

RECENT ADVANCES IN PALAEODEMOGRAPHY

Recent Advances in Palaeodemography

Data, Techniques, Patterns

edited by

Jean-Pierre Bocquet-Appel

CNRS, Paris, France

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Contributing Authors

Jean-Noël BACRO

Université de Montpellier, France

I3M, UMR CNRS 5149
Université Montpellier II
CC51 4 place E. Bataillon
34095 Montpellier cedex 5
France
Bacro@math.univ-montp2.fr

Matthew BANDY

*CNRS, UPR 2147
Paris, France*

UPR2147
CNRS, 44 rue de l'Amiral Mouchez
75014 Paris
France
inti@devnull.net

Jean-Pierre BOCQUET-APPEL

CNRS, UPR2147

44, rue de l'Amiral Mouchez
75014 Paris
France
bocquet-appel@ivry.cnrs.fr

Joseph E. BEAVER

University of Arizona, USA

Department of Anthropology University of Arizona
Tucson, AZ 85721
U.S.A.

Magali BELAIGUES-ROSSARD*INED, Paris, France*

INED (Institut National d'Études Démographiques)
133 Bd Davout
75980 Paris Cedex 20
France

Paul BEURNIER*INED, Paris, France*

INED (Institut National d'Études Démographiques)
133 Bd Davout
75980 Paris Cedex 20
France

Arnaud BRINGE*INED, Paris, France*

INED (Institut National d'Études Démographiques)
133 Bd Davout
75980 Paris Cedex 20
France
bringe@ined.fr

Luc BUCHET*CNRS, Nice, France*

CEPAM (UMR 6130, CNRS-Université de Nice-Sophia-Antipolis)
250 Avenue Albert Einstein
Sophia-Antipolis
06560 Valbonne
France
INED (Institut National d'Études Démographiques)
133 Bd Davout
75980 Paris Cedex 20
France
buchet@cepam.cnrs.fr

Jean-Nicolas CORVISIER*University of Artois, France*

Université d'Artois
9 rue du Temple
62030 Arras cedex
France
jn.corvisier@wanadoo.fr

Nadège COUVERT

INED, Paris, France

INED (Institut National d'Études Démographiques)
133 Bd Davout
75980 Paris Cedex 20
France

Nathan B. GOODALE

Hamilton College, USA

Department of Anthropology
Washington State University
Pullman, WA
99163
USA
ngoodale@wsu.edu

John HAWKS

University of Wisconsin, USA

Department of Anthropology–University of Wisconsin–Madison
Madison WI 53706
USA
jhawks@wisc.edu

Mary JACKES

University of Waterloo, Canada

Department of Anthropology
University of Waterloo
Waterloo, ON N2L 3G1
Canada
mkjacks@watarts.uwaterloo.ca

Ian KUIJT

Notre Dame University, USA

Department of Anthropology
Notre Dame University
ikuijt@nd.edu

C. Owen LOVEJOY

Kent State University, Ohio, USA

Kent State University
Department of Anthropology
P.O. Box 5190 - Kent OH 44242-0001
USA
olovejoy@aol.com

Marc A. LUY

University of Rostock, Germany

University of Rostock
Institute for Sociology and Demography
Ulmenstrasse 69
18055 Rostock
Germany
email@marc-luy.de

Christopher MEIKLEJOHN

University of Winnipeg, Canada

Department of Anthropology
University of Winnipeg
Winnipeg, MB R3B 2E9
Canada
c.meiklejohn@uwinnipeg.ca

Richard S. MEINDL

Kent State University, Ohio, USA

Kent State University - Department of Anthropology
Lowry Hall - P.O. Box 5190
Kent OH 44242-0001
USA
rmeindl@kent.edu

Robert P. MENSFORTH

Cleveland State University, Ohio, USA

Cleveland State University
Department of Anthropology
2121 Euclid Ave
Cleveland OH 44115
USA
r.mensforth@csuohio.edu

Natalie D. MUNRO

University of Connecticut, USA

Department of Anthropology
University of Connecticut
354 Mansfield Road
Storrs CT 06269
U.S.A.

Stephan NAJI

CNRS, UPR 2147

Paris, France

CNRS ACI "Détection de la transition démographique
néolithique à l'échelle mondiale"

44 rue de l'Amiral Mouchez Paris 75014

France

stephan_naji@hotmail.com

Carole PERRAUT

INED, Paris, France

INED (Institut National d'Études Démographiques)

133 Bd Davout

75980 Paris Cedex 20

France

Anna M. PRENTISS

University of Montana, USA

Department of Anthropology

University of Montana

Missoula

Isabelle SÉGUY

INED/CEPAM, Nice, France

INED/CEPAM

133 Boulevard Davout

75020 Paris

France

seguy@cepam.cnrs.fr

MARY C. STINER

University of Arizona, USA

Department of Anthropology

University of Arizona

Tucson, AZ 85721

U.S.A.

mstiner@email.arizona.edu

Todd A. SUROVELL

University of Wyoming, USA

Department of Anthropology

1000 E. University Avenue

University of Wyoming

Laramie, WY 82071

U.S.A.

Ursula WITTWER-BACKOFEN

University Clinics Freiburg, Germany

Institute for Human Genetics and Anthropology
University Clinics Freiburg
Albertstr. 9
79104 Freiburg
Germany

ursula.wittwer-backofen@uniklinik-freiburg.de

Recent Advances in Palaeodemography: Data, Techniques, Patterns

Written demographic records mainly cover the last few centuries. Since the emergence in Africa of *Homo ergaster*, our direct human ancestor, and its expansion through Eurasia around 1.8 million years ago until few centuries ago, there are no written records to reconstruct human demographic history in a form that can be interpreted using the conventional tools of demography. However, to be tested with any validity, the main demographic theories from Malthus to Boserup (and combinations) require knowledge of long-term or even very long-term trends. Therefore, sources of information other than written records need to be used, as well as techniques other than standard demographic methods. The information provided by archaeological research and archaeological models of interpretation therefore provides essential input. The intention of this book is to cover three broad topics, some of which were discussed during the 2005 international population conference:

- Palaeodemographic data, represented by the space-time distribution of archaeological remains (sites, ¹⁴C dates, urban) and of skeletons by age from burial sites;
- Techniques of demographic inference from the distributions and densities of palaeodemographic data, and methods to derive estimates of demographic parameters.
- Detection of demographic signals in archaeological data, such as those indicating the approaching limits of carrying capacity during the Middle Palaeolithic, or a major demographic change, like the Neolithic demographic transition on a worldwide scale.

INTRODUCTION

Jean-Pierre BOCQUET-APPEL

CNRS, Paris, France

The written data used by demographers essentially cover the last five centuries. Since *Homo ergaster* moved out of Africa around 1.8 million years ago and until the sub-contemporary periods, there is no data allowing us to reconstruct a demographic history that can be interpreted with the traditional tools of demography. If we want to be able to tackle demographic issues over a long evolutionary duration, trying to reconstitute our human demographic history and thinking out and testing macro-demographic theories, we need to draw on sources other than written data and on techniques other than those commonly used by demographers. This necessarily means using information of every kind, from archaeology, physical anthropology, paleontology, primatology or genetics, along with relevant models of interpretation.

The volume presented here has been developed from a core of papers selected for the paleodemographic session of the 25th World Population Congress (July 2005, Tours, France), to which further requested contributions have been added. The publication covers recent paleodemographic innovations, in terms of data, techniques and the detection of patterns making it possible to highlight hitherto unknown prehistoric demographic processes. Now that the anxiety over ways of defusing the population “time bomb”, which mobilized mainstream demographic thinking as from the 1960s (see, for authority, Bogue and Tsui 1979; Demeny 1979) has largely been dissipated, the focus has shifted to other important issues.

Looking back in time, there is the issue of the long duration of the human metapopulation’s demographic past, such as the planetary colonization scenario or the demographic transitions that were experienced over two million years. Looking forward, we have the issue of the future of an age pyramid in which, after the current accelerating decline in fertility and

possibly even its collapse, we will see hundreds of millions of old people having to provide for themselves without any pension funds and almost without any children, in the former Third World countries which had always been the world's reservoir of young people. Now that the demography of the human metapopulation has become an object of scientific study, shedding its burden of demographic policy contingencies, the place of paleodemography within the IUSSP, which was episodic before its 24th Congress (Salvador, Brazil, 2001; see also the 1969 Congress in London, with JN Biraben, L Henry and J Nemeskeri), is tending to become permanently established. In the interests, perhaps, of seeking a dialogue with demographers, the papers given at the Congress mainly gave demographic narratives on archaeological data, rather than addressing methodological or technical questions, despite the well-known fact that there is no consensus over even basic paleodemographic techniques. The volume's subtitle, "Data, Techniques and Patterns", reflects a necessarily loose subdivision among chapters, since so many of these items are embedded in one another.

In the first part, we look into two radically different categories of data: genetic data, with a critical re-reading of their interpretation models in demographic terms, and space-time distributions of archaeological remains, as reconstituted from systematic field surveys. The first data concern periods of humanity going back several hundreds of thousands of years to the Pleistocene. The second category concerns ancient Greece. The very different nature of these data is almost a caricature of the inevitable eclecticism of paleodemographic information. There is no such thing as a version of human demographic history written for genetic or archaeological semiotics. What does exist is simply the demographic history that we try to reconstruct from the mists of the past, using whatever comes to hand and, whenever possible, comparing the results. Because we are setting end to end the chronological periods with which various categories of data are coupled, we have to get used to the juxtaposition of eclectic data. It is important to remember that one of main goals of demography is simply the enumeration of human beings, otherwise known as the "census population size". The census population size does not mean exactly the same thing to an economist, a historian or an evolutionary biologist. But it is generally agreed that the overall interpretation of the size of a census population is a measurement of success – of an economic system, a society or an adaptation.

For a long time now, the genetic variation of a population has provided us with an estimator of this number, via the so-called "effective population size" (Wright, 1931). For the Pleistocene, the literature on genetic anthropology usually gives a number of 10,000 individuals, while carefully written

demographic literature (see Hawks below) usually gives 300,000. Why such a large discrepancy – of 1:30 – between these estimates? In chapter 1, John Hawks questions this discrepancy. Contrary to an insistent suggestion, he reminds us that genetic data are not, in themselves, demography. They need to be interpreted via a model, that of Wright-Fisher. In reality, there are any number of conditions of deviation from the model. Hawks reviews many of them and concludes, pessimistically, that the link between human genetic variation during the past million years and “*the relative importance of demography, selection and changing environments (. . .) remain unclear*”.

In chapter 2, Jean-Nicolas Corvisier describes the grid surveys made of archeological sites on the scale of Ancient Greece. The sheer number of surveys makes it possible to estimate the space-time distribution of settlement units, from cities to villages, hamlets and individual farms. But these distributions raise several primarily technical questions as to the influence of the grid size of archeological site surveys on their interpretation, in other words, as to the resolution degree of spatial distributions. Next, on a more strictly theoretical level, as Jean-Nicolas Corvisier writes, “*in a world dominated by the City-state phenomenon, does the civic phenomenon have any influence on the spatial distribution of the population, or is the logic simply that of urbanization, i.e. the creation of urban centres once human settlements have reached a certain level of concentration in the same place?*” (Corvisier, this volume: p. 34).

The techniques described in the next three chapters are designed to deal with two interconnected problems: estimating an age distribution of skeletons and its confidence interval. Two approaches are described to estimate an age distribution. Chapter 3 presents an iterative Bayesian procedure used by Jean-Noël Bacro and myself. This gives an age distribution from the distribution of an age indicator of physical anthropology in a cemetery. This is given in the knowledge, on the one hand, of the information provided by an anthropological reference collection and representing the relationship between biological age indicator and chronological age and, on the other hand, of the mortality law from which the cemetery was inferred. The statistical procedure varies the prior probability of two broad classes of preindustrial mortality: ordinary mortality (also called attritional mortality in the paleontological literature) and catastrophic mortality. These prior probabilities are kept in the procedure, which makes it possible to obtain the best approximation of the observed distribution of the age indicator in a cemetery. But, as always with this kind of approach, there is never any certainty of having the “true” prior probabilities, only the best of the two broad classes of models proposed. A confidence interval for the

distribution is then determined by bootstrapping the likelihood matrix of the reference anthropological collection, which represents the main source of error in the estimate (Bocquet-Appel and Masset, 1996).

In chapter 4, in order to estimate an age distribution, Isabelle Séguy, Luc Buchet, Arnaud Bringe, Carole Perraut, Nadège Couvert and Paul Beurnier have built up an array of pre-industrial Model Life-tables, obtained through successive linear regressions, in the manner of Coale, Demeny Vaughan (1983) or Ledermann (1969). The array input is one of the non-conventional demographic indicators observed in cemeteries, such as the various ratios of child and adult age classes (5–14/20+, 5–19/5+), or the average age at 20 years+. The limits indicated for the confidence intervals are those of the computed regressions, which the user will have to add the variation in the non-conventional demographic indicators that were used as input. Under the usual conditions of model life-table use, this new set would then have to replace the arrays built up from industrial populations or, worse, from archaeological populations (see Jackes and Meiklejohn, this volume: p. 179)

Now that we have an age distribution of skeletons, obtained not overall as in the approaches used in the two preceding chapters, but by grouping individual age estimates produced by any anthropological technique, with a confidence interval for each individual age, the question then is how to move from the individual confidence interval to the overall confidence interval of the distribution? In chapter 5, Marc A Luy and Ursula Wittwer-Backofen suggest drawing the individual age estimates in random sequences many times over (say 1000 distributions/cemeteries simulated), within their respective confidence interval limits, and building up the corresponding life table of each simulated distribution. The dispersion limits of the age-specific deaths in the 1000 life-table samples (the dx 's of the life-table), at the level $1 - \alpha$, then provide an estimate of the confidence interval for the age distribution.

