf et al. 1991; Ketterson et al. 1992]) and flattened wing length (male mean is 82 mm, female mean is 78 mm [Ketterson et al. 1991b]). The sexes are similar in coloration, although the predominant color, gray, is darker in males and males have more white in their rectrices. Juncos form socially monogamous pairs, females build the nest and perform all incubation, and both sexes help protect and feed nestlings and dependent fledglings. Most pair bonds are season-long (greater than 90% of cases in our population), and year-to-year fidelity to breeding sites is very high. The annual rate of return of breeders from the preceding season is approximately 50% (Ketterson et al. 1996; Nolan et al., unpubl. data). If both members of a pair return to breed next season, the bond is usually reformed (approximately 80% of cases [Ketterson et al. 1996]). Both sexes breed in their first year of life (Nolan et al., unpubl. data). If young juncos survive until about the middle of their first winter, further expectation of life is about 2 years.

Nest predation is common, reaching 75% of all attempts in some years, with 30% of these losses occurring between clutch completion and hatching (Ketterson et al. 1996). Many predators contribute to this mortality, but eastern chipmunks (*Tamius striatus*) are believed to be most important (Ketterson et al. 1996; Cawthorn et al., in prep.). Juncos in this population renest, sometimes repeatedly, after nest failure, and if successful they produce second and even third broods.

## METHODS

*Data collection in the field:* Data on mating success and reproductive success were collected during two breeding seasons, 1990–1991. All adults were individually color-marked, most of them as juveniles in the year they hatched and the rest early in the breeding seasons in which they were first studied as adults. As part of an ongoing study, a subset of the males (approximately one half) was treated with testosterone by placing hormone-packed silastic implants beneath the skin (see Ketterson et al. 1992). Control males were treated similarly in all respects except that their implants were empty. Implant status was assigned at random after blocking for age (first-year adults or older adults) and capture site within the study area. Males that were discovered breeding on the study area after a predetermined date in spring were not implanted, but because they were treated similarly in all other ways (e.g., caught, bled, weighed, and so on), we also considered them to be controls. This group comprised 1 of the total of 13 control males in 1990 and 3 of 13 in 1991.

Early in each season we mapped the locations of males and females and determined the identities of pair members on the basis of color bands. Adults seen together repeatedly during the initial nest-building and laying period were considered paired; if and when the eggs hatched, all such conclusions were confirmed. If we found nests only after hatching, we treated the adults that fed the nestlings as the social parents of these young. We maintained a season-long effort (from late April to early August) to monitor the reproductive status of all nesting pairs. Exceptions to social monogamy were rare. Over 14 years, <2% of pairings have involved simultaneous associations of more than one female with a single male, and <1% have involved the association of multiple males with the same female (Nolan et al., unpubl. data). Males that remained unmated for an entire season were also rare but easily detected by their constant advertising, and we also mapped their locations. Some pairs failed to leave any offspring because their nests were repeatedly raided by predators.

We bled adults when we captured them in the spring or at the time young left the nest, taking approximately 100 μl of whole blood from the alar vein. Blood was held on ice and returned to the laboratory where it was preserved in phosphate-buffered saline (3 mM KCl, 3 mM $Na_2HPO_4$, 2 mM $KH_2PO_4$, 0.14 M NaCl, 6 mM ethylenediaminetetraacetic acid 0.2% sodium azide) (see Rabenold et al. 1990). Nestlings were counted, weighed, and bled on day 6 (hatching of the first egg = day 0), and their blood was treated identically to that of adults.

*Laboratory work:* Genetic relatedness was determined by Parker and T. Peare using multilocus minisatellite DNA fingerprinting (Rabenold et al. 1990). We extracted DNA with phenol : chloroform, purified it with dialysis, cut it with the restriction enzyme *Hae*III, and transferred the digested fragments from agarose gels to nylon membranes. We probed the membranes with one to three radioactively labelled sequences, Jeffreys' 33.6, Jeffreys' 33.15, or M13 (Rabenold et al. 1990).

Gels were arranged so that DNA of offspring and social parents were in adjacent lanes, and, when there was sufficient room on the gel, we ran potential extra-pair sires (neighbors) on the same gels. Young that could not be assigned to their putative (social) sire or to other males represented on the original gel were run again on new gels until a match was obtained. On these subsequent gels we ran the female, the unassigned offspring, and additional neighboring males. We scored (using both Jeffreys' probes) an average of 41.3 bands for each individual, and a frequency distribution of bands shared between putative parents and offspring was distinctly bimodal. Young in the first mode were considered to have been produced by the putative sire and his social mate; young in the second mode were considered to have been sired by an extra-pair male. Young and assigned genetic parents differed by an average of 0.231 bands. Excluded young assigned to a male other than their social father differed from the social father by an average of 10 bands (extremes, 5–16) (Parker et al., in prep.).

*Terminology:* We define annual apparent reproductive success (AARS) of adults as the number of nestlings reared to the age of 6 days summed over all nests of the social pair during one breeding season. Day 6, the age at which we bled young, represents survival of about one half of the nestling stage and one quarter of the period of dependence after hatching (Wolf et al. 1988). Because genetic analysis revealed no cases of conspecific brood parasitism of females by other females, female AARS equals annual genetic success (AGS). This was not true for males, and for them we calculated the number of young lost to EPFs (EPF losses) and subtracted that number from their apparent reproductive success; we refer to the difference as home success (AARS − EPF losses = home success). We also determined the number of young these males sired with females other than their social mates, and we call these EPF gains or away success. Thus for males, AGS was the sum of home success and away success (home success + away success = annual genetic success).

For members of both sexes we calculated the number of individuals with which they produced at least one genetic offspring that survived to day 6, that is, mating success (MS; number of mates per season). For a female this was the number of different males that sired her offspring, and for a male it was the number of different females whose eggs he was known to have fertilized. Mates that were strictly social did not contribute to an individual's MS. Thus, for example, if a male with a social mate failed to sire any offspring with her or with any other female, he was classified as having had zero mates, and if all of a female's young were sired by a single extra-pair sire she was classified as having had only one mate.

*Statistical analyses and methodological considerations:* All statistical analyses were done using Systat 5 for the Macintosh (SYSTAT Inc., Evanston, IL). One of our first methodological concerns was how to treat individuals that were present in more than 1 year. Of the 50 males and 45 females studied in 1990–1991, 6 males and 6 females were present in both years, providing data from 56 male-years and 51 female-years.

We considered three methods for dealing with replication: one was to select at random 1 year to represent each individual that was present in more than 1 year, another was to average the data across years to represent each bird (e.g., Whittingham and Lifjeld 1995), and the third was to treat each year as an independent data point (e.g., Weatherhead and Boag 1995). We found no between-year correlation in RS of individuals present in more than 1 year (in these data and also in a larger set of data covering additional years), so it is arguable that we might have treated as independent the data collected on the same individual in more than 1 year. Nevertheless, we elected to use the first method as the most conservative, and we performed the random selections independently on females and males, so not all pair members entered the sample as pairs.

A second concern was that males treated with testosterone might have increased the population-level frequency of EPFs and increased variance in male and female RS. However, because male treatment had no significant effects on AARS, EPF losses, EPF gains, or AGS of this sample of males (Ketterson et al. 1996), we elected to pool males across treatments for all comparisons. Although legitimate statistically, we note that patterns described here should be verified from unmanipulated populations. Such a population is currently under investigation (Raouf et al., in prep.).

A third concern relates to the difficulty in obtaining accurate measures of RS in open-nesting species that can rear more than one brood and that are subject to heavy nest predation. Junco nests can be difficult to find in mountainous terrain,

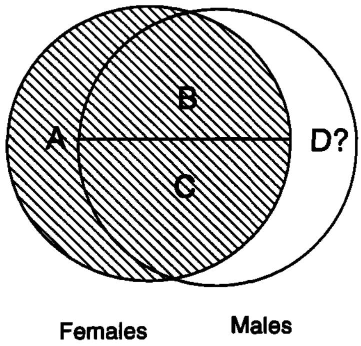

FIG. 2. Limits to accuracy when comparing reproductive success (RS) in the field for males and females of socially monogamous bird species in which extra-pair fertilizations (EPFs) occur and conspecific brood parasitism is absent; information for females will typically be more complete than for males. Circles represent RS of a set of males and females (left circle females, right circle males) occupying a study area. Offspring of females will have been sired by some combination of males entering the study area from outside its boundaries to engage in EPFs (region A), by social mates (region B), or by social mates of other females in the sample (region C). Males will probably have left the study area to sire offspring by females not occupying it (region D), but the magnitude of D is often unknowable.

and, despite our efforts to locate all of them for each pair throughout the season, we almost inevitably missed some. Pairs believed to have reared only one brood may actually have reared more than one, and pairs classified as having achieved zero apparent success (because all their known broods were lost to predators) might actually have reared a brood we missed. Both facts may have caused us to underestimate mean RS. Despite these limitations, we do not think this tendency to underestimate RS would have a differential effect on comparative estimates of male and female RS.

A final concern relates to the relative accuracy of measures of male and female RS (Fig. 2). In open populations in which there is no brood parasitism, data for females can be complete if they remain socially mated to the same male all season; that is, if all their nests are found, then all their eggs, regardless of how many males sired them, can be accounted for. Males, on the other hand, regardless of presence of their social mates on the study area, may sire young in nests located off the study area, and if they do those young will not be considered in calculations of male RS. To illustrate this point as applied to our sample: the adults that we used to compare males to females consisted of (1) individuals belonging to social pairs that tended the offspring that we bled, (2) individuals belonging to pairs that left no offspring because of nest predation, and (3) unmated males (no evidence indicated that any females were unmated). Some of the young in the sample were sired by the males that tended them (region B, Fig. 2), and some were sired by males socially mated to other females on the study area (region C, Fig. 2). Thus, the sample of males used to characterize male RS did not include any males whose territories lay outside the study area but that entered the area and sired young as the result of EPFs (region A, Fig. 2). These males were excluded because their social mates, assuming they had mates, lived off the study area and had young we therefore did not sample.

In this study of 50 males, 45 females, and 187 nestlings, 24 nestlings (12.8%)

were sired by 7 males that were not among the 50 males in the study sample (region A, Fig. 2). Although we might have assumed that the number of young in the study population sired by males from outside it was equal to the number of young sired outside the area by males from within it (i.e., region A and region D were equal, Fig. 2), we opted not to do this because we could not know which males increased their RS via EPFs and which did not.

## RESULTS

*Frequency of EPFs:* Of the 50 males, 42 had some degree of apparent success, 5 lost all broods to predators, and 3 were unmated. A total of 37 males had some genetic success, that is, sired at least one offspring (37 of 50, 74.0%; 37 of 42, 88%), and 5 males that were apparently successful had no genetic success. Nineteen of the 42 males with some apparent success lost paternity to EPFs (45.2%). Of 187 young, 53 were sired by extra-pair males, that is, 28.3% were produced by EPFs. Of the 45 females, 25 produced only young sired by social mates, 13 produced at least one young sired by an extra-pair male, and 7 had zero apparent and genetic success because of repeated losses to predators. Thus 34% of 38 successful females had multiple mates. As stated earlier, no young were found that could not be assigned to the females that tended them.

*Variation in AGS in males:* From the 50 males in the sample, we identified 9 that had EPF gains. An additional 7 males from outside the sample were sires of EPF young that were in the sample (see above), so the total number of sires that gained paternity on the study area via EPFs was 16. Comparing this number to the 19 males that lost paternity to EPFs indicates that some males sired EPF-young with more than one female.

Two clear a priori alternatives describe how EPFs might affect variation in male RS. If EPFs involve a trade-off such that the greater the number of EPF-young a male sires, the greater his loss of paternity at home, then gains and losses would be positively correlated and the impact of EPFs on variance in male RS would be small (trade-off relationship). Alternatively, if some males gain RS by EPFs without losing paternity to other males as the result of EPFs, and if others show the opposite pattern, then gains and losses could be negatively correlated and the impact on variance would be high (winners and losers relationship).

Figure 3 plots individuals according to the number of EPF gains and losses they accumulated and appears to describe three types of males: one group near the origin that neither gained nor lost RS by means of EPFs ($n = 25$), a second group in the lower right that suffered losses and had no gains ($n = 16$), and a third group in the upper left that accumulated gains and suffered few ($n = 3$) or no ($n = 6$) losses. When we considered either all males or all males with apparent success, fertilizations gained and lost by EPFs were neither positively nor negatively correlated ($r = 0.03$, $P = 0.84$, $n = 50$; $r = -0.08$, $P = 0.61$, $n = 42$). This result supports neither the trade-off nor the winners and losers relationship. However, when we considered only those males affected by EPFs, that is, males that experienced either losses or gains, there was a negative correlation between gains and losses ($r = -0.375$, $P = 0.06$, $n = 25$) and a significant negative correlation between gains and proportion of young lost to EPFs ($r = -0.453$, $P = 0.02$, $n = 25$). These results provide no support for the trade-off relationship and limited support for the winners and losers relationship.

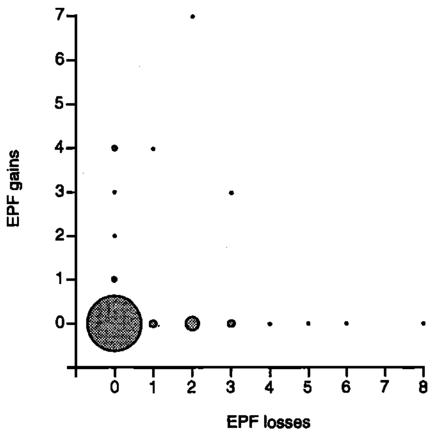

FIG. 3. Extra-pair fertilization (EPF) gains versus EPF losses in male Dark-eyed Juncos (size of circles proportional to number of observations, $n = 50$).

We next considered possible associations between a male's RS at home and his RS away from home (Fig. 4). A positive correlation would indicate that males successful in gaining EPFs were also successful both at preventing losses at home and in being socially mated to females with high success. We found no such correlation either among all males (home success vs. EPF gains) ($r = 0.07$, $P = 0.629$, $n = 50$) or among males with an apparent success of least one young ($r = -0.026$, $P = 0.870$, $n = 42$) (Fig. 4). Visual inspection of the pattern (Fig. 4) suggested that males with lowest and highest home success had few EPF gains, whereas those with low to intermediate home success were the ones that acquired EPF gains. To test this possibility that a nonliner relationship existed between home success and EPF gains, we divided observed values of home success into thirds: home success of zero to three offspring ($n = 29$, mean gains = 0.586, SE = 0.251), four to six offspring ($n = 18$, mean gains = 0.667, SE = 0.412), and

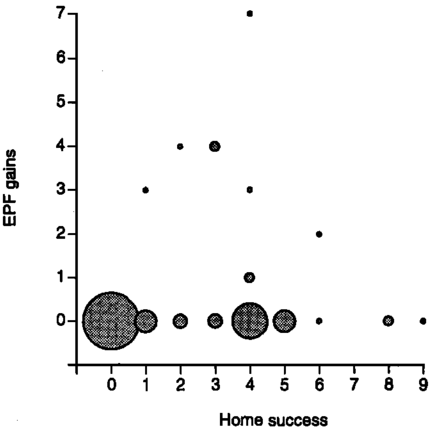

FIG. 4. Extra-pair fertilization (EPF) gains of males plotted in relation to their own home success (size of circles proportional to number of observations, $n = 50$).

TABLE 1. Comparing variance in annual apparent reproductive success (AARS) and annual genetic reproductive success (AGS) in male and female Dark-eyed Juncos.

| | Males ($n$ = 50) | | | Females ($n$ = 45) | |
|---|---|---|---|---|---|
| | Reproductive success | | Number of mates | Reproductive success* | Number of mates |
| | Apparent | Genetic | | | |
| Mean | 3.74 | 3.26 | 1.02 | 3.73 | 1.16 |
| Variance | 7.62 | 7.67 | 0.67 | 7.16 | 0.50 |
| Variance ratio (males/females) | 1.064 | 1.071 | 1.340 | | |
| Standardized variance (variance/mean$^2$) | 0.545 | 0.721 | 0.647 | 0.513 | 0.373 |
| Standardized variance ratio (males/females) | 1.060 | 1.407 | 1.734 | | |

* See text; for females AARS and AGS are the same.

seven to nine offspring ($n$ = 3, mean gains = 0). When we compared the three classes for gains, we found no significant differences ($F$ = 0.261, $P$ = 0.771).

To determine the impact of EPFs on variation in male RS, we compared variance in AARS to variance in AGS (Table 1, Wade and Arnold 1980), employing the standardized variance (SV, variance divided by the square of the mean [Wade and Arnold 1980]). AARS was somewhat less variable among males (SV = 0.54) than was AGS (SV = 0.72), suggesting that EPFs enhanced variance in male RS (ratio of standardized variances equaled 1.3, Table 1). We used $F$ ratios to compare the nonstandardized variances and found no significant differences. No test of significance was applied to the standardized variances.

Mean AGS of males was 3.26 young (SV = 0.721) (Table 1), and mean number of mates acquired was 1.02 (SV = 0.647) (Table 1). Analysis of the degree of dependence of RS on mating success (Table 2; Fig. 5; figure patterned after Arnold 1994, Fig. 1) showed that male RS increased with mating success. Males with zero known mating partners ($n$ = 13) left no known offspring. AGS of males with one mate averaged 3.65 young ($n$ = 26, SE = 0.39); with two mates 5.75 young ($n$ = 8, SE = 0.41), and with three mates 7.33 young ($n$ = 3, SE = 2.03) (RS = 2.63 MS + 0.58) (Table 2). RS also increased with MS when number of young per mate was held constant (partial regression coefficients significantly different from zero) (Table 2).

*Variation in AGS in females:* Mean AGS of females was 3.73 young (SV = 0.513), and mean number of mates acquired was 1.16 (SV = 0.373) (Table 1). Because we found no conspecific brood parasitism, AARS was the same as genetic success. AGS according to number of mates (Fig. 6) revealed that mean AGS of females with one mate was 3.52 young ($n$ = 25, SE = 0.27), whereas females with two mates averaged 5.83 young ($n$ = 12, SE = 0.78), and the single female with three mates produced 10 young. The genetic success of the seven females that produced no offspring was, of course, zero. RS increased significantly with MS (RS = 2.92 MS + 0.37) (Table 2; Fig. 6), and the effect was significant when number of young per mate was held constant (partial regression coefficients significantly different from zero) (Table 2).

Because the relationship between AGS and number of mates was surprising to us, we refer to a second female with three mates whose RS we determined. She was excluded from the sample by our method of randomly eliminating females present during both years of the study to avoid pseudoreplication (see section

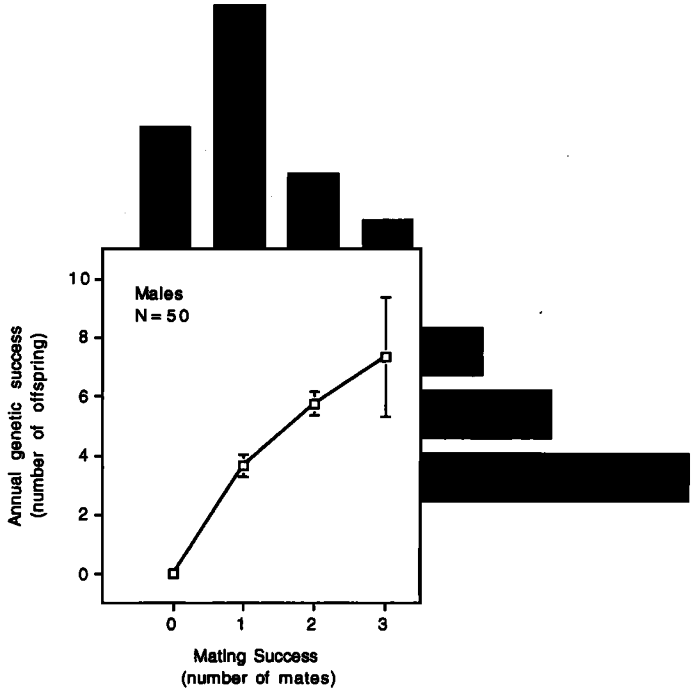

FIG. 5. Male annual genetic reproductive success (number of offspring, AGS; mean ± 1 SE) as a function of mating success (number of mates that served as genetic dams of young) in Dark-eyed Juncos (*n* = 50, 1990–1991) (after Arnold 1994; Fig. 1). Top histogram is a frequency distribution of numbers of males with zero to three mates (13, 26, 8, 3, left to right, respectively); right-hand histogram is a frequency distribution of total numbers of offspring produced by individuals with zero to three mates (0, 95, 46, 22, bottom to top, respectively).

*Statistical analyses and methodological considerations*). During the year for which this female was included, she had two mates and six young. During the year for which she was excluded, she had three mates and seven young. Thus high RS of females with three mates may occur more commonly than the single observation in Figure 6 would suggest.

Do females that are inherently more fecund attract more mates? If the null hypothesis is that male effort to sire young by EPFs is independent of a target female's potential RS, we would predict no relationship between AGS and the proportion of a female's young sired by EPFs (and thus potentially number of mates). We found instead that the proportion of young sired by EPFs increased with RS ($r = 0.475$, $P < 0.001$, $n = 45$) (Fig. 7). That correlation might have been driven by including in the analysis females that had zero RS. Therefore, we performed the same calculation limited to females with greater than zero RS ($n = 38$) and again found a positive correlation ($r = 0.425$, $P < 0.008$) (Fig. 7).

*Comparing males to females:* To ask whether the existence of EPFs generates stronger selection in males than in females, we compared means, variances, and standardized variances of key reproductive parameters of males and females (Table 1). Mean genetic success of males was 14% lower than that of females (3.26 vs. 3.73) (Table 1). This is consistent with the caveat that female RS can be

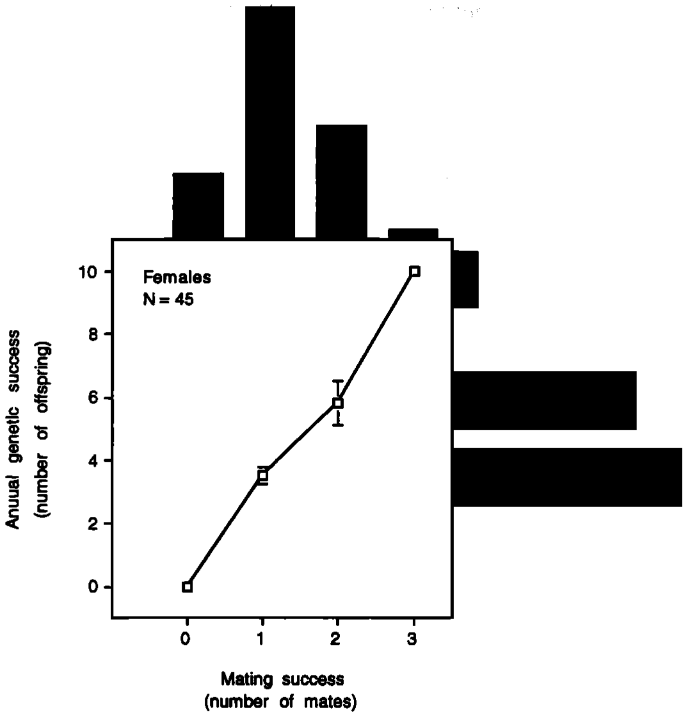

FIG. 6. Female annual genetic reproductive success (number of offspring, AGS; mean ± 1 SE) as a function of mating success (number of mates that served as genetic sires of young) in Dark-eyed Juncos ($n$ = 45, 1990–1991) (after Arnold 1994; Fig. 1). Top histogram is a frequency distribution of numbers of females with zero to three mates (7, 25, 12, 1, left to right, respectively); right-hand histogram is a frequency distribution of total numbers of offspring produced by individuals with zero to three mates (0, 88, 70, and 10, bottom to top, respectively).

known more accurately than male RS (see Methods), because females in the sample can be inseminated by males from outside the study population, whereas we would not detect cases in which males inseminate females not part of the study population. When we compared variance in genetic success, we found that it was 1.07 times greater in males than in females (7.67/7.16, [Table 1; right-hand histograms in Figs. 5, 6]); the standardized variance in genetic RS was 1.41 times greater in males than females (0.722/0.513) (Table 1). We used *F* ratios to compare the nonstandardized variances and found no significant differences. No test of significance was applied to the standardized variances.

Variance in number of mates obtained was also greater in males; the ratio of male to female variance in this measure was 1.34 (0.65/0.50) (Table 1; top histograms in Figs. 5, 6), and when variances were standardized, the ratio was 1.73 (0.647/0.373) (Table 1). *F* ratios revealed no significant differences in the nonstandardized variances, and no test of significance was applied to the standardized variances.

Consideration of the regression lines relating genetic RS to MS provides a comparison of the sexual selection gradient (Arnold 1994) in males and females (Figs. 5, 6; Table 2). The slopes did not differ.

TABLE 2. Regression analyses (simple and multiple) of the dependence of annual genetic reproductive success (AGS) on number of mates of males and females. For multiple regressions, second independent variable was number of young per mate.

| Independent variable/constant | Regression coefficient/constant | Standard error | $t$ | $P$ | $r^2$ |
|---|---|---|---|---|---|
| Males: dependent variable = AGS: $n$ = 50 | | | | | |
| Simple regression | | | | | 0.61 |
| Constant | 0.58 | 0.40 | 1.45 | 0.15 | |
| Number of mates | 2.63 | 0.30 | 8.62 | 0.00 | |
| Multiple regression | | | | | 0.91 |
| Constant | −0.54 | 0.21 | −2.54 | 0.01 | |
| Number of mates | 1.79 | 0.16 | 11.09 | 0.00 | |
| Young per mate | 0.79 | 0.06 | 12.61 | 0.00 | |
| Females: dependent variable = AGS, $n$ = 45 | | | | | |
| Simple regression | | | | | 0.59 |
| Constant | 0.37 | 0.50 | 0.73 | 0.47 | |
| Number of mates | 2.92 | 0.37 | 7.89 | 0.00 | |
| Multiple regression | | | | | 0.85 |
| Constant | −1.06 | 0.34 | −3.09 | 0.00 | |
| Number of mates | 2.04 | 0.24 | 8.35 | 0.00 | |
| Young per mate | 0.87 | 0.10 | 8.70 | 0.00 | |

## DISCUSSION

*Frequency of EPFs:* As in many songbirds studied to date (reviews in Westneat et al. 1990; Birkhead and Møller 1992; authors in this volume), EPFs are common in Dark-eyed Juncos: 45.2% of 42 males that had positive apparent success lost at least one offspring to an extra-pair sire, and the percentage of young sired by EPFs was 28%. No female laid an egg in the nest of another female. Interestingly, in 7 years of intensive field study prior to 1990, we had had no conclusive observational evidence of EPCs in juncos.

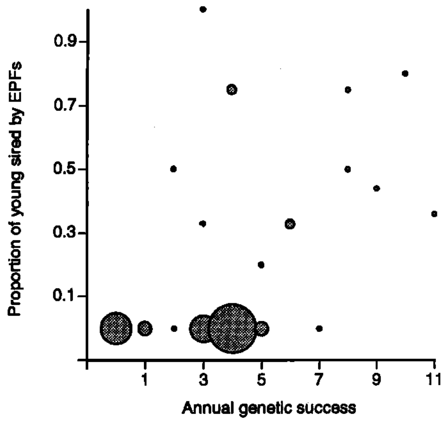

FIG. 7. Proportion of a female's young sired by extra-pair fertilizations in relation to annual genetic success of females (size of circles proportional to number of observations, $n$ = 45).

*EPFs and variation in male RS:* We had anticipated that if success at acquisition of EPFs was balanced by losses, EPFs might affect males equally. For example, when females begin to build nests synchronously and therefore are fertile simultaneously, the frequency of EPFs is known to rise in some species (Stutchbury and Morton 1995; Stutchbury and Neudorf, Chapter 5). In that case, a male's time spent off-territory inseminating other females might be at the cost of preventing his own social mate's access to EPFs. Under that hypothesis, the net effect of EPFs on variance in genetic success might be negligible, and a plot of EPF gains versus EPF losses would have a positive slope (trade-off relationship). Alternatively, if some males gain in genetic success via EPFs and are also successful at maintaining paternity at home, whereas other males are relatively unsuccessful both at home and away, the result would be that some males were highly successful, others were notable losers (Westneat 1992; Sorenson 1994), and still others were intermediate (winners and losers relationship).

In the juncos reported on here, EPFs did not affect all males equally (Fig. 3). Among those that either gained or lost paternity via EPFs, the two measures, gains and losses, were negatively correlated, significantly so when losses were expressed as a percentage of apparent success. Thus, male juncos tend either to gain or lose RS via EPFs but infrequently do both. This is an argument for the existence of differences in "male quality" in a free-living population of a monogamous species. Still, we saw more than one path to high genetic RS (home success + EPF gains) (Fig. 4).

Studies of patterns of EPF gains and losses across males in other species have shown them to be complex and varied (Gibbs et al. 1990; Westneat 1992; Dunn et al. 1994; Whittingham and Lifjeld 1995; Yezerinac et al. 1995; Dunn and Cockburn, Chapter 7). Juncos appear to resemble the pattern in Red-winged Blackbirds (*Agelaius phoeniceus* [Westneat 1993]) and Purple Martins (*Progne subis* [Morton et al. 1990]), in which males that gain from EPFs tend not to suffer EPF losses. In other species, such as Superb Fairy-wrens (*Malurus cyaneus* [Dunn and Cockburn, Chapter 7]), Yellow Warblers (*Dendroica petechia* [Yezerinac et al. 1995]), and House Martins (*Delichon urbica* [Whittingham and Lifjeld 1995]), males tend to experience both gains and some offsetting losses. In general, however, for males that acquire EPFs, the net effect on genetic RS is positive.

A related question is whether EPFs increase the opportunity for sexual selection (Wade and Arnold 1980). One way to answer this question is to compare variance in apparent success to that in genetic success, after standardizing the variances (Gowaty 1985; Westneat 1987; Arnold 1994; Whittingham and Lifjeld 1995). In male juncos, these variances were 0.545 versus 0.721 for apparent and genetic success, respectively, and the ratio of larger over smaller was 1.32. When these calculations were made on only those males that acquired a social mate and raised young (i.e., whose apparent success was greater than zero), the standardized variances were lower overall (0.296 vs. 0.444), and the ratio was actually greater (1.50).

These ratios in juncos are similar to or smaller than those reported from other species, for example, Red-winged Blackbirds (0.25 vs. 0.39, ratio = 1.56 [Gibbs et al. 1990]), Blue Tits (*Parus caeruleus*; 0.16 vs. 0.27, ratio = 1.69

[Kempenaers et al. 1992]), and House Martins (0.06 vs. 0.31, ratio = 5.17 [Whittingham and Lifjeld 1995]). Yezerinac et al. (1995) estimate that EPFs increased variance in RS in male Yellow Warblers 3- to 15-fold. Only Hill et al. (1994) do not report an increase in variance after considering the effects of EPFs on House Finches (*Carpodacus mexicanus*). Comparatively, the impact of EPFs on variance in male genetic RS in juncos is relatively low.