The final section of this volume covers the archaeological signatures left by identifiable demographic phenomena in (pre-)historical information, i.e. paleodemographic patterns. Here as in other areas, we need a demographic model of interpretation in order to move from an observable pattern in the data to demography. An initial set from the literature contains the simplest patterns, expressed by profiles representing skeleton age distribution, assuming, of course, that such profiles are constructible using current techniques. These age distribution profiles are directly interpretable simply by virtue of their resemblance to historical distributions, such as those produced by attritional mortality, warfare mortality – civilian or military – or plague epidemics (see Chamberlain, 2006; Gowland and Chamberlain, 2005;

Margerison and Knüsel, 2002; Paine, 2000; Keckler 1997). But when we depart from the catalogue of historical resemblances, the identification of a non-referenced signal which is not – or not adequately – measured in aggregate data from government offices, or which is unknown in ethno-historical demography (i.e. caused by a new demographic process), becomes more complex. A second set of paleodemographic patterns brings together signals that express temporal or space-time changes in variables compared to former stable states. This can be the case with an abrupt increase in frequencies, for example of hundreds of radiocarbon dates, interpreted as representing a re-colonization during the Late Glacial in Europe (Gamble et al., 2005), or even in the percentage of immature skeletons in more than 130 cemeteries, interpreted as the effect of a Neolithic demographic transition (Bocquet-Appel and Naji, 2006; Bocquet-Appel, 2002). It can also be the case with the variation in the space-time distribution of archaeological sites across Europe, reflecting an hitherto unknown distribution of populations under severe climatic constraint (Bocquet-Appel et al., 2005). But in these examples, which link up signatures and the demographic processes generating them, the distance is short and the model is simple. As we go further back in time, direct signatures of demographic processes become scarcer or non-existent. To come closer to demography, models for the interpretation of archaeological remains must become complex, with one or more additional layers of interpretation.

In chapter 6, from subtle changes in the archeozoological distributions of Mediterranean sites of the Late Pleistocene through Holocene periods, Mary C Stiner, Joseph E Beaver, Natalie D. Munro and Todd A Surovell detect a process of hunting intensification, where others might only have seen a simple change in fauna distribution due to climatic variations. This intensification is interpreted as indicating an increase in demographic density at the sub-continental scale. This detection of intensified hunting (and perhaps also of the law of diminishing returns) during OIS 2 was made possible thanks to a model where prey animals are classified on the one hand according to their long-term persistence (resilience) and on the other hand according to the expected return for the hunter-gatherer on his investment in time. This model provides an economic reference against which the observed data can be appraised. Stiner, Beaver, Munro and Surovell's approach can be extended to other sites and periods.

In chapter 7, Nathan B Goodale, Ian Kuijt and Anna M. Prentiss attempt a demographic interpretation of the Upper Columbia area of the Canadian Plateau between 4000 and 500 years ago, drawing on data representing variations in the temporal density of pithouses and C14 dates. These data

are used as proxy variables of human density. According to the authors, a small-scale society seems to have existed in Upper Columbia prior to the full onset of the Neo-glacial climatic period, at 3800–4200 calBP, and was replaced by a society of “complex” gatherers at 1400–2200 calBP. The detection by Goodale, Kuijt and Prentiss of major regional economic and social changes, under conditions of very low demographic density, has led them to take up a position in the ongoing debate on the validity of the Boserupian paradigm of the creative force of population pressure on cultural change.

The next two chapters focus on the increase in fertility during the transition from a forager to a producer economy, as measured by skeleton distributions in cemeteries. In chapter 8, Mary Jackes and Chris Meiklejohn present the distributions of skeletons dug up from three important Portuguese sites in European prehistory, including two Mesolithic shell midden cemeteries which they personally excavated. The authors’ tenacity along the years in gathering information on skeletal data which, in some cases, have been mixed up or dispersed since the first campaigns of the 1880s, must be underlined. Jackes and Meiklejohn then provide an in-depth ecological contextualisation of population data. Finally, tools for fertility estimation are presented. As will be seen, Jackes and Meiklejohn do not subscribe to the idea of a Neolithic demographic transition¹, which I have set out elsewhere. But this is a matter of scientific debate.

In chapter 9, Richard S Meindl, Robert P Mensforth and C Owen Lovejoy update their analysis of Libben, a Late Woodland forager cemetery (Northern Ohio, USA). We know that a skeleton age distribution, assuming of course that it can be obtained, is not in itself demography. To become demography, such a distribution has to be interpreted using a model. The preferred model is a Lotka stable population model, with its single parameter represented by the growth rate. This model is simple in its assumptions (the temporal stability of input/output parameters in a population) and robust in its results, having proven its reliability beyond reasonable doubt in countries where statistics are inadequate (Bourgeois-Pichat, 1994). Meindl, Mensforth and Lovejoy give a bounded continuum of a priori existing solutions, making it possible to provide a demographic interpretation (explanation) of their Libben age distribution, when fertility (and therefore their growth rate) varies, via the age-specific fertility rates of natural fertility populations (summarized by their TFR). The authors then set Libben within the long duration of evolutionary time in order to emphasize the need to take the growth rate into account in the demographic interpretation of skeleton distribution, because, as the authors write: “*it is the evolutionary nature of human populations to grow*”.

Finally, in chapter 10, Stephan Naji, Matthew Bandy and myself return to the paradigmatic question initially raised 30 years ago by Mark Cohen (Cohen, 1977): What were the consequences of the Neolithic demographic transition on the population's health? We know that in the five main centers of invention of plant domestication (the Levant, Meso-America, North America, Peru and Southern China), the transition from a forager to a horticulture-farming economy did not occur at the same time, ranging from 12,000 calBP to 500 calBP in North America alone. One of the main difficulties involved in answering Cohen's question concerns the integration of biodemographic information, taking its space-time dispersion into account. How, for example, can we compare the effects of a transition occurring between 12000–8000 BP in the Levant and 500 AD in Eastern North America? As with the detection of the signal of the Neolithic Demographic Transition, Naji, Bandy and myself provide an integrated representation of the pattern of change in a number of bioarchaeological indicators, positioning them in the reference frame of a relative chronology.

It is to be hoped that following the IUSSP meetings, other volumes will be published on paleodemography, reporting on progress in an active field of research as well as on the emergence of a consensus on methodologies and problematics, because it seems that the time has come to tackle the reconstruction of the demographic history of our global village. Finally, I am glad to acknowledge Lounès Chikhi, Christian Theureau, Monique Tersis and Ilona Bossanyi for their contribution to this volume.

NOTE

¹ I have not found, in Deevey (1960), the reference given by Jackes and Meiklejohn to a “demographic transition”, a concept that was developed between 1929 and 1945 by several scientists, including CP Blacker, K Davis, A Landry, F Notestein and W Thompson (see Kirk, 1996); the concept of a Neolithic demographic transition was set out by the demographer Livi-Bacci (1992) and, independently, by myself (Bocquet-Appel, 2002). The reality of the concept is based, now, on more than 130 cemeteries across the entire northern hemisphere (Bocquet-Appel and Bar-Yosef, 2007).

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Chapter 1

FROM GENES TO NUMBERS: EFFECTIVE POPULATION SIZES IN HUMAN EVOLUTION

John HAWKS

University of Wisconsin, USA

Abstract: The effective population size has become a central aspect of our understanding of the ancient structure of human populations. It is through this concept that the genetic variation of present-day humans may inform us about the number and relationships of humans in the past. However, effective population size itself is not a demographic parameter. If the theoretical model does not apply accurately to human evolution, then inferences based on the estimates of effective population size may be in error. Here, I present the theoretical basis of effective population size, including many of the demographic and evolutionary conditions that can confound the relationship of genetic variation and population size.

Demography is the engine of evolution. Changes in allele frequencies require differential births and deaths of the individuals who carry the alleles. Under natural selection, these births and deaths approximate a deterministic process favoring the survival and reproduction of carriers of a particular allele. The histories of alleles themselves are demographic phenomena: the fitness advantage of a selected allele may be expressed as a relative intrinsic growth rate; its frequency over time follows a logistic growth curve.

In the absence of selection, allele frequencies vary as a stochastic process. The parameters influencing this process are themselves demographic: population size and mating pattern. Ultimately, the rate of evolution of a population must be constrained by these parameters. This means that the observable genetic characteristics of populations are to some extent natural estimators of demographic characteristics. The relationship between the demographic parameters of a population and its genetic characteristics may in some cases be approximated by a single parameter: the “effective population size.” Effective population size refers the demographic complexity of some real population to the simplicity of some ideal

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Abstract: The effective population size has become a central aspect of our understanding of the ancient structure of human populations. It is through this concept that the genetic variation of present-day humans may inform us about the number and relationships of humans in the past. However, effective population size itself is not a demographic parameter. If the theoretical model does not apply accurately to human evolution, then inferences based on the estimates of effective population size may be in error. Here, I present the theoretical basis of effective population size, including many of the demographic and evolutionary conditions that can confound the relationship of genetic variation and population size.

Demography is the engine of evolution. Changes in allele frequencies require differential births and deaths of the individuals who carry the alleles. Under natural selection, these births and deaths approximate a deterministic process favoring the survival and reproduction of carriers of a particular allele. The histories of alleles themselves are demographic phenomena: the fitness advantage of a selected allele may be expressed as a relative intrinsic growth rate; its frequency over time follows a logistic growth curve.

In the absence of selection, allele frequencies vary as a stochastic process. The parameters influencing this process are themselves demographic: population size and mating pattern. Ultimately, the rate of evolution of a population must be constrained by these parameters. This means that the observable genetic characteristics of populations are to some extent natural estimators of demographic characteristics. The relationship between the demographic parameters of a population and its genetic characteristics may in some cases be approximated by a single parameter: the “effective population size.” Effective population size refers the demographic complexity of some real population to the simplicity of some ideal

population—in other words, it is a measure of the extent to which a natural population corresponds to some theoretical population model.

THE WRIGHT-FISHER MODEL

The mathematical theory of population genetics was developed early in the twentieth century, principally by Ronald A. Fisher, Sewall Wright, and J. B. S. Haldane (Provine, 1971). The initial success of population genetics was the development of mathematical account of inheritance that reconciled Mendelian inheritance with continuous traits (Fisher, 1918). This development made possible a deterministic model of Darwin's natural selection in terms of change in gene frequencies (Haldane, 1927; Fisher, 1930; Wright, 1931). However, the deterministic model depends on differential equations that are strictly true only in an infinite population. In a finite population, stochastic factors also change gene frequencies, even for genes under natural selection, but particularly for the sampling variance of allele frequencies in the absence of selection (Wright, 1955). The importance of the stochastic factor was considered by both Fisher (1930) and Wright (1931); their disagreement about its importance became a major focus of theoretical population genetics.

Many phenomena in finite populations may amplify or dampen stochastic change in gene frequencies. In an infinite population, the variance in the time or number of events such as births, deaths, and matings does not matter to the gene frequency. Absent selection or mutation, an infinite population does not evolve. In a finite population, variance in the times or numbers of births, deaths, and matings causes evolution even in the absence of selection and mutation, as gene frequencies fluctuate slightly from generation to generation. Other factors may increase or decrease the variance in births, deaths or matings, such as assortative instead of random mating, high variance in mating success, or inbreeding instead of outbreeding.

In the course of several publications, Wright and Fisher explored the stochastic factor by application of a simple population model (e.g. Wright, 1931; Fisher, 1930), which became known as the Wright-Fisher model. The model assumes a population of $2N$ genes replicating themselves in discrete non-overlapping generations. Each gene in generation t has d descendants in generation $t + 1$, where d is a random variate based on a binomial distribution with $2N$ trials and probability of success $1/(2N)$ for each trial. This model approximates the behavior of a population of N diploid individuals, but does not actually involve individuals; it corresponds

to the assumptions that individuals mate randomly, die immediately upon reproduction, and are monoecious (i.e. no sex-specific effects of alleles, selfing possible).

The main feature of this model is that it is mathematically tractable. The gene frequency in any given generation is a binomial random variable based on the frequency in the previous generation (Ewens, 2004). The expectation of a gene frequency p_t is simply its frequency in the preceding generation p_{t-1} —that is, no change in frequency on expectation. The variance in the gene frequency is equal to $p_{t-1}(1-p_{t-1})/(2N)$ —this variance is larger for smaller N and for gene frequencies near 0.5. The probability of fixation of a given allele is equal to the initial frequency of the allele, so that the fixation probability of a new introduced mutation is $1/2N$. Likewise the probability that two genes taken at random in the population are descendants of a single parent gene is $1/2N$. The model is a Markov process in which the transition matrix (probabilities of p_t given p_{t-1} has a maximum nonunit eigenvalue equal to $1-(1/2N)$). As can be seen from these relations (summarized in Ewens, 2004), stochastic evolution in the Wright-Fisher model is determined by the single parameter of population size—indeed, the model assumes all other possible factors constant.

Mutation may be added to the model, at a rate u per gene, in which case the expected number of new mutations in any given generation is $2Nu$ (Fisher, 1930). When mutations are included in the model, it is possible to derive expectations for sample characteristics such as the frequency spectrum of alleles and the probability of gene identity (Ewens, 1972). Such values involve the parameter $\phi = 4Nu$, which indicates that mutation and finite population size are inversely related stochastic factors: A small population with a high mutation rate may have similar sample characteristics to a large population with a low mutation rate.

No natural population reproduces according to this simple model. However, the model gives rise to calculations of the expectation and variance of many genetic characteristics that might be empirically observed in natural populations. Wright (1931) considered that deviations from the simple model might be treated in terms of their effects on sample characteristics. In this respect, a nonideal population with N individuals might behave in a similar way to the ideal population of some different size, N_e , which he termed the “effective population size.” The effective population size of a study population is therefore the number of individuals in an ideal Wright-Fisher model with the same sample characteristics as the nonideal population under study.

But from the considerations above, it is evident that different sample characteristics depend *differently* on population size in the Wright-Fisher model. In particular, the probability of identity of two randomly chosen genes depends on the probability of inbreeding ($1/2N$ in the Wright-Fisher model), while the change in gene frequency over time depends on the variance in gene frequency ($p_{t-1}(1-p_{t-1})/(2N)$ in the Wright-Fisher model). Departures from the Wright-Fisher model may affect these two values in different directions. For example, assortative mating may greatly increase the probability of gene identity without greatly affecting the allele frequency. This insight can be important to conservation, since inducing assortative mating may allow more effective selection against deleterious recessives without materially reducing the frequencies of other genes (Templeton and Read, 1994).