*MS and RS in males and females:* A priori, theory predicts that EPFs should increase variance in male RS more than in female RS (Trivers 1972; Wade and Arnold 1980; Andersson 1994). Female RS is usually thought to be limited by the numbers of eggs females can lay, not by access to extra-pair sires, whereas each offspring a male sires with a female mated to another male increases his EPF gains at the cost of the home success of the other male.

Nevertheless, of the three possible relationships between MS and RS outlined in the Introduction (Fig. 1), juncos appear to resemble most closely the third outcome, in which variance in both male and female RS is increased by EPFs, because genetic success increases with MS. This EPF-related increase in variance suggests that sexual selection (as defined here, dependence of RS on MS: individuals with more mates leave disproportionately larger numbers of offspring) is acting on both sexes. Thus, attributes that enhance multiple mating should be favored in both sexes.

Studies of males of other species are still relatively few and were summarized above. In general, male RS increases with MS (Webster et al. 1995). A few reports have also been made of enhanced RS in female birds that mate with more than one male (e.g., Westneat 1992; Wetton and Parkin 1991). Although EPFs are potentially costly, both for males (e.g., loss of opportunity to inseminate social mate, sexually transmitted disease) (Sorenson 1994; Stutchbury and Morton 1995; Stutchbury and Neudorf, Chapter 5) and for females (e.g., loss of paternal care, sexually transmitted disease) (Davies 1992; Whittingham et al. 1992; Westneat and Sherman 1993; Davies et al. 1996), most data seem to indicate that EPFs are either beneficial or neutral for the individuals involved.

How did males with multiple mates achieve greater RS? One explanation, that males that gain EPFs are socially mated to more fecund females, seems unlikely because our regression analysis showed that MS was a significant predictor of RS even when young produced per mate was held constant. Rather, some males apparently possess attributes that allow them to accomplish EPF gains without suffering EPF losses at home (Fig. 3). Our data say nothing about whether the attributes are associated with intersexual or intrasexual dynamics, or both.

To answer whether the lifetime fitness (survival and reproduction) of male juncos with high MS is also greater, we will need to relate survival to EPFs. Whittingham and Lifjeld (1995) found no relationship between annual survival and success at EPFs in House Martins, although they did find that high total success (herein AGS) was positively related to annual survival, as did Kempenaers et al. (1992) for the Blue Tit. A similar analysis for juncos is currently underway.

There are several possible answers to the question why females with more than one mate might produce more young: they may produce larger clutches, have greater hatching success, or produce more broods per season. These questions as well as whether females with extra-pair mating partners are larger, older, or otherwise more experienced will be addressed in a future paper (Parker et al., in prep.). Regardless of the reason(s), our results suggest multiple mating is beneficial to female juncos.

*Relative intensity of sexual selection in male and female juncos:* Whether our results should be taken to indicate that sexual selection acts on male and female Dark-eyed Juncos with similar intensity depends in part on how one defines sexual selection (Arnold 1994). If one defines it as the degree of dependence of RS on number of mates as we have done here, then, because the slopes of the lines relating RS to MS were nearly identical in male and female juncos, sexual selection can be said to be equally strong on both sexes. However, we are aware of two potential objections to this interpretation.

The first objection is that the relationship between RS and number of mates might arise purely as an artifact of sampling. If EPFs are visited randomly on females (in Poisson fashion), then females that achieve high RS may be more exposed to EPFs, and EPFs of such females would be more readily detected. Thus, if the probability of an EPF is 0.33 per egg laid, then a female that produces nine eggs and young should produce three by EPFs, whereas for a female that produces only one egg and young, in approximately two out of three cases it would not be EPF-sired. Under this hypothesis, EPFs, and thus potentially number of mates would increase with RS, but the reason would be simply that such fertilizations would be more detectable in more fecund females (see also Johnson and Burley, Chapter 2). However, our finding that the *proportion* of young sired by EPFs increases with AGS in female juncos (Fig. 7) makes it unlikely that the sole explanation for the observed relationship between RS and MS in the junco was an artifact of sampling.

A second objection addresses whether a statistical demonstration of dependence of RS on MS is sufficient to demonstrate sexual selection, particularly in females. This question challenges the definition of sexual selection used thus far in this paper and raises the issue of whether our results are interpretable as natural selection or sexual selection on females (compare McCauley 1983). Should we reserve the term sexual selection for situations in which female RS is enhanced directly or indirectly by additional mates, or should the term be extended to cover situations in which inherently more fecund females are more attractive to males and thus accumulate more matings?

It seems probable that some female juncos would have had higher RS than others, regardless of the number of males siring their offspring, because they were older or in better condition or possessed some other trait associated with fecundity. If we then suppose that males have means of assessing potential fecudity and more fecund females are more attractive to males, we might expect such females to have acquired more mates. The greater MS among females with higher RS would reflect male preference for females that would have been favored by natural selection, whether they had one mate or three. Greater mating success would be the result, not the cause, of higher RS, and, for those who hold that selection can be sexual only if mate acquisition causes differential RS, the situation in the junco would not suffice.

Stating this position in another way, in order for selection to be sexual, many would require not only evidence that RS increases with MS but also evidence that RS decreases in the absence of access to additional mates. The female that could leave equal numbers of young with or without access to extra males does not benefit from extra males. Her situation may be seen as fundamentally different from that of the male that can achieve higher RS only if he gains access to more females. Defined in this way, demonstration of sexual selection on females requires evidence of (1) direct enhancement of RS as the result of multiple matings, such as by greater fertility (percentage of eggs fertilized) (e.g., Wetton and Parkin 1991), protection from predators, or access to food (see Gray, Chapter 3) or (2) indirect enhancement such as by acquiring 'better genes' for her offspring (Kempenaers et al. 1992; Houtman 1992).

Sexual selection as it is defined by Arnold (1994) and Arnold and Duvall (1994) requires only demonstrated statistical dependence of RS on MS because when this condition holds—genetic RS increases with MS—it follows that the offspring of individuals that acquire more mates will be overrepresented in the next generation. Thus, phenotypic selection will have favored the attributes of parents that mate multiply. If the traits that made males or females more attractive or competitive or subject to chance-based advantages are heritable, then the traits too will be overrepresented in the next generation. But whether or not the traits are heritable, selection has occurred, and because that selection relates to mating success, it is sexual in nature.

Regardless of one's definition of sexual selection, most would probably agree that variation in RS that is related to variation in MS is the "raw material for sexual selection," because without such variation sexual selection cannot occur. In nature, selection on females is likely to be a blend of natural and sexual, and separating the quantitative effects of the two forms of selection poses a challenge (Webster and Westneat 1994; Webster et al. 1995). In the meantime, determining the degree of correlation of MS and RS should provide a useful comparative index of the potential for sexual selection, however it is defined.

As authors we do not fully agree as to which definition should be employed. We do note that if the standard for sexual selection is that access to multiple mates must be the cause of higher RS in the sense that RS would be diminished if that access were denied, then we are almost certain to conclude that sexual selection is generally less important in females than in males. If we continue to contemplate how female fecundity might serve as an attractant to males and have accompanying consequences for evolution of the female (and male) phenotype, our understanding of the role of mate choice in evolution as well as our understanding of differences between the sexes should be enhanced.

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# CHAPTER 5

# FEMALE CONTROL, BREEDING SYNCHRONY, AND THE EVOLUTION OF EXTRA-PAIR MATING SYSTEMS

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ABSTRACT.—When female control of EPCs is included as an important feature of extra-pair mating systems, our understanding of male mating strategies can become quite different. We illustrate this by examining how breeding synchrony of females affects extra-pair mating tactics. If females choose extra-pair mates, then breeding synchrony is expected to promote EPCs, rather than reduce opportunities for EPCs. When extra-pair mating systems are viewed as leks (Wagner, Chapter 6), it becomes clear that males should compete most intensely for EPCs when the availability of fertile females is highest. Likewise, females may also benefit directly from breeding synchrony if a simultaneous comparison of competing and displaying males allows for a more reliable assessment of male quality. We show how this model applies to the Hooded Warbler where males attempt EPCs when their mates are fertile, females seek EPCs from neighboring males, and EPFs are most common during the peak of fertility. Furthermore, in comparisons among species, breeding synchrony is generally associated with an extra-pair mating system.

DNA fingerprinting revolutionized the study of mating systems by detecting high frequencies of extra-pair fertilizations (EPFs) in a wide range of birds (e.g., Gibbs et al. 1990; Morton et al. 1990; Westneat 1990), many of which were previously considered to be both socially and genetically monogamous. This has been followed closely by another conceptual revolution, that female birds often seek and benefit from extra-pair copulations (EPCs) (e.g., Wagner 1991a; Kempenaers et al. 1992; Lifjeld and Robertson 1992). Early studies viewed EPCs as primarily a male strategy (Trivers 1972), and suggested that most EPCs resulted from forced copulations (Westneat 1987; Morton et al. 1990). This idea occurred in part because EPCs are forced in some species (McKinney et al. 1984; Sorenson 1994) and female resistance implies that copulations are forced (Birkhead et al. 1989). If EPCs are typically forced, it seems likely that females do not benefit from EPCs (e.g., McKinney and Evarts, Chapter 8). Recently, behavioral and genetic studies have shown that females of numerous species pursue EPCs and exert some level of choice over which males attain EPCs (e.g., Wagner 1991a; Kempenaers et al. 1992; Lifjeld and Robertson 1992; Mulder and Magrath 1994; Sheldon 1994; Wagner et al. 1996). Some studies view female resistance as a tactic to test male quality (Wagner 1991b), rather than strictly a response to forced

EPC attempts. Given the long history and recent popularity of female mate choice in behavioral ecology and evolution literature (e.g., Darwin 1871; Trivers 1972; Hamilton and Zuk 1982; Bateson 1983), it is perhaps surprising that female choice in extra-pair mating tactics was initially overlooked (but see Gowaty 1985; Smith 1988).

It is important to recognize that neither males nor females completely control EPCs; instead, there is often a conflict of interest between the sexes over fertilizations (Lifjeld et al. 1994; Johnson and Burley, Chapter 2). Both males and females have behavioral tactics to influence the outcome of extra-pair matings. Much of the initial theory on the evolution of extra-pair mating tactics focused primarily on male mating tactics (reviewed in Birkhead and Møller 1992) because the extent of female extra-pair mating tactics was not yet known. This theoretical framework is being revised as the sophistication and prevalence of female extra-pair mating tactics becomes better understood (Lifjeld et al. 1994). Here, we use the example of breeding synchrony (Stutchbury et al. 1994; Stutchbury and Morton 1995) to illustrate how far-reaching the effects of female extra-pair mating tactics can be for understanding the evolution of mating systems.

Breeding synchrony is a little-studied aspect of mating systems (Dunn et al. 1994b; Stutchbury and Morton 1995), despite its potential importance in the evolution of extra-pair mating tactics. Social mating systems are strongly affected by the availability of females in space and time (Emlen and Oring 1977). The temporal pattern of female fertility (i.e., breeding synchrony) is well recognized as an important determinant of social mating systems, because breeding synchrony affects a male's ability to defend fertile females as a resource from other males (Emlen and Oring 1977). When males provide parental care, synchronization of breeding among females tends to favor socially monogamous mating systems. However, when EPCs are an important part of the mating system, male mating success is no longer constrained by parental care. Extra-pair matings allow males to fertilize many females without defending additional mates or provisioning extra-pair offspring. Thus, the variation in male mating success can become highly skewed, even in species with long-term monogamous pair bonds (Wagner, Chapter 6).

Breeding synchrony affects the availability of EPC opportunities, and so should have an important effect on extra-pair mating tactics. The mate guarding hypothesis (Birkhead and Biggins 1987; Westneat et al. 1990; Birkhead and Møller 1992) emphasizes male mating tactics, and predicts that breeding synchrony *reduces* the frequency of EPCs because males must guard their own mates from extra-pair mating attempts instead of seeking EPCs with other females. Thus, when females are fertile simultaneously, few males are able to seek EPCs. An alternative hypothesis (Stutchbury and Morton 1995) assumes that females have extra-pair mating tactics and that males do not face a strong tradeoff between mate guarding and seeking EPCs. In this case breeding synchrony *increases* the benefits of extra-pair mating tactics for both males and females because they have more opportunities for EPCs when breeding is synchronized. The predictions of these two hypotheses are completely opposite, because different assumptions are made regarding the role of females in EPCs. This provides us with an interesting focus for exploring female extra-pair mating tactics and their effects on male extra-pair mating tactics.

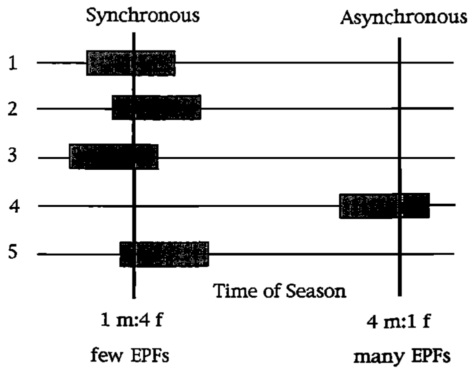

FIG. 1. The mate guarding hypothesis is illustrated for a hypothetical migratory songbird. The nesting chronology of each of five females is shown, with the fertile period of each female shaded. During synchronous nesting early in the season, the ratio of males seeking extra-pair matings (i.e., those not guarding their own mates) to fertile females is low (1:4), so each fertile female receives few EPC attempts. As a result, the frequency of EPFs should be low. Later in the season, the ratio of males seeking extra-pair matings to fertile females is high (4:1), so asynchronously nesting females receive many EPC attempts and should be more likely to produce extra-pair young.

In this paper we first outline the mate guarding hypothesis for the effect of breeding synchrony on the frequency of EPFs, and show that there is little evidence to support it. We argue that this results because the mate guarding hypothesis does not incorporate female extra-pair mating tactics, hence its two main assumptions do not generally hold. The first assumption of male control is clearly refuted by the broad range of female extra-pair mating tactics reviewed here. We then evaluate the second assumption that males usually face a trade-off between mate guarding and seeking EPCs. We show how breeding synchrony can promote extra-pair mating tactics and illustrate this idea using a case study of the Hooded Warbler (*Wilsonia citrina*). Finally, we discuss how this new view of breeding synchrony is important for understanding broader patterns in extra-pair mating tactics. Important aspects of ecology (breeding latitude, number of broods per season, predation frequency) affect the temporal distribution of fertile females, and thus result in predictable differences in extra-pair mating tactics among species.

## THE MATE GUARDING HYPOTHESIS

The mate guarding hypothesis for the effect of breeding synchrony on EPCs predicts that breeding synchrony reduces opportunities for EPCs (Birkhead and Biggins 1987; Westneat et al. 1990; Birkhead and Møller 1992), because males risk low parentage if they leave their fertile mates unattended (e.g., Westneat 1987; Morton et al. 1990; Hanski 1992). Thus, when the fertile periods of females in a population are synchronized, few males are free to seek EPCs and the operational sex ratio (ratio of number of males without fertile mates to number of fertile females) is low (Fig. 1). Females that breed asynchronously should produce many extra-pair young because they are subjected to numerous EPC attempts by males who are no longer guarding mates. This hypothesis assumes that females do not seek EPCs, and that females are unable or unwilling to reject repeated EPC attempts.

Although the mate guarding hypothesis is widely cited (e.g., Birkhead and Møller 1992; Meek et al. 1994; Hasselquist et al. 1995), few empirical studies have explicitly examined the effect of breeding synchrony or even reported how the frequency of EPCs varies seasonally. Evidence thus far seems to contradict the mate guarding hypothesis. First, species that breed very synchronously nevertheless have high frequencies of extra-pair young (e.g., Stutchbury et al. 1994; Whittingham and Lifjeld 1995, Yezerinac et al. 1995). Second, many species that breed relatively asynchronously do not have the predicted high levels of EPFs (Hill et al. 1994; Hasselquist et al. 1995). An interspecific comparison among many genera of songbirds found a positive, not negative, correlation between breeding synchrony and the frequency of EPFs (Stutchbury and Morton 1995).

The degree of breeding synchrony can also vary between and within populations, allowing additional tests of the mate guarding hypothesis. Here, too, the evidence does not provide general support. Dunn et al. (1994b) compared two populations of Tree Swallows (*Tachycineta bicolor*) that differed in breeding synchrony, but found no significant difference in the frequency of EPFs. In House Sparrows (*Passer domesticus*) Yellow Warblers (*Dendroica petechia*), Blue Tits (*Parus caeruleus*) and Red-winged Blackbirds (*Pheoniceus ageliaus*) there was no correlation between time of season and EPFs (Wetton and Parkin 1991; Westneat 1992; Kempenaers 1997; Weatherhead 1997; Yezerinac and Weatherhead 1997). In Eastern Bluebirds (*Sialia sialis*) and Hooded Warblers, relatively synchronous first broods had a *higher* EPF frequency than relatively asynchronous second broods (Gowaty and Bridges 1991a; Stutchbury et al. 1994, 1997).

In general, there is little support for the mate guarding hypothesis in comparisons among or within species. This hypothesis was based on logical assumptions at the time it was developed; in the next two sections we review these assumptions in light of recent literature.

## FEMALE EXTRA-PAIR MATING TACTICS

Female extra-pair mating tactics have been reported in at least 18 species from 10 families and two orders of birds (Table 1). In our summary we conservatively include only studies incorporating genetic and behavioral data or studies with extensive behavioral observations of EPCs. Female extra-pair mating tactics vary from rejecting unwanted EPC attempts to actively seeking EPCs from particular males. Extra-pair mating tactics give females some control of EPCs, thereby influencing the likelihood that a given male will fertilize a female's eggs (Lifjeld et al. 1994). Females can have extensive control of EPCs (EPC rejection, fertility advertisement) without being able to exercise optimal mate choice, because these tactics alone do not ensure access to the highest quality male. The actual paternity of the young results from the dynamics of female and male extra-pair mating tactics, male–male competition, and the possible conflict of interest between a female and her mate (Johnson and Burley, Chapter 2).

The first tactic we consider is female rejection of EPCs. This includes female interruption of the copulation (Wagner 1991b), evasive flights by the female (Kempenaers et al. 1995), and aggression directed toward the male (Burley et al. 1994). Females may also eject sperm after copulation as a way of influencing sperm competition (reviewed in Birkhead and Møller 1992). The ability to reject copulations allows females to prevent fertilizations by undesirable mates (Lifjeld

TABLE 1. Summary of species in which female extra-pair mating tactics have been reported.

| Order | Family | Species | Tactic* | Reference |
|---|---|---|---|---|
| Ciconiiformes | Scolopacidae | *Actitis macularia* | Sperm storage | Oring et al. 1992; Oring et al. 1993 |
| | Lariidae | *Larus novaehollandiae scopulinus*† | Rejection | Mills 1994 |
| | | *Alca torda*† | Rejection; foray | Wagner 1991a, b |
| | Phalacrocoracidae | *Phalacrocorax aristotelis*† | Foray | Graves et al. 1993 |
| | Procellaridae | *Fulmarus glacialis*† | Rejection; foray | Hatch 1987 |
| Passeriformes | Maluridae | *Malurus cyaneus* | Unknown | Mulder et al. 1994 |
| | Muscicapidae | *Sialia sialis* | Foray | Gowaty and Bridges 1991b |
| | | *Luscinia svecica* | Foray | Smiseth and Amundsen 1995 |
| | | *Panurus biarmicus* | Rejection; solicit | Hoi 1997 |
| | Paridae | *Parus atricapillus* | Foray | Smith 1988; Otter et al. 1994 |
| | | *Parus major* | Rejection | Björklund et al. 1992 |
| | | *Parus caeruleus* | Foray | Kempenaers et al. 1992 |
| | Hirundinidae | *Tachycineta bicolor* | Rejection; foray | Lifjeld and Robertson 1992; Venier et al. 1993 |
| | | *Progne subis* | Rejection | Wagner et al. 1996 |
| | | *Hirundo rustica* | Rejection | Møller 1988 |
| | Passeridae | *Taeniopygia guttata* | Rejection; solicit | Houtman 1992; Burley et al. 1994 |
| | Fringillidae | *Fringilla coelebs* | Solicit; foray | Sheldon 1994 |
| | | *Wilsonia citrina* | Solicit; foray | Neudorf et al., in press |
| | | *Agelaius phoeniceus* | Rejection; foray | Gray, this volume |

* See text for definitions of tactics.
† Based on behavioural observations only.

and Robertson 1992) but does not give them control over which males attempt EPCs. This tactic may not allow females to choose particular males as extra-pair partners.

The potential exists for females to exhibit postcopulatory control of EPFs via sperm storage, but there is no evidence to date that females have direct control over which sperm in their sperm storage tubules will eventually fertilize their eggs (Gilbert 1979; Birkhead et al. 1991; Birkhead and Møller 1992). Many species of birds store sperm in sperm storage tubules (Hatch 1983; Birkhead and Møller 1992; Briskie and Montgomerie 1992, 1993), so sperm from multiple males may be present in the reproductive tract of a female, leading to sperm competition (Parker 1970; Birkhead 1988; Birkhead et al. 1993). Females may be able to use the mechanism of last male sperm precedence (which results from sperm storage) to control paternity of their young (Compton et al. 1978; but see Birkhead et al. 1990; Sheldon and Birkhead 1994), a subject that requires further investigation.

Females can increase their probability of encountering extra-pair mates by solicitation or fertility advertisement. Montgomerie and Thornhill (1989) suggest that loud calls given by some species of female birds during the nesting period may function to advertise fertility and incite male–male competition. This type of behavior has been reported in the Chaffinch *Fringilla coelebs* (Sheldon 1994) and Hooded Warbler (see below). Males attracted to female displays often fight with the resident male, which could allow females to assess their quality as potential extra-pair mates (Sheldon 1994; Neudorf 1996; Hoi 1997). Females may have more choice of extra-pair mates when they actively solicit EPCs from neighboring males.

Females actively seek EPCs by visiting the territories of neighboring males (e.g., Kempenaers et al. 1992; Otter et al. 1994; Smiseth and Amundsen 1995) or a mating arena (Wagner 1991a). This tactic may give females more control of EPCs because they can choose an extra-pair mate and avoid interference from the social mate. Extra-territorial forays are a common form of female control (Table 1). Kempenaers et al. (1992) observed female Blue Tits soliciting copulations from males on neighboring territories and these females preferentially mated with extra-pair males that had high survival rates. Female Black-capped Chickadees (*Parus atricapillus*) enter territories and solicit EPCs from males that were most dominant in winter foraging flocks (Smith 1988; Otter et al. 1994). These studies indicate that females actively choose males for EPCs, and in many cases choose males of high quality (e.g., Bollinger and Gavin 1991; Graves et al. 1993; Houtman 1992; Ketterson et al., Chapter 4).

In some species there is good evidence for female control of EPCs, but the behavioral tactics involved are not well understood (Table 1). In the Superb Fairy-wren (*Malurus cyaneus*) the frequency of extra-pair young is extraordinarily high (76%) and there is clear female control of EPCs (Mulder and Magrath 1994; Mulder et al. 1994). Males visit other territories to display to females for EPCs, but copulations do not immediately follow. The geographic distribution of displays differs from that of EPFs, suggesting that females are not simply mating with males that display to them often (Mulder et al. 1994). In Purple Martins (*Progne subis*) there is strong genetic evidence for female choice for older males as genetic mates likely via copulation rejection (Wagner et al. 1996).

In a number of species, females exhibit more than one type of extra-pair mating tactic (Table 1). Several species can reject male EPC attempts as well as seek EPCs off their territory, so females have extensive control of copulations and actual paternity. Less common are species that both solicit EPC intrusions from their territory and seek EPCs off their territory (Sheldon 1994; Neudorf 1996). These phenomena indicate that females benefit from a mixed mating strategy, even if the actual benefits have proven difficult to quantify (Wagner 1992a; Dunn et al. 1994a). Extensive behavioral studies are necessary, and possibly insufficient (Westneat 1992), to rule out female control of EPCs because female tactics may be subtle and difficult to document.

When females seek and/or reject EPCs, the frequency of EPFs will not depend on the ratio of males attempting EPCs to fertile females, as assumed by the mate guarding hypothesis (Fig. 1). Furthermore, female extra-pair mating tactics may make paternity guards ineffective or unnecessary for some males (Kempenaers et al. 1995), allowing males to seek EPCs when their own mate is fertile. Below we evaluate the assumption that mate guarding constrains male extra-pair mating tactics when female fertility is synchronized.

## MATE GUARDING AND EXTRA-PAIR MATING TACTICS

A trade-off between mate guarding and seeking EPCs is intuitively appealing, because many studies have shown that removing a guarding male increases EPC attempts on the female (Björklund and Westman 1983; Møller 1987; Birkhead et al. 1989; Björklund et al. 1992; Riley et al. 1995). Therefore, many studies assume that mate guarding increases paternity (e.g., Gowaty and Plissner 1987; Hartley et al. 1993; Meek et al. 1994; Ritchison et al. 1994). Few studies, however, have directly tested whether increased mate guarding intensity actually increases paternity of eggs laid by a male's mate.

In Purple Martins, increased mate guarding is correlated with increased paternity, but only for young males (Wagner et al. 1996). In Eastern Bluebirds and Blue Tits increased mate guarding is associated with reduced paternity (Gowaty and Bridges 1991b; Kempenaers et al. 1995). Males that do not guard their mates closely have high paternity, and low quality males guard their mates who nevertheless seek EPCs from higher quality males (Gowaty and Bridges 1991b; Kempenaers et al. 1995; Wagner et al. 1996). An alternative paternity guard is frequent copulation with the mate, but in Tree Swallows within-pair copulation rate was also not significantly correlated with paternity (Lifjeld et al. 1993). These studies suggest that mate guarding may not be an effective paternity guard, so the trade-off between mate guarding and seeking EPCs may be weak in these and other species.

Close and persistent mate guarding is a common behavior in birds (Beecher and Beecher 1979; Birkhead 1979; Morton 1987; Møller and Birkhead 1991), so the mate guarding hypothesis could apply to those species. Males with fertile mates are expected to have a lower EPC effort than males with nonfertile mates. In some species male EPC effort is highest before or after their mate's fertile period (Westneat 1987; Morton et al. 1990; Hanski 1992). However, other studies report that males seek EPCs when their own mate is fertile (Sorenson 1994; Green et al. 1995; Wetton et al. 1995; Kempenaers 1997; Stutchbury, in press). Demonstrating a strong trade-off requires quantification of male EPC and mate guarding effort, and experimental manipulation to show the causal link between the two.

Male mate guarding tactics cannot be considered in isolation from female extra-pair mating tactics. The extensive control of EPCs by females (Table 1) reduces the effectiveness of mate guarding as a paternity guard. The prevalence and complexity of female extra-pair mating tactics means that our intuitive assumptions about extra-pair matings and mate guarding will not likely hold. We now know why the key prediction of the mate guarding hypothesis, that synchrony reduces the frequency of EPFs, is not supported by the evidence in the literature. Specifically, in many species, close mate guarding by males is not an effective tactic for ensuring paternity because females can reject unwanted EPCs (Björklund et al. 1992; Lifjeld and Robertson 1992; Westneat 1994; Kempenaers et al. 1995) and choose extra-pair mates despite male mate guarding (Table 1). Although there may be some risk from not mate guarding, in many species this cost is not so great as to preclude EPC attempts by males when their mates are fertile.

## FEMALE TACTICS, LEKS, AND BREEDING SYNCHRONY

The evidence that females actively seek EPCs has a broad range of implications, perhaps the most important being that females place strong sexual selection pressure on males to compete and display for EPCs (Wagner, Chapter 6). Wagner (1992b, 1993, Chapter 6) proposed that when females seek EPCs, the same mechanisms of female mate choice and sexual selection that operate in a lek will occur in the mating system of socially monogamous species. Females obtain only sperm from extra-pair males, and males must compete with each other directly, or via display, to obtain matings. Male displays and EPC tactics provide females with cues for discriminating among males (e.g., Kempenaers et al. 1992; Mulder and Magrath 1994; Sheldon 1994; Hasselquist et al. 1996), as occurs in leks (e.g., Bradbury and Gibson 1983; Höglund and Lundberg 1987; Alatalo et al. 1992; Andersson 1992).

If extra-pair mating tactics are similar to mating tactics in leks, then breeding synchrony could promote EPCs for two reasons. First, males are expected to compete most intensely for EPCs when the opportunities for EPCs are greatest. Second, females may be more likely to participate in, and seek, EPCs when male–male competition is intense. Thus, a concentration of female fertility in time increases male EPC effort, which in turn increases the likelihood that females will seek and accept EPCs. This assumes that females use relative competitive ability to assess male quality.

Breeding synchrony creates operational sex ratios that are relatively female-biased, which increases opportunities for males to obtain EPCs. Males must compete intensely with each other for EPCs, and are predicted to invest the most time and energy in seeking EPCs when the stakes are highest. Male EPC effort is predicted to increase as breeding synchrony increases, assuming that males do not face a strong trade-off between mate guarding and seeking EPCs. Depending on the cues females use to accept/seek EPCs, males may be able display to several extra-pair mates simultaneously (e.g., via song cues [Kempenaers et al. 1992; Hasselquist et al. 1996]). When few females are fertile at one time, the potential benefits to be gained from competing with other males for EPCs are relatively small.

Remarkably little is known about the energetic, survival, and time costs of male EPC tactics, or how these change with the availability of fertile females. The costs to males of EPC attempts are likely high, and include energetic and survival costs of male–male aggression (Wagner 1992b), and the costs of display to potential extra-pair mates (Kempenaers et al. 1992; Mulder and Magrath 1994; Hasselquist et al. 1996). In Razorbills (*Alca torda*), male–male competition for EPCs peaks when female fertility peaks (Wagner 1992b). In Hooded Warblers, male EPC effort is high early in the season when breeding synchrony is high (Stutchbury, in press).

Testing the prediction that male EPC effort is positively correlated with breeding synchrony requires controlling for the possible influence of paternal care, because male care to young often coincides with a period of low breeding synchrony late in the season. A seasonal decline in male EPC effort could result if males face a trade-off between feeding young and seeking EPCs (Westneat et al. 1990; Dunn and Cockburn, Chapter 7), rather than because breeding synchrony is low. These alternative hypotheses can be tested by quantifying EPC effort of nonparental versus parental males at the same time of year. The breeding synchrony hypothesis predicts low EPC effort even for males without nestlings.

Females can avoid or resist unwanted EPC attempts, so high male EPC effort does not necessarily translate into high EPF frequency. Nevertheless, breeding synchrony should also increase female receptivity to EPCs because their opportunities for evaluating male quality will increase as male–male competition for EPC partners increases (Bradbury and Gibson 1983; Höglund and Lundberg 1987; Alatalo et al. 1992; Andersson 1992; Kempenaers et al. 1992). Weatherhead (1997) stated that synchrony should not affect EPC behavior because it does not alter the *number* of extra-pair mates available to females. It is not the number of potential mates which is important in female choice, however, but whether females can reliably assess male quality. In other words, breeding synchrony produces a lek (Wagner, Chapter 6).