Evidently, a single “effective” population size cannot summarize all departures from the Wright-Fisher model: natural populations are not described by a single stochastic parameter. For this reason, three distinct concepts of effective population size are often considered. The *inbreeding effective population size* is the size of the Wright-Fisher population with the same probability of inbreeding as the study population. The *variance effective population size* is the size of the Wright-Fisher population with the same variance in gene frequencies as the study population. The *eigenvalue effective population size* is the size of the Wright-Fisher population in which the maximum nonunit eigenvalue is the same as the study population. It is important to note that “study population” here may refer to an empirically observed natural population, or it may apply to a population model. It is also worth noting that population models other than the Wright-Fisher model are sometimes considered, such as the Cannings model (Cannings, 1974) or the Moran model (Moran, 1958). These models sometimes give rise to different effective population sizes, because the parameterization of population size may differ from the Wright-Fisher version.

These effective population sizes have different uses. Molecular data empirically provides estimates of sample characteristics such as the probability of gene identity and the frequency spectrum of alleles, both of which depend on the probability of inbreeding. For this reason, the inbreeding effective size is most relevant for most studies of genetic data. Sometimes inbreeding is relevant to ecological comparisons; in other cases the variance in gene frequencies may be more relevant. In particular, the variance effective size is relevant to conservation because conservation efforts often attempt to assess the rate of gene frequency change (Crow and

Denniston, 1988). The eigenvalue effective population size is based on the transition probabilities among gene frequencies, with a leading nonunit eigenvalue of $1-(1/2N)$ in the Wright-Fisher model. Like variances in gene frequencies, these transition probabilities are not easily estimable from empirical molecular samples, and the eigenvalue effective size has rarely been applied in human population genetics. However, it is important in modeling and has emerged recently in considerations of metapopulation dynamics (e.g. Whitlock and Barton, 1997; Lehmann and Perrin, 2006).

The model-dependence of effective population size is rarely considered in analyses of molecular data. Ewens (2004) gives a good account of the problem:

Except in simple cases, the concept [of effective population size] is not directly related to the actual size of the population. For example, a population might have an actual size of 200 but, because of a distorted sex ratio, have an effective population size of only 25. This implies that some characteristic of the model describing this population, for example a leading eigenvalue, has the same numerical value as that of a Wright-Fisher model with a population size of 25. It would be more indicative of the concept if the adjective “effective” were replaced by “in some given respect Wright-Fisher model equivalent.” Misinterpretations of effective population size calculations frequently follow from a misunderstanding of this fact (Ewens, 2004, 37–38).

CHANGING POPULATION SIZE

The utility of effective population size comes from the fact that it concatenates many separate stochastic phenomena into a single parameter. As an example, a gene frequency is a single value, with a single degree of freedom. It is therefore sufficient to estimate only a single parameter. This approach obviously runs into trouble when more than one stochastic factor varies in the population.

One of the most troublesome cases is a change in population size. A population that changes in size violates a basic element of the Wright-Fisher population model. Sjödin et al. (2005) assert that “effective population size” is meaningless in the context of most changes in population size, because the allele frequency spectrum, variance in gene identity, and other sample characteristics will be altered in ways that have no equivalent in the Wright-Fisher model. In their view, only changes in size that occur on a different

time scale (either much shorter or much longer) than genealogical events can be reconciled with the concept of effective size. Indeed, a survey of the literature on human prehistoric population dynamics shows that changes in size create much confusion, with divergent definitions and concepts of “long-term effective population size.”

Nevertheless, the treatment of changing population size in terms of effective size originated with Wright himself and is well-entrenched. Wright (1938) considered the effect of fluctuating population size on inbreeding, finding that the effective size of a population that fluctuates in size is approximated by the harmonic mean of population size taken across all generations. The harmonic mean is much closer to the smallest of a set of values than the largest; effective population size is generally closer to the minimum population size than the maximum. This is the inbreeding effective population size, which predicts gene identity and other sample characteristics that derive from it, such as allele frequency spectra.

The harmonic mean approximation breaks down as changes in population size become more and more rare or exceptional. For example, we might estimate an “effective size” for a population that has undergone a bottleneck, a period of small population size flanked by which would be useful for predicting the expected heterozygosity. But the coalescence times of different genetic loci would be much more variable than expected for the corresponding Wright-Fisher population. In essence, a population bottleneck is a five-parameter model of demographic history, including the time of onset, time of release, and the effective population sizes before, during, and after the bottleneck event. Different genes may therefore show apparently discordant genealogies under such a population history—some genes having been fixed by drift during the bottleneck, others having escaped fixation (Fay and Wu, 1999).

Simple population growth induces a disequilibrium compared to the Wright-Fisher model, in which the number of new alleles arising by mutation increases more rapidly than the mean difference between individuals (Tajima, 1989). For growing populations, different characteristics of single molecular samples may lead to very divergent estimates of effective population size. For instance, allele number may lead to a large effective population size estimate at the same time that gene identity generates a small estimate. The discrepancy emerges from the temporal scope of inbreeding underlying the two observed values—some are influenced by population growth more rapidly than others. The disequilibrium itself serves as a test of population growth (Tajima, 1989; Fu and Li, 1997).

NATURAL SELECTION

Generally, analyses of effective population size assume neutrality—that is, they attempt to quantify the stochastic factor in the absence of selection. Natural selection is a deterministic force, which itself is influenced by the stochastic factors in finite populations. Still, genes under selection are influenced by demography. For example, the long-term selective balance affecting many HLA loci has preserved their allelic diversity over millions of years, but the major functional alleles themselves occur on different haplotypes that are neutral relative to each other, and respond to the population effective size (Takahata and Satta, 1998). Balancing selection may extend gene genealogies over longer times than would be predicted from demographic considerations; this may obscure genetic “signatures” of genuine population expansions (Harpending and Rogers, 2000). Contrarywise, positive selection may generate an excess of rare genetic variants similar to demographic expansion (Wall and Przeworski, 2000). And the long-term survival of polymorphisms under selection assumes some demographic prerequisites (Ayala, 1995), which may be used to test demographic hypotheses.

Linkage to selected sites may impact the variation of neutral sites, distorting estimates of effective size. The relationship of recombination rate and genetic diversity may reflect these selective processes (Nachman et al., 1998; Nachman, 2001). “Genetic hitchhiking” is a phenomenon in which neutral sites linked to a positively selected allele show vast reductions in variability (Braverman et al., 1995; Kim and Stephan, 2000). Hitchhiking induces disequilibria that resemble those resulting from population growth, naturally because positive selection is the logistic growth of one adaptive allele. Constant purifying selection across the genome can reduce the variation of linked neutral alleles, a phenomenon called “background selection” (Charlesworth et al., 1993; Kim and Stephan, 2000). Gillespie (2000) showed that recurrent positive selection could restrict the variation of weakly linked neutral sites even in a population of infinite size. This gives rise to a stochastic effect called “pseudohitchhiking,” which generates an estimate of effective population size even for evolutionary models where it is undefined. If the force is powerful in natural populations, it would greatly restrict genetic variation below the amount expected for the Wright-Fisher population model. Pseudohitchhiking may even generate an “effective population size” for a population of infinite numbers (Gillespie, 2001).

As evolutionary factors, both genetic drift (influenced by population size and mating structure) and natural selection influence the genetic variability of natural populations. For any particular locus, these factors may confound each other, so that the reasons for a particular level of genetic variability may not easily be attributed to either. For any bias in the genetic parameters that might result from selection, an equivalent bias may be found as a product of some demographic history. Indeed, this equivalence marks a deep symmetry between the stochastic effects of drift and selection: ultimately, selection is a demographic phenomenon as concerns a particular allele, as opposed to a full population. It has often been assumed that the effects of drift and selection may be clearly differentiated by among-locus analyses—while selection should affect different functional loci differently, genetic drift should affect all loci in the same way. However, pseudohitchhiking exerts stochastic effects across many loci (Gillespie, 2000). This may explain some cross-species comparisons, which show that genetic diversity does not correlate strongly with population size (Nei and Graur, 1984), including mtDNA where there is no correlation between population size and diversity across large groups of animal species (Bazin et al., 2006). The importance of selection in shaping genome-wide variation remains an unresolved question.

GENETIC VERSUS ECOLOGICAL ESTIMATES

From its definition and application to theoretical populations, it should be clear that the utility of “effective population size” is that it provides a way of relating the genetic characteristics of a population to those expected of an ideal population under the Wright-Fisher model. Yet, the genetic characteristics of a population always trail to some extent the demographic and ecological factors that influence them. Because genetic variation “looks to the past” in this way, a discrepancy arises between estimates of effective size based on genes and so-called “ecological” estimates based on observations of demography and behavior. It should be noted that estimates based on site distributions, cemetery samples, or other archaeological observations fall in the category of “ecological” estimates: in abstract, such efforts concern the place of a population in the context of its ecology rather than the statistical properties of gene genealogies.

Nunney and Elam (1994) reviewed genetic approaches to estimating effective population size, compared to approaches based on field observations of ecology. Genetic approaches are very straightforward: mathematical expressions derived from the Wright-Fisher model generally include

population size. Genetic data from a natural population may be entered into these expressions, yielding a solution for population size. This solution is the effective population size: the value of population size in the Wright-Fisher model that corresponds to the observed genetic data. Nunney and Elam (1994) divided genetic approaches into “long-term” and “short-term” methods. Long-term methods track the changes in gene frequencies over time, and require recurrent sampling of populations over timescales long relative to their generation lengths. Such surveys may be plausible for genes that are phenotypically apparent (e.g. coat color polymorphisms), although estimates must ensure that such traits are neutral. Sampling of molecular characteristics is more costly, and tracking gene frequency change in long-lived populations may be impractical—for example, no such study has been performed on a human population. Nevertheless, such long-term studies have great relevance to conservation because they assess the variance effective size. Most important, they estimate the *current* variance effective size, without being confounded by the cumulative effects of genetic drift in the past.

The vast majority of studies that estimate effective population size from genetic data are short-term studies. These use the characteristics of a single genetic sample, taken at one time, and the result is generally an estimate of the inbreeding effective size. This estimate entails all of the potential confounding factors that have influenced gene frequencies over a long, long time in the study population; generally over a period spanning four times as many generations as the estimate of effective size. Thus, an estimated effective size of 10,000 individuals is an assertion that the gene frequencies have been changing by drift in a population of this size for a time period on the order of 40,000 generations. Such estimates obviously have weaknesses as applied to conservation: although they may assess the current level of variation, they do not inform about the current rate of change in gene frequencies. Most important, because the potential confounding effects include both ancient demographic changes and ancient selection over a very long time period, these estimates have a necessarily uncertain connection to current or historic demography.

Ecological estimates require observations relevant to natural population densities, migration rates, life history, sex ratio and other aspects of mating pattern. The practical interest in conserving natural populations has engendered a substantial body of theoretical work on the relationship between census and effective population sizes, considering variation in these factors. The following list discusses several classes of factors that influence the ratio of effective to census population size. The list is not intended to be

comprehensive, but gives a sampling of important phenomena in natural populations and their effects on neutral genetic variation. These factors are considered in terms of their effects on the *inbreeding* effective population size, although for the most part they influence variance and eigenvalue effective sizes in similar ways.

Age structure

Age-structured populations are all those in which death is not coincident with reproduction. For mammals, the reproductive lifespan is relatively long and features intermittent births of single or multiple offspring. This life history pattern leads to an overlap of two or more generations within the population at any given time. Because a large proportion of individuals are either pre- or post-reproductive, the effective population size of an age-structured population is generally half or less the census size (Hill, 1972).

1. **Maturation age:** A higher maturation age leads to a higher proportion of nonreproductive juveniles in the population, reducing effective size relative to census size (Hill, 1972; Nunney, 1993).
2. **Variance in breeding age:** Earlier breeding has a greater effect than later breeding on changes in gene frequencies (Fisher, 1930), so that a population with a high variance in reproductive ages will have a reduced effective size.
3. **Postreproductive lifespan:** A long postreproductive lifespan increases the number of individuals without increasing the birth rate, reducing effective size relative to census size. Postreproductive helpers may enable a higher birth rate than otherwise possible, but only among those females for which mothers or other postreproductive helpers have survived. In this way, helpers may also tend to decrease effective population size relative to census size.

Population structure

Splitting a population into partially isolated subpopulations or groups tends to impede the fixation of alleles in the population as a whole. But if these subpopulations themselves undergo evolutionary stochasticity, then the fate of alleles will be tied to the fate of the subpopulations. When the population behaves as a metapopulation (Levins, 1969), different subpopulations may have greatly different net reproduction, some areas of suitable habitat may be unoccupied, and the fission and subsequent growth of successful subpopulations may dominate the population history (Gilpin, 1991).

1. **Subpopulations:** A population divided into partially inbred subpopulations retains more genetic variation than a panmictic population of the same size. This is a major factor *increasing* effective population size in geographically dispersed populations.
2. **Isolation by distance:** Wright (1943) defined the concept of effective population size in his isolation by distance model to encompass a finite “neighborhood” of spatially proximate individuals. The neighborhood size is used to estimate the inbreeding coefficient for this model, and is much smaller than the total population size.
3. **Source/sink dynamics:** A species with static population size may nevertheless occupy geographic areas that differ in productivity. Areas where reproduction is lower than the replacement rate will contribute relatively little to the ancestry of the total population over the long term. The effective population number is reduced by such variation (Beerli and Felsenstein, 2001; Wakeley, 2001).
4. **Extinction and recolonization:** At an extreme, local groups frequently become extinct and are replaced by colonists from other groups. The population will be derived from a small number of groups at earlier times, which may drastically reduce genetic variation and effective population size (Maruyama and Kimura, 1980).

Family size

Family size is simply the number of offspring per individual. Under the Wright-Fisher population model, a substantial proportion of individuals have no offspring at all—which makes genetic drift possible. But when the variation in family size exceeds the binomial number predicted under the Wright-Fisher model, genetic drift may be substantially stronger.