The effects of breeding synchrony on extra-pair mating tactics depend on the extent of female control, and whether males actually face a strong trade-off between mate guarding and seeking EPCs. The mate guarding hypothesis may still apply to some species. However, the mate guarding hypothesis thus far has little empirical support because EPFs are not uncommon when breeding is synchronous (Dunn et al. 1994b; Stutchbury et al. 1994; Stutchbury and Morton 1995). Below, we use our long-term study of Hooded Warblers to illustrate how the breeding synchrony hypothesis applies to a typical migratory songbird.

## A CASE STUDY: THE HOODED WARBLER

We studied a population of Hooded Warblers, a Neotropical migrant songbird, nesting in mixed hardwood forest in northwestern Pennsylvania, USA (Stutchbury et al. 1994). A color-banded population of 40 breeding pairs was monitored from 1991 to 1995, and blood was collected from adults and nestlings for use in DNA fingerprinting. Parentage of nestlings from 118 broods was determined using multilocus DNA fingerprinting with the 33.15 Jeffrey's probes (Stutchbury et al. 1997). We used a synchrony index (Kempenaers 1993) to quantify the overlap among females within the population in their fertile period. The breeding synchrony index for a given nesting attempt is the average percentage of females in

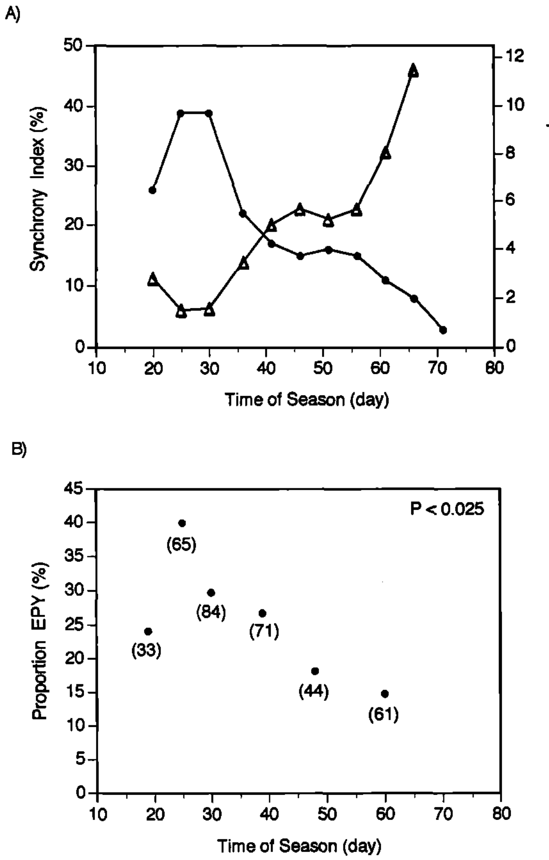

FIG. 2. (*A*) Seasonal variation in breeding synchrony (% females fertile simultaneously) and operational sex ratio (males without fertile mates to fertile females) of Hooded Warblers averaged over five breeding seasons. (*B*) The percentage of extra-pair young produced from nests at different times of the season follows a similar pattern as breeding synchrony. Median day of period sampled is plotted, and number of young fingerprinted for each period is shown in brackets. The first day of the breeding season is defined as 1 May.

the population that were fertile on the same days as the female in question. The fertile period for a female was conservatively defined as the period 5 days before laying the first egg to the laying of the penultimate egg in the clutch (e.g., Kempenaers 1993). Birds can likely use sperm that has been stored for longer than 5 days to fertilize eggs (Oring et al. 1992) but fertilization success tends to drop below 80% after about 5 days even under controlled conditions (Birkhead et al. 1989; Birkhead 1992).

*Synchrony and EPFs:* About 40% of females in the population were simultaneously fertile at the beginning of the breeding season (late May), but this dropped to 15–20% for the remainder of the season (Fig. 2A). Hooded Warblers are double-brooded and about one half of early nests are depredated (Evans Ogden and Stutchbury 1994), so nesting continues through late June and early July. The operational sex ratio follows a pattern opposite to breeding synchrony (Fig. 2A). If the operational sex ratio determines EPF frequency then EPFs should be un-

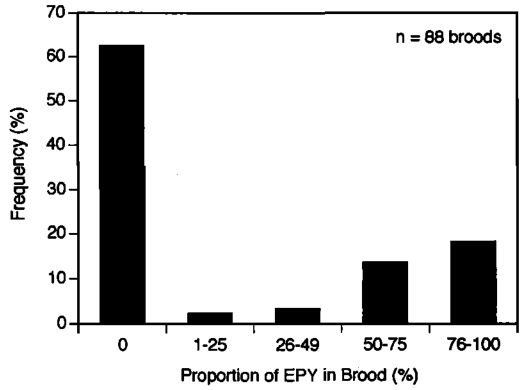

FIG. 3. Distribution of the proportion of extra-pair young per brood in Hooded Warblers for 1991–1995. Only broods with three or more young fingerprinted were included.

common early in the breeding season (Fig. 1; Westneat et al. 1990). However, if breeding synchrony promotes extra-pair mating tactics, the EPF frequency should be highest during the peak of breeding synchrony.

The proportion of young that resulted from EPFs varied seasonally (*G*-test, $G = 12.3$, d.f. $= 5$, $P < 0.05$), and followed the same temporal pattern as breeding synchrony (Fig. 2B). Females that breed asynchronously produced 50% fewer extra-pair young compared with females that breed synchronously. These results reject the mate guarding hypothesis and support the prediction that EPFs are positively correlated with breeding synchrony.

Behavioral and genetic data suggest that male Hooded Warblers do not face a trade-off between mate guarding and seeking EPCs. Males do not follow their mates closely during the fertile period (Neudorf 1996; Stutchbury, in press), although they do attack intruding males that attempt EPCs. Radio-tracking of male Hooded Warblers revealed they frequently seek EPCs on neighboring territories when their own mate is fertile (Stutchbury, in press). Furthermore, extra-pair males who obtained EPFs when their own mate was fertile ($n = 6$) did not suffer lost parentage at their own nests. Males can apparently seek EPCs without losing parentage at their own nests, likely because females have extensive control of EPCs (see below). Radio-tracking is being used to quantify the costs of male EPC attempts, and to test the prediction that male EPC effort is highest during the peak of breeding synchrony.

*Female extra-pair mating tactics:* Growing genetic and behavioral evidence indicates that female Hooded Warblers pursue EPCs. The proportion of extra-pair young within broods forms a strongly bimodal distribution (Fig. 3), which suggests that some females may be choosing to participate in EPCs and others are not. Within broods, all extra-pair young were usually fathered by one extra-pair male even though each female typically had four to six neighbors with which they could have had EPCs. These findings suggest that females may be selective in their choice of extra-pair mates because they are mating with one, presumably high-quality male (Stutchbury et al. 1997). There is a strong skew in male EPF success and males who obtain EPFs usually have full paternity of young in their own nests (Stutchbury et al. 1997). This pattern is consistent with either female

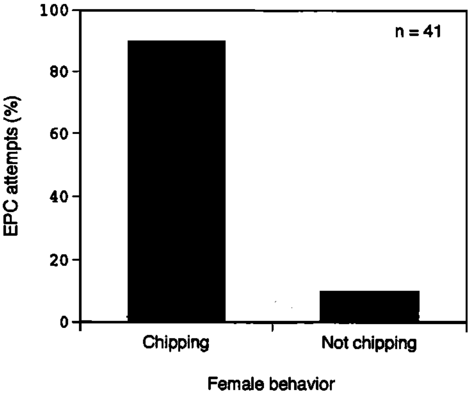

FIG. 4. Male extra-pair copulation attempts versus female chipping behavior in Hooded Warblers.

choice of EPC partners or male dominance in intrasexual competition. Some neighboring males may be particularly aggressive and persistent at pursuing EPCs and females may simply accept EPCs to minimize their costs (Westneat et al. 1990).

If female Hooded Warblers are simply accepting EPCs to minimize costs, then we would expect them to be secretive during their fertile period in order to avoid unwanted EPCs. However, the opposite is true. Female Hooded Warblers give a conspicuous "*chip*" call during the nesting period (Evans Ogden and Stutchbury 1994), the effect of which is to advertise their fertility (Neudorf 1996). Neighboring males are attracted to female chip calls. Ninety percent of EPC attempts we observed occurred after a female had begun a bout of chipping (Fig. 4). We define an EPC attempt as the intrusion by a male onto the territory of another male to within 10 m of the resident female. Successful EPCs were not observed because intruding males frequently were chased away by the resident male before they could attempt copulation. Furthermore, individuals often became obscured by vegetation during interactions, thus some EPCs may have occurred out of sight.

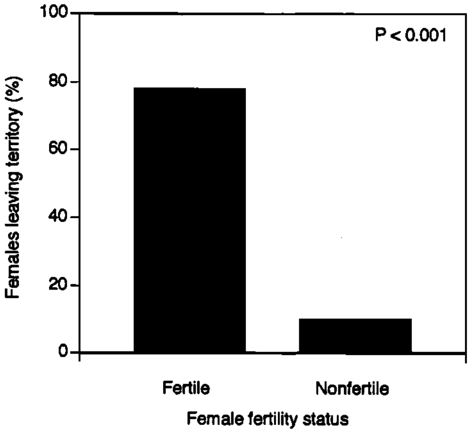

FIG. 5. Proportion of fertile ($n = 13$) and nonfertile ($n = 10$) radio-tagged female Hooded Warblers that visited neighboring territories.

Female chipping incited male–male competition (see Cox and Le Boeuf 1977; Montgomerie and Thornhill 1989) as intruding and resident males frequently engaged in aggressive interactions including chases, displays, and contacts (Neudorf 1996). These behaviors could allow females to directly assess male quality (e.g., Sheldon 1994).

Not only do female Hooded Warblers attract extra-pair males onto their territories by chipping, but they also leave their territories when they are fertile, presumably in search of EPCs (Neudorf 1996). We radio-tracked female Hooded Warblers from nest-building through incubation and found that almost 80% of females visited neighboring territories while they were fertile, but females rarely left their territories when incubating (Fig. 5). Only through the use of radio-tracking were we able to determine that females left their territories. We had never before documented females off their own territory either through behavioral observations or mist netting. In habitats where females are not easily seen or followed, radio-tracking may be the only way to determine the existence of female pursuit of extra-pair matings.

In summary, evidence from Hooded Warblers, a typical migratory songbird, is consistent with the breeding synchrony hypothesis. Below we present available evidence for other migratory temperate-breeding songbirds, and compare data available on tropical resident species.

## ECOLOGY, SYNCHRONY, AND THE EVOLUTION OF EXTRA-PAIR MATING TACTICS

The degree of breeding synchrony may be an important factor accounting for interspecific variation in EPF frequency. The extreme variation in EPF frequencies among birds has not been fully explained, partly because the original emphasis on ecology in mating system theory has been replaced by a strong emphasis on the tactics of individuals in obtaining EPCs (Reynolds 1996). Breeding synchrony is important because it is closely tied to ecology, allowing one to predict a priori the mating system of a given species. Ecological factors that promote high breeding synchrony are short breeding seasons, long-distance migration, single broods, and low predation frequencies. Ecology and life history determine breeding synchrony, which in turn sets the stage for sexual selection to favor the evolution of extra-pair mating tactics.

Generally speaking, breeding synchrony varies consistently with latitude, so on a broad scale important differences in extra-pair mating tactics are expected when comparing tropical versus temperate latitudes (Stutchbury and Morton 1995). Temperate zone songbirds, especially long-distance migrants, are constrained to breed synchronously because climate limits the length of the breeding season (Fig. 6A, B). Tropical species, however, are characterized by prolonged breeding seasons and asynchronous breeding (Fig. 6C). Morton et al. (1990) first suggested that latitude has an important influence on the evolution of extra-pair mating strategies because migratory songbirds appeared to have consistently high levels of extra-pair matings. Recent studies have confirmed that many temperate zone breeders have high EPF frequencies (e.g., Kempenaers et al. 1992; Dunn et al. 1994a; Stutchbury et al. 1994; Whittingham and Lifjeld 1995; Yezerinac et al. 1995). The few socially monogamous tropical species for which DNA fingerprinting has been done are genetically monogamous (Fleischer et al. 1994; Robertson

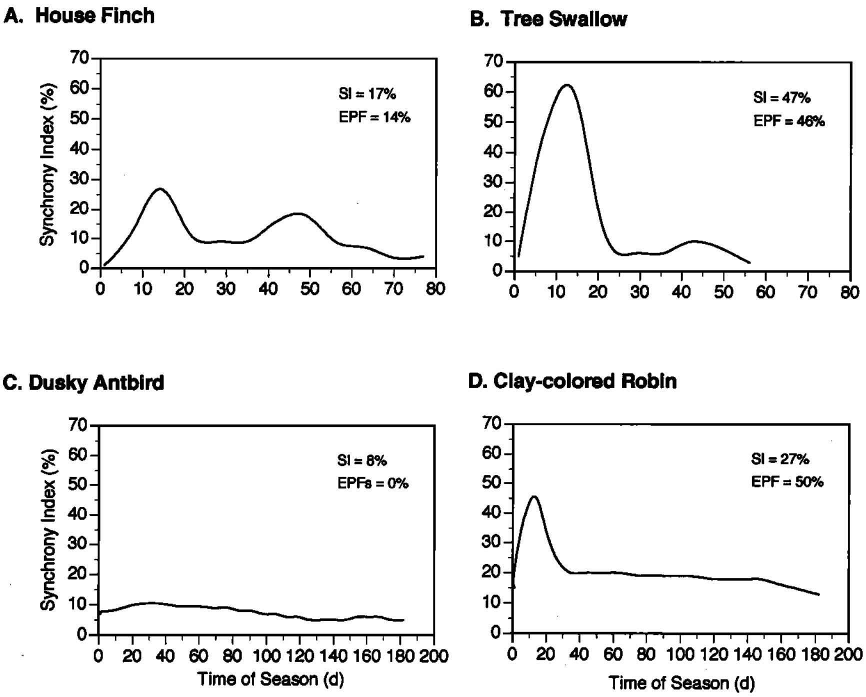

FIG. 6. Synchrony index versus time of season for temperate zone species that (*A*) breed asynchronously (House Finch [G. Hill, unpubl. data]) and (*B*) breed synchronously (Tree Swallow [R. Robertson, unpubl. data]) versus tropical species that are (*C*) asynchronous (Dusky Antbird [Fleischer et al., unpubl data]) and (*D*) synchronous (Clay-colored Robin [Stutchbury et al. 1998]). Note the prolonged breeding season of tropical songbirds.

and Kikkawa 1994; Fleischer et al. 1997). Testis mass correlates well with EPF frequency (Møller 1991; Møller and Briskie 1995), and tropical songbirds have significantly smaller testis mass compared with temperate zone birds (Stutchbury and Morton 1995). Tropical songbirds that do breed relatively synchronously (Fig. 6D), such as the Clay-colored Robin (*Turdus grayi* [Morton 1971]) and Yellow-green Vireo (*Vireo flavoviridis* [Morton 1977]) are expected to have abundant extra-pair matings. This has recently been confirmed for the Clay-colored Robin using DNA fingerprinting (Stutchbury et al. 1998).

Among temperate zone songbirds, variation in the degree of breeding synchrony correlates with EPF frequency (Stutchbury and Morton 1995). Species with relatively low breeding synchrony (Fig. 6A), such as the House Finch (*Carpodacus mexicanus*) (Hill et al. 1994), tend to have a low frequency of EPFs compared with highly synchronous breeders such as the Tree Swallow (Fig. 6B; Lifjeld et al. 1993). Tree Swallows are migratory, have low predation frequencies, and only a single brood per season (Robertson et al. 1992). This implies that ecological factors that affect synchrony can be important in predicting the evolution of extra-mating tactics among species. One way to test these ideas is to compare closely related species that differ in ecology. For instance, the Solitary Vireo (*Vireo solitarius*) and Red-eyed Vireo (*Vireo olivaceus*) are both migratory, but Solitary Vireos arrive much earlier to begin breeding and have a protracted and relatively asynchronous breeding season. As expected, the EPF frequency is low (6% of broods) in Solitary Vireos but high (57%) for Red-eyed Vireos (Morton, Stutchbury, and Piper, unpubl. data). These results suggest that breeding synchrony may be an important ecological predictor of extra-pair mating systems, although other social and ecological factors may also be important (Westneat et al. 1990; Møller and Birkhead 1993; Wagner, Chapter 6).

## CONCLUSIONS

Female control of EPCs is widespread and occurs in many species from diverse taxonomic backgrounds. Many different female extra-pair mating tactics exist, ranging from copulation rejection to active solicitation of EPCs. When female control is included as an important feature of extra-pair mating systems, our understanding of male mating strategies can become quite different, as in the case of breeding synchrony. When extra-pair mating tactics are viewed as leks (Wagner, Chapter 6), it becomes clear that males should compete most intensely for EPCs when the availability of fertile females is highest. Likewise, females may also benefit directly from breeding synchrony if a simultaneous comparison of competing and displaying males allows for a more reliable assessment of male quality. This revised and more complex view of extra-pair mating tactics results in a complete reversal of predictions regarding breeding synchrony. Rather than deterring EPCs, breeding synchrony is expected to promote EPCs. This model works well for the Hooded Warbler because males attempt EPCs when their mates are fertile, females seek EPCs from neighboring males, and EPFs are most common during the peak of fertility. We hope that this paper will encourage a closer examination of how male and female extra-pair mating tactics vary seasonally, and the extent to which female receptivity to EPCs depends on the intensity of male–male competition.

The association between high breeding synchrony and extra-pair matings seems robust in comparisons among species. This is encouraging in terms of being able to use ecological correlates as a first step in predicting when extra-pair mating systems are expected to evolve. Such ecological correlates are well established for social mating systems (Emlen and Oring 1977) but only beginning to be understood for genetic mating systems.

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# CHAPTER 6

# HIDDEN LEKS: SEXUAL SELECTION AND THE CLUSTERING OF AVIAN TERRITORIES

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ABSTRACT.—The discovery that socially monogamous birds copulate outside the pair-bond compels us to view mating and parental care relationships separately. The operation of sexual selection via extra-pair copulation suggests that the mating behaviors of monogamous species are more similar to those of promiscuous species than previously thought. Males in many promiscuous species aggregate in display arenas called leks, which form in response to females seeking copulation. This chapter reviews and synthesizes evidence that the mating systems of monogamous birds that pursue extra-pair copulations resemble those of promiscuous species. Razorbills (*Alca torda*) demonstrate that males in a monogamous species form leks for extra-pair copulation. Results from studies of Purple Martins (*Progne subis*) indicate that lek mechanisms may contribute to colony formation. These studies, combined with other evidence, suggest that the lek models can operate in many more contexts than those in which they were originally proposed. The "hidden lek" hypothesis predicts that the same mechanisms that form leks in promiscuous species can also explain certain aggregations of territories of monogamous species.

Beginning with Darwin (1871), sexual selection has been thought to operate much more intensely in promiscuous than in monogamous species. This is because there is high potential for variation in male mating success in promiscuous species, in which a minority of males often obtain a majority of matings (Emlen and Oring 1977). Sexual selection would operate much less intensely in monogamous species if each male copulated only with the one female with whom he provides parental care, as had traditionally been assumed. However, as Trivers (1972) predicted, the provision of parental care by monogamous males should not prevent them from attempting to fertilize females in addition to their mates. The discovery that male and female monogamous birds pursue extra-pair copulations (EPCs) and that males often do not sire the offspring in their broods (Birkhead and Møller 1992) suggests that monogamous species are more similar in mating behavior to promiscuous species than previously thought.

The prevalence of multiple mating in monogamous species has generated discussion over new definitions of mating systems. The term "social monogamy" has been defined in terms of biparental care, and "genetic monogamy" refers to copulations and fertilizations that occur exclusively within pairs (Westneat et al. 1990). Here, I refer to monogamy strictly in the social sense of a system of parental care in which one male and one female cooperate in raising offspring.

This makes no assumptions about which males copulate with a given female and fertilize her eggs. In contrast to monogamous species, promiscuous species are those in which males and females associate for copulation only, and in which the male provides no parental care (Gill 1995). Because males of monogamous species also do not provide parental care to extra-pair females, I refer to extra-pair matings by monogamous species as promiscuous copulations, the same as matings by promiscuous species. The ideas proposed here for monogamous species also apply to polygynous species, because polygynous males also form bonds with females for the purpose of providing parental care, and females can obtain EPCs.

This chapter develops the idea that when copulation is viewed separately from parental care relationships, sexual selection in monogamous birds operates similarly as in promiscuous species. In many promiscuous species, males aggregate for copulations into display arenas called leks, which will be discussed in the following section. My thesis is that the prevalence of EPC in monogamous species has created similar conditions to those that have produced leks. Just as males of some promiscuous species cluster into leks when females seek copulations, males of monogamous species may also cluster when females seek extra-pair copulations. The difference is that monogamous males defend territories to provide parental care. These territories may consist of a nesting territory only, such as in colonies (Wittenberger and Hunt 1985), or can be all-purpose territories that contain nesting sites and food. Monogamous males that defend all-purpose territories are often spaced much more widely than promiscuous males in leks. However, as I illustrate, all territory types can potentially become aggregated as a result of females pursuing EPCs. I suggest that the wider spacing of monogamous males in their territories disguises the effect of female behavior on their distribution. My aim is to demonstrate that when copulation is viewed separately from parental care, a lek may be "hidden" among the territories of monogamous birds.

The "hidden lek" hypothesis of territory clustering is an extension of the "EPC hypothesis" of colony formation (Wagner 1993). In that paper I proposed that sexual selection via EPC can contribute to colony formation. That prediction was not incompatible with hypothetical naturally selected benefits of high-density nesting (reviewed by Wittenberger and Hunt 1985). Here I develop the idea that the same mechanisms that produce leks can cause the clustering of males in all territory types, and not only in colonies. As in the case of colony formation, this prediction is not mutually exclusive with resource-based ideas that explain the distribution of avian territories (reviewed by Weins 1976) because numerous forces can interact to cause aggregation (Siegel-Causey and Kharitonov 1990). Rather, my goal is to suggest how sexual selection may act as one factor contributing to the clustering of territories.

## THE HIDDEN LEK HYPOTHESIS OF TERRITORY CLUSTERING

To understand how the hidden lek hypothesis can explain the clustering of territories of monogamous birds, it is necessary to define leks and examine how they may have evolved. Leks are aggregations of males that females visit for copulation. Males provide no parental contributions, and the area on which the lek is located contains no female-required resources other than males (Bradbury 1981; Höglund and Alatalo 1995). Typically, there is a male-biased sex ratio in the lek, with many males displaying to one or several females at a given time

(Emlen and Oring 1977). There is nearly always a skew in mating success, with one or several males obtaining a majority of the matings and most males obtaining none (Beehler and Foster 1988). There is often aggressive male–male competition, sometimes involving courtship disruption (Foster 1983; Trail and Koutnik 1986; Gratson et al. 1991), although females are generally able to obtain copulations (Bradbury 1981). The skew in male mating success in leks, combined with the lack of male parental care, has permitted the study of sexual selection without the confounding effects of male parental contributions (Bradbury 1981; Höglund and Alatalo 1995). This contrasts with monogamous species in which male parental care creates difficulties in discerning whether females prefer males for their phenotypic quality or for their value as providers to offspring. However, the relative convenience of studying sexual selection in leks does not preclude the operation of it in monogamous species. In fact, biparental care may set the stage for sexual selection by creating incentives for females to copulate with more than one male (Møller 1992).

In monogamous species, only one female can pair with the highest quality male in an area, but many females can obtain EPCs from him. This may select for females to preferentially pair with males that provide them with access to top males (Wagner 1993; Wagner et al. 1996a). Males that claim territories far away from more favored males may be less able to attract a mate, forcing them to readjust their territorial claims and breed near other males who might copulate with their mates. In species in which males are already paired when searching for a territory, a male may be compelled to follow his mate to her preferred territory near a higher quality male. Although breeding close to high quality males may cause other males to lose paternity, such a risk is preferable to not breeding at all. Additionally, even males that risk losing paternity might cluster to attempt EPCs from receptive females. Thus, the pursuit of EPCs by females could cause males to cluster in order to obtain breeding partners and/or extra-pair copulations.

## THE LEK MODELS AND EXTRA-PAIR COPULATION

The above sequence may be produced by the mechanisms of either of two models of lek formation, the hotshot model (Beehler and Foster 1988) and the female preference model (Bradbury 1981). The hotshot model predicts that leks form when secondary males cluster around a dominant male, or "hotshot" who obtains a disproportionate share of matings because of his superior competitive abilities (Beehler and Foster 1988) or his greater attractiveness to females (Höglund and Robertson 1990). The prevalence of females around the hotshot draws in secondary males, resulting in the formation of a lek around the top male. The female preference model proposes that males cluster in response to female preferences for appraising males in groups, where females can make side-by-side comparisons. The mechanism is simply that females bypass males that display solitarily, forcing them to display near other males. This mechanism may also cause the clustering of the territories of monogamous males (Wagner 1993). The difference between promiscuous and monogamous males is that promiscuous males defend only a display territory whereas monogamous males defend a breeding territory. However, the additional uses (and often the greater sizes) of the territories of monogamous males should not necessarily prevent these territories from becoming aggregated by the same mechanisms that aggregate lekking males.

An implicit difference in the assumptions of the two lek models is that, according to the female preference model, females benefit from male clustering. The hotshot model, in contrast, does not assume that females benefit from male clustering, and Beehler and Foster (1988) suggest that females may actually suffer costs from male clustering because of the increased frequency of courtship disruptions by secondary males. Therefore, the hotshot model implies that male clustering is merely an incidental by-product of female behavior. To apply the two models, with their contrasting assumptions, to monogamous species, I proposed two alternative routes to aggregation (Wagner 1993). In the first route, which is an application of the female preference model, females benefit from male clustering. In the second route, which is an application of the hotshot model, females do not benefit from male clustering. The different assumptions of the two models have ramifications for the relationship between EPC frequency and breeding density, which will be discussed in the section on Breeding density and EPC frequency.

I predict that the most important factor producing male clustering for EPCs is the opportunity of males to obtain EPCs, which is primarily determined by the proportion of females receptive to EPCs. Thus, I stress that the hidden lek hypothesis, like the lek models, is driven by the sexual *behavior* of males and females, more than by the genetic outcome of their behavior. Therefore, records of extra-pair copulation may be more predictive of male clustering than are data on extra-pair fertilization (EPF). Recent studies of EPF, however, are useful because the occurrence of EPF is proof that EPCs were performed. Genetic studies provide minimum estimates of EPC frequency because males are expected to employ paternity assurace tactics that should reduce EPFs (Birkhead and Møller 1992). For example, in Northern Fulmars (*Fulmarus glacialis*), 16% of females accepted EPCs, but 0% of offspring were sired by extra-pair males, presumably because pair males copulated with their mates frequently (Hunter et al. 1992). Willow Warblers (*Phylloscopus trochilus*) provide another example of a species in which EPCs, but not EPFs, were observed (Gyllensten et al. 1990). I assume that marked skews in EPF success result from skews in EPC success, which cannot be verified by existing studies. This assumption is useful for identifying potential similarities between promiscuous and monogamous species in patterns of male mating success. However, this assumption is not required by the hidden lek hypothesis because, as noted, male clustering is predicted to be driven directly by copulation behavior rather than by fertilization.

When EPC is rare relative to within-pair copulation, the percentage of females that are receptive to EPC may, nevertheless, be high. For example, in Razorbills (*Alca torda*), 50% of females accepted EPCs, but due to the high rate of within-pair copulation, only 2% of all copulations were extra-pair (Wagner 1992b). Similarly, in White Storks (*Ciconia ciconia*), 21% of females accepted EPCs whereas only 0.4% of copulations were extra-pair (Tortosa and Redondo 1992). If the percentage of females that engage in EPC is a key determinant of male clustering, then that variable is more predictive than the more widely reported percentage of copulations that are extra-pair.

## EPCS IN A LEK

The hidden lek hypothesis was developed from the mating system of Razorbills. Razorbills are typical of many seabirds in being colonial and monogamous, with a high degree of biparental care (Wagner 1992a). However, there is one unique feature of the Razorbill mating system that reveals with uncommon clarity how the pursuit of EPCs can cause the aggregation of monogamous male birds. Whereas other monogamous, colonial species usually copulate in their nesting territories, Razorbills perform most copulations outside their nesting colony on ledges that serve as mating arenas. The mating arenas permit the viewing of prelaying sexual behaviors of a monogamous species separately from nesting behaviors associated with nest defense, incubation, and chick rearing. When prelaying sexual behaviors are viewed independently from nesting behaviors, it is apparent that, prior to laying, monogamous Razorbills behave similarly to lekking species.

In this section I review evidence that the Razorbill mating arenas are formed by the same mechanisms as leks. To support this conclusion, I summarize the findings that all of the major features that characterize leks are also exhibited in the mating arena: the pursuit of copulations by females, male clustering for copulations, no female-required resources, no male parental care to extra-pair females, a male-biased sex ratio, male–male competition, and a skew in male mating success (Höglund and Alatalo 1995). The similarity of the Razorbill mating arena to leks suggests that the same mechanisms may have produced both types of arenas. In turn, I propose that these mechanisms can also produce the aggregation of breeding territories of some monogamous species.

Razorbills at my study population on Skomer Island, Wales, nest under boulders where their eggs and chicks are protected from predators (Hudson 1982). Although providing safety, the boulders also hinder social interaction, a factor that was thought to explain why Razorbills congregate on nearby ledges (Hudson 1979) that serve as mating arenas. Pairs commonly copulated in the colony near the nest site; however, 74% of within-pair copulations were performed in the mating arenas (Wagner 1992b). Unless indicated, the following account is from Wagner (1992d).

Conditions in the arenas changed markedly from the prelaying period to the laying period, when females became fertile fairly synchronously. During the prelaying period the arena resembled a typical colony of monogamous birds prior to egg-laying: the sex ratio was approximately equal and pair members usually arrived and attended together and copulated with each other frequently. However, as females became fertile, the conditions in the arenas dramatically changed and began to resemble those in a lek. First, the arena sex ratio became increasingly male-biased as females reduced attendance to feed at sea. As an increasing proportion of females became fertile, male–male aggression increased markedly. Males frequently initiated attacks against other males and attempted to drive them off the arenas (Wagner 1996a). Females demonstrated their receptivity to EPCs by visiting the arenas at this time, when virtually all females received aggressive-appearing mountings by extra-pair males, most of which were resisted by females. Despite the appearance of female resistance to EPCs, the mating arena provided clear evidence that females actively sought and controlled copulations (Wagner 1991a, b, 1996b). Unlike females of other colonial species that are subjected to such EPC attempts within their nesting territories, female Razorbills were not required to attend the arenas because there were no resources on those open ledges other than males (Wagner 1992b).