1. **Variation in family size:** Low variance in family size tends to increase effective size relative to census size; high variance tends to decrease effective size.
2. **Heritability of family size:** If large families generate offspring that themselves tend to have large families, this inheritance can vastly decrease effective population size (Nei and Murata, 1966).
3. **Polygyny/polyandry:** These mating systems tend to alter effective sex ratio away from 1.0, which increases the variance in family size in the population, and decreases effective population size.
4. **Distribution of family size:** The Wright-Fisher model predicts that family size will follow a Poisson distribution (Hudson, 1990);

different distributions (e.g. binomial) may increase or decrease effective population size.

The majority of these phenomena tend to *reduce* genetic variability below that expected for a Wright-Fisher model of the same population size, although there are several exceptions to this trend. This bias toward factors that reduce variation may emerge as a natural consequence of fitness-seeking by organisms: if given a chance, individuals should tend to increase the representation of their own genes at the expense of other individuals. Equal representation of all individuals in the gene pool—as in the Wright-Fisher model—is an unlikely outcome. Natural factors that deviate from the Wright-Fisher model should often bias the gene pool toward a subset of individuals, which increases both inbreeding and the rate of change of gene frequency.

HUMAN SOCIETIES

No study of a human population has considered more than a handful of the factors that might influence the relation of effective population size and census size. Some of the factors, such as the effect of age structure or migration, are relatively visible in the ethnographic present. In a village census, the demographer can note the ages of respondents and their place of birth. She may be able to determine inbreeding patterns (e.g. cousin marriages) and factors influencing reproductive variance (e.g. polygyny). But longer-term factors such as population extinction and recolonization, imbalanced migration, or fluctuations in population size are generally beyond measuring with ecological or demographic means in humans. But although no study of ecological factors influencing effective population size in humans is comprehensive, each provides important evidence about the constraints that affect gene frequencies and gene identity over the short run. They may be evaluated in the context of longer-term genetic data to examine the way that human demography itself may have evolved over time.

Wood (1987) applied the ecological approach to a human society, using the methods of Hill (1972). He estimated the ratio of effective to census population size for the Gainj tribe of highland New Guinea, a group of slash-and-burn horticulturalists numbering around 1500 individuals at the time of the study. There were two important departures in this study population compared to the Wright-Fisher model: overlapping generations and a high

male reproductive variance. Both features tend to decrease effective size compared to census size; with a census count of 1318 individuals in the study, Wood estimated an effective population size of 650.5, for a ratio of N_e/N of approximately 1/2. In the Gainj, reproductive heterogeneity in males was mainly a result of polygyny. However, although the male reproductive variance was approximately three times that of females, this mating structure was estimated to decrease effective population size by a relatively modest 7 percent. However, Wood noted that the estimate of approximately 1/2 for N_e/N is substantially higher than the value of 1/3 that had often been taken for humans. He interpreted this discrepancy in terms of reproductive lifespan—in his sample, individuals of reproductive age made up a larger proportion than 1/3 of the population. High infant mortality and higher adult mortality rates tend to increase the ratio of effective to census population size.

Austerlitz and Heyer, (1998) (see also Gagnon and Heyer, 2001) examined pedigrees from French Canadian families, finding an autocorrelation in family size from one generation to the next. In this population, large families themselves tended to beget large families, leading to a strong reduction in the effective population size. They estimated that the harmonic mean of this growing population to have been ca. 17000; but the inheritance of family size reduces the effective size to only ca. 1000 individuals. This leads to an estimate of the ratio of effective to census size well under 1/10. Sibert et al. (2002) found that such intergenerational correlations in family size could affect gene genealogies in a similar pattern as population size bottlenecks. It is not known to what extent family size may be inherited in most human population. Québécois may be an extreme example where rapid growth is concentrated in large families, or perhaps stationary populations may also have such strong intergenerational correlations.

Migration is an important influence on genetic diversity in most human populations. It is very difficult to examine the effect of migration apart from other factors, because migration patterns have depended strongly on local population growth. Cavalli-Sforza (1959) considered the effect of migration on effective population size for village isolates in Parma, Italy. With a unique knowledge of the historical context of migration among these villages, Cavalli-Sforza was able to demonstrate that their present genetic differentiation was significantly associated with past patterns of movement among localities. This genetic differentiation does not characterize all human populations, but provides an important reason why genetic diversity may exceed estimates based on other demographic observations.

Social stratification by cultural mechanisms may affect genetic differentiation within and among human groups. A single society with little gene flow from outside will tend to have a reduction in heterozygosity if stratification affects mating, just as for assortative mating and other deviations from panmixia. Estimates of effective population size will be more strongly influenced by differential gene flow into different social strata. For example, Bamshad et al. (2001) found that genetic samples from higher-ranking castes in India tended to share more alleles with Europeans than samples from lower-ranking castes, which share more alleles with other Asians. Since gene flow from different source populations appears to have been correlated with caste, the overall effect of stratification has been to inflate the overall genetic diversity of the population while limiting within-caste variation. Likewise, differences in admixture rates between Africans and other populations within the New World has influenced the genetic diversity of local geographic regions. For example, Parra et al. (2001) assessed the frequencies of genetic markers in African Americans in different parts of South Carolina, finding that European gene flow increased with distance from the Atlantic Coast, and exhibited a historic sex bias. The net effect was an increase in genetic diversity and differentiation with geographic location. Boundaries between living hunter-gatherers and agricultural populations may exhibit differential gene flow that generates similar patterns of differentiation. This may be an important reason for the apparent high genetic diversity of living hunter-gatherer populations within Africa, despite their current small census sizes (Chen et al., 2000; Tishkoff and Williams, 2002).

PLEISTOCENE HUMAN POPULATIONS

Ancient human material and skeletal remains have been found across large parts of Africa, Asia, and Europe. By the beginning of the Middle Pleistocene, some 780,000 years ago, ancient humans occupied at least 35 million square kilometers (Hawks, 1999; Biraben, 1979; Weiss, 1984). This estimate includes large parts of the tropical and subtropical Old World, but excludes constant and periodic desert, rain forest, inundated continental shelf, and the northern tier of steppe and boreal forest. Although there were likely substantial fluctuations in geographic range over time, the estimate of 35 million km² is conservatively low for the past 500,000–800,000 years.

To arrive at an estimate of population numbers, the geographic range must be multiplied by some population density. The range includes areas with varying resource densities, some of which may have been marginal

for ancient hunter-gatherers without projectile weapons or sophisticated organizational strategies (Whallon, 1989; Gamble, 1994). Therefore, the population density applied across this entire range would be substantially lower than might have obtained within long-lasting local breeding populations. Observations of population densities in ethnographic hunter-gatherers vary substantially. Weiss (1984) applied estimates of population density based on ethnographic observations in recent Native Australian groups (Birdsell, 1972; Tindale, 1940). The overall estimate of Australian population density before European contact was approximately 0.28 persons per square kilometer (Weiss, 1984). However, this overall continental estimate includes groups with widely varying ecologies, from those living in subtropical rainforests, to temperate open woodlands or desert. Birdsell (1993) estimated that the range of population densities among Australian groups may have varied from 1 person per square kilometer in areas of dense resource availability to 1 person per 100 square kilometers in marginal desert regions. Applying the minimum estimate of 1 person per 100 km² yields a global census size estimate of 350,000 individuals. This is likely to have been near the minimum of a long-term fluctuating population of Pleistocene humans.

This estimate of 350,000 individuals would be of the census population size of humans globally during the Middle Pleistocene. In strong contrast, the effective population size of humans globally during this time period has been estimated from many sources at only 10,000 individuals.

The earliest studies of variation used protein polymorphisms to arrive at this figure (Nei, 1970; Haigh and MaynardSmith, 1972; Nei and Roychoudhury, 1982). Haigh and MaynardSmith (1972) proposed that the slight amount of human polymorphism might be explained by an ancient bottleneck of population size—a period of time during which human populations were very small compared to their present numbers. This hypothesis was later applied to a broader range of protein polymorphism data (Nei and Graur, 1984), and then RFLP data from the mitochondrial DNA (Cann et al., 1987). Later studies discovered consistent levels of variation for Y chromosome (Underhill et al., 1997) and autosomal genes (Wang et al., 1998; The International HapMap Consortium, 2005). The Wright-Fisher equivalent of the ancestral human population would have contained 10,000 persons.

Considering the number of ways that natural populations may differ from the Wright-Fisher model, there might have been many reasons that human populations had such low genetic variation compared to their census numbers. It is important to note that this discrepancy between

census and effective sizes characterizes most mammal species to some extent, with carnivores and primates in particular showing low genetic variation compared to their census sizes (Nei and Graur, 1984). A number of phenomena may explain this discrepancy, at the same time providing valuable information about the dynamics of Pleistocene human groups.

One explanation for low human genetic variation is that ancient population structures resulted in higher inbreeding than typical today. Takahata (1994) applied a model of extinction and recolonization of subpopulations to human evolution. In this model, the human population is assumed to have consisted of small groups that frequently became extinct and were replaced by other groups. Eller et al. (2004) extended the model to demographic parameters drawn from the ranges observed in recent hunter-gatherers. This kind of model can account for a severe reduction in genetic variation compared to the expectations for the census size of a population, because most of the population will be descended from a few ancestors at any earlier time. Considering the fluidity of hunter-gatherer groups, it may be unclear whether a model of recurrent extinctions and low migration is appropriate (Yellen and Harpending, 1972).

In many other respects, it seems likely that the ratio of effective to census population size actually decreased over time. For example, overlapping generations present more of a limit on genetic variability today than at any time during the Pleistocene, because the human lifespan is much longer (Caspari and Lee, 2004), generating a much larger number of postreproductive individuals. Likewise, migration distances greatly reduced after the advent of agricultural economies, increasing the genetic differentiation of local populations from each other.

A second explanation for low genetic variation relative to census population size is that the census population size used to be much smaller. A bottleneck with a short duration can explain some aspects of human genetic variation, such as the much lower variation of mtDNA and Y chromosome compared to autosomes and the X chromosome (Fay and Wu, 2000). However, a short bottleneck can have only a slight effect on the overall level of genetic variation. A number of researchers adopted the hypothesis that current human genetic variation is the product of a very long history of small population size in equilibrium (Harpending et al., 1993, 1998; Sherry et al., 1997). In this view, the reason why human genetic systems have an inbreeding effective size on the order of 10,000 is that the number of breeding individuals in the human species was in fact near 10,000 during most of the Pleistocene. A corollary of this hypothesis is that many ancient human fossils must represent different species not ancestral

to any living people—otherwise, their genes should remain with us today and inflate the current level of genetic variation.

Since the population size is clearly much larger than 10,000 today, the bottleneck hypothesis also requires a massive expansion of population size during the late Pleistocene. It is clear from archaeological data that human populations did expand massively during the Late Pleistocene (Stiner et al., 2000). But it has proved complicated to relate genetic data to this archaeological record. Single genes have provided different estimates of the time and existence of ancient population size changes, with some genes (mtDNA and Y chromosome in particular) showing strong evidence of recent expansion, while other genes show no sign of expansion at all (Hawks et al., 2000; Harpending and Rogers, 2000; Wall and Przeworski, 2000). Comparisons that include many genomic regions in one model have suggested a very slight bottleneck during the past 70,000 years (Marth et al., 2003, 2004). Further complicating attempts to narrow the range of population size estimates, some genes suggest that archaic populations of Eurasia may have appreciably contributed to human ancestry (Evans et al., 2006; Plagnol and Wall, 2006). These genes, together with anatomical evidence (Freyer et al., 1994; Wolpoff et al., 2001), suggest a substantial geographic extent to the ancient human population, which would be inconsistent with a small census population size (Harpending et al., 1998).

A third hypothesis is that selection has limited the genetic variation of humans and other species. The discrepancy between census and genetic estimates of effective size is widespread among animal species. In order to affect both functional and apparently nonfunctional sites, selection might involve widespread hitchhiking or pseudohitchhiking, or strong background selection. Theoretical models suggest that pseudohitchhiking may explain some empirical results, such as the lack of relationship of mtDNA variation and census size across animal species (Bazin et al., 2006), or the association of genetic diversity and local recombination rate in *Drosophila* (Betancourt et al., 2004).

It is now known that recent selection was very widespread in human prehistory (Wang et al., 2006; Voight et al., 2006). This selection is largely recent, however, and a large proportion may be attributable to demographic and ecological changes in the terminal Pleistocene and Holocene. Whether recurrent selection may have restricted human genetic variation throughout the past million years or more remains an open question. There is no strong association of local recombination rate and genetic diversity in humans (Hellmann et al., 2003), even though such an association would be predicted if widespread genetic hitchhiking did occur (Nachman, 2001). Background

selection of deleterious variants has been estimated to be relatively weak in its effect on N_e in humans (Charlesworth et al., 1993). Eswaran (2002) has proposed that selection of a coadapted gene complex in ancient humans might have restricted neutral genetic variation across the genome by assortative mating at a wavefront of dispersing adaptive alleles. Many other such models may be possible, and further research will need to determine which models of selection can be compatible with the observed pattern of data.

None of these three hypotheses yet provides a compelling account of human effective population size. It is clear today that an effective size of 10,000 individuals refers only to a theoretical model that is inaccurate in many possible ways. But we do not know whether a more correct population model would have 30,000 individuals or 300,000—or even more. Therefore, it is not yet obvious whether human genetic variation can inform us about the geographic location or mating systems of ancient people. The few estimators available are very coarse in their resolution. Deciding which factors actually operated on Pleistocene humans remains an active area of theoretical interest. At present, the relative importance of demography, selection, and changing environments to human genetic variation during the past million years remain unclear.