All paired females ($n$ = 49) visited the arenas where 96% received 1–14 EPC

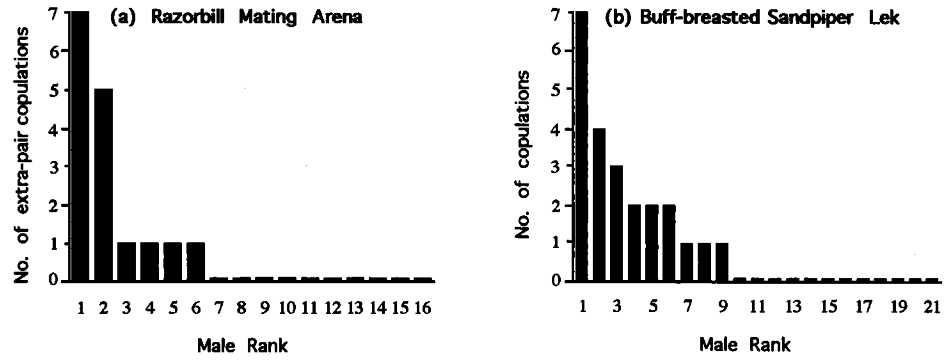

FIG. 1. The similarity between the distributions of (*a*) male extra-pair copulation success in a mating arena of monogamous Razorbills (Wagner 1992d) and (*b*) male copulation success in a lek of promiscuous Buff-breasted Sandpipers (*Tryngites subruficollis* [Pruett-Jones 1988]).

attempts prior to laying. Fifty percent of females accepted one to seven EPCs, and 82% of EPCs were performed in the mating arenas. In response to female receptivity, males aggregated in the arenas and competed for EPCs, with 87% of males making 1–39 EPC attempts. The distribution of EPC success was skewed, with the two most successful males obtaining 75% of the EPCs (Fig. 1a).

## THE MATING ARENA AND THE LEK MODELS

The conditions in the Razorbill mating arena closely matched those predicted to produce lek formation in the hotshot model. Beehler and Foster (1988) predicted that the skew in male mating success is caused by a skew in male dominance, rather than by female preferences for measurable phenotypic differences. In the Razorbill mating arena, there was a skew in male EPC success that was similar to the skew in male mating success found in many lekking species, such as the Buff-breasted Sandpiper (*Tryngites subruficollis* [Pruett-Jones 1988]) (Fig. 1b). In another lekking species, the Guianan Cock-of-the-Rock (*Rupicola rupicola*), the principal correlate of male copulatory success was the frequency of courtship disruptions, the distribution of which was skewed (Trail and Koutnik 1986) (Fig. 2a). This is strikingly similar to the finding that male Razorbill EPC success was determined by male fighting ability, primarily in the form of EPC disruptions, the distribution of which was similarly skewed (Fig. 2b). Also consistent with Beehler and Foster's prediction that male dominance explains mating success, there were no significant correlations between male Razorbill EPC success and any of numerous phenotypic variables. In contrast, the number of EPC disruptions, which could be a measure of male dominance, explained a majority (57%) of the variance in male EPC success (Wagner 1992d). Thus, the mechanism of the hotshot model that hypothetically produces leks may also have produced the Razorbill mating arena. This may have been accomplished by females visiting a ledge outside the nesting colony in order to rendezvous with a top male away from the females' mates. The increased presence of females could have then attracted other males to the ledge to attempt EPCs, causing the ledge to serve as a lek-like mating arena.

The female preference model (Bradbury 1981) could also explain the formation

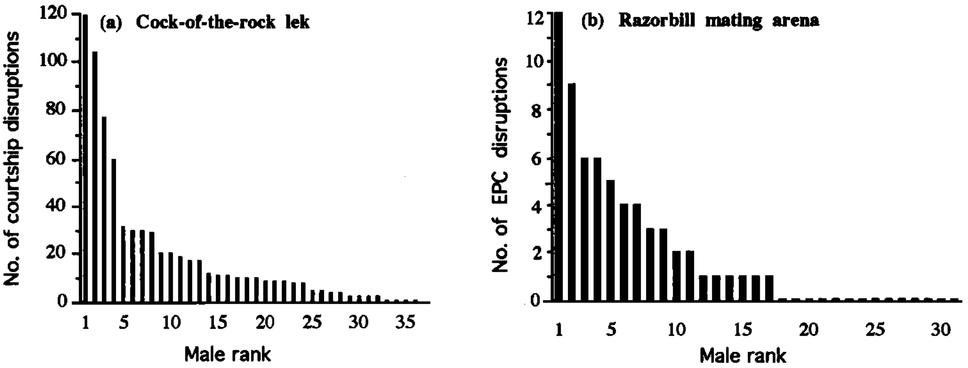

FIG. 2. The similarity between the distributions of the number of (*a*) male courtship disruptions in a Guianan Cock-of-the-Rock lek (Trail and Koutnik 1986), and (*b*) male extra-pair copulation disruptions in a Razorbill mating arena (Wagner 1992). In both the promiscuous and the monogamous species, disruptions were the most significant correlate of male mating success.

of the mating arena. The model's mechanism is that males gather in the open arena to be evaluated side by side by females, in this case for EPCs. Males that avoided being evaluated by remaining in the sparser nesting colony, where large boulders visually and physically separated individuals, might have been ignored by females, forcing them to join the aggregation of males in the arena to vie for EPCs. Additionally, given that Razorbills also require nesting partners, the arena can also attract unpaired males attempting to acquire mates (Wagner 1991c). In this context, the arena resembles a colony prior to egg-laying, in which sexual selection might operate on female selection of male nesting partners of varying quality (Zahavi 1986; Draulans 1988).

In summary, the Razorbill mating arena clearly exhibits all of the major features of a lek (Table 1). Males cluster in response to the pursuit of copulations by females. The arena contains no resources for females other than males. Like males in leks, male Razorbills in the mating arenas contributed only sperm to the females with whom they had promiscuous copulations (Wagner 1992a). There was also a male-biased skew in the sex ratio. And as in many leks, there was a skew in male dominance that was correlated with a skew in male mating success.

TABLE 1. The convergence of features of leks and the Razorbill mating arena. The same features exhibited in leks for promiscuous copulations exist in the mating arenas of socially monogamous Razorbills for extra-pair copulations.

| | Lek | Razorbill mating arena |
|---|---|---|
| Males aggregate where there are no resources | + | + |
| Females visit for copulations | + | + |
| Males provide no parental contributions* | + | + |
| Aggressive male–male competition | + | + |
| Skew in male dominance | + | + |
| Skew in male mating success | + | + |

* Monogamous males provide no parental contributions to extra-pair females.

## THE HIDDEN LEK IN THE PURPLE MARTIN COLONY

Razorbills have illustrated that by pursuing extra-pair copulations, monogamous birds can form a lek outside of their nesting colony. In this section, I address the question of whether the pursuit of EPCs can cause a lek to form in the same location where birds nest, thereby contributing to colony formation. The idea that EPCs can lead to colony formation differs from previous views that EPCs are a cost of coloniality (Birkhead et al. 1985; Emlen and Wrege 1986; Møller 1991). In contrast, Morton et al. (1990) viewed EPC as a benefit, to some males, that could contribute to colony formation. Their idea stemmed from their study of Purple Martins (*Progne subis*), in which they found a marked relationship between male age class and paternity. Whereas yearlings lost most of their paternity through EPFs, older males achieved nearly complete paternity of their broods. Morton et al. (1990) observed that older males could increase their fitness by recruiting young males to the colony and fertilizing their mates. The acquisition of extra-pair paternity would accrue major fitness benefits to old males because reproduction in Purple Martins is limited by food, of which males provision half to the nestlings (Wagner et al., 1996b). Morton et al. (1990) suggested that the benefits old males accrued from EPCs selected for coloniality. This idea was based on the different breeding schedules of the two age classes, with older martins arriving from migration and breeding earlier (Morton and Derrickson 1990). When the mates of the old males complete egg-laying, old males perform a loud predawn song which appears to attract migrating young males and females to the colony. At this time, old males are emancipated from nest-building and mate-guarding and can pursue the mates of the young males for EPCs, which appear to be forced (Morton 1987).

However, for the hidden lek hypothesis to explain colony formation it is necessary that females willingly accept EPCs, despite appearing to resist male attempts to mount them. Although some old males would clearly benefit by obtaining EPCs, young males and their mates would pay a cost. The mates of young males should therefore avoid nesting near old males if EPCs are forced, and young males should avoid nesting near old males if it means losing paternity. Alternatively, it is possible that females prefer to pair with old males, and if none are available then they pursue a mixed mating strategy of pairing with a young male and accepting EPCs from an old male. If so, then unpaired females may be drawn to old males in the colony and young males may be drawn to the unpaired females. Young males that attempt to nest far from old males might be unable to attract mates, as is suggested by the observation that a single old male is able to attract a female and establish a new colony whereas a single young male is not (Morton et al. 1990). Although sharing paternity with old males would be disadvantageous to young males, they could achieve greater fitness by breeding in a colony near old males who might fertilize their mates, than by foregoing breeding that year. The question of whether a lek is hidden in the martin colony, therefore, depends upon whether EPCs are forced or subtly accepted by females.

To test whether males or females control EPFs, I collaborated with Eugene S. Morton and Malcolm D. Schug. Our DNA fingerprinting analyses confirmed the marked relationship between paternity and male age class reported by Morton et al. (1990). Whereas old males lost only 4% of their paternity to EPFs, young males lost 43% (Wagner et al. 1996a). This could be caused either by old males forcibly inseminating the mates of the young males, or by those females permitting EPCs. Most EPC attempts occur on the ground when females alight to collect nesting material (Brown 1978; Morton 1987). The EPC attempts appear aggressive and females resist, but their resistance occurs in a wide range of forms. Some fly away before males can approach near enough to attempt mountings, whereas others continue foraging for material until the male is able to mount, at which point females emit an alarm call and struggle to escape (Morton 1987). This range in responses could be caused by variation in female experience in avoiding EPCs or in female receptivity to EPCs. In the latter case, receptive females may subtly permit mountings while also resisting as a ploy to test males (Westneat et al. 1990), as illustrated by female Razorbills in the mating arena (Wagner 1991b).

We found several lines of evidence that female Purple Martins did not receive forced EPCs, but subtly accepted EPCs. Contrary to the hypothesis that EPCs are forced by males, the number of extra-pair offspring females had was unrelated to the number of males that were available to pursue them. Consistent with the female control hypothesis, extra-pair paternity was strongly correlated with male age and not at all with female age: generally, old females paired to young males had EPFs whereas young females paired to old males did not. The much higher paternity of older males was not caused by more effective mate-guarding because old males guarded significantly less intensely than young males. The higher mate-guarding intensity of young males, despite their much lower paternity, suggests that young males guarded their mates to limit the females' ability to accept EPCs. We therefore concluded that EPCs were not forced, and that females paired with young males pursued a mixed mating strategy whereas females paired with old males avoided EPCs.

The question we then addressed was: which males obtained the EPFs? As expected, all assignable EPFs were obtained by old males. What was striking was the distribution of EPF success, with one old male obtaining seven of eight EPFs the first year (Fig. 3a) and another obtaining five of six the second year. This skew in EPF success matches the skew in mating success by lekking species (Fig. 1b) and the skew in EPC success by males in the Razorbill mating arena (Fig. 1a).

Thus, elements exists in the Purple Martin mating system that suggest a lek may be hidden in the colony. Although more work is required to confirm this view, the following scenario is suggested by the findings. Old males arrive at the colony early and defend extra nest cavities (Morton and Derrickson 1990). Their predawn song appears to recruit young females and males. Females are drawn to the colony by old males and young males are drawn by females. After all of the old males are paired, females pair with young males (who are permitted to occupy cavities previously defended by old males) and obtain EPCs from old males. These conditions, and especially the striking skew in EPF success achieved by old males, suggest that the mechanisms that produce leks may also contribute to the formation of Purple Martin colonies.

## HIDDEN LEKS IN ALL-PURPOSE TERRITORIES

As studies of Razorbills illustrate and Purple Martins suggest, the copulatory patterns of monogamous, colonial species can resemble those of lekking species.

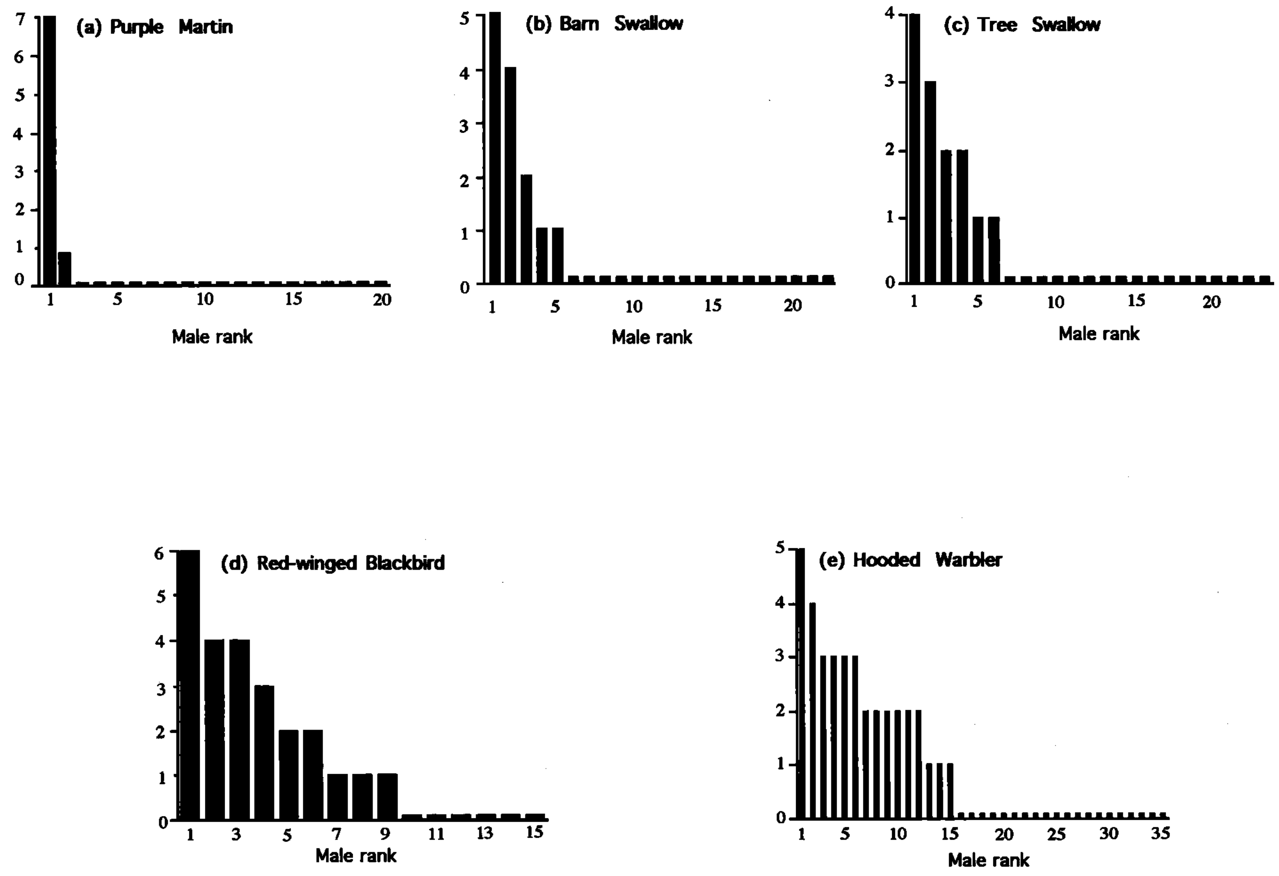

FIG. 3. Skews of extra-pair fertilization success of males of four monogamous species (*a*) Purple Martin (Wagner et al. 1996a), (*b*) Barn Swallow (*Hirundo rustica* [Møller 1993]), (*c*) Tree Swallow (*Tachycineta bicolor* [Dunn et al. 1994]), and (*e*) Hooded Warbler (Stutchbury et al. 1994), and one polygynous species, (*d*) the Red-winged Blackbird (Gibbs et al. 1990).

The Razorbill mating arena revealed that males in a monogamous species cluster for EPCs outside of their nesting colony. Results from our studies of Purple Martins imply that a lek may also exist within a colony, but is hidden by nesting territories. In this section I address how the hidden lek hypothesis applies to the majority of monogamous species that are not colonial, but defend much larger all-purpose territories.

A general approach for discerning whether all-purpose territories may be aggregated by sexual selection is to examine populations that exist in unsaturated habitats of uniform quality (see Stamps 1988). Highly clumped territories have been reported in several *Phylloscopus* warblers, such as in the Bonelli's Warbler (*P. bonelli*), Wood Warbler (*P. sibilatrix*), and Willow Warbler (Tianen et al. 1983), as well as in European Robins (*Erithacus rubecula* [Lack 1948]), Pied Flycatchers (*Ficedula hypoleuca* [Alatalo et al. 1982; Tianen et al., 1984]), and Goldcrests (*Regulus regulus* [Tianen et al. 1983]). This issue has been reviewed for North American warblers by Morse (1989). In the Kirtland's Warbler (*Dendroica kirtlandii*), territories were clumped within homogeneous stands of pine, and social factors were considered to affect their distribution. Other species that nest in aggregated territories in areas of apparently uniform habitat are Swainson's (*Limnothylpsis swainsonii*), Bay-breasted (*Dendroica castanea*), Blue-winged (*Vermivora pinus*), and Golden-winged (*Vermivora chrysoptera*) warblers (Morse 1989), and Yellow-breasted Chats (*Ictera virens* [Dennis 1958]).

These examples show that the clumping of all-purpose territories occurs. However, evidence that the hidden lek hypothesis can explain such clumping requires the exclusion of ecological habitat features as the primary cause of clumping. This was achieved in the long-term study at Hubbard Brook, New Hampshire, in which Sherry and Holmes (1985) found that the all-purpose territories of Least Flycatchers (*Epidonax minimus*) were significantly clumped for nonecological reasons (see Fig. 4). They found that the highly clumped distributions were produced by strong aggregative behavior that overrode features of vegetation, territories were aggregated in all sample transects, there were no measurable differences within occupied clumps of flycatchers versus adjacent unoccupied territories, and some aggregations had moved to adjacent areas between years, suggesting that suitable habitats were available nearby. Sherry and Holmes (1985:302) concluded that: "The significantly clumped dispersion of territories, in addition to their relatively small size, suggests to us that proximity of neighbors (i.e. sociality) is an important, if not essential, dimension of Least Flycatcher ecology."

Least Flycatchers demonstrate that all-purpose territories may be clumped for reasons unrelated to the distribution of resources. However, the territories of most species are probably affected by a combination of ecological and sexual factors. Thus, in order to identify the role that sexual selection hypothetically plays in aggregating males' territories, it will be fruitful to begin by applying the methods of Sherry and Holmes (1985) to other species with conspicuously clumped distributions, and to collect both genetic and behavioral data, as well as measurements of resource distribution. A specific prediction of the hidden lek hypothesis is proposed in the following section.

## DOES SEXUAL SELECTION NECESSARILY CAUSE CLUSTERING?

A question that is central to the hidden lek hypothesis is whether sexual selection via EPC is necessarily linked to clustering. It is likely that in some situations,

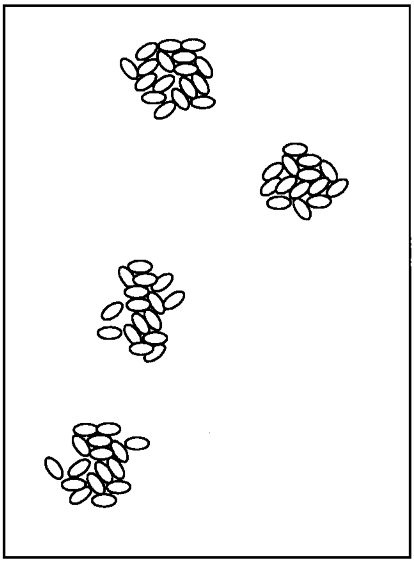

FIG. 4. A highly clumped distribution of all-purpose territories of a monogamous species, the Least Flycatcher (redrawn from Sherry and Holmes 1985). The aggregations existed in habitat of uniform quality, suggesting a social explanation for clumping (Sherry and Holmes 1985).

promiscuous mating interactions occur between monogamous birds without causing males to aggregate. Relatively large all-purpose territories contrast with the small display territories of lekking males and the small nesting territories of colonial males, yet similar sexual behaviors are performed (see Fig. 5). Females can pursue EPCs even across several territories (Stutchbury and Neudorf, Chapter 5), and males can compete for EPCs wherever there are receptive females. Evidence that similar interactions occur in an all-purpose territorial species as in lekking species is suggested by the skew in EPF success found in Hooded Warblers (*Wilsonia citrina* [Stutchbury and Neudorf, Chapter 5]) (Fig. 3e). Thus, a skewed distribution of mating success may occur even in saturated all-purpose territories of monogamous species. Evidence that the aggregation of male display sites is not essential for a lek-type mating system to operate can be found in the examples of so-called "exploded leks" in which males are dispersed relatively widely, and yet other typical lek features exist (Emlen and Oring 1977). Therefore, although clustering is often a product of sexual selection, it is not a prerequisite of it.

## ARE SOME HABITATS CLUMPED BEFORE BECOMING SATURATED?

Another important question is how sexual selection might have affected the distribution of territories in habitat that became saturated. When uniform habitat is saturated, by definition, there cannot be a clumped distribution. Nevertheless, it is possible that during settlement, clustering for EPCs had initially occurred but was later disguised by subsequent saturation. The difficulty in identifying whether clumping preceded saturation is that the initial clumping becomes hidden by the eventually even distribution of territories. This is analogous to human settlement patterns in which separate towns each grow into cities, then expand to the borders

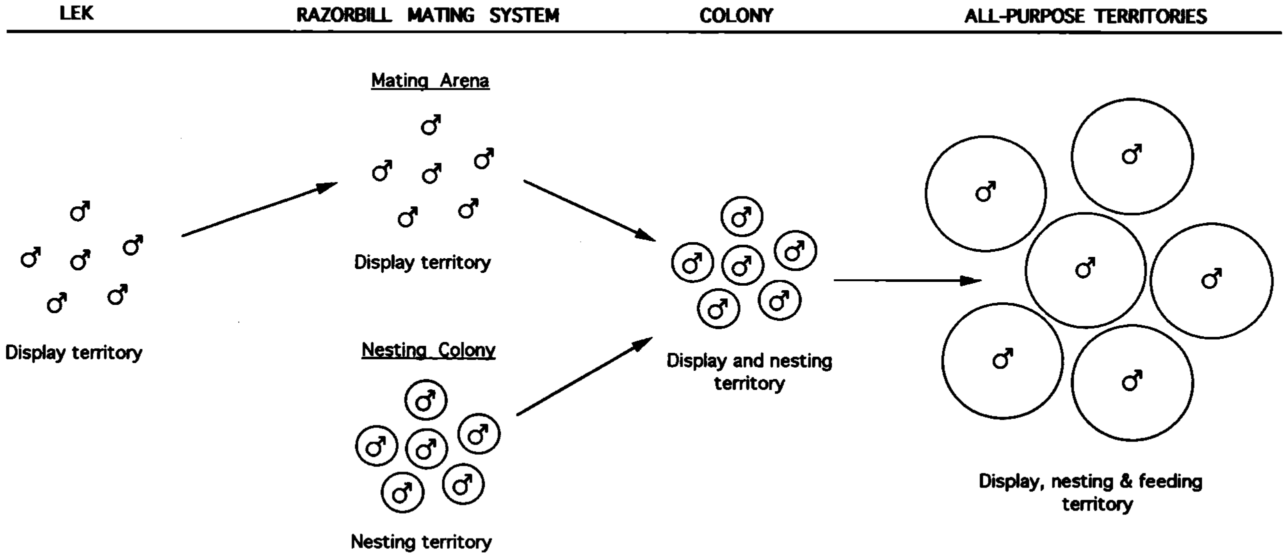

FIG. 5. The pursuit of copulations by females of promiscuous species cause males to cluster in (*A*) leks. When monogamous birds pursue EPCs, the same mechanisms that produce leks can also cause males of monogamous species to cluster into (*B*) mating arenas, (*C*) colonies, and (*D*) all-purpose territories. The figure illustrates that there is a continuum of lek "hiddenness," depending upon the number of uses and the size of the territories. It is clear that leks are formed by males seeking copulations. Beyond the unhidden lek of promiscuous species, the clearest example of male clustering for copulations is the Razorbill mating arena, in which males cluster for extra-pair copulations. A colony of monogamous species can show a similar degree of clustering in their nesting territories as male Razorbills do in their mating arena, but the nesting territory overlaps with and "hides" the display territory. All-purpose territories can also be clumped by the lek mechanisms. However, display territories overlap with relatively large nesting and feeding territories, which disguise the role of sexual selection in contributing to clumped distributions of territories.

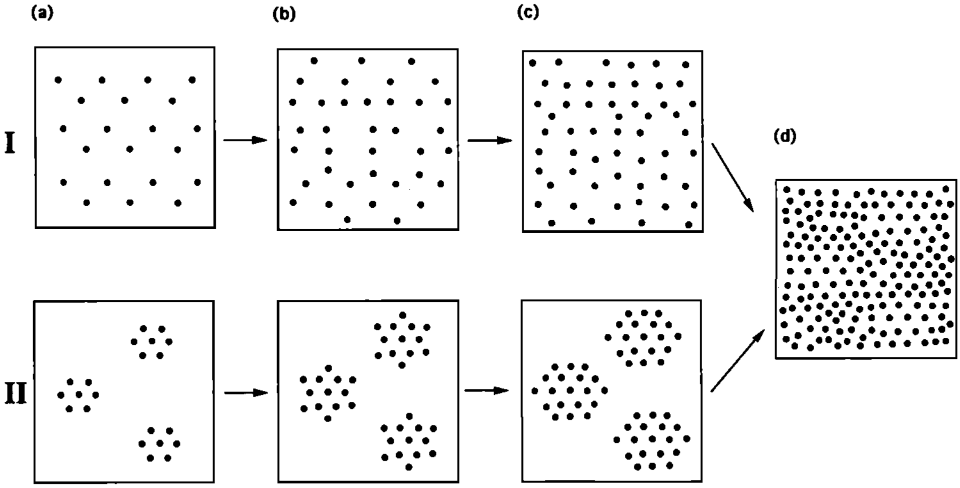

FIG. 6. Two routes to saturation in a patch of habitat of uniform quality. In the top sequence, I, newly arriving males are repulsed by previously settled males. Consequently, males maximize their distances from each other in an ideal-free distribution. As the habitat becomes saturated (d), males are forced to settle closer to each other. The same pattern of saturation can also develop from a very different process. In the lower sequence, II, males are drawn to each other, and settle in a clumped distribution. However, as the habitat becomes saturated, the original clumping becomes hidden. I term the phasing together of multiple aggregations the "metropolitan" process of habitat saturation.

of neighboring cities, until a metropolitan sprawl disguises the original clumped distribution.

If territorial male birds are repelled by each other, then we would expect them to claim territories that maximize their distances from each other, forming ideal-free or despotic distributions (Fretwell and Lucas 1970). In contrast, the hidden lek hypothesis predicts that males are drawn to each other because they are better able to access females by aggregating. Thus, there are two contrasting routes to saturation in uniform habitat (Fig. 6). A population-level test of the hidden lek hypothesis is to remove all males from a patch of uniform habitat and observe whether the area is resettled according to an ideal-free or despotic distribution, versus a clumped distribution that is produced by what I term the "metropolitan" process, in which aggregations converge (Fig. 6). At the level of individual males, the hypothesis predicts that later arriving males will preferentially settle near occupied territories, as was suggested in a study of Whitethroats (*Sylvia communis* [Persson 1971]). More specifically, the hypothesis predicts that young or low quality males will attempt to settle near males that are more attractive to females, as is suggested by Purple Martins.

## BREEDING DENSITY AND EPC FREQUENCY

Given that the hidden lek hypothesis predicts the aggregation of male territories, it is relevant to consider how breeding density and EPC frequency may interact. I stress that a positive relationship between density and EPCs *is not required* by the hidden lek hypothesis. I predict that what typically occurs is: (1) females seek EPCs, (2) males aggregate, *if they can*, and (3) females may obtain EPCs regardless of density. No matter how strong a force multiple mating by females exerts on males to aggregate, males are probably often constrained from aggregating by the need to defend all-purpose territories in resource-limiting habitats. The economic necessity of defending a large territory, therefore, should often play a more significant role in determining intermale distances than will female behavior. Nevertheless, situations exist in which there are positive correlations between breeding density and the rate at which EPCs are attempted (MacRoberts 1973; Birkhead 1978; Emlen and Wrege 1986; Hatchwell 1988; Møller 1991). There have also been several genetic studies showing that EPFs increase with density, such as in House Finches (*Carpodacus mexicanus* [Hill et al. 1994]), Great Reed Warblers (*Acrocephalus arundinaceus* [Hasselquist et al. 1995]), Red-winged Blackbirds (*Agelaius phoeniceus* [Gibbs et al. 1990]), and Eastern Bluebirds (*Sialia sialis* [Gowaty and Bridges 1991]). Correlations between density and EPC or EPF frequency suggest that a causal relationship may exist in some circumstances. The question is, what is the source of this hypothetical relationship? Rather than assuming that high breeding density promotes high EPC frequencies, the hidden lek hypothesis predicts the reverse, that *EPC promotes density*—the more that females seek EPCs, the more males aggregate.

A finding that is related to the positive relationship between density and EPC is that males often lose paternity to adjacent neighbors (Gibbs et al. 1990; Stutchbury et al. 1994; Hasselquist et al. 1995; Wetton et al. 1995). This pattern might be stochastic because fertile females may simply encounter neighboring males more often than distantly settled males. However, to conclude that neighboring males obtain most EPCs merely because of a high random encounter rate may, as in the density example, reverse cause and effect. The hidden lek hypothesis offers the alternative prediction that males become neighbors to the males that later inseminate their mates because their mates select them to be, as appears to be the case in Bearded Tits (*Panurus biarmicus* [Hoi and Hoi-Leitner, 1997]). In Purple Martins, young males lose paternity as a result of breeding in colonies near old males. If our interpretation is correct (Wagner et al. 1996a), young males do not breed near old males randomly—they do so for access to females, who are drawn to old males.

The circumstances that determine whether EPCs will promote density may depend upon whether the mechanisms of the hotshot model or of the female preference model are operating. The female preference model assumes that females benefit from male clustering because females can better appraise males that are densely aggregated. Once male aggregation is produced by this mechanism, the receptivity of females to EPC may increase along with their enhanced ability to appraise males. Thus, a feedback system may have evolved, wherein female preferences for males in groups produces density, which in turn creates greater female receptivity to EPCs. In this event, positive correlations between density and EPC frequency could be partially due to high density, not necessarily because of a higher encounter rate, but rather because of the enhanced ability of females to compare males.

In contrast, the hotshot model does not assume that females benefit from male clustering. In fact, females may actually suffer from male clustering if higher density leads to more frequent courtship disruption (Beehler and Foster 1988). Unlike the female preference model, the clustering of males by the hotshot mechanism should not necessarily increase female receptivity to EPC. If females can identify a top male without male clustering, then EPC frequency may be high regardless of breeding density. A general prediction that follows is that a positive correlation is expected between breeding density and EPC frequency when high density is produced by the female preference model but not when it is produced by the hotshot model.

### DENSITY AND SYNCHRONY

A new hypothesis that may have ramifications for the relationship between EPC frequency and density is the prediction that reproductive synchrony increases the opportunities of males and females to pursue EPCs. Stutchbury and Morton (1995) reported a positive correlation between breeding synchrony and extra-pair paternity among songbird taxa and proposed that variation in synchrony may explain much of the considerable interspecific variation in EPF frequency. As Stutchbury and Neudorf (Chapter 5) stress, the relationship between synchrony and EPF frequency may be caused by males attempting most EPCs during the peak of female fertility. In turn, females hypothetically respond with enhanced receptivity to the increased display rates of males. This prediction assumes that the female preference model is operating in that females are most receptive to EPCs when they can appraise multiple males simultaneously. Conversely, low extra-pair activity should occur when few females are fertile (i.e., during periods of asynchrony) because female receptivity should decrease as few males display. Thus, if synchrony and density covary, it could be because high synchrony creates EPC opportunity, which in turn produces aggregations.

## ARE THE LEK MECHANISMS CONSTRAINED BY MONOGAMY?

Throughout this chapter, I have strived to simplify the mating strategies of monogamous species by viewing copulation separately from parental care. The hidden lek hypothesis assumes that monogamous birds experience similar conditions in finding promiscuous copulation partners as do lekking species. The fact remains, however, that monogamous species have constraints on their ability to obtain promiscuous copulations that lekking species lack. The existence of constraints is a challenge to the hidden lek hypothesis because if constraints are sufficiently severe, then the lek mechanisms could be prevented from operating. Therefore, it is necessary to identify these constraints and evaluate whether they could prevent the lek mechanisms from aggregating the territories of monogamous species.

### CONSTRAINTS AGAINST FEMALE PURPLE MARTINS

A major constraint experienced by monogamous species that promiscuous species lack is the possession of a nesting partner. In the example of Purple Martins, females paired to young males accepted EPCs from old males, at a considerable fitness cost to their mates. The young males, therefore, are expected to reduce the risk of losing paternity by trying to prevent their mates from accepting EPCs. Observations of young males attacking their mates (Morton and Derrickson 1990) might be explained by young males steering the female away from extra-pair males (Wagner et al. 1996a). The conflict between young males and their mates could explain why the paternity achieved by young males was largely determined by two variables that apparently constrained their mates from obtaining EPCs. One variable was mate-guarding intensity, which was significantly and positively correlated with paternity achieved by young males ($r_s$ = 0.66). Young males apparently escorted their mates not only to deprive other males of access to the female, but also to deprive the female of access to other males. The second correlate of paternity for young males was their body size relative to that of their mate. Young males that possessed longer wings than their mates achieved a mean of 87% paternity, compared to only 21% by those that had shorter wings than their mates, and wing difference was significantly correlated with paternity ($r_s$ = 0.69). Additionally, mass difference was almost significantly correlated with paternity ($r_s$ = 0.49). Given the occurrence of male–female aggression, a likely explanation for these correlations is that young males that were larger than their mates were able to physically prevent them from obtaining EPCs, whereas those that were smaller failed to control the female. Wing difference, body mass difference, and mate guarding intensity together explained 77% of the variance in paternity of young males, and all three variables apparently constrained females from obtaining EPCs (Wagner et al. 1996a).

Our results suggest that females paired to young males attempted to be fertilized by old males, but were constrained by their mates' attempts to prevent them from encountering old males. Thus, it is possible that all females paired to young males preferred to be fertilized by old males, but 53% of these females failed to obtain EPFs because of limitations imposed by their mates. Because typically one half of the breeding males are of the young age class, it is reasonable to predict that one half of the females seek EPCs. This is lower than females in those promiscuous species in which all females can obtain copulations in leks. This difference raises the question of whether 50% of females seeking EPCs provides a sufficient selective force for monogamous males to cluster for EPCs in a colony, as males of some promiscuous species cluster in leks.

## CONSTRAINTS AGAINST RAZORBILLS

One way to appraise constraints against females is to examine the proportion of females that had opportunities to obtain EPCs. Because of the pursuit of EPCs by female Razorbills in mating arenas, Razorbills provide a clear case study of female opportunity. Although females were never inseminated by force (Wagner 1991a; Wagner 1996), their ability to willingly accept EPCs was constrained by two factors, the presence of their mates and disruptions of extra-pair mountings by other males. Thus, an EPC opportunity for females consisted of receiving an undisrupted extra-pair mounting in the absence of their mates. Although 31 of 33 females received such opportunities in the arenas prior to laying, 22 (71%) rejected all (range 1–7) EPC opportunities (Wagner 1992c). Given that females apparently created many of these opportunities by visiting the arenas when their mates were absent (Wagner 1992b), the rejection of all opportunities in the arenas by a majority of females suggests that most females did not necessarily seek fertilizable EPCs in the arenas. The most significant observation, however, is that whatever the reason for the high frequency of female EPC rejection, nearly all males clustered for EPCs.

Razorbills also demonstrate that males suffer similar constraints as females, because as noted in the section on EPCs in a lek, females also disrupt their mates'

EPC attempts (Wagner 1992e). Females attended during 67% of the days their mates attended, and when females were present, they disrupted at least 46% of their mates' EPC attempts, creating a substantial constraint for males (Wagner 1992e). Female interference may explain why males made 94% of their EPC attempts when their mates were absent. Another constraint against male Razorbills is the need for both mates to incubate. This resulted in males markedly reducing their arena attendance after their mates had laid. At the same time that monogamous male Razorbills suffer these constraints that males in lekking species lack, they must also compete with an aggressive intensity that is similar to that of males in leks.

Given these constraints, it may seem surprising that monogamous male Razorbills and males in lekking species show a comparable proclivity to cluster. However, these differences might be bridged by a notable similarity in the distribution of mating success of the males of both mating systems. As Figure 1 and 3 illustrate, the distribution of both lek matings and EPCs or EPFs are highly skewed, with most males obtaining no matings or fertilizations. Thus, what monogamous and lekking males have in common is a very high probability of failure. These skewed distributions of male mating success indicate that even when most males consistently fail to obtain matings or fertilizations, most males will attempt them anyway. This similarity suggests that the benefits of obtaining promiscuous matings generally outweigh the costs for males of both mating systems, and may help explain why monogamous male Razorbills cluster for EPCs despite their additional constraints. The 50% of female Razorbills observed accepting EPCs (mostly in the arenas) is comparable to the estimated 50% of female Purple Martins seeking EPCs in their colony. The question is, what proportion of females seeking EPCs in other monogamous species is necessary to cause males to cluster? The answer is probably that males cluster according to EPC opportunity, which includes various factors, such as the proportion of fertile females available at a given time (Stutchbury and Morton 1995).

The existence of constraints imposed by nesting partners might suggest that female behavior is less likely to drive male clustering in monogamous than in promiscuous species. However, an interesting difference is that the relative lack of constraints on promiscuous females results in their usually copulating with only one male (Birkhead and Møller 1993). For monogamous females, in contrast, the constraint of having a nesting partner selects for multiple mating (Møller 1992). If the pursuit of multiple matings by females drives males to cluster, then males of monogamous species may paradoxically be more, not less, prone to cluster than males in promiscuous species.

## FEMALE LEVERAGE AND MALE-BIASED SEX RATIOS

Given that males often try to prevent their mates from obtaining EPCs, a question raised is: why do females succeed in obtaining EPCs as often as they do? For example, males might be expected to retaliate against unfaithful mates by withholding parental care (Møller and Birkhead 1993; Wright and Cotton 1994) or by evicting the female from the territory. This could compel females to cease or reduce their pursuit of EPCs. However, the ability of the male to win this conflict depends in large part on his ability to attract a replacement mate. In this section, I consider how one factor, a male-biased sex ratio, may give females leverage with their mates.

It appears that male-biased skews are the rule in birds (Lack 1954), as evidenced by all of 26 species surveyed showing surpluses of males (Breitwisch 1989). Purple Martins, for example, have a male-biased skew in the breeding population that results in the failure of some young males to acquire mates each year (Wagner et al. 1996a). The male-biased sex ratio may provide females with leverage at two stages of reproduction: during pair-bonding, and when seeking EPCs after pair-bonding. At the first stage, the sex ratio imbalance may provide females with influence over where males claim nesting territories. For example, young males may be drawn into the colony because of female preferences for mates that provide them with access to old males. At the second stage, the male-biased sex ratio could provide females with the ability to pursue EPCs without risking male-imposed sanctions. Although young males often attempted to prevent their mates from obtaining EPCs, even males that did not mate-guard effectively did not reduce their parental effort (Wagner et al. 1996b) or evict the female prior to laying.

Another example of a male-biased sex ratio providing female leverage can be deduced from a study of House Finches in which there was a strong male bias in the breeding sex ratio and all nests with EPFs were aggregated (Hill et al. 1994). As suggested in the second section, the clumping of nesting territories might be caused by female preferences for mates that provide them with access to more favored males, from whom the female can obtain EPCs. The male-biased sex ratio would force solitary males to nest near more preferred males to find mates, resulting in the observed pattern of clumping. Given male-biased skews in the sex ratios of many species, the ability of females to force males to aggregate may be widespread.

## CONCLUSIONS

The discovery that EPC produces sexual selection in monogamous birds provides great scope for reinterpreting avian mating systems. In this chapter I have proposed that the pursuit of EPCs by monogamous (and polygynous) species creates similar conditions to those that produce leks. Males may aggregate in response to female behavior for two reasons: to obtain EPCs and/or to obtain a nesting partner. Strictly, it is the clustering of monogamous males for EPCs rather than for nesting partners that resembles leks. The main similarity is that for both lek matings and EPCs, male mating success is often highly skewed, creating intense sexual selection. In contrast, there is usually much less variation among monogamous or polygynous males in the acquisition of nesting partners. However, when such variation is produced by a male-biased sex ratio (Breitwisch 1989; Hill et al. 1994) or polygyny (Searcy and Yasukawa 1995), the lek mechanisms may also cause males to cluster to acquire nesting partners. In Purple Martins, young males may join colonies to find mates. As predicted by the hotshot model, young male martins, like males in lekking species, may be drawn to more attractive males to gain access to females. In contrast, old males may cluster in colonies for EPCs. Thus, the simple mechanism of the hotshot model can operate whether the male incentive is to acquire females as breeding partners or for promiscuous copulations. The female preference model also provides a simple mechanism that can operate in a wide range of circumstances—males cluster because females prefer to select among males in groups. This mechanism also may produce male clustering for nesting partners and EPCs.

The hidden lek hypothesis does not require a positive relationship between breeding density and EPC or EPF frequency. However, when such a relationship exists, it might be explained by female receptivity to EPCs producing high density, more than by high density producing EPC opportunity. With the same logic, the hidden lek hypothesis might also explain the common finding that most EPFs are obtained by neighboring males. The hidden lek hypothesis predicts that this pattern is not stochastic, but is a result of a priori female preferences for mates that provide them with access to other males.

The hidden lek hypothesis also predicts that when all males are removed from saturated uniform habitat, resettlement should occur in a clumped distribution. A "metropolitan" process may eventually cause groups of territories to converge and conceal the initial aggregations. This prediction provides a sharp contrast to the assumption that territorial males are repelled by each other and will therefore attempt to maximize their distances. At the individual level, the hidden lek hypothesis predicts that males will preferentially breed near previously settled males, and that low quality males will attempt to settle near males that are more attractive to females.

The revolution in our perceptions of mating systems has only recently begun. We can now see that copulatory patterns of monogamous species often resemble those of promiscuous species. The central challenge is to determine whether, and the degree to which, these patterns are caused by similar processes. Another goal is to determine whether the constraint of possessing a nesting partner inhibits monogamous females, relative to lekking females, from pursuing multiple matings, thereby possibly limiting selection for male clustering. Alternatively, the constraint of being paired may provide monogamous females with more, rather than less, incentive to mate multiply (Møller 1992). In this case, monogamous species could, paradoxically, be more prone to aggregate than many promiscuous species. Evidence that leks may be hidden among the territories of monogamous birds highlights the importance of separating copulation behavior and parental care when viewing the relationships between males and females.

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# CHAPTER 7

# COSTS AND BENEFITS OF EXTRA-GROUP PATERNITY IN SUPERB FAIRY-WRENS

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ABSTRACT.—One of the most extreme examples of conflict between the sexes occurs in the Superb Fairy-wren (*Malurus cyaneus*), a cooperatively breeding bird in which 72% of nestlings were produced by extra-pair fertilizations. Males that gained extra-pair paternity were almost exclusively dominant breeding males outside the group and not helpers. Group size had a significant effect on the number of young sired by males on their own territory. Males breeding in a pair (no helpers) sired more young (41%, 71/175 young) and provided more parental care (42% of feeding visits) than dominant breeding males that lived in groups with helpers (19%, 56/292 young; 25% of feeding visits). This pattern of extra-group paternity was a result of female choice and control of fertilization. When females lived in a group, helpers compensated for the lower parental assistance of the dominant breeding male, so all offspring were provisioned fully and there was no cost to the female or male in terms of reduced nestling survival. Thus, the mate choice of females with helpers was not constrained by the importance of male parental assistance. In unassisted pairs, females had no alternative source of parental assistance and may have allowed their mates greater paternity to ensure the assistance of the mates in providing parental care. The reduced workload of dominant breeding males in groups did not increase their survival; rather, it allowed them more time to engage in courtship displays to females on other territories. This increased display rate of males in groups was associated with a greater likelihood of gaining extra-group fertilizations, and it may have compensated males in groups for their lower within-pair paternity. The release of females from the constraint of male parental care was due to helpers, whereas the reduction in male parental care was most likely the result of a paternity cue and not simply the presence of helpers per se. After controlling statistically for group size, males provided less parental care when they had lower paternity. Thus, a detailed knowledge of the alternatives available to females (other sources of parental assistance) and males (opportunities for extra-pair matings) may be necessary to understand male and female reproductive strategies.

Many recent studies have used genetic methods to describe patterns of extra-pair paternity in birds. One of the most important consequences of this research is a shift in our view of the role of females. Previously, the interests and strategies of females were virtually ignored in the literature on sperm competition. This bias arose because it was thought that females had little to gain, and much to lose, from mating with extra-pair males (reviewed by Lifjeld et al. 1994). However, there is mounting evidence from genetic studies that females often initiate extra-pair matings and control their success in terms of fertilization (Lifjeld and Robertson 1992; see also Lifjeld et al. 1994). If females benefit from extra-pair matings, then their reproductive interests will conflict with those of their mate.

In biparental species this conflict between mates over paternity may result in a conflict over parental care. Selection should favor males that do not provide parental care to unrelated nestlings, all else being equal. Thus, females must weigh the potential benefits of extra-pair matings against the potential cost of reduced male parental care. Males must weigh a number of potential costs and benefits as well. Males with low paternity may provide less parental care if they benefit relatively more from a greater probability of survival or greater opportunities for extra-pair matings. On the other hand, males cannot recognize individual offspring in many birds, and thus males that reduce their level of parental care in relation to overall paternity may reduce the survival of their own as well as unrelated nestlings (Whittingham et al. 1992).

Few studies have been able to demonstrate convincingly this trade-off between male parental care and paternity (reviewed by Whittingham et al. 1993; Dunn and Cockburn 1996). Previous studies may have been limited by insufficient variation within species in terms of paternity or the importance of male parental care. In most biparental species relatively little variation exists in paternity as males usually sire most of the young they care for (mean = 83% of young [Dunn et al. 1994]). Also, in most monogamous species male parental care is important to reproductive success (reviewed by Wolf et al. 1988; Dunn and Hannon 1989), and thus males usually do not vary widely in the level of parental care provided, as a reduction in male care would risk the survival of any young they have sired (Whittingham et al. 1992, 1993). Cooperative breeders provide an novel perspective because they have helpers that may influence both paternity and the cost to males of providing parental care. Indeed, some of the best examples of the trade-off between male parental care and paternity come from cooperatively polyandrous birds (Burke et al. 1989; Hartley et al. 1995).

One of the most extreme examples of the conflict of interests between males and females occurs in the Superb Fairy-wren (*Malurus cyaneus*) of Australia. This species has the highest known frequency of extra-pair paternity (72–76% extra-pair young [Mulder et al. 1994; this study; see also Brooker et al. 1990]), and it lives in both pairs and cooperatively breeding groups in which all males contribute parental care (nest defense and feeding young). The high level of extra-pair paternity and the presence of helpers that can modify some of the costs of extra-pair paternity make this species ideal for examining male and female reproductive strategies. In this chapter we examine the costs and benefits of extra-group paternity for both sexes in the Superb Fairy-wren, and how these costs and benefits are modified by the presence of helpers. We suggest that these costs and benefits are not specific to cooperatively breeding birds, and thus similar types of reproductive trade-offs may occur in other socially monogamous species.

## METHODS

*Study species:* Superb Fairy-wrens are small (8–11-g) insectivorous birds endemic to Australia and New Guinea (family Maluridae, superfamily Meliphagoidea [Sibley and Ahlquist 1990]). Superb Fairy-wrens were one of the first cooperative breeders to be studied using individually marked birds (Bradley and Bradley 1958; Rowley 1961, 1965). They live both in pairs and stable year-round social groups. Territories of pairs are always occupied by two birds, a breeding male and female; there are no auxiliary birds that live on the territory and do not assist with parental care, as occurs in some other cooperatively breeding species. Groups are composed of a single breeding female and one to five adult males (helpers), all of whom provide parental care and defend a permanent territory. Pair-bonds between the dominant male and female are relatively stable from year to year; to date the longest known pair-bond on our study area is 5.75 yr. Individual males and females have held breeding territories on our study area for at least 8 yr. The single putative father typically is the oldest male in the group, and he is always behaviorally dominant over the helpers (Mulder and Langmore 1993; Dunn et al. 1995). Male helpers usually remain on their natal territory throughout their lives because of a shortage of females with territories (Pruett-Jones and Lewis 1990). In contrast, all females disperse from their natal territory and die if they do not gain a breeding vacancy at the start of their first breeding season (Mulder 1995).

Female fairy-wrens may lay up to eight clutches (two to four eggs each) and produce up to three successful broods during a 5-mo breeding season that spans two calendar years (September to February). For convenience we designate breeding seasons by the year in which they start (e.g., 1992/1993 is the 1992 season). Females alone build the nests and incubate the eggs. All males in groups contribute to nest defense and provisioning of nestlings and fledglings (Rowley 1965). Incubation lasts 14 days and nestlings fledge after approximately 12 days in the nest. Fledglings require four more weeks of care before they become independent.

Superb Fairy-wrens are sexually dichromatic. In the breeding season females are brown, whereas males have a dark purple throat and light blue crown and ear coverts outlined in black. In the winter both males and females are mostly brown, although males retain a blue tail. All males attain breeding plumage and are capable of breeding regardless of age or social status (Mulder and Cockburn 1993; Mulder and Magrath 1994; Mulder et al. 1994). Male fairy-wrens in breeding plumage engage in conspicuous courtship displays (Rowley and Russell 1990), which are directed almost exclusively at extra-group females (Mulder et al. 1994; Mulder 1995). These displays are highly stereotyped; males erect their ear coverts, lower their tails, and display the contrasting blue and black feathers of their plumage by twisting their bodies to one side. Intruding males are usually from an adjacent territory, but some males have been observed to cross up to six territories to display (Mulder et al. 1994). Displays can occur year-round, but peak early in the breeding season (September and October; Mulder 1997). For any given female, displays peak 4–5 days before egg laying, when up to seven males may be observed displaying during a 20-min period (Mulder et al. 1994). Despite their frequency, displays rarely result in immediate copulation (3 of 1,930 displays; 0.2%) and, instead, may be used by males to advertise themselves for later extra-group copulations (Mulder et al. 1994; Green et al. 1995).

*Study area:* Our study area is located in and adjacent to the Australian National Botanic Gardens (ANBG), a 40-ha reserve on the southeastern slope of Black Mountain, Canberra, Australia. Dry sclerophyll forest covers most of the ANBG, which contains only native Australian trees and shrubs. Wrens were individually color-marked with plastic leg bands starting in 1986, and we have detailed reproductive data on individuals from 1988 to 1995. Currently all individuals in 80 territories within and adjacent to the ANBG are individually color-marked. The composition and social relationships within these groups have been determined from weekly censuses during the nonbreeding season, and daily visits during the breeding season. Thus, mate switching, although rare, is detected within a few days. During seven breeding seasons from 1988 to 1994 we assigned the dominant male on each territory into one of four social categories: (1) males living in unassisted pairs ($n$ = 155 male-seasons); (2) males living with one helper ($n$ = 109); (3) males living with two or more helpers ($n$ = 84); and (4) males without a female, or with a female that did not breed (solitary; $n$ = 16). For all territories we measured the number of young that fledged and survived to independence (at least 4 wk), and determined whether the dominant male survived until the start of the following breeding season.

*Behavioral observations:* We conducted behavioral observations on parental care for 35 broods on 33 territories during the 1992 season (28 November 1992 to 19 January 1993, see Dunn et al. 1995; Dunn and Cockburn 1996). Paternity analyses using DNA fingerprinting have been completed for this sample. We observed 14 pairs, 13 groups with one helper, five groups with two helpers, and one group with three helpers. During each 1-hr observation session we counted the number of nest visits with food by each individual in the group. Observations were made once a day when nestlings were 3 and 4 days old and twice a day (a.m. and p.m.) when the nestlings were 5–11 days old (16-hr maximum per group). Observations of parental care were not conducted after fledging because it was difficult to observe adults delivering food to young in dense cover.

Data on extra-group courtship displays were obtained by watching 22 dominant males during the 1994 season (4 October 1994 to 19 January 1995; see Green et al. 1995). This sample contained 10 pairs, six groups with one helper, and six groups with two helpers. Paternity analyses have not yet been completed for these samples. During 30-min observation sessions observers recorded: (1) the distance between the dominant male and his mate at 30-s intervals, (2) the timing of any departure by the male from his territory, and (3) the time that the male was first observed on his return. Two observers, one watching the male and the other the female, were used generally during these sessions. The time when males departed from their territory could be determined relatively accurately as the habitat was open *Eucalyptus* woodland and territories had distinct and stable boundaries during the breeding season. On their return males often flew directly to the female. We attempted to watch the focal males five times each during the fertile (1–14 days before laying), incubation, and nestling periods. Nestling period observations were conducted when the nestlings were 3, 5, 7, 9, and 11 days old. Some nests were depredated before fledging, so our data were incomplete for some males.

*Paternity analyses:* We used DNA fingerprinting to conduct paternity analyses of 618 nestlings over six breeding seasons from 1988 to 1993, and were able to determine the paternity of some male helpers from the 1986 and 1987 cohorts. We analyzed all nestlings in 172 broods over five seasons from 1989 to 1993 (in chronological order: 19, 21, 48, 69, and 15 broods). In 1991 and 1992 sampling was nearly complete for all territories on the study area.

Our DNA fingerprinting procedures are described in detail by Mulder et al. (1994). Briefly, our fingerprints consisted of *Hae*III-digested DNA that was probed separately with radioactively labelled *per* (Shin et al. 1985), 33.15 (Jeffreys et al. 1985), and, lastly, molecular size marker DNA (BRL 1-kb ladder) to produce three separate autoradiographs. The molecular size markers allowed us to correct for distortions in the migration of DNA across the gel and to use a computer database of fragment sizes to search for potential extra-pair fathers (see Mulder et al. 1994). To date we have found no cases of egg-dumping. Nestlings that had three or more novel fragments (both probes combined) and low band-sharing ($<0.40$) with the putative father were attributed to extra-pair fertilization (see Mulder et al. 1994). We assigned paternity to males when their fragments matched ($\pm 1\%$ error in size) all or all but one of the nonmaternal fragments (both probes combined) of an extra-pair nestling, and a visual comparison of autoradiographs revealed that bands differed less than twofold in intensity. These assignments were confirmed by two scorers using fingerprints that had the suspected extra-pair father and extra-pair nestling next to each other on the same autoradiograph. For the 1991, 1992, and 1993 seasons, we ran 25 additional fingerprint gels (24 individuals/gel) to confirm these suspected paternities. We estimated the probability of misassigning a parent as $1.4 \times 10^{-6}$ (Mulder et al. 1994).

## RESULTS

*Extra-pair/extra-group paternity:* DNA fingerprinting revealed that 92% of 157 broods contained at least one extra-pair nestling (data from broods with every nestling fingerprinted; 1989–1992 seasons). Overall, 72% (447/618) of nestlings were sired by extra-pair males and 69% (429/618) of nestlings were sired by extra-group males (data from all nestlings, 1986–1993). The 3% difference between extra-pair and extra-group paternity was the result of helpers siring extra-pair young within their own group. Thus, extra-group males were responsible for 96% (429/447) of all extra-pair paternity. Of young sired by males (dominant or helper) within the same social group, the dominant male sired the vast majority (91%, 171/189). Helpers also sired relatively few extra-group young (11%, 21/197 extra-group young with known sires). Extra-pair paternity was not influenced by male body mass, brood size, or time of the season (Mulder et al. 1994).

Group size had a significant effect on the number of young sired by males on their own territory. Dominant males breeding in a pair (0 helpers) sired more young (41%, 71/175) than males that had one or more helpers in their group (19%, 56/292; $G = 24.8$, d.f. $= 1$, $P < 0.001$; data from 1989–1992 seasons). On a per brood basis, dominant males in pairs again sired more young ($\bar{x} \pm$ SE $= 38 \pm 5.5\%$ of young, $n = 47$ broods) than males that lived in groups ($21 \pm 3.9\%$, $n = 70$ broods; $Z = 2.49$, $P = 0.013$; data from completely sampled broods in 1991 and 1992). Similarly, the percentage of broods containing at least one young sired by the dominant male was greater for males breeding in a pair (68%, 41/60) than for males breeding in groups (35%, 34/97; $G = 16.1$, d.f. $= 1$, $P < 0.002$). Thus, the presence of helpers was associated with a strong paternity cost to dominant males in groups. However, males from other territories gained almost all of this paternity, not the helpers of the dominant male. Below we will address whether or not there is any benefit from helpers that compensates dominant males for this large paternity cost.

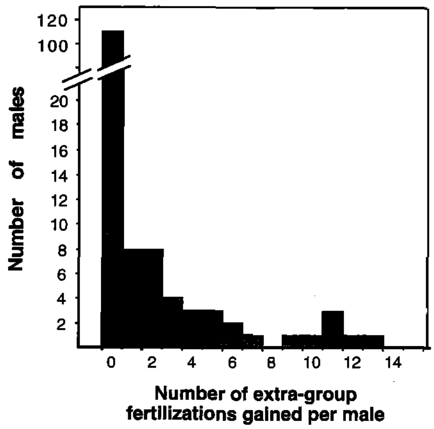

FIG. 1. The distribution of extra-group fertilizations gained by known sires during the 1991, 1992, and 1993 seasons. In this sample we were able to determine the true fathers of 58% (162/280) of extra-group young in the entire study area. Note that most males (115) gained no extra-group fertilizations and 36 males gained at least one.

*Female mate choice:* Our evidence indicates that the high level of extra-group paternity in fairy-wrens is not the result of direct male–male competition, but rather female choice and control of fertilization (Mulder et al. 1994). Females easily evade males during extra-territorial displays and just 0.2% of these displays result in copulations. During several thousand hours of field work we have observed 46 copulations, including three extra-group copulations. One of the extra-group copulations was on the female's territory, one was on the male's territory, and one was on the border between two territories. Females appeared to solicit all of these copulations, which suggests that males are not forcing copulations. Males do not closely guard their mates and will even perform courtship displays to females on other territories when their own mate is fertile (Green et al. 1995). In addition, we know that the most successful extra-group males often sire young some distance from their own territory (crossing up to five territories), whereas most of the intruding males that display to females are from neighboring territories (Mulder et al. 1994). This provides evidence that females are making an active choice rather than simply mating with a nearby male that visits them often.

Further evidence for female choice comes from the skewed distribution of males that gained extra-group fertilizations (Fig. 1). In the 1991, 1992, and 1993 seasons we were able to determine the true fathers of 58% (162/280) of extra-group young in the entire study area. In this sample, just eight males, which is approximately 5% of all males in the area, sired 52% (84/162) of the extra-group young whose father was known. The most successful male (YRG) sired 8% of the extra-group young (13/162). These values may be biased by unequal sampling throughout the study area. However, a similar skew in male mating success was evident in the center of our study area where, over the same three seasons, we were able to determine the true fathers of 78% (58/74) of extra-group young. In this sample three males, which were 11% of all males in the area, sired 48% (28/58) of the extra-group young whose father was known. The most successful male

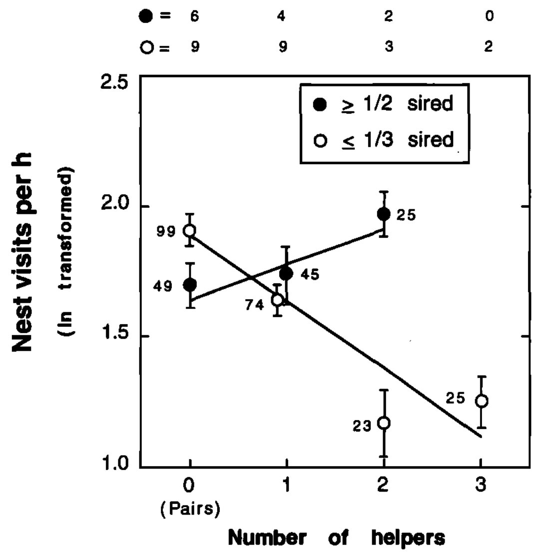

FIG. 2. Nest visit rate (ln transformed) of the dominant male in relation to the number of helpers at the nest and whether the dominant had sired one half or more of the clutch (high paternity) or one third or less (low paternity). The interaction between these variables was significant, but all other factors and interactions proved to be nonsignificant. Symbols indicate the means of the actual data (with standard errors, and the number of hours of observation associated with each point). The lines depict maximum likelihood estimates, which are based on all observation sessions and control for differences among broods (see Dunn and Cockburn 1996). The number of broods for each paternity category is given above the graph. The paternity of males in this data set fell into two distinct categories of paternity; those that sired one third or less of their young and those that sired one half or more. The median number of young sired for these two groups was no young sired for the ≤⅓ paternity group, and 88% of young sired for the ≥½ paternity group. Redrawn from Dunn and Cockburn (1996) with the permission of the Society for the Study of Evolution.

(YRG) sired 22% (13/58) of the extra-group young. Thus females were choosing a select subset of males for extra-group matings.