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Chapter 2

ASSESSMENT OF LAND SURVEYS IN GREECE: CONTRIBUTIONS AND LIMITATIONS

Jean-Nicolas CORVISIER

University of Artois, France

Abstract: For over a quarter of century, successive surveys, which are still continuing, have supplied a considerable though varied collection of data on the lands of ancient Greece. From around 1990, a fresh start was made with the grid-based method of systematic exploration, used in particular by J. Cherry in Keos and subsequently practised elsewhere. The idea is no longer merely to produce synopses on published sites or to conduct new explorations with the ultimate aim of locating and identifying habitats mentioned in written sources. Rather, it is to make a systematic exploration of a specific zone, which is intended to be used as an example, in order to index all archaeological vestiges that suggest the existence of habitats, whether permanent or not

For over a quarter of century, successive surveys, which are still continuing, have supplied a considerable though varied collection of data on the lands of ancient Greece. From around 1990, a fresh start was made with the grid-based method of systematic exploration, used in particular by J. Cherry in Keos, and then practised elsewhere. The idea is no longer merely to produce synopses on published sites or to carry out a new exploration with the ultimate aim of locating and identifying habitats mentioned in written sources. Rather, it is to make a systematic exploration of a specific zone, which is intended to be used as an example, in order to index all archaeological vestiges that suggest the existence of habitats, whether permanent or not.

Rather than focusing on historical periods (Archaic, Classical or Hellenistic), the chronological scope of investigations now seeks to be as broad as possible, extending from the Neolithic era to the Ottoman period. The choice of the study area must take into account soils of different nature. Grid squares on a smaller scale are revealing even small-sized rural

settlements, making it possible to reconstitute land-use histories. Although the aim of such investigations is not strictly demographic (their authors only seldom offer population assessments), they deal with demography insofar as habitats can be surveyed through successive periods. Our intention is to explore all the advantages, in terms of both methods and primary results, that not only demographers but also paleodemographers can draw from such investigations, since our information source is based not on texts but on long time-scales.

Under these conditions, questions need to be raised on the links between sites and populations. Is there a direct relationship between the number of given sites and the level of their population? Is the relationship indirect only, with the size of the site being taken into account, and if so, how? Secondly, in a world dominated by the City-state phenomenon, does the civic phenomenon have any influence on the spatial distribution of the population, or is the logic simply that of urbanization, i.e. the creation of urban centres once human settlements have reached a certain level of concentration in the same place? Similarly, is it possible to apply the “grid” concept to the Greek world, whether before or after the creation of the political – and not only urban – entity that the City represents, i.e. the concept of regular distances from one habitat to the other, whether in urban or rural sites and excepting major topographical features?

To answer these questions, raw survey results are not sufficient; they need to be considered as sources of information to which demographic reasoning is applied. However, different survey results contradict one another. Do these contradictions stem from faults that are inherent to the survey technique, or do they reflect the existence of several spatial organisation models and/or geographical variation in demographic densities?

SURVEYS AND DEMOGRAPHY: CONVERGENCE OR DISCREPANCY?

Using surveys in demography is not without its dangers. This is obvious if we look at the history of spatial exploration in the Greek world. At first, the idea was to chart and identify urban habitats. This phase culminated with the publication of *Griechische Landschaften* by A. Philippson and E. Kirsten between 1950 and 1962. Subsequently, the objective sought was also demographic. Based on a typology of habitats put forward by A. Doxiadis, a new systematic inventory of these was drawn up for often peripheral areas of the Greek world, as part of the *Archaies Hellenikes Poleis*

series, between 1971 and 1973. But as far as population was concerned, the inventory merely assigned an average coefficient per hectare, usually 300, which was then added up for successive periods.

These studies, which were purely circumstantial in origin, were followed by a number of historical studies and regional explorations, such as those of P. Cartledge, or R. Tomlinson on Laconia or Argolid. Finally, in the late 1980s, a new phase gradually emerged. This called on the techniques of the new urban geography in order to classify sites in order of importance and to define the pattern of the urban fabric, but they did not generally attempt to determine population levels.

This development gave rise either to studies primarily founded on synopses of published works, like those of J. Fossey on Boeotia and my own on northern Greece (with, it is true, an emphasis on demographic concerns), or to new systematic explorations – those of J-C Decourt in the Enipeus valley or J. Fossey in Lokris or Phokis – and even to surveys using improved techniques, combining very fine-meshed grid explorations (squares of 25 or 50 metres) with systematic research into the slightest traces of habitats, in the islands (C. Renfrew and M. Wagstaff in Melos or J-F Cherry in Keos), in Crete (L.V. Watrous in Lasithi, or L. Nixon in Sphakia) and in the Peloponnese (Mr. Jameson in the south of Argolid, W. Cavanagh in Laconia, J-C Wright in the Nemean Valley), to quote only a few of the main studies¹.

This brief historical overview shows the difficulties involved in our approach: how can links be made between studies based on different methods and sometimes with different goals in mind? Can any demographic conclusions be drawn from gazettes of sites and maps of land use patterns over time, other than simple observations of decreasing or increasing numbers of settlements?

One point can already be taken as certain: the *direct* link between demography and the number of sites, which was considered self-evident from 1970 to 1990 or so, is in fact far from certain, even though it had been used to support the theory of an abrupt population decline during the “dark age”, followed by an equally rapid demographic surge at the beginning of the archaic period. It also reinforced the old idea of a depopulation of the Greek world during the Hellenistic and especially the Roman periods. These points of view need to be substantially qualified, for several reasons:

- 1) The sudden decline in the number of sites does not necessarily imply a corresponding demographic decline. This is obvious in Thessaly during the “dark age”: according to my 1987 study, the sites occupied in the

Table 1: Numbers of sites and graphs for Crete, the islands and peninsular Greece

	N	EH	EH1	EH2	EH3	MH	LH1-2	LH3	LH3C	LH	AM	MM	LM	PG	G	A	C	H	R	LR
Keos (Ko)		10				12				12						22	41	22	6	17
(Ka)																30	66	50	13	47
(Po)																26	52	25	10	34
Melos	8	32				6				8					39	39	28	15	51	
Lasithi	15										8	45	18	4	4	22	7	7	28	
Messara	9													2	13	13	26	52		
Kavousi	9										9	53	7	9					19	
Sphakia (An)															48	48	48	20		
(Frang)																23	23	23	23	
Praisos	2										14	4	8	1	4	6	25	29	4	
Kythera	1										7	5	5				9	10	6	1
Argolid	16	40				31	35	56	32					8	32	43	75	73	60	
S. Argolid	7		30	30	2	4				21					16	18	34	71	22	59
P Pylos	7	14				37	37	33		21				10	10	13	13	27	60	
<i>S. Messenia</i>														14	24	55				
<i>Laconia 1</i>	13	44				30	18	35						11	13	39	87			

<i>Laconia 2</i>	15	62							38						83		9	21	54	196	194	164	37
N. Laconia	18	48							18						83				152	197	171	150	26
<i>Corinthia</i>																	3	10	30	35			
Achaia	6	5							3						9				5	17	23	14	7
<i>Attic</i>															9		15	26	50	70			
Boeotia		46							31						38		12	17	46	74	58	39	
Phokis/Doris																	1	6	4	17			
E. Phokis	1	3							4	2	8	3					4	5	7	16	14	11	4
W. Lokris	3		1	2	3				5		6	4					2	7	12	16	14	11	4
<i>Thessaly</i>	28	26							36	26	49	16					27	26	68	112			
Enipeus	83										30												71

Abbreviations: N: Neolithic; Prehis: Prehistoric; E H: Early Helladic; M H: Middle Helladic; L H: Late Helladic; A M: Ancient Minoan; M. M: Middle Minoan; L M: Late Minoan; P G: Protogeometric; G: Geometric; A: Archaic; C: Classical; H: Hellenistic; R: Roman; L R: Late Roman; Med: Mediterranean.

LH III C and reoccupied later are of average and large size, usually more than 4 ha and often more than 10 ha; the sites occupied in the LH III A-b, for which no trace of occupation during the “dark age” exists, but which were later reoccupied, vary from 1 to 3 ha. On the other hand, sites that were not reoccupied mainly cover 1 hectare or less. It is therefore clear that large-sized habitats were in fact maintained, and therefore that, in difficult periods, the population tended to gather together². If we examine the data from the surveys, the same observation can be made for other places. The reader will find examples along the way. We therefore need to take into account not only the number of sites, but also their size.

- 2) A comparison of the survey results given in the table and graphs³ shows that they vary according to their date of publication. A continuous increase from the Geometric to the Classical period corresponds to early publications or explorations (Argolid, S. Messenia, Laconia, Corinth, Attic, Thessaly). The others are more recent and give a less uniform picture: the increase continues in Keos, Kythera or Boeotia, but a levelling-off or classical type of ceiling is observed in Melos and Pylos. There is a Hellenistic levelling-off in Keos and Melos, but the rate of increase is maintained and even accelerated in Argolid, Pylos, Phokis and Lokris.

Lastly, in the Roman period, we observe a collapse in Keos, in one of the Sphakia sites, in Praisos and in the south of Argolid; a levelling-off in Kythera and a slight decrease in Laconia, but the trend is maintained overall and sometimes rises rapidly, as in Melos, Lasithi, Kavousi, in the second Sphakia site, in Pylos, Phokis and Lokris. Moreover, the trend resumes strongly in the late Roman period in Keos and in the south of Argolid. This may have been due to specific local factors, but even more so to changes in the way the space was used: as we will show later, new sites or those which were reoccupied during the Roman period were rural and of small size, and therefore correspond to an increasingly rural population.

Under these conditions, we need to be wary of applying survey results too directly to demography. Admittedly, given the paucity of our sources, they offer useful and even irreplaceable indications for demographers. But to be fully convincing indicators of demographic trends, variations in the number of sites should be applied to identical space structures, i.e. identical rural and urban land uses. Furthermore, because numerical variations almost always concern the smallest sites, they considerably amplify, any putative demographic trends, whether declining or rising⁴.

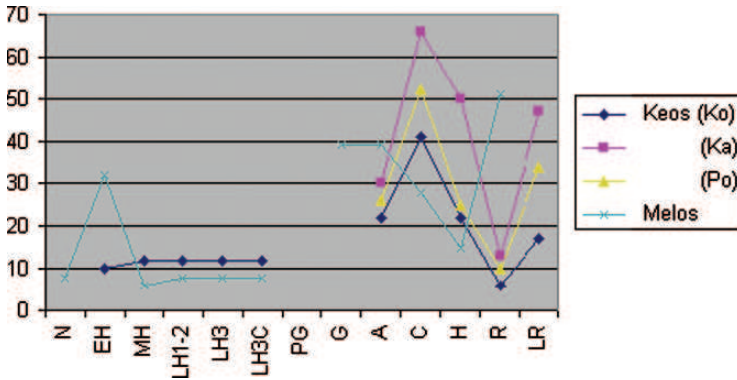


Figure 1: The Islands

TWO APPARENTLY CONTRADICTORY STUDIES: KEOS AND MELOS

The recent surveys of Keos and Melos were carried out with similar methods but have produced contradictory results, as evidenced by the following:

There were four Cities on the 103 km² island of Keos: Koressia, Poiessa, Karthaia, and Ioulis. The study related to the first three (see table 2⁵). But the exploration and the most systematic publication centred on the north of the island, essentially around Koressia. The City is a habitat of at least 3 hectares. Outside, there are 70 closed and 28 open habitats. Although the density is high, they are small in size, with only 15 covering more than one hectare. The other habitats very small, and not occupied continuously. According to the authors, these may be non-permanent farms. To turn our attention to the former, according to our calculations, they are at a distance of 1.8 to 4.3 km from the centre of the City. There is also evidence of prehistoric occupation in 8 sites, Archaic in 3 sites, Classical in 2, Hellenistic in 1, and Roman in 6.

This leads us to the conclusion that the creation and development of the City gradually suppressed other permanent types of habitat such as villages. The habitat distribution tables obtained by members of the team give the same impression, as they clearly show how far the Classical period, and the Hellenistic even more so, reflect the absence of real villages and the grouping together of the inhabitants as sites were abandoned. There is also the greater concentration of the shards found near Koressos, in a radius that does not exceed 4 km, and beyond which the space was little used.

Table 2: *Keos*: Distances from cities

Stavoti	1,6 ha	1,8 km	Prehist.	(A)	(C)	(H)	(R?)
Roukounas	1	2,4 km		(A)	(C)	H	R
Ay. Irini	1	2	Prehist.	A	C		R
Troullos	1,3	2,3	Prehist.				
Képhala	1,5	2,4	Prehist.				
Ammoudias	1,3	2,7	A	A	(C)	(H)	(R?)
Vourkari	2	2,5		(A?)	(C?)	(H)	(R)
Ay. Vervari	1,4	2,5			(C)	(H?)	R
Olzias	1,2	3,1	Prehist.	(A)	(C)	(H?)	(R)
Kephala	1	3,3	Prehist.	(A)	(C)	(H?)	
Képhala	1,25	3,3	Prehist.	(A)	(C)	(H?)	
Otzias	1,3	3,7			(A-C?)	(H)	R
Otzias	1,2	3,7			(A?) (C?)	(H)	R
Otzias	2	3,8			(A-C?)	(H?)	R
Paoiera	1,5	4,3	Prehist.		(A-C?)		

N-B: The brackets indicate that the habitat is not certain.

? indicates that there is little chance that the site is a habitat.

Distribution of habitats (%):

	0–0,4 ha	0,4–0,8 ha	0,8–1,2 ha	1,2–1,6 ha	1,6–2 ha
A	78	10	4	8	
C	86	10		2	2
H	88	10	2		
R A	75	13			12
R T	62	21	3	3	10

Habitat re-use (%):

	Re-use	Abandon
A	80	20
C	54	46
H	21	79
R A	90	10

It thus appears that land use in the Keos area was influenced by City development. Four Cities in an area of 103 km² means one City every 5 km, each covering an average area of 25 km². There is no need for permanent village-type habitats when a city flourishes and expands in this way. Moreover, those covering 1 to 2 ha are 0.5 to 1.2 km apart. Isolated farms are much more numerous but not necessarily occupied permanently.