*Costs of extra-group mating:* It is unlikely that searching for extra-group mates is very costly to females because males travel to the female to perform their display. However, extra-group mating may be costly if females generally have to travel to the territory of a male to gain an extra-group copulation. We do not know if these copulations generally occur as a result of females travelling to the territories of males or vice versa (both behaviors have been seen a few times). One of the most frequently discussed costs to females is a reduction in parental care by males that have low paternity. Below we examine the potential costs and benefits of reduced male parental care to females and dominant males.

Analysis of the parental care and paternity of dominant males in the 1992 season revealed that males with low paternity (≤⅓ of the brood sired) reduced their level of parental care when they had helpers, but dominant males without helpers (or with just one) provided similar levels of parental care regardless of their paternity (Fig. 2 [see also Dunn and Cockburn 1996]). Brood size, nestling age, and age of the male (1–2, 3–4, or 5+ yr) did not influence significantly the nest visit rate of males. The only variable affecting the nest visit rate of dominant males was the interaction of the number of males provisioning nestlings and the level of paternity of the dominant male (Fig. 2; $P < 0.05$). Males that had high paternity (sired ≥½ of their nestlings) maintained high feeding rates regardless of the number of helpers; in contrast, feeding rates for males with low paternity dropped sharply when two or three helpers were present (Fig. 2). Note that these results also suggest that dominant males are responding to their level of paternity (presumably through some cue other than paternity per se) and are not adjusting their level of care simply to the number of helpers. Males with low paternity reduced their effort by 64% from 5.6 feeds per hour in a pair to 2.1 feeds per hour with three helpers (back-transformed data). In contrast, the feeding rate of males with high paternity showed no significant change as the number of helpers increased (Fig. 2; i.e. the apparent increase was not significant).

We also analyzed male parental care in relation to whether or not the male sired any young (Dunn and Cockburn 1996). In this analysis we corrected for the number of helpers by examining nest vists made by the dominant male in two categories: one helper ($n = 15$ broods) or two or more helpers ($n = 7$ broods). Across both categories of group size, we found that dominant males that sired at least one young made a greater proportion of all male nest visits (dominant and helpers combined) than males that sired no young ($F_{1,15} = 10.0$, $P = 0.007$ [Dunn and Cockburn 1996]). Both of these analyses correct for group size, which suggests that males decrease their level of parental care in relation to some paternity cue, rather than simply in relation to the number of helpers. As a consequence, there is a potential cost to females from engaging in extra-group copulations, because if the male has low paternity and helpers are present, then the dominant male provides less parental care.

Nevertheless, females and nestlings did not incur any apparent cost of reduced parental care because helpers compensated completely for the reduction in nest visits by the dominant male. Indeed, nestlings in groups were provided with more food than nestlings in pairs, because as group size increased, so did the total feeding rate (Dunn and Cockburn 1996). This effect was the result of the presence of helpers because female feeding rate did not change as group size increased. There also was no significant effect of paternity (or its interaction terms) on the rate of total or female nest visits. The only variables that significantly affected total feeding rate were nestling age and the number of males feeding. The net result of this compensation by helpers was that the total nest visit rate did not decrease when dominant males with low paternity decreased their feeding rate. As a consequence, males with low paternity did not risk the survival of their nestlings. Although groups had higher productivity than pairs in our study population, this appeared to be because good territories and/or females were more likely to produce helpers, rather than a direct effect of the parental assistance from helpers. Females that changed social circumstances (pair to group or vice versa) during the study showed no evidence of increased fecundity when they had helpers (Green et al. 1995).

*Are dominant males in groups compensated for their lower paternity?:* Dominant males in groups generally incurred lower paternity and, consequently, provided less parental care than males in pairs (Fig. 2). This reduction in parental care could benefit dominant males in groups in terms of greater survival or more extra-group mating opportunities. However, data from seven breeding seasons indicated that there was no difference between the annual survival rates of males in pairs (71%, 90/127) and groups (77%, 112/146), so it did not appear that dominant males in groups were gaining a survival benefit from reducing male parental care (Dunn et al. 1995; Green et al. 1995).

Instead, it appears that dominant males in groups were spending more time displaying to females on other territories (Green et al. 1995). Overall, males left their territories about once every hour in the 1994 season (each departure lasted about 10 min). We assume that these males were displaying to females on other territories because birds did not feed off their territory during the breeding season and only displaying males were seen intruding onto other territories at this time. Green et al. (1995) found that the number of helpers had little effect on the probability that a male left his territory during his female's fertile and incubation periods. Thus, the lower paternity of males living in groups than in pairs was not a simple consequence of males in groups spending less time guarding their fertile mate (see also Mulder 1997). In contrast, during the nestling period, when males probably provide most of their parental care, the dominant male departed his territory significantly more often if he had helpers than if he had no helpers. On average, the addition of two helpers reduced the nest visit rate of the dominant male by about 40% and increased his overall display rate by about 20% during the peak of breeding (October to January; Green et al. 1995).

Thus, when dominant males in groups had low paternity they could feed their nestlings less and display more to females; but what effect did this have on their overall reproductive success? To examine this question we took data on paternity from 7 to 11 contiguous territories over three seasons in the center of our study area where we were able to explain the paternity of 86% of all nestlings and 78% of the extra-group nestlings (Fig. 3). This relatively high percentage of young with known parentage allowed us to make a reasonable estimate of the total reproductive success of males in the central area.

In this sample, dominant males in groups tended to sire fewer within-group young per season than males in pairs (Fig. 3; $\chi^2 = 7.8$, d.f. $= 6$, $P = 0.05$; categories compared were 0, 1, 2, and 3+ young sired by males in pairs versus groups). This result was similar to that from a larger sample for the entire study area (Mulder et al. 1994; see above). In contrast, dominant males in groups tended to gain more extra-group fertilizations than did males breeding in pairs (Fig. 3; $\chi^2 = 7.0$, d.f. $= 6$, $P = 0.07$). Overall, the total fertilization success (within territory and extra-group) of dominant males in pairs and groups was not significantly different (Fig. 3; $\chi^2 = 0.29$, d.f. $= 6$, $P = 0.96$). Thus, dominant males in groups may have been compensated for their generally lower paternity within their own territory by a higher likelihood of gaining extra-group fertilizations on other territories. We caution, however, that extra-group fertilizations were gained over a wide area (see above), and thus we probably underestimated the extra-group fertilization success of some males that lived in the central area but gained matings far away from the center. In addition, a relatively small number of males gained most of these extra-group fertilizations (e.g., Fig. 1), and this subset of males may have been the main reason for the relatively similar fertilization success of males in pairs and groups. Future analyses will reveal if these highly successful males gain most extra-group fertilizations as well as retain high paternity within their own nests, regardless of their group size.

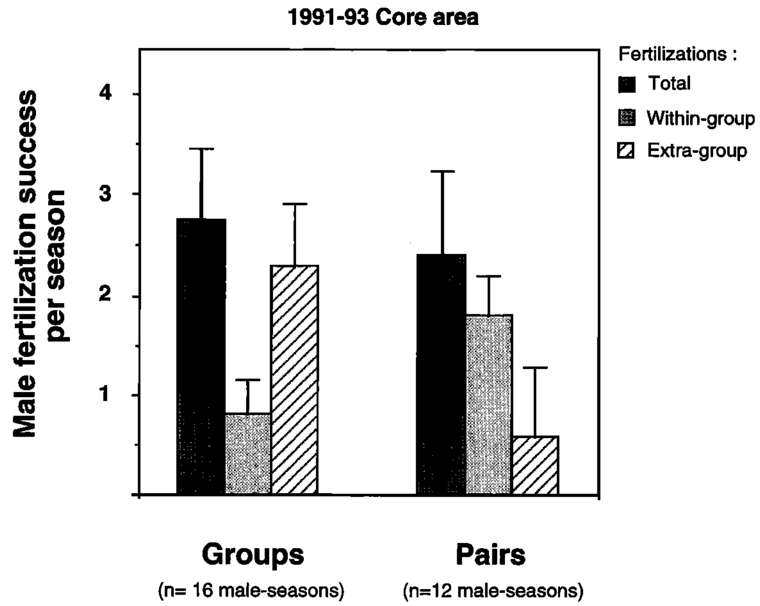

FIG. 3. The mean fertilization success of dominant males per season in relation to group size. Total fertilization success is composed of fertilizations gained by dominant males on their own territory (within-pair, $n = 35$ young) and on the territories of other males (extra-group, $n = 44$ young). Data are from 16 dominant males (28 male-seasons) living on 7–11 territories in the center of our study area over three seasons (1991, 1992, and 1993).

## DISCUSSION

Extra-pair paternity occurred in more than 90% of nests in the Superb Fairy-wren (Mulder et al. 1994; this study). Our evidence indicates that this high level of extra-pair paternity was the result of female choice and control of fertilization and not the result of direct male–male competition (Mulder et al. 1994). Obviously it is not in the interests of males to raise so many unrelated nestlings, so how is this system maintained, and are there any parallels that may help to explain extra-pair paternity in other species?

*Female costs and benefits:* Female Superb Fairy-wrens benefit from the presence of helpers because they allow females greater opportunity to gain extra-group fertilizations (Mulder et al. 1994). Preliminary evidence suggests that females are choosing extra-group mates for a particular trait (see Mulder and Magrath 1994), but the reason for this choice is still under study. Nevertheless, the high levels of extra-group paternity in fairy-wrens indicate that females are receiving some type of benefit that outweighs the costs. Helpers facilitate the extra-group mate choice of females because they compensate completely for any reduction in parental care by dominant males that have low paternity. As a consequence, the extra-pair mating options of females with helpers are less constrained by the importance of parental care from the dominant male.

Mulder et al. (1994) suggested that the level of extra-pair paternity in other species with female control of fertilization is based on a similar balance between the benefits to females from extra-pair paternity and the potential costs arising from reduced male parental care. A prediction from this hypothesis is that levels of extra-pair paternity will be greater in species or populations of birds in which male parental care is less important to reproductive success (see also Johnson and Burley, Chapter 2). This relationship should occur if selection favors males that redirect their parental effort into alternative mating opportunities (extra-pair copulations or polygyny) as their parental care becomes relatively less important to their overall fitness. This hypothesis would not apply to situations in which there is no trade-off between parental and mating effort, which might occur if male parental care occurs after all mating is completed, although even in this case an energetic trade-off is still possible. At a broader level, this idea is supported by theory and some empirical evidence among species that suggests an overall increase in the intensity of sexual selection as levels of male parental investment decrease (e.g., Trivers 1972; Clutton-Brock 1991; Searcy and Yasukawa 1995). Assuming that helpers allow dominant males to redirect more of their total reproductive effort into extra-pair copulations, one might predict that levels of extra-pair paternity will be higher in species with helpers than in those without helpers. Contrary to this prediction, the available studies suggest that levels of extra-pair paternity are relatively low in cooperative breeders (e.g., Mumme et al. 1985; Wrege and Emlen 1987; Rabenold et al. 1990; Poldmaa et al. 1995). However, in this type of comparison it must be known if males have the opportunity to redirect their parental effort into mating effort (i.e., extra-pair copulations), if fertilization patterns are controlled mostly by females, and if helpers compensate for decreases in parental care by males with low paternity. In almost all cases these assumptions have yet to be tested.

In Superb Fairy-wrens the most likely costs to females of extra-group mating include searching for extra-group mates and reduced male parental care from dominant males with low paternity. Females probably do not incur a large search cost as many males frequently travel from other territories to display to the female on her own territory (Mulder 1997). However, females may travel to the territory of a male to gain an extra-group copulation. We do not know if extra-group copulations generally occur as a result of females travelling to the territories of males or vice versa. The most frequently discussed cost to females of extra-pair mating is a reduction in male parental care; however, relatively little evidence exists for its occurrence outside cooperatively breeding birds (reviewed by Whittingham et al. 1993; Dunn and Cockburn 1996). In fairy-wrens we found that males reduced their parental care in relation to paternity, as has been found in some other cooperative species (e.g., Davies et al. 1992). However, this was not costly to females living in groups because helpers compensated for the reduction in male parental care, and, as a consequence, there was no effect on the production of young. Apparently, female fairy-wrens with helpers have the best of both worlds; they can gain the benefits of extra-pair paternity while not incurring any significant reproductive costs. Females living in pairs do not have helpers and do not gain as many extra-group fertilizations, but they do have relatively more parental assistance from their mate. We are currently testing the hypothesis that females in pairs gain fewer extra-group fertilizations because males display to them less frequently. However, we suspect that female choice in fairy-wrens is not limited simply by the number of displaying males (see Mulder 1997).

In studies of male parental care and paternity it is important to realize that if extra-pair fertilizations are the result of female choice, then the benefits to females of extra-pair paternity must outweigh the potential costs, including the consequences of reduced male parental care, such as reduced fledging success or nestling survival. As in our study, others have reported a positive relationship between male parental care and paternity (e.g., Møller 1988; Dixon et al. 1994), but they have not reported the cost (if any) of extra-pair mating. Data on reduced fledging success or survival are important because these are potential costs incurred by both the male and female. For example, in some populations of Red-winged Blackbirds (*Agelaius phoeniceus*) females that engage in extra-pair matings may gain better quality offspring, but they also incur lower nesting success, as a result of reduced nest defense by males with lower paternity (Weatherhead et al. 1994; but see also Gray, Chapter 3). Thus, we should expect any cost of extra-pair paternity to the female to be outweighed by some benefit such as better quality offspring (e.g., Kempenaers et al. 1992). Similarly, any cost of extra-pair paternity to males should be outweighed by a benefit to the male in terms of more extra-pair fertilizations or increased survival. These complex trade-offs between and within the sexes must all be examined when testing theories of male parental care and paternity (Whittingham et al. 1992; Westneat and Sherman 1993).

*Male costs and benefits:* In contrast to females, many male fairy-wrens appear to be making the best of a bad situation. The average male fairy-wren sires less than a third (28%) of his nestlings. When dominant males live in groups they incur a greater cost of extra-pair paternity than males living in unassisted pairs (19% vs. 41% of young sired, respectively). Males that gain extra-pair paternity are almost exclusively males outside the group and not helpers. As a consequence, both dominants and helpers are frequently unrelated to any of the young they help rear (Dunn et al. 1995). Thus, extra-pair paternity results in few indirect kin benefits for either dominants or helpers. However, dominant males in groups typically provide less parental care than males in pairs (25% of all feeding visits). Helpers compensate completely for this lower level of care by the dominant male. Thus, any offspring the dominant male may have sired are provisioned fully and there is no cost to the male in terms of nestling survival (Green et al. 1995). The reduced workload of dominant males in groups does not increase their survival; however, it does allow them more time to engage in courtship displays to females on other territories (Green et al. 1995). This increased display rate of males in groups is associated with a greater likelihood of gaining extra-group fertilizations, and it may compensate males in groups for their lower within-pair paternity. However, it is quite likely that just a small proportion of dominant males in groups receive benefits from extra-group mating, because about one half of all extra-group fertilizations are gained by just 5–11% of males (Fig. 1).

Pairs make up 45% (155/348 male-seasons) of breeding associations. Males in pairs sire more of the young in their nest (41%), spend less time seeking extra-pair matings, and provide more parental care (42% of feeding visits) than dominant males living in groups. Males in pairs have levels of paternity and parental care that are similar to those in some other socially monogamous species such as Tree Swallows (*Tachycineta bicolor*) in which males provide 40–50% of feeds and sire 47–62% of nestlings (Lifjeld et al. 1993; Dunn et al. 1994). Thus, male fairy-wrens in pairs have trade-offs that are similar in magnitude to those of males in other socially monogamous species. Male fairy-wrens do not have a choice as to whether they live in pairs. Pairs become groups if male nestlings survive to breeding age (71–79% of territories produce some fledglings [Dunn et al. 1995]). Dominant males do not attempt to force these potential helpers from their territory, even though they are related to just 31% of them (Dunn et al. 1995).

Male helpers appear to gain the fewest reproductive benefits. In general, they sire few of the young sired by males on their own territory (9%, 18/189), so they receive few direct reproductive benefits on their own territory. Helpers likely receive few indirect benefits as well, because their assistance does not increase reproductive success and 36% of the young they help raise are unrelated ($r <$ 0.25; this percentage climbs to 56% for helpers 2+ yr old [Dunn et al. 1995]). Finally, helpers sire few young on other territories (11%, 21/197 extra-group young), so they are not receiving any potential compensation as do dominant males in groups.

There are several unanswered questions arising from our recent studies of fairy-wrens. First, why do dominant males with both helpers and high paternity contribute substantial amounts of parental care (see Fig. 2)? One might expect these dominant males to redirect some of their parental care into extra-group mating effort, as they have helpers that potentially can compensate for their reduction in parental care. In this case providing relatively high levels of parental care may be more beneficial to the male in terms of subsequent paternity or the production of related offspring (Dunn and Cockburn 1996) (e.g., it may be more productive to provide care to related sons if they have a greater probability of reproducing when they inherit their father's territory). Second, how does the timing and frequency of extra-group displays by males relate to their success at gaining extra-group fertilizations? Do males gain most of their extra-group fertilizations from displays made during the nestling season (when helpers have the greatest effect on male display rate [Green et al. 1995])? Males display to females on other territories up to 5 mos before the breeding season begins (Mulder 1997), but we do not know yet if these displays are more important to gaining extra-group fertilizations than displays made during the breeding season itself. This question will be addressed in future studies that combine data collected simultaneously on display rates, paternity, and male parental care.

The fairy-wren mating system may seem complex and unusual when compared to most other monogamous birds. However, male and female fairy-wrens are similar to other species in the sense that the sexes face similar types of trade-offs. For example, females face a trade-off between the benefits of extra-group paternity and the costs of reduced male parental care. Males may face trade-offs between providing parental care and seeking extra-pair paternity and between protecting within-pair paternity and seeking extra-pair paternity. The relative importance of these trade-offs may vary among species depending, in part, on the level of female control of fertilization. The important difference between fairy-wrens and most other species is that they have helpers that reduce some of the costs constraining mating options in other species. Fairy-wrens may serve as an extreme example that helps us to understand some of the general reproductive strategies of male and female birds.

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# CHAPTER 8

# SEXUAL COERCION IN WATERFOWL AND OTHER BIRDS

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ABSTRACT.—Sexual coercion was defined previously as "use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female." Forced extra-pair copulation (FEPC), a well-known phenomenon in waterfowl, is reexamined in detail as a prime example of sexual coercion in birds. Monogamy is the basic mating system in almost all waterfowl, opportunities for polygyny are rare, and males of many species seek extra-pair copulations (EPCs). Presence of a male intromittent organ in waterfowl, thought to have evolved in association with copulation while swimming, makes forced EPC feasible. Evidence (as follows) for FEPC as a secondary male reproductive strategy is reviewed: males involved are usually paired, eggs can be fertilized, FEPC attempts focus on fertile females, males have elaborate tactics to secure FEPCs, males defend their mates against FEPC by other males, and males perform forced pair copulation after FEPC has occurred on their mates. Females resist FEPC and show elaborate escape behavior (flying, diving, hiding, sneaking). Female resistance may be a tactic to preserve the pair-bond and the investment of the mate. Incubating female dabbling ducks have special "repulsion" behavior that indicates their nonfertile status and seems to discourage males from FEPC. Females incur costs from FEPC, including risk of injury or death during multimale FEPC attempts, energetic costs of escape behavior, and abandonment of nesting attempts caused by harassment. FEPC has been recorded in 55 species of waterfowl in 17 genera. FEPC apparently is absent in swans, shelducks and sheldgeese, steamer ducks, and most sea ducks. In some of these cases, there may be a trade-off between territoriality and FEPC. Other avian groups in which FEPC has been reported include albatrosses, pelicans, herons, gulls, auks, bee-eaters, swallows, waxbills, and corvids. Females may be especially vulnerable to FEPC in breeding colonies when left unguarded by the mate. In general, FEPC appears to be uncommon in birds other than waterfowl, but there are some species in which males do appear to be able to overpower females. Many opportunities for future research are noted.

Most research on the mechanisms of sexual selection in animals has focussed on mate choice and contests between males, but recent reviews of the vast literature in this field have drawn attention to additional ways in which members of one sex (usually males) compete with one another for mates or matings. The lists compiled by Andersson (1994) and Andersson and Iwasa (1996) include lesser known mechanisms such as scrambles, endurance rivalry, sperm competition, infanticide, and coercion. Although sperm competition and infanticide have received considerable attention from ornithologists (Birkhead and Møller 1992; Mock and Parker, in press), the topic of coercion has been neglected. Indeed, the identification of coercion as a distinct source of sexual selection was not clearly made until very recently (Smuts and Smuts 1993; Clutton-Brock and Parker 1995), and it is an appropriate time to consider how important this phenomenon may be in birds.

Smuts and Smuts (1993:2) defined sexual coercion as

> use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female.

This definition, developed from studies of nonhuman primates, combines behavioral description and functional explanation. Therefore, sexual coercion cannot be identified solely by observing the immediate behavior of the aggressor; it is also necessary to observe the subsequent behavior of the aggressor, the target, and even of other individuals. Smuts and Smuts (1993) use the term "male aggression" (toward females) rather than "sexual coercion" whenever the functional consequences of the behavior are uncertain.

Examples of sexual coercion in primates described by Smuts and Smuts (1993) include forced copulation (as in the great apes, especially orangutans), male use of aggression to herd mates away from strange males (hamadryas baboons) or to force a female to follow him (consortships in chimpanzees), cooperative aggression by several males against breeding females (spider monkeys), and infanticide (as in many nonhuman primates). Infanticide is included because it entails the use of force to manipulate the female's sexual state and mating behavior to the male's advantage, and there is a cost to the female. Other costs to female primates include physical injury, stress-related effects, abortion, loss of time and energy in being vigilant, and constraining influences on female movements and free mate choice. Female primates have various counterstrategies to male aggression including mating with a dominant male (to reduce harassment of themselves or their infants by other males), forming a "friendship" with a particular male (preferring him as a sexual partner in exchange for his protection), and forming female–female coalitions against males (many species).

The concept of sexual coercion can be applied to a number of other mammalian groups (Smuts and Smuts 1993; Clutton-Brock and Parker 1995) and forced copulation has been reported also in various invertebrates (Parker 1974; Thornhill and Alcock 1983; Rowe et al. 1994). In birds, copulations that appear to be forced have been reported in various species, especially waterfowl (McKinney et al. 1983, 1984), but the occurrence of forced copulation in passerine birds has been controversial for several reasons. Many ornithologists remain unconvinced that a male passerine bird can force copulation with a female (e.g., Fitch and Shugart 1984; Weatherhead and McRae 1990). Male–female chases do occur, and males are seen to attempt mounting, but females usually seem to be able to prevent forcible copulation. Conversely, some observers working on passerine birds have reported seeing forced copulations and they interpret these events as being of biological significance (Emlen and Wrege 1986; Westneat et al. 1990; Burley and Price 1991; Birkhead and Møller 1992). In any event, it is generally agreed that we need to be cautious in using the word "forced" because it is possible that females resist forced copulation attempts as a tactic to test male quality and ensure receipt of sperm from highly competitive males.

Early studies of extra-pair copulations (EPCs) in birds focussed on the prediction by Trivers (1972) that in monogamous species paired males could be increasing their production of offspring by fertilizing eggs via EPCs. This prediction was supported by observations on a variety of species, and such observations directed attention to research on male reproductive strategies and sperm competition mechanisms (Beecher and Beecher 1979; McKinney et al. 1984; Westneat 1987a, b). Recent research has shown, however, that females of some species solicit or preferentially accept EPCs from certain males, and therefore females are largely in control of extra-pair fertilizations (EPFs) (Smith 1988; Wagner 1991, 1993; Kempenaers et al. 1992; Lifjeld and Robertson 1992; Birkhead and Møller 1993; Graves et al. 1993; Sheldon 1994; Stutchbury and Neudorf, Chapter 5). For example, male Purple Martins (*Progne subis*) were reported to perform forced EPCs on females (Morton 1987), but it is now known that females mated to young males accept EPCs from old males whereas those females that acquired old males as mates avoid EPCs (Morton et al. 1990; Wagner 1993; Wagner et al. 1996). Such findings show that the benefits and costs of EPCs for each sex need to be examined with great care, and the use of the term "forced" in relation to EPCs should be critically reexamined.

Smuts and Smuts (1993) argue that morphological and behavioral traits have been selected specifically in the context of coercive behavior, and that the study of these traits will be enhanced if their unique features are recognized in the broad context of sexual selection theory. We are impressed by this argument, and suggest that it be applied to the study of sexual coercion in birds. In this paper, we argue that a strong case can be made for use of the term "forced" in referring to EPC in waterfowl, and we suggest that the FEPC phenomenon in waterfowl may be a useful model in enabling researchers to distinguish between male coercion of females and female manipulation of males in other birds.

We follow the taxonomy in the checklist by Howard and Moore (1991), except for the waterfowl (Anatidae), where we follow Johnsgard (1978) and the recent generic rearrangements (and in most cases the specific nomenclature) proposed by Livezey (1986, 1991, 1995a, b, 1996).

## EVIDENCE OF SEXUAL COERCION IN WATERFOWL

*Copulatory behavior in waterfowl:* In view of the difficulties involved in making field observations of copulatory behavior in many kinds of birds, the descriptive literature often lacks the detail necessary to judge whether forced extra-pair copulations (FEPCs) were indeed observed. There are three main practical problems: (1) Were the identities of the individuals and their mated status correctly recorded? Incidental observations on unmarked birds are not enough; the social status of identifiable individuals must be known from behavioral observations. (2) Was the copulation really forced? Here we need to decide on what is meant by "forced" and how it is to be identified. (3) Was the copulation attempt successful? Usually the best that can be done in the field is to define behavioral criteria and use them systematically. Ideally we want to know whether sperm transfer has occurred, and this cannot always be inferred even from information on paternity of offspring because of possibilities for sperm competition.

Three kinds of copulation have been described in waterfowl (McKinney et al. 1983; Afton 1985; Sorenson 1994a, b), and it is important to note that the paired status of the individuals concerned and the details of the behavior observed are used to distinguish them.

Pair copulations (PCs) occur between socially mated individuals, and in almost all species of waterfowl they take place while both birds are swimming. PCs are usually preceded by precopulatory displays by one or both partners (see Johnsgard 1965); the female adopts a prone posture with head stretched forward; the male climbs on to the female's back, grasps her crown feathers is his bill, and adjusts his position by making treading movements; the male's tail is moved around the left side of the female's tail (called "tail-bend") and there is a pronounced thrust as the male achieves intromission; the male's breast moves to the side off the female's back, he releases his hold of the female's crown feathers, and dismounts. The male typically performs one or more postcopulatory displays, in some species the female also gives displays, and then the female (or both birds) begin to bathe. Often the male performs vigorous tailwags, associated with retraction of the male's everted phallus into the cloaca. Key features of PCs are that either partner can initiate the behavior, copulation does not occur unless the female adopts the receptive posture and allows the male to mount, and the tail-bend and thrust are the best indicators that intromission is taking place. It seems likely that in many species the performance of male postcopulatory displays indicates that sperm transfer has been successfully achieved, but this is an assumption at this stage.

Forced extra-pair copulations (FEPCs), involving a male and female that are not social mates, are initiated aggressively by the male. The male approaches the female, dashes at her, and, if he succeeds in grasping and forcibly restraining her, mounts, performs tail-bend and thrust, and then dismounts. An FEPC attempt is an event in which the male chases the female and makes physical contact by grasping her; successful copulation may or may not follow. There are no precopulatory displays, and the male may or may not perform postcopulatory displays. The occurrence of tail-bend and thrust are believed to be more reliable indications of successful sperm transfer than are postcopulatory displays in dabbling ducks (*Anas* species) (McKinney et al. 1983; Sorenson 1994a), but Afton (1985) used the presence of postcopulatory displays as the criterion for success in Lesser Scaup (*Aythya affinis*). Male ducks intent on FEPC engage in prolonged and vigorous aerial, terrestrial, or underwater chases (called "sexual chases"). Females actively flee or hide from a pursuing male. Male–female pursuits can attract additional males and multimale FEPCs may follow, with several males achieving copulation in sequence. FEPC attempts take place on land or water, wherever the female is captured. In several goose species, FEPCs take place on land, in the nesting colony, with males typically approaching and grasping a female on her nest. In this situation, females may remain on the nest rather than fleeing, but this probably reflects reluctance to leave the eggs rather than purposeful "acceptance" of EPC. Unforced EPCs, in which females solicit or accept EPCs from males other than their social mates, have not been reported in waterfowl.

Forced pair copulations (FPCs) between a male and his mate have been observed in many duck species. Typically they occur soon after a male has witnessed

TABLE 1. Relative success of copulations in wild Mallards (Evarts 1990), White-cheeked Pintails (Sorenson 1994a), and Lesser Scaup (Afton 1985).*

| | Total PC attempts | Total FEPC attempts | Total FPC attempts |
|---|---|---|---|
| Mallards | | | |
| *n* | 28 | 19 | 12 |
| Success rate (%) | 100 | 39.8 | 50 |
| White-cheeked Pintails | | | |
| *n* | 84 | 96 | 7 |
| Success rate (%) | 80 | 19 | 57 |
| Lesser Scaup | | | |
| *n* | 230 | 276 | 3 |
| Success rate (%) | 96.5 | 19.6 | 0 |

* PC = pair copulation; FEPC = forced extra-pair copulation; FPC = forced pair copulation.

an FEPC attempt on his own mate. When an FPC occurs on land, the male attempts to grasp and mount the female and the female resists and moves away by walking or running a short distance. The male may persist with repeated mounting attempts, and the female continues to avoid him, but usually without extreme escape maneuvers involving flying or diving. Often the male appears half-hearted in his mounting attempts, and the female's escape behavior is similarly halfhearted. Nevertheless, these activities often culminate in copulations that appear to be successful.

The relative success rates for these three kinds of copulations are summarized for three species of ducks in Table 1. These data illustrate patterns of copulatory behavior in species in which males actively pursue FEPCs, but there are important specific variations in the frequency of FEPCs in waterfowl (see below).

*FEPC as a secondary reproductive strategy of males:* Monogamy is the basic mating system in most waterfowl and, although males are emancipated from parental care in many species, opportunities for polygyny are rare (Oring and Sayler 1992). Females of many species pair prior to the breeding season, often in flocks away from breeding areas, so resource defense polygyny, as practiced by many passerine bird species, is not an option for males (Rohwer and Anderson 1988). Therefore, in waterfowl, it appears that the stage is set for EPC to be exploited by males as a secondary reproductive strategy (Trivers 1972), and the presence of a male intromittent organ in waterfowl (rare in other birds) could make forced EPCs feasible (King 1981). Six hypotheses for the occurrence of FEPCs in waterfowl were reviewed in detail by McKinney et al. (1983), and most evidence supported the hypothesis that FEPC is a secondary male reproductive strategy. Predictions from this hypothesis were: the males involved are paired, eggs are fertilized by sperm delivered during FEPC, FEPCs are directed at fertile females, males have tactics whereby they achieve FEPCs, and males protect their mates from FEPC by other males. Key findings relating to these predictions are summarized here. (See also Afton 1985 and Sorenson 1994a, b for discussions of additional predictions.)

*Status of males:* Evidence that FEPCs are performed primarily by paired males has been presented for Lesser Scaup (Afton 1985), Mallard (*Anas platyrhynchos* [Evarts 1990]), White-fronted Goose (*Anser albifrons* [Ely and Dzubin 1994]), White-cheeked Pintail (*Anas bahamensis* [Sorenson 1994a, b]), Mottled Duck

(*Anas fulvigula* [Paulus 1984]), and a number of other species (McKinney et al. 1983). Although unpaired males are present on the breeding grounds in many duck species, they are mostly involved in courtship rather than FEPC activities (Seymour and Titman 1979; McKinney et al. 1983; Seymour 1990). Several records of FEPCs by unpaired males (in White-cheeked Pintails [Sorenson 1994b] and Lesser Scaup [Afton 1985]) were performed by old, experienced males that had been paired in previous years with females breeding on the same study area.

*Fertilization of eggs via FEPC:* The presence of sperm in the female's reproductive tract following an FEPC on a female Lesser Scaup was confirmed in one case by Afton (1985). A study of captive Mallards using a genetic plumage marker (Burns et al. 1980) provided strong evidence that eggs can be fertilized by FEPC. Multiple paternity of clutches was demonstrated, and observed FEPC events on particular females were correlated with the fertilization of eggs laid by these females on subsequent days. Multiple paternity was documented by electrophoresis in 8 of 46 clutches (17.4%) taken from wild Mallards (Evarts and Williams 1987), and multiple paternity was also shown in Lesser Snow Geese (*Anser caerulescens* [Quinn et al. 1987; Lank et al. 1989]).

Time of day is likely to be important if FEPC is to be effective in fertilizing eggs, but findings are contradictory. In Mallards, Evarts (1990) found that FEPC chases (with no mounting) ($n$ = 97) and FEPC attempts (with grasping and mounting) ($n$ = 19) peaked in frequency in late afternoon. Several other duck studies, however, suggest that FEPCs are more frequent in the morning than in the afternoon (Cheng et al. 1982; Afton 1985; Sorenson 1994a). The latter pattern has been associated with the postovulatory "fertilization window" (Cheng et al. 1982) that is likely to occur between the laying of one egg and the ovulation and fertilization of the next egg in the clutch. In species laying one egg per day (e.g., many dabbling ducks), these physiological events produce a short period (believed to be about 1 hr) during which stored sperm within the female's reproductive tract are in competition for fertilization of the newly ovulated egg. Because eggs are believed to be laid and fertilized in the morning, this could provide an especially favorable opportunity for males to inseminate laying females as soon as possible after egg-laying. However, the precise time of egg-laying (and hence of the "window") has not been determined in any species, and it is not known whether the window period occurs before or after females leave the nest (see Sorenson 1994a). There could be variation in egg-laying intervals between species and populations, and research on this topic is needed.

Sperm can remain viable for up to 17 days within the female Mallard's reproductive tract (Elder and Weller 1954), and therefore the mechanisms of sperm storage and control of fertilization must have important influences on which male's sperm are successful. The rules of sperm competition in Mallards have been investigated using artificial insemination techniques by Cheng et al. (1983). If several ejaculates are introduced within a short space of time, sperm from any of the males can have a chance of fertilizing the next egg in the clutch. If ejaculates are introduced more than 6 hr apart, however, the last insemination is most likely to be successful in fertilization. Thus, for example, sperm from a pair copulation could compete effectively with sperm from a different male introduced by FEPC 6 hr previously.

*Status of females involved in FEPC:* Several studies have provided convincing evidence that males direct FEPCs primarily at fertile females. In Lesser Scaup, Afton (1985) reported that rates of FEPCs and FEPC attempts were 2.4 times higher on fertilizable females (prelaying and laying) than on nonfertilizable females (incubating, premolting, nonbreeding birds). In White-cheeked Pintails, the rate of FEPC attempts on fertile females was 7.2 times the rate on nonfertile females, and when males were resident on the same pond with both fertile and nonfertile females they directed 13 of 14 FEPCs at fertile females (Sorenson 1994a, b). In Mallards, 13 of 22 FEPC attempts were directed at fertile females, and all seven attempts that were successful were on fertile females (Evarts 1990). In Arctic-nesting Lesser Snow Geese with highly synchronous egg-laying in breeding colonies, however, Mineau and Cooke (1979) found that only 10 of 54 FEPC attempts were directed at laying females and most attempts were on incubating birds.

*Male FEPC tactics:* Males use a variety of sophisticated tactics to detect fertile females and achieve FEPCs (McKinney et al. 1983). One method entails monitoring the breeding activities of neighboring pairs. Male Mallards frequently associate with neighboring males, in groups of two or three birds, while their females are absent at the nest, and similar male–male associations occurred in captive Chiloe Wigeon (*Anas sibilatrix*) (Brewer 1990). In two instances when a male Mallard was associating with a "waiting male," the female flew in to join her mate and the associating male attempted FEPC with her (Evarts 1990). Sorenson (1994b) reports that male White-cheeked Pintails also appear to monitor the activities of neighboring females. Behavioral cues males are likely monitoring include the intensity of territorial aggression shown by the breeding male (territory size and male aggression are at a maximum during the mate's laying stage) and secretive behavior characteristic of laying females. Male White-cheeked Pintails may also use sexual chases to assess female reproductive status. Fertile females were chased more persistently and at a much higher rate than nonfertile females, suggesting that males gather information on a female's condition by chasing her in flight.

Little is known about the behavioral mechanism involved in FEPC attempts by male ducks, although some of the triggers that stimulate males to engage in pursuits and/or assaults apparently come from the behavior of the target bird. Females that behave as though trying to escape (by fleeing, crouching, sneaking away, diving, hiding) are pursued especially vigorously, and even conspecific males (or females of other duck species) can trigger pursuit, grasping, and mounting behavior by eager males (McKinney et al. 1983, unpubl. obs.). In wild Mallards, interspecific FEPC attempts have been recorded involving North American Black Ducks (*Anas rubripes* [Seymour 1990]). There are also records of males attempting to copulate with dead birds (Greater Snow Goose, *Anser caerulescens atlanticus* [Gauthier and Tardif 1991]; Mallard [Lehner 1988]), which probably represent FEPC attempts.

Recent studies of wild dabbling ducks confirm that males are very adept at capturing females for FEPC. In a study of Mallards, eight of nine females that dived while being pursued by a male were captured underwater and the male was mounted on the female's back when the birds surfaced (Evarts 1990). Sorenson (1994b) reported underwater captures in 27% of 96 FEPC attempts observed in White-cheeked Pintails. Male White-cheeked Pintails also approached females surreptitiously, notably when thwarted by the aggressive behavior of a strongly defending mate. In these cases, males sneaked through shoreline vegetation or swam with body submerged with only the top of the head and back showing above the water surface.

Most FEPC attempts involve one male and one female, but multimale attempts occur when the chasing and splashing attract other males (McKinney et al. 1983). In White-cheeked Pintails, two to five males were involved in 63 of 139 FEPC attempts (each male's attempt scored separately), but FEPC success per male was lower in multimale than in single-male attempts, perhaps because of interference between males (Sorenson 1994b). Joining males try to mount the female simultaneously, so that the female becomes submerged under a pile of males, all trying to grasp her crown feathers, mount her back, and dislodge other males.

*Male paternity guards:* There are many ways in which male ducks protect their paternity (e.g., close following of the mate, escorting the mate to her nest and waiting on a nearby wetland while she is on the nest, defending a territory in which the mate feeds, attacking males that attempt FEPC on the mate, and engaging in FPCs after the mate has been exposed to FEPC [McKinney 1988]). The timing and intensity of mate guarding in Mallards was studied by Goodburn (1984), who showed that males guard their mates especially closely during the females' fertile periods.

The relatively low success rate of FEPC attempts in comparison with PC attempts reported for various species (Table 1) can be attributed to a combination of female resistance and male defense. Defending males usually attack the assaulting male, at least when only one male is involved, and this is often successful in preventing FEPC. In White-cheeked Pintails, the frequency of FEPC attempts on females was 3.4 times higher when they were alone than when their mates were present, and FEPC success was higher when the female was alone (33%) than when the female's mate was present (14%) (Sorenson 1994a).

Experiments in which paired males have been removed from their breeding females are instructive in showing effects on females of loss of mate guarding and the incidence of FEPC attempts by other males when a female is left unguarded. Removal experiments involving male Lesser Snow Geese (Martin et al. 1985) resulted in several prompt FEPC attempts by neighboring males, and widows were subjected to frequent sexual and physical harassment during the first week of incubation. The experimenters concluded that "increased physical or sexual harassment is one potentially significant, but as yet unmeasured, consequence of mate loss." In contrast, removal of seven male Buffleheads (*Bucephala albeola*) during the laying period (Gauthier 1986) led to territorial attacks on most females by neighboring males and in two cases males mated polygynously with widowed females. No FEPC attempts were made, confirming the absence of FEPC as a male strategy in this highly territorial species.

Forced pair copulations (FPCs) have been recorded in many duck species during the period when females are involved in FEPCs: Mallard, Green-winged Teal (*Anas carolinensis*), Northern Pintail (*Anas acuta*), North American Black Duck, African Yellowbill (*Anas undulata*), American Wigeon (*Anas americana*), Blue-winged Teal (*Anas discors*), Red-billed Pintail (*Anas erythrorhyncha*), White-cheeked Pintail, Speckled Teal (*Anas flavirostris*), and Lesser Scaup (references in McKinney et al. 1983). FPCs have also been recorded in Chiloe Wigeon (Brewer 1997), Auckland Island Teal (*Anas aucklandica aucklandica* [Williams 1995]), Canvasback (*Aythya valisineria* [Anderson 1985]), and Tufted Duck (*Aythya fuligula* [Gillham 1986]). These copulations could be important in sperm competition, and they are believed to be an adaptive response by paired males to FEPC on the mate. Sorenson's (1994a, b) observations of seven FPC attempts in White-cheeked Pintails support this idea. In four of these cases (three involving laying females), the FPC occurred less than 80 min after the female had been subjected to an FEPC attempt in the presence of her mate. In two other cases, the female was known to have been involved in frequent FEPC attempts during the previous 7 days. In Mallards, Evarts (1990) recorded 12 FPC attempts (6 of which were successful), and 3 attempts were made within 1 hr of an FEPC attempt on the female.

The timing of PCs (in which mates cooperate) could also be important in sperm competition during the period when females are fertile. PCs are common in Mallards after the female leaves the nest and returns to her mate (within 10 min of arrival in five of six instances) (Evarts 1990). All-day observations on captive Mallards during the females' fertile period (Cheng et al. 1982; McKinney et al. 1983) suggested that PCs are more frequent in the afternoon than in the morning (10 vs. 3), although this result could be influenced by frequent absence of females on the nest in the mornings. In White-cheeked Pintails, Sorenson (1994a) found that the diurnal timing of PC was influenced greatly by the periods that females were on the nest. Laying females left the nest later each day as the clutch progressed. Late in the laying period, all PCs were in the afternoon ($n = 6$), whereas five of seven PCs during the first half of the laying period occurred in the morning.

*Conclusions about FEPC as a secondary male strategy:* There is strong evidence supporting the hypothesis that FEPC is a male insemination strategy in well-studied species such as the Mallard, Lesser Scaup, Lesser Snow Goose, and White-cheeked Pintail. We know of no evidence that is inconsistent with the hypothesis for these species, although there remain important questions about the frequency of FEPC in other waterfowl species.

## DO FEMALE WATERFOWL BENEFIT FROM FEPC?

So far, waterfowl studies have focused on male benefits and tactics with regard to FEPC. Because these copulations appear to be forced, and there is no evidence so far that female waterfowl solicit or even passively accept copulations from males other than their mates, it has been assumed that there is no benefit of FEPC for females. Indeed, the behavior of females is consistent with active resistance to FEPCs. When pursued by males, female ducks try to escape (e.g., by flying, diving underwater, hiding in vegetation, moving to secure locations), and when grasped they resist attempts by males to achieve FEPCs (McKinney et al. 1983; Goodburn 1984; Sorenson 1994b). Females that are frequently subjected to FEPCs crouch when males fly over, and are more secretive when rejoining their mates after leaving the nest. For females, it appears that the costs of FEPCs outweigh any potential benefits, but studies with female strategies as the focus have not been done.

The costs and benefits of EPCs for female birds in general have been discussed very thoroughly by Westneat et al. (1990) and Hunter et al. (1993), although these discussions focus primarily on species in which the female cooperates with or solicits EPCs. We consider here the potential benefits of FEPCs for female waterfowl.

*Good genes:* Female waterfowl play active roles in mate choice, paying attention to various morphological and behavioral characteristics that probably vary between species (e.g., Choudhury and Black 1993; Sorenson and Derrickson 1994). In the Northern Hemisphere, pair formation begins in the fall or winter and continues through early spring (Rohwer and Anderson 1988). Females (and males) spend a great deal of time choosing a mate and assessing the pair-bond, but the "best" males are limited in number and chosen males are defended by their mates. Thus, females may have to settle for a mate that is less than optimal, and females might benefit by obtaining inseminations via EPC from males that otherwise would be unavailable to them.

Some observers have suggested that female ducks draw attention to themselves during EPC attempts by flying, calling, splashing, and so on (e.g., Christoleit 1929a, b; Sowls 1955; Phillips and van Tienhoven 1962), in order to incite competition between males. The activities involved in FEPC attempts in ducks are usually noisy and they make the birds conspicuous so that additional males are attracted and may join in the pursuit. Often several males attempt FEPC on the same female, and presumably the most competent and persistent males are those that gain copulations first. Each male typically departs after copulating, however, and less competent males may then be able to copulate with a female with weakened resistance. In such multimale events, it is difficult to envisage how females could control which male(s) inseminate them, and the benefits for females of such induced competition are unpredictable.

*Increasing genetic diversity of offspring:* Female ducks (e.g., Mallard) nest in relatively diverse and temporally variable habitats (Bellrose 1979), and because pairs are often formed on the wintering grounds, the female may have no way to judge whether the genes from her mate will help to produce offspring that are well adapted to her breeding area. A female might benefit by obtaining inseminations from several males, thereby increasing the genetic diversity of her offspring. The possibility that females benefit in this way from multiple paternity of their clutches remains an open question.

*Securing fertilizations:* In many migratory duck species, pair-bonds break during incubation and males desert their females. If the female should lose her clutch or brood after her mate has departed, some authors have suggested that she could profit by obtaining sperm for a renest clutch via EPC (Milstein 1979). In most species, however, the old pair-bonds are renewed, or new pair-bonds are formed before renest clutches are laid (e.g., Gates 1962; Humburg et al. 1978) and, therefore, eggs can be fertilized via PCs. Inseminations via EPCs, however, may be advantageous to females in guarding against sterility of mates.

## DO COSTS OF FEPC OUTWEIGH BENEFITS FOR FEMALES?

*Risk of injury and death:* Females can be injured or killed as a result of repeated FEPC attempts. At the Tring reservoirs in southern England, Huxley (1912) reported that about 70 Mallard females were killed annually (estimated to be 7–10% of the breeding population) as a result of FEPCs. In the Doñana National Park in southwestern Spain, Amat (1983) found up to 10 dead Mallard females in May of each of 2 years, and one dead Gadwall (*Anas strepera*) female, all with "their heads and backs without feathers and completely bloody" suggesting that "all such females were repeatedly mounted by several males, causing their deaths." Similar observations have been reported in a crowded population of Mallards (Titman and Lowther 1975), among captive-raised and released Northern Pintails (*Anas acuta* [Smith 1968]), in a natural population of Laysan Teal (*Anas laysanensis* [Moulton and Weller 1984]), and in several other dabbling ducks (McKinney et al. 1983). In White-cheeked Pintails, Sorenson (1994b) observed two females that were exhausted (unable to walk without collapsing) during multimale FEPC attempts, but no mortalities were noted in this species.

We have examined several female Mallards found dead after being subjected to repeated FEPC attempts. They had very few feathers left on the back of their heads (where males grasp females during copulation), and they had deep scratches on their backs made by the claws of males during mounting attempts. Some females also had internal injuries (ruptured organs and eggs). Females can also be drowned by being held under water for extended periods of time during multimale FEPC attempts. Injuries and mortality of females occur especially frequently in crowded or park populations, where the sex ratio is often heavily male-biased and females have difficulty avoiding harassment (S. Evarts, unpubl. observations).

*Energy loss:* Although energetic costs of resisting FEPCs have not been measured, females often expend large amounts of energy flying, struggling, and diving to avoid FEPC attempts. This is an especially serious cost for females during the period of egg production when their reserves are needed to produce eggs.

*Abandonment of breeding attempt:* Females that are harassed continually by males intent on FEPC may abandon nests. Afton (1985) documented one case in Lesser Scaup in which the mate of a female that was subjected to many FEPC attempts gradually ceased to defend her, the female abandoned breeding, and then the male left the study area. Sorenson (1994a) found that female White-cheeked Pintails that abandoned nesting attempts ($n = 17$) had been exposed to a higher frequency of FEPC attempts and sexual chases than females that completed clutches and initiated incubation ($n = 23$).

Male ducks whose female mates are continually subjected to FEPCs may sometimes desert them prematurely (Afton 1985), and this could be costly for females. Although males of many species do not invest directly in the care of eggs or young, they may contribute indirectly by escorting their mates during the prelaying, laying, and early incubation periods, by remaining vigilant for predators, and by discouraging approach by other males (McKinney 1985, 1986). In this way, males can reduce the amount of time females spend in vigilance, increase the time females have for feeding, and minimize harassment to females by other males (Ashcroft 1976; McLandress and Raveling 1981; Afton and Sayler 1982). The time spent feeding by female White-cheeked Pintails that eventually abandoned a nesting attempt was significantly less than in females that nested successfully (Sorenson 1992). Therefore, effective guarding by the female's mate against harassment and chasing was essential to successful nesting in this species.

*Reduced fertility of eggs:* Amat (1987) has reported data on the relative frequency of infertile eggs in clutches of four species of dabbling ducks, indicating that infertility is more frequent in three species with high rates of FEPC (Northern Pintail, Mallard, Gadwall) than in the highly territorial Northern Shoveler (*Anas* *clypeata*). Amat suggests that the lower frequency of infertile eggs in the Northern Shoveler could be attributed to strong mate guarding and absence of disruptive FEPC activity in this species.

*Conclusions on FEPCs and females:* The fact that female waterfowl are willing to expend large amounts of energy resisting EPCs (especially during a period when energy reserves are needed to produce eggs), coupled with the risk of injury or death from these copulations, indicates that these copulations really are forced. Male waterfowl have an intromittent organ and copulations usually occur on water so it is possible for a male to force a copulation on an unwilling female.

Female waterfowl, like other birds, may be able to control some aspects of sperm competition (Birkhead and Møller 1993). Females have sperm storage organs and so may be able to control which sperm fertilize eggs. Females may also control the timing of PCs so that the mate may have a better or worse chance of fertilizing that day's egg. FPCs by the male may be a behavior that has evolved to counter this. Females may also be able to eject sperm (Davies 1983; Birkhead and Møller 1992), but this is difficult to determine with copulations on water.

## WHY DO FEMALE WATERFOWL RESIST FEPCS?

It appears that there are substantial costs to females associated with FEPCs, and because the costs and risks of prolonging FEPC attempts until they become multimale affairs are severe, it is puzzling to find that females vigorously resist FEPCs. Why do females not accept EPCs to minimize the risk of attracting additional males? By accepting EPCs, the female could save much time and energy expended in flying, diving, and otherwise trying to escape from the pursuing male. Sorenson (1994b) has discussed this question and has examined the following three hypotheses.

(1) Perhaps the female's resistance of EPCs is a tactic to test male quality. For the reasons already detailed above, Sorenson believes that the "resistance-as-a-ploy" hypothesis is unlikely to apply to waterfowl because the costs of resistance are so high (as McKinney et al. [1983] and Birkhead and Møller [1992] also concluded).

(2) Perhaps females resist EPCs because they are already paired to a high-quality male, and by resisting they avoid the costs of copulating with a male of inferior or unknown quality. But, Sorenson argues, male mates vary in quality as do males attempting FEPC, and therefore females should accept EPCs from some males and reject them from others. This has been the finding in several studies on nonwaterfowl species (Smith 1988; Burley and Price 1991; Kempenaers et al. 1992; Wagner et al. 1996). In White-cheeked Pintails, however, Sorenson (1994a) found that high-quality males attempted EPCs most frequently, and often with females paired with low-quality males, but females always resisted these attempts. Nor did females show less resistance to paired versus unpaired males (although the former would probably be readily identifiable and be likely of higher quality than the latter). In summary, there was no detectable difference in female resistance to EPCs in relation to the male's quality or pair status, and, therefore, this hypothesis is not supported.

(3) Perhaps females resist EPCs to preserve the pair-bond and the investment of the mate. Sorenson argues that if a female cooperates in an EPC and her mate witnesses the copulation, he may defend her less vigorously or even desert her.

The open habitats occupied by many waterfowl probably make it more difficult for females to cooperate in EPCs without their mate observing it, and loss of confidence of paternity could be a powerful factor promoting reduced male reproductive effort. Although this seems to be the most promising hypothesis, data on paternity and lifetime reproductive success are needed to test it.

## FEMALE DISPLAYS

Female dabbling ducks have distinctive postures with accompanying vocalizations that they perform when approached or pursued by males other than the mate (Lorenz 1951–1953; McKinney et al. 1983). From the time of pair formation until the beginning of the breeding season, females threaten approaching males and effectively discourage them by performing the distinctive "inciting" display. This is performed beside the female's mate, and entails ritualized threat motions toward the rejected male accompanied by rhythmical calls. Inciting signals the female's bond to her mate and rejection of the stranger, and it is the major female display during the prebreeding period.

For several days or weeks before laying the first egg of a clutch, female dabbling ducks frequently give long bouts of "persistent quacking," a display believed to be designed to stimulate terrestrial predators to betray their presence (McKinney et al. 1990). Persistent quacking is associated with flights by pairs over nesting cover, and although such females are often pursued in the air by males (e.g., in "three-bird flights" [McKinney and Stolen 1982]), persistent quacking does not stimulate males to attempt FEPC. This is perhaps surprising, because some calling females may well be fertile, but the duration of persistent quacking (up to several weeks) may be too long and variable to provide males with an accurate indicator of a female's fertility.

When egg-laying begins, inciting is no longer effective in deterring determined males intent on FEPC, and after a female has been subjected to vigorous chases and FEPC attempts, she gives inciting infrequently and becomes silent while attempting to escape by flying, diving, or hiding.

After a female begins to incubate, her mate continues to maintain the pair-bond by waiting on a nearby wetland and escorting her during recess periods. (The duration of the bond varies with the season and among species.) When approached and/or chased by males other than their mates, incubating females adopt distinctive "repulsion" postures, with retracted head and ruffled feathers, and they give loud irregular quacking calls and squeals. Although females giving repulsion behavior may be harassed by persistent males, their behavior appears to deter males from FEPC attempts and this is believed to be the function of the display. During the "renest interval" (e.g., after loss of a clutch to predation), the female's responses to being chased gradually change from repulsion to inciting or silent retreat as she nears egg-laying again.

Results of one study of breeding Mallards (Evarts 1990) illustrate responses to these female displays. No FEPC attempts were directed at females giving persistent quacking ($n = 698$ calling bouts). Of FEPC chases directed at calling females ($n = 129$), 69.8% were on females giving inciting and 30.2% were on females giving repulsion. Aerial chases directed at females giving inciting averaged 3.26 min in duration ($n = 90$), whereas chases at females giving repulsion lasted on average 1.19 min ($n = 39$), a significant difference ($G_{\text{adj}} = 20.64$; $P < 0.001$).

Of 15 FEPC attempts, 14 were on females giving inciting, and 1 was on a female giving repulsion.

Although repulsion displays are widely recognized as indicative of "broody" female ducks, further detailed studies are needed to explore the probable role of these displays as a behavioral adaptation evolved specifically as a response to male FEPC.

## FEPC AND MATE ACQUISITION

The behavior of male waterfowl during courtship leading to pair formation and during FEPC attempts is so different that the two kinds of activity are often regarded as alternative, incompatible male strategies. For example, in migratory Northern Hemisphere ducks, the two activities are temporally separated; pairs form during competitive courtship in winter and FEPC occurs in spring when breeding begins. This sharp separation can become blurred, however, when extra-pair courtship, renewal of bonds, or mate-switching occur during the breeding season, for example prior to renesting attempts. In some waterfowl, males follow one or the other strategy; Canvasbacks use extra-pair courtship, sometimes leading to mate-switching before renesting, but Lesser Scaup pursue FEPCs and renesting is rare (Afton 1985; Anderson 1985). In some dabbling ducks, males engage in both FEPC and extra-pair courtship during the same breeding season (e.g., Green-winged Teal [McKinney and Stolen 1982]) and it is possible that the different goals (EPC vs. acquiring a mate) conflict.

In tropical and Southern Hemisphere dabbling ducks, breeding seasons are often extended and/or irregular (McKinney 1985) and breeding patterns and mating systems can be variable, including bigamy, serial monogamy, and double brooding (Sorenson 1992; Sorenson et al. 1992). Studies on two Southern Hemisphere species breeding in flight pens showed that paired males are capable of combining FEPC with mate acquisition (Cape Teal, *Anas capensis* [Stolen and McKinney 1983]; Speckled Teal, *Anas flavirostris* [McKinney 1985]). In both cases, a paired male directed FEPC attempts at another female while his mate was in prelaying or laying phases; then abruptly the relationship to the second female changed to that typical of a pair-bond (including PC and close attendance), and the male became bigamous. Initially, these males engaged in PCs with the first mate and FEPCs with the second female, but all time was spent with the mate; after the sudden onset of bigamous behavior, the males divided their time between the two females. In both cases of bigamy, the females solicited PCs from the male they shared, and the male actively partitioned his time so as to maintain his bond to both females.

Additional observations on the behavior of captive Speckled Teal during the formation of bigamous bonds have shown that there is much variation from case to case, with the relationships between the birds involved being dynamic and complex (F. McKinney, unpubl. data). Extra-pair courtship by males, dominance relations between males, female interest in specific males, aggression between females, and female mate-holding tactics all seemed to be involved. In some cases, FEPC did occur before a bigamous bond developed, but in other cases no FEPCs were recorded.

We conclude that FEPC may possibly play a role in the acquisition of second mates in those waterfowl species where bigamy occurs. Further study of this intriguing topic is needed.

## FEPC, MATE GUARDING, AND BREEDING SYNCHRONY

The reproductive strategies of male birds are likely to be greatly influenced by the degree of breeding synchrony in the local population because of effects on the operational sex ratio (Emlen and Oring 1977). In species with social partners (pair-bonds), breeding synchrony can be expected to affect the ways in which paired males reach a compromise between the competing demands of mate guarding and pursuit of EPCs (Birkhead et al. 1985; Björklund and Westman 1986; Birkhead and Biggins 1987; Birkhead and Møller 1992; Kempenaers 1993; Stutchbury and Morton 1995; Stutchbury and Neudorf, Chapter 5). Two quite different arguments have been made, yielding the following opposing predictions. (1) Paired males cannot pursue EPCs and guard their mates simultaneously; therefore mate guarding must have priority while the mate is fertile and males will pursue EPCs at other times (e.g., later in the breeding season); so males will have more opportunities for EPCs in an asynchronously breeding population. (2) The payoff for males seeking EPCs will be highest during the period when most females are fertile; therefore, EPC attempts by males are expected to be most frequent in synchronously breeding populations.

One approach to these questions has been to look for correlations between specific differences in breeding synchrony and the frequency of EPFs in the mating system. Stutchbury and Morton (1995) examined this possibility in songbirds, and showed that EPFs are most common in species where females breed synchronously. This analysis is not possible for waterfowl, because EPFs have been documented in only two species (Mallard and Lesser Snow Goose). Based on FEPC frequencies, however, the songbird pattern does not seem likely to apply in dabbling ducks or pochards, in which only moderately asynchronously breeding north temperate species exhibit both high and low frequencies.

Considering the different question of how individual males partition their time in relation to breeding synchrony, there is no clear pattern in waterfowl. In some species, males appear to temporally partition mate guarding and FEPC attempts, guarding during their mate's fertile period and pursuing FEPCs after the mate begins incubation (Lesser Snow Goose [Mineau and Cooke 1979]; Mallard [Goodburn 1984; Evarts 1990]). In other species, however, males engage in both activities during their mate's fertile period (Lesser Scaup [Afton 1985]; White-cheeked Pintail [Sorenson 1994a]). In Lesser Snow Goose and Lesser Scaup, breeding synchrony is high and renesting is rare. Males in these species may therefore have a very limited period during the annual breeding season when FEPCs can be profitably pursued. Moreover, the potential costs to males of exposing their mates to FEPC (in terms of risk of cuckoldry and exposure of the mate to harassment) may differ markedly between species, and the costs are likely to be especially high in this colonially nesting goose.

In general, the two dabbling duck species (Mallard and White-cheeked Pintail) have moderately asynchronous breeding patterns (with frequent renesting in the case of the Mallard). However, Sorenson's White-cheeked Pintail population was sedentary, and paired males differed markedly in "quality" as measured by their effectiveness in *both* mate guarding (including defense of a breeding territory) and FEPC. Therefore, it may be that the costs of engaging in FEPC attempts while the mate is fertile were minimal for high-quality males in this population (as in some passerine species; e.g., Stutchbury et al. 1994), whereas temporal partitioning of mate guarding and FEPC was favored in the Mallard populations studied by Goodburn and Evarts.

In addition to the various factors noted above that may have influenced the trade-off between mate guarding and FEPC in these four waterfowl species (renesting, colonial nesting, sedentary behavior, territoriality), other factors could also be involved (e.g., vulnerability of females to FEPC in different habitats, effectiveness of female defenses against FEPC). Therefore, at least in the case of waterfowl, we expect that relationships between degrees of breeding synchrony and male strategies will vary considerably between species, and further research on these and other species is badly needed.

## COMPARATIVE EVIDENCE FOR WATERFOWL

Since attention was drawn to the phenomenon two decades ago, FEPC has been a topic of widespread interest to students of waterfowl biology, and careful studies have revealed that this behavior occurs commonly and regularly in certain species, uncommonly and opportunistically in other species, and rarely or never in some species. Several factors could contribute to these distributional patterns.

Forced extra-pair copulation has been recorded in 55 species of waterfowl in 17 genera (*Anseranas, Dendrocygna, Anser, Branta, Cereopsis, Sarkidiornis, Aix, Anas, Callonetta, Chenonetta, Marmaronetta, Netta, Aythya, Melanitta, Mergus, Heteronetta, and Oxyura*) (see Table 2). The wide distribution of FEPC in the family Anatidae indicates that this behavior is either an ancient one in this lineage or that it has evolved multiple times during the radiation of anatid types. Morphological, physiological, or ecological constraints appear to inhibit or prevent the use of FEPC in certain species, and the factors involved are of special interest.