In Melos, as we can judge from table 3⁶, the situation is somewhat different. The city is of course large, occupying 15 ha at least, with a territorial extent of 151 km². 111 sites have been discovered. Even taking into account some losses in the number of sites, their density was lower than at Keos. According to the authors of the publication, they tended to retreat after the prehistoric period to the east and centre-south part of the

Table 3: Melos

	Site	Size in ha	Distance (km) from Melos	Occupation				
Group 1	Areti	1, 5		Prehist.				
	Mandrakia	3	2, 5		A	C	(H)	R
	Mandrakia	1	5	Prehist.				
	Kaminia	1	5	Prehist.				R
		0, 8				C		R
		4, 5	4		A	C	H	R
Group 2	Agrilia	6, 9	6	N	(A?)			
	Philikopi	1, 8		Prehist.				
	Pelloudi	4, 5?						R
	Kouphi	2, 8		Prehist.				
Group 3	Kato Kômia	3, 5	8					R
	Soleti	4	10	Prehist.	(G/A?)			R
	Spathi	1	12	Prehist.				R
	Paliochôri	9						R
	Zephyria	12, 2	7				(C?)	Med
Group 4	Aya Kyraki	6						R
	Stous Dekatas	2, 5	9/3, 5 ¹	Prehist			(C?)	R
Group 5	Provotas	7	10/7 ¹	Prehist.	A	C		R
Group 6	Ay Spiridon	2	5 ² /6 ¹	Prehist. G				R?
	Emborio	10	/6 ¹	Prehist.				R
	Asprochavo	1, 5						R
Group 7	Xylokeratia	2	12/6 ³	Prehist G	A		(C?)	R
Group 8	Phakos	2	/8 ⁴	Prehist				
	St. Glastria a)	1, 5	/9 ⁴					R
	St. Glastria b)	2	/9 ⁴		(A?)		H	R

¹ distance from Zephyria.² as the crow flies, but 15 km by road.³ distance from Provotas.⁴ distance from Xylokrateia.

island, i.e. the city area, where 21 of the 28 traditional sites and 10 of the 15 Hellenistic sites were found. The rural sites were obviously abandoned. During the Roman period, occupation of the island became denser again.

Of still more interest is the existence of preferred habitat zones. According to the habitat map and typology, I have noted 8 of these, which are not necessarily contiguous. The data in table 3 show the scarcity (except for Melos), after a well represented prehistoric period (14 sites), of archaic occupation (7 sites) and especially Classical (7 at most), or Hellenistic (3), even for large habitats; and the density of Roman occupation (18 sites in all, including 6 entirely new and often reasonably large sites). There is also one notably atypical case: between zones 3 and 4, Zephyria, a rather isolated site, is quite large, and could have been a true urban centre, given its distance from Melos. Unfortunately, its Classical occupation has not been fully ascertained.

In the light of this spatial distribution, the following conclusions can be hazarded:

- 1) It was possible for principal habitats, towns or large villages, to form within 7–12 km of Melos.
- 2) Although such habitats existed in the prehistoric period, the City phenomenon caused them to disappear. Zephyria, which covered 12.2 ha but was too close to Melos, was clearly an aborted City.
- 3) Outside the City, habitats of the Classical period are less numerous and very small (usually less than 0.5 ha): these were hamlets or more or less permanent isolated farms.
- 4) When the influence of the City began to diminish, in the Roman period, the principal habitats reappeared and a new level of spatial organisation becomes perceptible: the city (15 ha), with main habitats situated about every 5 km and scattered rural habitats every 500 metres as, judging by the habitat chart, the countryside became more intensively used.

These are two very precise studies, but also two very different models. We now need to assess their validity outside the area considered.

SURVEYS OUTSIDE MELOS OR KEOS

With the possible exception of the south of the Argolid, the surveys were not as thorough with regard rural areas – or have not yet been published with the same precision. It is advisable to group them together into larger areas.

Crete

In Crete, six explorations were carried out, with similar results overall, in the Lasithi plain, the Mesara, Sphakia, Praisos, Kythera, and Kavousi.

In the 66 km² of the Lasithi plain (data table 4⁷), a total of 77 sites have been found for all historical periods. However, main sites are scarce, with 10 covering more than 1 ha, 3 more than 3 ha and 2 covering 5 ha or more. The trend in numbers peaks during the Middle Minoan (45 sites), the Classical period (22 sites) and the Roman period (28 sites), when the plain was densely inhabited. The existence of potential principal habitats during the archaic period is perceptible. The distance between them, with only one exception, is about 3 km.

Very small scattered farm-type habitats are discernible every 500 metres or so. For the Classical and Hellenistic periods, only principal habitats remain; the scattered hillside habitats have almost all disappeared. Clearly, only one City seems possible in an area of 66 km². This corresponds to an urban pattern, barring relief accidents, of one City per 9–10 km. During the Roman period, the clear increase in the number of sites corresponds to a return to the valley bottom, with a new pattern of four major sites plus secondary sites every 1 to 2 km. Some of these Roman farms were new (5), others merely reappeared.

The publication does not allow a thorough analysis of the results in the Messara. However, the number of sites steadily increased between the Neolithic and Recent Minoan eras, with rural depopulation and concentration in Phaistos. The resumption of rural occupation starts up again with the Protogeometric. For the Archaic period, there are 13 sites of which 3 appear to cover 0.5 ha, while the others are all clearly smaller. The 26 Classical sites, with the exception of Phaistos, almost all cover less than 0.2 ha, and are therefore only simple farms. During the Hellenistic period, Phaistos covered more than 50 ha. Sivas developed elsewhere, growing from 1 ha to 48 ha. A hierarchy of the rural sites begins to take shape, with farms covering less than half a hectare, and villages 1 or 2 hectares. Apart from Phaistos,

Table 4: Lasithi

Kardamoutsa	5 ha	Prehist.	G	A	C		R	3,2 km from Plati
	8	Prehist	G	A	C?			1,3 km from Plati
Tzermiada	2	Prehist.	G	A	C	H	LR	3,2
Angousti	3,3	Prehist.		A	C	H	R	2,8
Plati	+0,5	Prehist	G	A				3,8

the seat of the City, there are 3 principal sites about 3–4 km distant from each other: Haghia, Kommas and Sivas. Despite the destruction of Phaistos by Gortyne, the rural population was maintained, except in the immediate vicinity of the old site. This structure notably corresponds to a large grid pattern, with Gortyne and Phaistos nearly 14 km apart.

In the plain of Sphakia, there are at least 2 Cities, Anopolis and Frangokastello, a little less than 10 km apart, in a fairly extensive area where each City-state covered about 170 km². A certain continuity is perceptible in the former, since, in 55 known sites from all historical periods, 48 (87%) were occupied more or less continuously from the Archaic to the Roman period (with the exception of the late Roman period). There is a clear hierarchy, since the City covers 10 ha, while 38 sites cover less than 1 ha and 10 cover 1 to 3 ha. The small sites seem to be individual farms. For the City of Frangokastello, the picture is slightly different, numerically speaking: 8.5 ha for the City, 46 sites in all, of which 23, or 50%, were occupied more or less continuously from the Archaic to the Roman period; 8 (36%) in the early Iron Age and 5 (13%) during the Late Roman period. In both cases, habitats were not necessarily occupied continuously.

The Kythera region, covering approximately 5% of the island, is located on the central plateau. The sites are small and rural in nature. The preliminary report does not make it possible to distinguish the grid pattern, but it is clear (see table 5⁸) that after Early Bronze Age to Middle Minoan settlements followed by a long period of vacancy, came a Classical and Hellenistic system based on habitats that were fewer in number but much larger.

In the case of Praisos, covering about 25 km², the sites, for which no area is given, seem primarily rural and, therefore of small size and relatively dense. Occupation is notably volatile: the relatively numerous Neolithic sites, or those of the Ancient Minoan, are not the same as those, fewer in number, with later prehistoric settlements. The acropolises, where the seat of the City of Praisos would later be established, were inhabited only at a much later stage, in the late Minoan IIIC, and then essentially from the start of the Protogeometric. Continuity would only appear with the Archaic, and

Table 5: Kythera

–1 ha:	14 sites of which AM: 7; MM: 2; C and H: 1; R: 2
1–2 ha:	3 sites of which C and H: 2; H and R: 1
2–4 ha:	2 of which AM, MM, C and H: 1; C, H and R: 1
+4 ha:	1 C, H and R

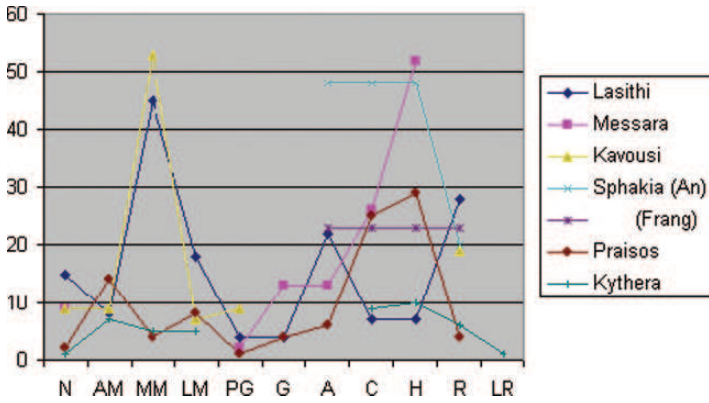


Figure 2: Crete

especially the Classical and Hellenistic worlds. The somewhat surprising Roman collapse seems linked to the capture of Praisos by Hierapytna.

Finally, in the Kavousi plain, there is a steady decrease in the number of sites between the Middle Minoan, when the 53 sites in the plain were about 2 km apart overall, and the dark age, when habitats were located in the hills. With no nearby City, the plain was abandoned until the Roman period. Thus, in the Cretan world, it seems that the hierarchy of the sites, with significant sites outside the heart and head of the city, corresponds to a large grid pattern (more than 13 km between Cities). The smaller the grid, the fewer cities are found. They are still found, however scarce, in a 10 km grid pattern. Hence the question: what happens when the grid pattern is smaller?

The Peloponnese

The most accurate exploration published to date concentrates on the south of the Argolid, in a zone covering a total area of 338 km². The essential data is given in table 6⁹. The study covers two cities, Hermione (276 km²) and Halieis (84 km²). In the neighbourhood, Epidaurus covered 473 km², Argos 360 km², and Trezen, 10 km from Hermione, 364 km², the distance being what it is because of a chain of very high hills. Hermione is 8 km from Halieis. Here we have two contrasting cases. Halieis eventually covered 15.12 ha, but was surrounded by only a small number of very small sites, while sites of more than 1 ha tended to disappear, except those near the City.

Table 6: The South of Argolid

Archaic: Hermioné	10 ha		
Halieis	5 ha		
Mases	5 ha	7 km from Hermioné	
Kineta	6 ha	3–4 km from Hermioné	
Stavros	2,7 ha	1,5 km from Halieis	
Flamboura	2 ha	2,5/3 km from Halieis	
Ayos Ioannis	1,4 ha	2,5 km of Mases	
+5 sites 0,2 to 1 ha, 27 sites with – of 0,2 ha.			
Classical: Hermione	16,8 ha		
Halieis	4,5 ha		
Mases	5 ha	7 km from Hermioné	
Eileioi	1,5 ha	7 km from Hermioné	
Stavros	2,7 ha	1,5 km from Halieis	
Ayos Ioannis	1,4 ha	2,5 km from Mases	
Kesari	1,1 ha	0,5 km from Mases	
+3 sites 0,2 to 0,6 ha, 44 to – 0,2 ha.			
Classical and Hellenistic	Hermioné	16,8 ha	
Halieis	5,12 ha		
Mases	5	7 km from Hermioné	
Eileoi	2	7 km from Hermioné	
Koukouras	1,9	5 km from Halieis	
Pikrodhani	1,7	6 km from Hermioné, 6,5 from Halieis	
Kapari	1,5	3/5 km from Hermioné	
Ayos Ioannis	1,4	2,5 km from Mases	
Petrothalassa	1	5 km from Halieis, 7 from Hermioné	
+98 small sites with 6 of 0,2 ha.			
Hellenistic and roman period	Hermioné	11, 3 ha	
Kineta	6	3–4 km from Hermioné	
E 51	2	5 km from Hermioné	
Kesari	1,1	0,5 km from Mases	
Emioni	1	4–5 km from Hermioné	
+2 sites 0,7 to 0,9 ha and 17 sites to – 0,2 ha.			
Late Roman. 16 sites with + than 1 ha 82 sites with 2 of 0,2 ha Distances in km			
Mases-Hermioné	7	Didymoi-Boleoi/Philinoreia	3/4 km
Hermioné-Eileoi	7	Boleoi-Mases	4
Eileoi-Didymoi	8		

Hermione grew to 16.8 ha, but its extent accounts for the existence of other main sites: Mases, with 5 ha, Eileoi, which reached 2 ha, and a few others. The distances between them range from 4 to 8 km. When we look at the detail, there is a distinct and noticeable change between the Archaic and Roman periods. Village-type sites tended to disappear as the two Cities became stronger. Eventually, they only remained in Hermione, the largest territory. Again, Mases, Eileoi and a few others tended to disappear. Thus habitats tended to cluster together as the secondary sites, except small farms, began to disappear, leaving nothing to indicate whether they were permanent or not.

In the Nemea valley, in an 80 km² zone, the situation seems very similar to what we know about the south of Argolid. Here, the Cities were less than 10 km apart: 5.5 between Nemea and Kleonai and 7.5 between Nemea and Phlious. The latter's 16.5 ha were very densely occupied. The numerical evolution masks the fact that a large number of prehistoric sites existed which cover about 1 ha and even 3 ha, like the Tsoungiza hill. They disappeared in the Archaic period, leaving a purely rural habitat of small hamlets or more probably simple farms, to which should be added 41 towers and rural sanctuaries. Sites from all periods are 0.8 to 1.2 km apart, except near the Nemea, where the average distance is 2.5 km.

In this much explored part of the Peloponnese, then, the logic of the habitat seems linked to the size of grid pattern. When this is very large (a territory of at least 250 km², corresponding to a grid pattern of about 15 km), there seems to be a need for small, permanent village-type sites, or small townships, which, however, cannot be called Cities. When the grid pattern is small (8–9 km, which corresponds to an area of less than 80 km², or even 5 km, corresponding to an area of about 25 km²), there are only small, more or less permanent farms.