There is much evidence to show that FEPC is either very rare or absent in certain waterfowl groups. FEPC appears to be absent in swans (*Coscoroba, Cygnus, Olor*), shelducks and sheldgeese (*Tadorna, Alopochen, Chloephaga*), steamer ducks (*Tachyeres*), and most genera of sea ducks (*Polysticta, Somateria, Histrionicus, Clangula, Bucephala*). In many of these waterfowl, males defend exclusive breeding territories and this appears to take priority over the different kinds of activities that would be involved in pursuing FEPCs (Oring and Sayler 1992). FEPC is also absent in two river species—the African Black Duck (*Anas sparsa*) and the Blue Duck (*Hymenolaimus malacorhynchos*)—in which pairs cooperate in defending all-purpose territories and mate-stealing tactics appear to be incompatible with FEPC (McKinney et al. 1978; Williams 1991; Williams and McKinney 1996). DNA fingerprinting also confirmed the absence of multiple paternity in Blue Ducks (Triggs et al. 1991).

Among *Aythya* species, Anderson (1985) showed that Canvasback males pursue extra-pair courtship instead of FEPC, and he suggested that this is related to the early nesting and frequent renesting behavior of this species. Liaisons with extra-pair females may pay off for male Canvasbacks in a second breeding sequence provided some mate switches occur between nesting attempts. This strategy contrasts with that of Lesser Scaup, which breed later in the season and seldom renest. In this species, FEPC is frequent and apparently replaces extra-pair courtship as

TABLE 2. Distribution of forced extra-pair copulation (FEPC) in major groups of waterfowl.

| | Number of species | | | |
|---|---|---|---|---|
| | In group | With FEPC present | With FEPC absent | References* |
| Anseranatidae (Magpie Goose) | 1 | 1† | | 1 |
| Dendrocygninae (Whistling Ducks) | 9 | 2 | | 2 |
| Cygnini (Swans) | 7 | | 7† | 3 |
| Anserini (Geese) | 15 | 5† | 1(?+)† | 2, 4, 5 |
| Sarkidiornini (Comb Duck) | 1 | 1 | | 2 |
| Tadornini (Shelduck and allies) | 15 | | 3(?+)† | 6 |
| Tachyerini (Steamer Ducks) | 4 | | 4† | 7 |
| Anatini (Dabbling Ducks and allies) | 55 | 34† | 2† | 2, 8, 9, 10 |
| Aythyini (Pochards) | 16 | 6† | 1† | 2, 11, 12 |
| Mergini (Sea Ducks) | 23 | 3 | 4(?+)† | 2, 13 |
| Oxyurini (Stiff-tails) | 9 | 3† | | 2, 14 |

* 1. S.J.J.F. Davies in Marchant and Higgins (1990). 2. References in McKinney et al. (1983). 3. Absent in *Cygnus columbianus, Cygnus buccinator* (J. Cooper, pers. comm.); absent in all swans (Kear 1972). 4. *Anser albifrons* (Ely 1989; Ely and Dzubin 1994), *Anser rossi* (add,‡ A. Afton, pers. comm.), *Branta bernicla* (Welsh and Sedinger 1990), *Cereopsis novaehollandiae* (c,‡ Veselovsky 1970). 5. Absent in *Branta canadensis* (J. Cooper, pers. comm.) 6. Absent in *Tadorna tadorna* (Cramp and Simmons 1977), *Tadorna tadornoides* (Marchant and Higgins 1990); *Tadorna variegata* (Williams 1979). 7. Livezey and Humphrey (1985). 8. *Chenonetta jubata* (Kingsford 1986), *Callonetta leucophrys* (add, c, Brewer 1988), *Aix galericulata* (add, c, Bruggers and Jackson 1981), *Aix sponsa* (add, Bellrose and Holm 1994), *Anas fulvigula* (Paulus 1984; Moorman and Gray 1994), *Anas penelope* (Ugelvik 1986), *Anas bahamensis* (add, Sorenson 1994a, b), *Anas melleri* (c, Young 1995), *Anas laysanensis* (Moulton and Weller 1984), *Anas versicolor* (c, J. Port, pers. comm.), *Anas chlorotis* (Dumbell 1987), *Anas aucklandica aucklandica* and *A. a. nesiotis* (Williams 1995; M. Williams, pers. comm.), *Anas flavirostris oxyptera* (add, G. Brewer, pers. comm.), *Anas sibilatrix* (Brewer 1997), *Anas querquedula* (c, F. McKinney, unpubl. obs.), *Anas clypeata* (add, Poston 1974), *Marmaronetta angustirostris* (c, J. Port, pers. comm.). 9. Correction to McKinney et al. (1983): delete records for *Anas poecilorhyncha*; add *Anas superciliosa* (W. Braithwaite, pers. comm.; F. McKinney, unpubl. obs. for *A. s. rogersi*). 10. Absent in *Anas sparsa* (McKinney et al. 1978), *Hymenolaimus malacorhynchus* (Triggs et al. 1991; Williams 1991). 11. *Aythya fuligula* (add, Gillham 1986). 12. Absent in *Aythya ferina* (Gillham 1986). 13. Absent in *Bucephala islandica, Bucephala clangula, Bucephala albeola* (Gauthier 1986; Savard 1988), and *Histrionicus histrionicus* (Inglis et al. 1989). 14. *Oxyura vittata, Heteronetta atricapilla* (Carbonell 1983).

† Includes additional species not recorded in McKinney et al. [1983].

‡ add = additional sources since McKinney et al. 1983; c = observed in captives.

a secondary male reproductive strategy (Afton 1985). Two Palearctic *Aythya* species may provide parallel contrasting strategies, with FEPC being rare or absent in the European Pochard (*Aythya ferina*) but frequent in the Tufted Duck (Gillham 1986).

Within the dabbling ducks, there are similar specific variations in the incidence of FEPC (Titman and Seymour 1981; McKinney et al. 1983). FEPC is frequent and apparently functional as a secondary male reproductive strategy in some species (e.g., Mallard, Northern Pintail, White-cheeked Pintail), it is uncommon in other species (e.g., Northern Shoveler, Blue-winged Teal), and it appears to be absent in one species (African Black Duck). Many ecological and social factors could be involved in producing such diversity in this group, and it is difficult to categorize many species. As noted in other waterfowl tribes, males of those species exhibiting strong territoriality may have limited opportunities to engage in FEPCs as well as defending an area. This might account for the rarity of FEPC in some of the species noted above (e.g., Northern Shoveler), although White-cheeked Pintails are able to combine these two activities. Gauthier (1988) reviewed the trade-off between territoriality and FEPC in ducks, and concluded that territoriality is closely associated with stable habitats. He proposed that in species occupying stable habitats, males will do better to defend their mates and promote the mate's breeding effort, whereas in unstable habitats males have more to gain from FEPC. Variations in the frequency of FEPC from year to year within populations of a species, as detected by Afton (1985) in Lesser Scaup, may be anticipated.

Although the breeding behavior of many species of waterfowl has been intensively studied, further research with a focus on FEPC is needed. Much of the information currently available on Northern Hemisphere ducks was collected by observers with diverse primary interests, under different habitat conditions, and on populations of ducks in various densities. Research is particularly needed on tropical and Southern Hemisphere species, which have received less attention. For example, the whistling ducks deserve special study, because FEPC behavior has been reported in two species only.

## FORCED COPULATION IN OTHER BIRDS

There are special problems of interpretation in observations of forced copulations, and there has been a tendency to focus on the genetic payoffs rather than the coercive aspects of the phenomenon. Although great advances have been made in revealing the roles that females can have in controlling paternity (Birkhead and Møller 1993; Wagner 1993; Stutchbury and Neudorf, Chapter 5), the ability of males to impose copulations on unwilling females remains poorly understood in birds. Most observers have been concerned with the possibility of forced copulation in the context of EPCs, and little attention has been given to the occurrence of sexual coercion in other contexts. Also, evidence of coercion is less clear in species without pair-bonds. The following review is inevitably incomplete. We have not tried to cover the literature on bird behavior to ferret out indications of coercive behavior. Instead we point to those cases where authors have noted attempts by males to force EPCs.

In cases where males are observed to pursue females or to mount females without preliminaries, the main problem is to decide whether females that resist or accept copulations are engaging in a subtle mixed reproductive strategy or are making the best of a bad job by trying to minimize the costs of EPCs. As Westneat (1992) has pointed out in a careful discussion of this topic, the difference lies in whether the female is incurring a net benefit or a net cost from the EPC event. The costs or benefits involved may have phenotypic and/or genotypic components and it is presumably the balance between these varied costs and benefits that has shaped the evolution of female behavior. In tackling these difficult questions from a female perspective, Westneat (1992) recommends that we begin by making careful behavioral observations to determine whether females initiate extra-pair events. If they do not initiate, but they either accept or resist EPCs, we can learn from a combination of information on the costs and benefits involved and what females actually do in different contexts. Intensive studies revealing costs and benefits in particular species are still uncommon, but some new behavioral evidence has been presented in a number of cases.

Although several researchers working on passerine birds appear to be convinced that they have observed FEPCs, most observers maintain that females must cooperate if a male is to be successful in achieving cloacal contact. One difficulty is that in many species it is extremely difficult to determine by observation whether FEPCs are occurring because copulations of any sort are not seen (e.g., Northern Cardinal, *Cardinalis cardinalis* [Ritchison et al. 1994]), the birds are usually obscured by vegetation or are out of sight in the nesting cavity, or the female's behavior is ambiguous.

The following systematic account updates the previous review (McKinney et al. 1984), which should be checked for additional earlier records.

### DIOMEDEIDAE (ALBATROSSES)

C. J. R. Robertson (pers. comm.) reported seeing forced copulations by male Royal Albatrosses (*Diomedea epomophora*) whose mates from the year before had not returned and were presumably dead. Once these males repaired, the forced copulation activity stopped.

### PELECANIDAE (PELICANS)

R. Evans (pers. comm.) saw several forced copulation attempts per day in American White Pelicans (*Pelecanus erythrorhynchos*). These copulation attempts occurred during the early stages of nesting, but Evans considered them generally to be unsuccessful. B. Ploger (pers. comm.) has observed apparently forced copulation attempts in Brown Pelicans (*Pelecanus occidentalis*) in a breeding colony.

### ARDEIDAE (HERONS)

M. Fujioka (pers. comm.) observed 1,888 EPC attempts in Little Egrets (*Egretta garzetta*), 326 (17%) of which were forced, and only 14 (1%) of the latter were successful. Earlier indications that FEPC is part of a mixed male strategy in Cattle Egrets (*Bubulcus ibis* [Blaker 1969; Lancaster 1970; Fujioka and Yamagishi 1981]) are supported by new evidence of EPFs and multimale FEPC attempts (D. Mock and J. Gieg, pers. comm.). Frequent FEPC attempts occurring in a dense breeding colony of Grey Herons (*Ardea cinerea*) when females were left unguarded supports the sperm competition hypothesis for this species also (Ramo 1993).

### THESKIORNITHIDAE (IBISES, SPOONBILLS)

Detailed information on the copulatory behavior of the White Ibis (*Eudocimus albus* [Frederick 1987a, b]) and the White Spoonbill (*Platalea leucorodia* [Aguilera and Alvarez 1989]) shows that although males initiate EPCs by approaching and trying to mount females on neighboring nests, females appear to control whether copulation occurs. Females accept EPCs from some males and refuse them from others. Therefore the label "FEPC" (Gladstone 1979) should not be applied in these or other members of this group without intensive study. It may be that both males and females are engaging in mixed mating strategies. EPCs, usually between paired birds on neighboring nests, have also been reported in the

Australian White Ibis (*Theskiornis molucca*); females never leave the nest to avoid EPCs and they sometimes bill-poke at the male (Marchant and Higgins 1990).

### ACCIPITRIDAE (HAWKS, EAGLES)

On a roosting cliff adjacent to a nesting colony of Cape Vultures (*Gyps coprotheres*), Robertson (1986) observed 76 copulations, of which 11 were classed as FEPCs. In 6 of the 11 instances, one of the birds involved (four males, two females) was from a known nest site.

### PHASIANIDAE (PHEASANTS, GROUSE)

Forced extra-pair copulations have been observed in captive Japanese Quail (*Coturnix japonica*; both domesticated and feral types), which have basically monogamous mating systems (Nichols 1991; Adkins-Regan 1995).

### LARIDAE (GULLS)

Forced extra-pair copulation attempts have been regularly observed in Western Gulls (*Larus occidentalis*), but do not often result in successful copulations (less than 1 in 100 [Pierotti 1981; Pierotti et al. 1997]). Most FEPC attempts occurred during the period from egg-laying until the middle of incubation. Males whose mates had completed laying were the primary participants in FEPCs. They approached females that were sitting on nests (males never approached females that were off the nest). Females would strike or snap at the male, but they were rarely able to deter a determined male who would leap upon the back of the female and attempt to force cloacal contact. Similar FEPC attempts were very frequent in a Lake Ontario colony of Ring-billed Gulls (*Larus delawarensis*) early in the breeding season when many birds were laying (R. Pierotti, pers. comm.)

Mills (1994) has reported results of studies on Red-billed Gulls (*Larus novaehollandiae scopulinus*) indicating that females vary in their responses to males attempting EPC. Females that were well fed by their mates during courtship feeding resisted all EPC attempts and kept the same mate the next breeding season. Females who were poorly fed during courtship divorced the next season, and one such female solicited EPC. This suggests that females can control EPCs and, although EPCs occur when females are fertile, the advantages of EPCs were greater for females than for males. Further studies on these and other species of gulls in which FEPCs have been reported (references in McKinney et al. 1984) are needed to investigate whether females as well as males may be using mixed strategies.

### ALCIDAE (AUKS)

Forced extra-pair copulations are frequent on ledges in breeding colonies of Common Murres (*Uria aalge* [Birkhead et al. 1985; Hatchwell 1988]). Unguarded females are particularly vulnerable to FEPC, and multimale assaults can occur. Only a small proportion of FEPCs is believed to result in successful sperm transer. Females usually respond aggressively or try to evade or escape, but sometimes females solicit EPCs and cooperate with the male by allowing cloacal contact.

Wagner (1991) presented evidence that female Razorbills (*Alca torda*) visit special sites near the nesting places where they solicit EPCs, and in this species females appear to control which males inseminate them. FEPCs are not reported in this species.

### MEROPIDAE (BEE-EATERS)

Colonially nesting White-fronted Bee-eaters (*Merops bullockoides*) engage in multimale FEPC attempts when a female leaves the nest cavity and is not guarded by her mate (Emlen and Wrege 1986). In such instances, females may be chased by as many as 12 males, and the chases sometimes end with the female being forced to the ground and mounted by numerous males. Females apparently try to prevent these copulations by spreading the wings and pressing the cloaca against the ground. If the female is forced to land on tree branches, she spreads her tail (making cloacal contact difficult) and may escape by flying out from under the male(s). Most sexual chases are directed at laying females by paired males, and males usually closely guard their mates during the fertile period. Emlen and Wrege (1986) consider FEPC to be a low yield/low cost secondary reproductive tactic of breeding males.

### HIRUNDINIDAE (SWALLOWS, MARTINS)

The swallow group has been much studied in recent years, and emphasis on apparent FEPCs in several species in earlier studies has been replaced by emphasis on female ability to accept or reject EPCs. In Tree Swallows (*Tachycineta bicolor* [Venier and Robertson 1991; Lifjeld and Robertson 1992]), PCs and EPCs occur on the nest box or on nearby branches and can be readily observed. In one 6-yr study (Venier et al. 1993), 73% of 45 EPC attempts were initiated by the male, and about one half of these were successful, because the female cooperated. Of the remaining EPC attempts, 12 (27%) were initiated by the female and 11 of these were successful. Therefore, females appear to be largely in control of the occurrence of sperm transfer. Only one instance of probable FEPC was recorded (inside the nest box). Nevertheless, observations of EPCs were rare relative to the incidence of extra-pair paternity (50% of families [Lifjeld et al. 1993]) in this population. Similarly, in Barn Swallows (*Hirundo rustica*), descriptions by Møller (1994) show that males frequently attempt EPCs on females but are unable to force copulations.

In House Martins (*Delichon urbica*), copulations apparently take place in the nest and so are not visible to observers (D. Bryant, pers. comm.). EPCs must occur because intruder males are seen to enter nests containing a female, and paternity analyses show that extra-pair nestlings are common (present in about one third of broods in studies by Riley et al. [1995] and Whittingham and Lifjeld [1995]). In this species, the extent to which males or females have control of the paternity of extra-pair offspring is unknown. One possibility, in both Tree Swallows and House Martins, is that some EPCs are taking place away from the nest site.

Assaults on females while they are gathering mud for nests have been reported in some swallow species. For example, in Cliff Swallows (*Hirundo pyrrhonota*), Brown and Brown (1996) estimated that over one half of all EPCs at mud holes were forced. Males occasionally achieved cloacal contact despite being fought against by the female. In Purple Martins, FEPCs were reported on unguarded females on the ground as they collected nest material (Morton 1987). In this situation, it appeared that females could be overpowered and inseminated by older experienced males, whereas young males were unsuccessful. Morton et al. (1990) showed that older males achieved 96% paternity of their broods, and increased their fecundity at the expense of young males, which achieved only 29% paternity. Wagner et al. (1996) now suggest that females are controlling EPCs, and are actually pursuing two different reproductive strategies, either pairing with old males and avoiding EPCs, or using a mixed strategy of pairing with young males and accepting EPCs from old males. Wagner (1993) also suggests that coloniality in this species is a response to females seeking EPCs. Møller (1994) reports that hybrids between Barn Swallows and House Martins arise as a result of FEPCs, and suggests that they may also account for some other hirundine hybrids.

### PARIDAE (TITS)

B. Kempenaers (pers. comm.) observed FEPC attempts in Blue Tits (*Parus caeruleus*) but only under experimental conditions. FEPC attempts never occurred when the male mate was on the territory, only when he was removed. Females did not solicit these copulations, and many times males rather violently chased the female and attempted to copulate. FPC attempts were also observed, but neither type of copulation was successful, and they appear to be unimportant in this species.

### EMBERIZIDAE (BUNTINGS, CARDINALS, TANAGERS)

Westneat (1987a, b) reported that female Indigo Buntings (*Passerina cyanea*) resist EPCs and vigorous male–female chases can occur. He never saw a female solicit an EPC. All EPCs were performed by solitary males entering the focal territory, and EPCs made up 12.8% of the total copulation attempts. Only two of the EPC attempts observed were clearly successful, although genetic analyses on two populations showed unexpectedly high rates of EPFs (27–40% and 35%, respectively [Westneat 1987b, 1990]). Westneat (1987b) also observed 28 instances where a male attacked his own mate and attempted FPC despite her resistance. Apparently females are not controlling copulations in this species.

Forced pair copulations (but not FEPCs) have been reported also in Dark-eyed Juncos (*Junco hyemalis*). E. Ketterson (pers. comm.) reports observing fertile females foraging on the ground who were copulated with by their mates in a way that appeared forced. In one case, a male dropped from a branch, landed on the female and, with no preliminaries, attempted to copulate. The female resisted by vocalizing and moving her wings "as if to free herself." There is also evidence of EPFs in this species (15–26% of the offspring produced [S. Raouf, pers. comm.]).

### PARULIDAE (NEW WORLD WARBLERS)

Ford (1983) described behavior suggestive of FEPC in Yellow Warblers (*Dendroica petechia*). Males intruded on the territories of resident females that were nest-building. Males followed females closely, chased them in flight, and in two instances grappled with the females in mid-air. FEPCs were not observed, however.

### ICTERIDAE (NEW WORLD BLACKBIRDS)

Forced extra-pair copulations had been recorded in Red-winged Blackbirds (*Agelaius phoeniceus*) by Nero (1956), but Searcy and Yasukawa (1995) consider its occurrence debatable. Gray (Chapter 3) compared differences in EPC activity between two populations of Red-winged Blackbirds. In a population in Washington State (Gray 1996), females actively sought EPCs in order to gain additional nest defense from extra-pair males and access to food on extra-pair territories. Gray also observed males attempting FPCs on their mates, but did not see FEPCs. In a population in New York State, males sought EPCs, but females did not. Females either resisted EPC attempts or passively accepted them.

Edinger (1988) reported three EPC attempts in Northern Orioles (*Icterus galbula*) in which the females fled and were chased to the ground by males intruding in their territories. In two cases, the male mounted the female after catching up with her, and in one case the male behaved similarly but the copulation (if it occurred) was obscured by vegetation.

### FRINGILLIDAE (FINCHES)

In Chaffinch (*Fringilla coelebs*), Sheldon (1994) reported FEPCs (8 of 20 EPCs) and FPCs (16 of 238 PCs) as well as the more usual female-solicited EPCs (12 of 20 EPCs). Three FEPCs and 3 FPCs were judged successful (B. Sheldon, pers. comm.). Extra-pair paternity occurred in 23% of broods, and it appears that females are largely in control of selection of fathers for their offspring (Sheldon and Burke 1994).

### ESTRILDIDAE (WAXBILLS)

Burley et al. (1994, 1996) distinguished FEPCs and unforced EPCs in captive Zebra Finches (*Taeniopygia guttata*). EPCs were considered to be forced if females resisted mounting attempts by males other than their mates by pecking and/or attempting to fly or hop away. If females did not resist mounting by males, EPCs were considered to be unforced. Burley et al. (1994) reported that 80% of observed EPCs in zebra finches were FEPCs. Birkhead et al. (1989) and Birkhead and Møller (1992) also described FEPCs in captive Zebra Finches as well as FPCs. In two species of waxbills (African Silverbills [*Lonchura cantans*] and White-backed Munias [*Lonchura striata*]), strange birds introduced to a caged male were subject to forced copulation attempts (L. Baptista, pers. comm).

### PLOCEIDAE (WEAVERS, SPARROWS)

Møller (1987) reported that FEPC attempts are frequent in House Sparrows (*Passer domesticus*) during the egg-laying period. Females usually vigorously resist FEPC attempts, but cloacal contact may occur occasionally, especially when the female's mate is not present. A high frequency of extra-pair paternity has been demonstrated in this species (26.8% of broods), but females actively solicit EPCs and fertilization of eggs via FEPC may be rare (Wetton and Parkin 1991). The factors responsible for the high frequency of infertile eggs in this species are uncertain, but some evidence suggests that harassment of females during FEPC attempts can cause embryo mortality (Lifjeld 1994; Birkhead et al. 1995).

## PTILONORHYNCHIDAE (BOWERBIRDS)

G. Borgia (pers. comm.) has observed forced copulations in bowerbirds, which have a leklike mating system. Males may attempt to force copulations both on females visiting bowers who may not be ready to copulate and at bowers of other males while the bower owner is courting the female. In Tooth-billed Catbirds (*Scenopoeetes dentirostris*), the normal courtship involves capture of the female and resistance during copulation (Borgia 1995).

## CORVIDAE (CROWS, MAGPIES)

The promiscuous behavior of colonially breeding Rooks (*Corvus frugilegus*), involving frequent FEPCs on females on the nest, has been known from earlier studies and was confirmed by Røskaft (1983). Apparent FEPC attempts have been reported in Black-billed Magpies (*Pica pica*) and Yellow-billed Magpies (*Pica nuttalli*) (Birkhead 1991).

Common Ravens (*Corvus corax*) in Idaho behaved similarly to Rooks (J. Marzluff, pers. comm.). FEPCs were always performed on laying females sitting on the nest. These ravens nest in an area dominated by sage brush, and in a higher density than ravens nesting in woods. Consequently, males are able to keep track of other nests even though they may be more than a mile apart. Males are very quick to approach nests where the male mate has left to forage. The visiting males land on the female's back and attempt to copulate. Females resist the copulations, but not always (perhaps to protect the eggs from damage or predation). Marzluff observed successful FEPCs and also FEPCs performed on the same female by several males over a period of a few hours.

## CONCLUSIONS ON FEPC IN OTHER BIRDS

In recent years, the growing evidence that females can control the success of EPC attempts by males of passerine birds (Stutchbury and Neudorf, Chapter 5) has forced researchers to become more critical of the view that males can actually force copulation in this group. This is probably a healthy state of affairs, and the onus should now be on those who claim to have observed FEPCs to convince us all.

Several factors that may promote or inhibit the occurrence of EPCs in particular species have been suggested (e.g., Westneat et al. 1990; Birkhead and Møller 1992; Stutchbury and Morton 1995), and these may also open possibilities for forced copulations specifically. Our survey suggests that colonial breeding may favor the occurrence of FEPC in some taxa, although the comparative evidence on closely related solitary nesting species is often weak. Females are likely to be more vulnerable to FEPC in nesting colonies, because females may be left unguarded when their mates leave to feed, and neighbors are easily monitored. However, the degree to which females can prevent males from forcing copulation on them may well vary in relation to body size and morphology (e.g., ibises vs. Rooks), age and experience of the male (e.g., Purple Martins), and the confines of the nest-site (e.g., murres, species nesting in cavities). In particular, we need to be alert to the possibility that females are especially vulnerable when occupied in certain activities (e.g., gathering nest material in swallows and martins), when breeding in open habitats, and when they are "unguarded." The effects of density on extra-pair mating strategies in birds have been reviewed by Westneat and Sherman (in press).

The use of FEPC as a secondary male strategy (as in waterfowl) may conflict with the major breeding strategy in many kinds of birds. Wiley (1991) notes that FEPC is incompatible with the elaborate female-luring tactics used by males of lekking species, although even here there could be exceptions (e.g., bowerbirds, as discussed by Borgia [1995]).

## FUTURE RESEARCH

Our review of the literature on sexual coercion in birds has revealed a dearth of detailed descriptions of behavior relating to this phenomenon. The incidents reported for many species were often noted by observers intent on other problems, and the potential significance of coercive behavior has frequently been overlooked. Undoubtedly the difficulties of making such observations are formidable in species that use vegetation or cavities as refuges from harassment. Nevertheless, there are many species in which the behavior leading up to EPCs is poorly known, and there is a need for careful observations to indicate which sex initiates such sequences and whether forced copulation is possible. The review provides some promising leads pointing to those groups that seem likely to repay special study (e.g., albatrosses, pelicans, herons, gulls, bee-eaters, swallows, buntings, waxbills, and corvids).

We believe that waterfowl warrant further research because many species exhibit forced copulation and often the behavior can be observed in open habitats. The arms races relating to forced copulation, involving male adaptations and female counteradaptations, have been studied in only a few species, and they provide a fruitful field for discoveries. Better measures of costs and benefits to both males and females are needed if we are to distinguish between true forced copulation and resistence as a female tactic to incite male sexual competition. Experimental removal of mates, as already carried out on a few species, can be very instructive. A promising field for study is the relationship between FEPC and mate acquisition, notably in duck species in which males have polygynous tendencies. In some circumstances, FEPC by a paired male may be an initial step in securing a second mate, and if the second female benefits from being paired there could be subtle changes in female behavior that have yet to be detected.

One of the most challenging problems relating to costs and benefits of FEPC in waterfowl concerns questions of "male quality." Are females using the same criteria when they choose mates during pair formation in winter as they use on the breeding grounds when assessing mates for renesting attempts? Do females uniformly reject and try to avoid all FEPC attempts, or do they have (partial?) control of which male ultimately fertilizes their eggs? Do females reject FEPC attempts to guard against desertion or reduced attentiveness by their mates? Such questions require research on sperm competition and sperm storage mechanisms as well as behavioral work on how males apportion their effort and ejaculates in FEPC, FPC, and PC strategies.

By recognizing the kinds of behavior involved in "sexual coercion" as a distinct category of sexual selection mechanisms, the implications of behavior associated with "forced copulation" are more readily appreciated. The time and effort that female ducks spend avoiding harassment by males appears to be considerable, and we have little information on the benefits of mate guarding to females in minimizing the costs of harassment. The constraints imposed on female movements by the presence of males seeking FEPC has not been studied. How real is the possibility that males devalue their commitment to their primary pair-bond in relation to observing FEPC on their mates? Perhaps there are subtle costs to females in terms of reduction in indirect parental investment by male ducks (the antiharassment aspects of mate guarding) that outweight any potential benefits they might gain by submitting to FEPCs?

As shown by Smuts and Smuts (1993) in primates and Clutton-Brock and Parker (1995) in ungulates, there is room for considerable diversity in the nature and consequences of sexual coercion in birds. The environmental conditions that could facilitate FEPC as a male strategy in colonial seabirds or ardeids are obviously quite different from those influencing breeding strategies in woodland or marshland passerine birds. We suspect that many discoveries are still to be made concerning the presence of sexual coercion as a significant phenomenon in birds.

## CONCLUSIONS

Sexual coercion, in the form of forced copulation, occurs in many species of ducks and geese. The presence of a phallus in male waterfowl (presumably an adaptation for copulation while swimming) appears to facilitate sperm transfer by force and has probably been a key factor in promoting forced copulation by males. In species where it occurs regularly, forced copulation appears to be an important secondary reproductive strategy of paired males (FEPC). Forced copulations are also performed by paired males on their own mates (FPC) after the latter have been subjected to FEPC. Although it is difficult to rule out some potential benefits to females, the costs to females of being exposed to FEPC attempts probably outweigh any incidental benefits. There is no evidence that female waterfowl solicit or willingly accept EPCs; females resist and try to avoid EPCs when possible.

The most likely explanation for female resistance (rather than passive acceptance to minimize costs of resistance), is to ensure maintenance of the pair-bond. Female waterfowl are dependent on their mates for support during breeding (reducing harassment by other males; defense of feeding areas; guarding the female, eggs, and/or young from predators), and any reduction in the mate's confidence of paternity could jeopardize his fidelity and support effort.

The occurrence and frequency of FEPC varies among waterfowl species. In some groups (e.g., shelducks) male investment in territory defense probably precludes FEPC as a male strategy, and this trade-off may explain specific variations in FEPC occurrence in various duck groups. Physical factors associated with body size and/or proportions may prevent males from achieving FEPC (e.g., swans), whereas some breeding strategies (e.g., renesting after loss of early clutches) may favor courtship and mate-switching rather than FEPC (e.g., some pochards).

In birds other than waterfowl, EPCs usually do not appear to be forced. In some species females obviously solicit EPCs, and often it appears that females can deter male EPC attempts by avoidance or rejection behavior. There remain a number of nonwaterfowl species in which males do appear to be able to overpower females and achieve copulation in spite of the female's rejection efforts (e.g., bee-eaters). Such FEPC attempts tend to take place when the female is especially vulnerable (e.g., on the nest, when her mate is absent).

Apart from forced copulation itself, sexual coercion in the form of persistent harassment of females by males is an important phenomenon in those waterfowl that regularly engage in FEPC. As in primates, males of these species actively protect their mates from harassment, and effective mate guarding by males appears to be essential to successful breeding. Little attention has been given to the possibility that sexual coercion through harassment occurs in nonwaterfowl species of birds.

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