The results, although they are provisional, of the still partial exploration of Achaia corroborate these conclusions to some extent. Table 8 systematizes the relevant data¹⁰. In the Peiros basin and the western plain, the major City is Dyme, which grew to a maximum of 80 ha during the Hellenistic period. Before its foundation, the habitat – where there is no clear distinction between principal and secondary sites – was organized roughly into a pattern with an average grid size of 3 ha. The Classical period saw a fundamental change in spatial organisation.

The foundation of Dyme choked off the scattered habitats that gravitated around it within a 6 km radius. According to the authors of the exploration, the small signs of occupation found all around do not necessarily correspond to habitats. We would be very much inclined to see in them an indication

of non-permanent occupation, a notion we will go into further on. We do, however, see a clue in the fact that the occupation of such sites is only occasionally attested in the chronology, and that their use very seldom led to permanent occupation. Only a small number of sites were inhabited for any length of time.

These observations are valid not only around Dyme, but also for the whole explored zone. New habitats can be found there, but only more than 6 km from Dyme. These were roughly grouped around a core, and situated about 2 km apart on average. The cores of the 3 groups thus formed were 8 to 10 km apart. During the Hellenistic period, when the Achaean Confederation flourished, Dyme reached its furthest extension and the number of sites is at its highest. A scattered type of habitat flourished, and rural occupation was at its most dense. All the sites are about 2 km apart. The imperial period saw the disappearance of this well-ordered system.

In comparison, the survey made in Laconia produced rather different results, though not so much in terms of evolution as in terms of the grid pattern. Some of these results are given in table 7¹¹. The small proportion of occupied sites during the prehistoric period is noticeable in comparison to the historical period – the collapse of the dark ages being linked with the arrival of the Dorians.

Essentially, these are small rural sites, hamlets or isolated farms. They were highly volatile, not only between the Bronze and Iron Ages, but from one period to the next. Except during the Archaic and Classical periods, and to a lesser extent the Hellenistic period, occupation rarely lasted over more than two periods, and thus was rarely maintained for more than three centuries (whether on a continuous basis or not: we cannot make an in-depth analysis here). Sites where relatively steady occupation is perceptible, between the Early Bronze Age and the Roman period, are mainly of average size (+3 ha) or large (+25 ha). Generally speaking, the most extensive sites developed during the historical period.

It is in fact from the archaic period onwards that sites can be classified as large (+3 ha, 2 sites), as hamlets (0.3 to 1 ha, 4 sites) and as isolated farms (0.15 to 0.3 ha, 17 sites). These data only concern fully proven habitats and do not take chance ceramic finds into account. Extensive sites are 3–4 km apart, while the other smaller sites are less than a kilometre apart, a pattern that was maintained during the classical period with the disappearance of some of the smaller sites (–0.13 ha) and an increase in the number of habitats, especially villages or small cities (2, 7 and 27 respectively). The trend continues during the Hellenistic period, in terms of the increased number of both proven and probable habitats, which could have reached 75 on the

Table 7: **Laconia:** Distribution of the sites and places of ceramic finds within the survey area

	N	EH	MH	LH	PG	G	A	C	H	R	LR
-0,3 ha	11	37	14	16			120	159	141	118	19
0,3-1 ha	5	7	1	2			21	26	23	21	2
1-3 ha				2			4	5	2	5	2
3-10 ha	1	3	3				4	4	4	2	2
+25 ha	1	1	1	1			1	1	1	1	1

Volatility of the sites and places of ceramic finds:

	N	EH	MH	LH
Later prehistoric reoccupation	5	8	10	
Without later prehistoric reoccupation	10	49	3	
Former prehistoric occupation		6	5	15
Without former prehistoric reoccupation		49	9	7
Later historical reoccupation		31	4	17
Without later historical reoccupation		20	5	4

	A	AC	C	C-H	H	H-R	R	LR
Former prehistoric occupation	26	24	27	10	17	10	17	3
Without former prehistoric occupation	126	115	170	80	154	86	133	23
Former historical occupation		139	41	97	42	101	24	
Without former historical occupation			58	49	74	54	49	2
Later historical occupation	146	56	105	37	91	16	21	
Without later historical occupation	6	81	92	53	80	80	129	

grid. This pattern continued into the beginning of the imperial period, and vanished later.

Although they differ slightly, none of these data are incompatible with the results of other surveys of the Peloponnese, if we remember that we are on Spartan territory. It is logical to find no other City, not even any real townships, and only dispersed rural habitats. This situation corresponds to the helotism characterising Sparta's political and social system, in which the dependent helots were tied to the earth which they cultivated to pay their master the royalty that allowed them to live and to keep their full citizenship. The tendency was therefore for the rural component to gradually fall apart. This can also be noted in the recently explored Pylos region. The

Table 8: **Achaia**: Distances in km

H. R.	Niphoreika C-Haghio Vlasitika A	4	Myrtos A-Petsas A et B	6
	Haghio Vlasitika A-Lousika D	1,8	Myrtos A-Riolos D	4
	Lousika D-Lousika F	2,2	Riolos D-Araxos F	7
	Lousika F-Phostanea A	1	Araxos F-Araxos A	5,5
	Phostanea A-Phlokas H	4,3	Niphoreika C-Limnochorion B:	4,5
	Phostanea A-Myrtos A	6	Limnochorion B-A	1,2

Classical period: Group 1 (around Dymè)

Dymè-(Kato Achaia C)	1,8	Dymè-(Haghios Nikolaos A)	7
(Kato Achaia C)-(Anô Achaia D)	3,5	(Anô Achaia D)-(H Nikolaos B)	4,2
Dymè-(Haghios Nikolaos B)	6,8	(H. Nikolaos A)-(H Nikolaos B)	0,5

Groupe 2 (autour de Anô Soudheneika A)

A Soudheneika A-K Mazarakion A	2	A Soudheneika A-Petrochorion B	6
A Soudheneika A-Phlokas A	0,5	Petrochorion B-Petrochorion A	1,5

Distance groupe 1-group 2 (distances maximales et minimales)

Dymè-Katô Mazarakion A	8	Katô Achaia C-K. Mazarakion A	7,5
Dymè-Anô Soudheneika A	10	(Anô Achaia D)-(H Nikolaos B)	3,5
Dymè-Petrochôrion A	6		

Group 3 (Around Lakkopetra F)

(Limnochorion A)-(Lakkopetra G)	1,5	Lakkopetra F-Lakkopetra H	2
(Lakkopetra G)-Lakkopetra F	0,5	Lakkopetra F-(Lakkopetra A)	2,5

Hellenistic period: Groups 1 et 2

Dymè-(Niphoreika A)	1,8	K.Mazarakion A-A. Soudheneika A	2,5
Dymè-Haghio Vlastika B	2,5	A. Soudheneika A-Phlokas E	1,5
Haghio Vlastika B-(H. VI. A)	0,5	Phlokas B-Phlokas C	0,5
(H. Vlastika A)-A Achaia A	1	Lousika F-Elaeochôrion A	2,5
Anô Achaia A-Lousika F	2,5	Elaeokhôrion A-Petrochorion A	3
Lousika F-Haghios Nikolaos A	2	Petrochorion A-B	0,8
H. Nikolaos A-K. Mazarakion A	1,8	Petrochorion B-Myrtos B	2,2

Groupe 3 (autour de Lakkopetra F)

Lakkopetra F-(Lakkopetra H)	0,6	Lakkopetra F-(Lakkopetra B)	2,5
Lakkopetra G-(Lakkopetra H)	0,6	Lakkopetra C-Lakkopetra B	1
Lakkopetra F-Lakkopetra C	2,5	Lakkopetra B-Araxos E	2,5

Distance group 1-group 3

Dymè-(Limnochorion A)	7	Dymè-Lakkopetra	8
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Imperial period

Dymè-(Therianon B)	7	Elaeochorion A-Petrochorion C	3
Dymè-(Therianon A)	8	Petrochorion C-E	2
(Therianon A)-(Therianon B)	1	Petrochorion C-Riolos B	8
Dymè-Lousika E	6	Riolos C-(Riolos C)	0,5
Lousika E-Elaeochorion A	2,5	Dymè-Limnochorion A	6,5
Elaeochorion A-A. Soudheneika B	4	Limnochorioon A-(Lakkopetra I)	1,5
Anô Soudheneika B-A	0,5	(Lakkopetra I)-(Lakkopetra G)	1,5
Elaeochorion A-Petrochorion E	3	Limnochorion A-Lakkopetra F	2,8

N-B: The brackets indicate that the site is not entirely certain as a habitat

Volatility of sites in Achaïe

Araxos A			H	R
Araxos B	HR		C	C
Metochion A			(C)	(H)
Lakkopetra A			(C)	
Lakkopetra B				(H)
Lakkopetra F			C	H
Lakkopetra G (farm)			C	H
Lakkopetra H			C	H
Limnochorion A	HR		C	H
Niphoreika A				(H)
Dymè		A	C	H
Kato Achaia C			(C)	
Haghio Vlasitika A				(H)
Anô Achaia A				H
Anô Achaia D			(C)	
Anô Achaia E				H
Lousika A		A		
Lousika E (farm)				(H)
Therianon A			C	H
Therianon B (farm)				(R)
Haghios Niokolaos B		(A)	C	
Anô Soudheneika A			C	H
Phlokas C				H
Phlokas D			(C)	H
Elaeochorion A		(A)		H
Petrochorion A		A	C	H
Petrochorion E				
Riolos C				(R)

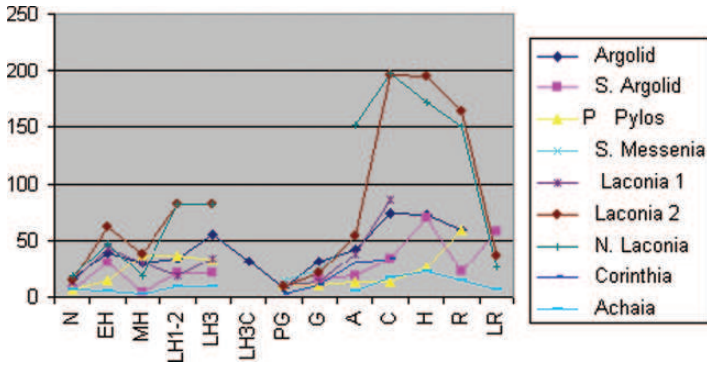


Figure 3: Peloponnese

preliminary report does not give a precise picture of the situation, but it seems close to that of Laconia, in that both regions are essentially rural.

However, the habitat was largely influenced by historical developments, with a peak during the recent Helladic, a major decline during the Protogeometric and Geometric – although the habitats did not disappear – and very depressed Archaic and Classical periods. A new start occurred in the Roman period and its numerous *villae*. History has an explanatory role, but it can be seen that from the PG to the Hellenistic period, the grid pattern tends to become larger, reaching 1 km to 1.5 km between sites, even when their number increases, contrary to the wider dispersion of the Recent Helladic and Roman periods (0.5 km between sites). Even in a region dominated by Sparta, the clustering tendency, even though it was interrupted by history, is still perceptible.

Central Greece or Thessaly

The surveys made in this region, although very thorough, are not comparable in their methods to those just described. In doubt, should we reject their conclusions? Or are we under a false impression? The question can be answered at least partially by examining the grid pattern.

One surprising finding is that in Boeotia, there are a number of important habitats that are not Cities. In the classical period in Boeotia, up to 23 Cities were detected by Fossey¹², or 1 City every 112 km, and a total of 51 important habitats, or 1 every 50 km². In terms of the grid pattern, the average in the first case would be 10 km, and 7 km in the second. The case here is that of important cities, which appear to have occupied a large area.

This theoretical distance of 7 km (3.5 km on each side of the inhabited site) allows us to take a considerable number of small villages into account, and even rural farms, which of course does not exclude the possibility that others may be found in the future. Are these just theoretical imaginings? In fact, the reality is not fundamentally different.

If we look at the case of the Cities alone, the actual grid pattern varies from 4.8 to 21.2 km, with an average of 10, according to the figures calculated by J-C Decourt¹³. However, the habitat situation in these zones is different. The Tanagra territory¹⁴ for example – the largest, because its nearest neighbour is 21.2 km away – has 20 known habitats, from all periods.

From the Archaic to the Hellenistic periods, Kastri of Vratzi seems to have been a refuge of 0.2 ha, but Archaic and Hellenistic tombs have been discovered nearby. Kleidheti, 2.5 km from Tanagra, seems to have been a true urban site; the site identified at Gephyra is described as a *polis* by Strabon and by Stephen of Byzantium, but in reality it is probably one of the large townships that made up Tanagra. Liatani, near Gephyra, seems to have been a farm or a small hamlet, Staniates (Oinophyta?), 6 km away from Tanagra, could have been a small village, like Kakosalesi, Bathiza or Delion (6 km from Staniates, 9 from Tanagra), where at least burials are known. Dhramesi/Graia, on a large hill 8 km from Tanagra, seems to have been a large township.

Mikro-Vathy, which seems to be the old Aulis, is 6 km from Graia and 12 from Tanagra. It has an acropolis covering 0.8 ha, and traces of a low city which probably covered around 2 ha, which makes it at least a large township. Tseloneri (Hyria), 12 km from Tanagra, was a *polidion* according to Strabon and Stephen of Byzantium, and was girdled by walls. 16 km from Tanagra, Khalia was described as a *polis* by Theopompe. 19 km away, Salganeus, covering 2.2 ha and inhabited during the prehistoric period, seems to have been reoccupied later on during the Classical period. Mykalessos, 12 km from Tanagra, described as a *kômé* by Strabon and a *polis* by Pausanias, could either have been a large village or a small city. Lykovouni (Harma), 10 km from Tanagra, had a wall encircling 0.7 ha. 10 km from Tanagra, Dhritsa (Heleon) had walls encircling 2.5 ha. Lastly, Ayos Pandeimon (6 km from Delion, 8 from Tanagra) could have been Pharai, Tanagra's *kômé*.

We thus have 15 sites, which were either small cities or villages. For a theoretical territory of about 300 km², we come to a figure, including Tanagra, of 1 site every 18 km², which corresponds to a grid pattern of small sites about 4.3 km apart. This is still within reason, and a large number of farms is not indispensable. However, looking to the small cities of Siphai

or Thisbe, there seem to be very few scattered sites. Thisbe, 7 km from Chorsiai, only covered 5 to 6 ha, and did not possess, outside the city, anything other than its port¹⁵. Siphai covered only 4 ha at the very most, and no other site has been attested in the region¹⁶. Looking now at Phokis, we have a completely different grid pattern. According to Demosthenes (*On the Embassy*, 123), the whole region had 22 Cities (*poleis*), while Pausanias (X, 3, 1–2) names twenty of them. For a region of about 700 km², we thus have a theoretical territory of 32 km² for every City, which means a grid pattern of about 5.6 km. If we calculate the distances between the 19 different sites, they range from 3.5 to 7 km from the nearest neighbour, which tallies exactly. The size of the habitats found (with the exception of the kastro, which cover 2.5 to 10 ha) is of 5 ha on average, which brings them into the category of small Cities. There is little space for scattered habitats. Accordingly, the 3 kastro and 4 secondary habitats found in the 19 sites could also be the only ones. The data in Table 9, resulting from a study on part of the area, were confirmed by a very recent study on all the fortified enclosures in Phokis¹⁷.

The situation in Opuntian Lokris (see table 10)¹⁸ is *a priori* appreciably the same: 22 sites for around 500 km², or 1 per 22 km². The distances between them range from 2 to 12 km, the average being around 5. But the typology of the sites differs. For those where the area is perceptible, 11 cover less than 3 ha and are mostly forts or prehistoric sites. Only 4 cover more than 3 ha and may be qualified as Cities. These are Larymnai, Halai, Boumelitsa and Alope, to which should be added Kyrtones (2.6 ha) Korsezia (1.6 ha?), Anastases (2 ha) and Oion (2 ha). We thus have 8 possible cities, that is to say a theoretical grid pattern of 8 km. The existence of rural and permanent habitats is not entirely indispensable. The fortifications enabled farms of a more or less permanent nature to exist, assuming that the nature of the ground made this possible.

Table 9: Phokis

Typology of habitats			Distance to nearest neighbour		
	Fossey	Typaldou-Fakiris		Fossey	Typaldou-Fakiris
–1 ha:	2 patterns	2 patterns	–3 km	6 patterns	11 patterns
1–3 ha:	2	6	3–5 km	6	9
3–5 ha:	2		5–7 km	4	4
5–10 ha:	3	9			
+10 ha:	1	4			

Table 10: Lokris

Typology of habitats		Distance to nearest neighbour	
-1 ha:	4 patterns	-3 km:	1 patterns
1-3 ha:	7	3-5 km	4
3-5 ha:	1	5-7 km	5
5-7 ha:	1	8-10 km	2
7-10 ha:	1	+10 km	2
+10 ha:	1		

Finally, in Thessaly, it is clear that the grid pattern of the City ranges, depending on the place, from 8 to 12 km, which gives us theoretical territories covering 64 to 120 km². There obviously a need for secondary habitats. In the Enipeus plain, where the Cities were 10 to 11 km apart, we know of 12 Cities, 18 forts, 23 habitats and 18 chance finds, from which the existence of permanent habitats cannot necessarily be deduced. Overall, we thus have 3.5 examples of *komai*, or traces of more or less permanent habitats, for each City. Between the heart of the City and the village, the distance is of 3 to 6 km, and 2 to 3 km between each *komai*.

To conclude: outline of a general framework, proposals and reintroduction of demography

Linking the surveys and the lessons that we can draw from them within a general framework is of course difficult, in view of the variety of cases. However, we believe the following conclusions can be drawn:

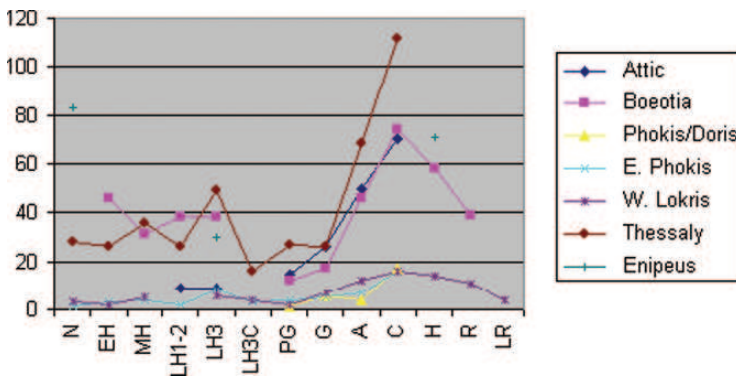


Figure 4: Peninsular Greece

- 1) The major element, at least during the Hellenistic period, is the grid pattern. It seems that, when the grid pattern is large (more than 12 km between Cities, not including major natural relief), intermediate sites should be found between the core of the city and the small rural habitats. This is particularly noticeable in Melos (which covers 151 km²) and Hermione (276 km²). In both cases, the intermediate habitats are generally situated roughly 5 km from the City, and cover 3 to 4 ha, which qualifies them as largish villages. When the grid pattern is smaller, the number of intermediate sites steadily diminishes, as well as their size (1 to 2 ha, only in Keos), and may actually disappear altogether when the grid pattern falls strictly below 5 km. When the grid pattern widens, however, intermediate habitats tend to become larger, and the space around them tends to become organized. Should these be considered as villages? Terminological uncertainty reigns in these cases, as can be observed in the Tanagra territories: for these habitats, the Ancient Greeks use words such as *kome*, *polidnion* or *polis*. In reality, they are sometimes small cities, often surrounded by walls, with a grid pattern of around 4/5 km, which works out as a theoretical territory of 18 km²
- 2) These observations raise the question of the relationship between cities, or towns, and the City. The link between the two, as we know, is not absolute. There are Cities that do not really make up a city, like Sparta (an incomplete grouping of 5 villages) or Lyttos¹⁹. The most frequent case is still that the political heart of the state are a city. But this was not necessarily the only city from the state. Some Cities-state were aborted because they were too close to their neighbours (Asine compared to Argos for example), or for historical reasons. They had cities nonetheless, and the rural area was organised around these. The idea of intermediate cities can also be applied to giant Cities, like Athens. Athens was a giant city and the core and the heart of the City; but in the state territory Athens was also real cities covering 12 to 20 ha, such as Eleusis, Thorikon or Sounion²⁰.
- 3) In rural areas, the City imposed its dominion. Either the area actually used was nearby, as in Melos, where part of the island was abandoned between the archaic and imperial periods, or there were only more or less permanent hamlets or isolated farms within a radius of about 3 km. Farmers could live in the city and also own a small cottage near their lands. This is why ceramic finds do not necessarily indicate permanent occupation. This is perceptible even in regions affected by rural decline, like Laconia.

- 4) The location of permanent habitats of the hamlet or village type varies over time, at least when there are nearby hills. From valley-bottom locations in prehistoric times, they shifted to average sized hills during the Archaic period, as can be seen in the Lasithi plain or the Enipeus valley. Did fear and insecurity cause habitats to move higher up? In our view, the answers lie more in the activities of these rural populations, which combined crop farming, livestock breeding and arboriculture. The latter two relied more on permanent habitat than traditional agriculture, at least when the animals could not be left to graze freely. Should this be considered as a general rule? If so, further studies would obviously be needed.
- 5) The density of farms or very small habitats fluctuates widely from one place to the next (1 every 0.5 km² in Keos, 1 every 1.5 km² in the part of Melos that was actually used, 1 every 10 km² in Argolid during the Classical period). The density tends to increase in the Imperial and Late Imperial periods, reflecting a habitat shift back to the plains. But above all, the higher the density, the greater the volatility of the habitats, and an increasing sense of their impermanence.

Given these conclusions, there are grounds for raising a further question and for risking a hypothesis. The question concerns the evolution of urban habitats during the Hellenistic period and how this related to the rural habitat. In many places, there is a noticeable tendency for cities to cluster together and become larger towards the end of the Classical and Hellenistic periods. However, there is no corresponding increase in rural sites, even when the area covered by the City-states increases. Does this mean that part of the country ceased to be exploited? This could corroborate the impressions of Polybe or Strabon on Greece in their times²¹.

Polybe, as we know, stigmatizes the egoism and birth restrictions that caused “the cities to empty and the lands to lie fallow”. Pausanias mentions the desertion of the countryside on several occasions. Strabon notes the desertion of some cities, like Megalopolis (which can easily be explained by the fact that the city was created as the capital of a federal State, but lost all its importance during its time), but especially, he mentions the abandon of rural zones in Arcadia, Laconia or Boeotia. It is clear that both authors noted a real phenomenon. Did depopulation really occur, as many have believed? For the time being, there is much doubt on this point, which tallies very well with our knowledge of the City-states between the third and first centuries, but which also requires us to cast doubt on the early evidence²². A reduction of the rural population with no overall depopulation would overcome the difficulties. This interpretation would of course need to be

verified. Our hypothesis concerns non-permanent habitats. Could these not be indicators of young people settling when they have not come into their family inheritance? The largest number of these habitats appear during the Classical period, which is also when the average age at death seems to have been at its highest in Greece²³.

With opportunities for emigration through colonization having largely disappeared, is there not a case for arguing that, before young people took over their family farms, those who did not go off to the city to learn a trade before settling down might have either gone to live on a part of the family property, if it was large enough, or in areas more distant from the City, in the plains, hills, or *eschatiai*? Although written sources are almost totally lacking on this subject²⁴, in a society based on agriculture, the question has to be raised. The surveys would therefore have demographic implications after all, but through the rural economy angle.

These remarks are an encouragement to reintroduce the archaeological data into the reasoning on demography²⁵. To do so, there are several possibilities:

1) Modelling. The results obtained for a small area of a region can be used as a model for the whole of that region. This main justification for the surveys could have given rise to one or more general or regional studies on the Greek world. The wide diversity of the models thus obtained makes this task rather hazardous but not impossible. A calculation will in any case have to be made with the model.

2) Calculations on the habitats. The systematic and inadequately differentiated nature of the method (only one coefficient of the “200 or 300 inhabitants per ha” type), even though it has been used since the beginning of the twentieth century for population calculations²⁶, means that it has been considered as random by a great many perhaps overly critical scientists, especially because of the risk of unknown small rural sites – which would imply an inevitable arbitrary adjustment – or the problem, in many cases, of finding out the actual area covered by the inhabited site. This problem affects even studies as precise and careful as those of J. Bintliff on Boeotia²⁷.

Nevertheless, using a detailed typology of the sites within the survey framework allows us to draw a few conclusions. In their study of Laconia, the authors have put forward estimations based on a site typology that distinguishes between farms, *villae*, hamlets and villages according to size, even though they admit there is no certainty as to whether these were habitats occupied permanently and simultaneously, or whether all of them are known²⁸.

But in any case, there has to be a standard, benchmark number of inhabitants per ha, which is still difficult to determine²⁹.

Consequently, the 14 inhabitants per km² obtained for the 70 km² covered by the survey seemed relatively low, as compared to what we know of classical Sparta. The authors therefore propose a number closer to 25 inhabitants per km² for the whole territory, taking the military quotas into account³⁰. The difference could have arisen from a benchmark figure that may be too low, or from the specific characteristics of the sample surveyed (70 km², which represents 1.9% of the current figure for Laconia).

Under these conditions, the samples need to be more varied, and systematic surveys, which give an accurate idea of the most rural populations, need to be replaced by geographically broader habitat surveys. Although the grid pattern is larger, the general studies made, published, and based on the antique geographers at least provide some knowledge on the important sites, those where, at least during historical periods, the majority of the populations lived. We also need to work with time bands and vary the approach. For this and for the historical periods at least, the method that I proposed in 1980 is still valid, in my opinion. This involves obtaining a ceiling figure based on an investigation made independently of the carrying capacity of the region (since A. Jardé, 36 inhabitants per km² has been considered as a maximum figure for the Greek world, above which the area could be considered overpopulated, although it is obviously advisable to adapt this figure to each region considered); a minimum figure based on the military quotas that include only the citizens; and finally, an intermediate figure based on the habitats, given that there is no certainty that all of them are known. Any other system would suggest that our information is not fully useable³¹.

Furthermore, it seems essential to adapt the number of inhabitants per ha according to the typology of the site, and therefore its size. To adopt a single figure seems rather hazardous, since differences must be taken into account between villages without collective buildings, or pre- or proto-cities with necessarily denser human occupation, and cities of the historical period (in the Greek world and the Classical, Hellenistic or Roman Periods) with a "looser" pattern of occupation. For urban sites or villages during the historical periods, 250 inhabitants/ha for those of less than 5 ha, 200 for those of 5 to 50 ha and 150 for those of more than 50 ha appear to be a reasonable order of magnitude³². During the prehistoric periods, the area scale must be reduced, and the orders of magnitude slightly increased to take into account the fact that streets were not common in the pre- and proto-urban habitats of the Near Eastern world, or even of the Creto-Mycenaean

world, just as public places, or squares, (except the Minoan palace) were particularly rare.

3) Pin-pointing anomalies as a way of ensuring the validity or non-validity of the surveys. A simple examination of the graphs will show, over and above the differences that are inherent to our sources, that some correspondences in time are perceptible in the graph curves, especially between the Neolithic/Ancient Bronze, and the Roman/Late Roman periods. To a certain extent, over-large differences would suggest that we do not have enough information to draw entirely reliable conclusions. It was in fact through similar comparisons that J. Bintliff, using the Cities of Boeotia as a basis, recently suggested the existence of a cyclical pattern in urban and rural demography, with cycles of about 500 years, between the ninth century B.C. and the eighth century B.C.³³.

In our opinion, this covers the survey assessment that can be drawn up at present. The surveys have enabled us to restore villages or hamlets, but they are still not entirely satisfactory: of what type were these farms or farming groups and villages? Were they simple peasant habitats, decentralised locations of artisanal production, places where people lived freely or in serfdom? To find out, other elements have to be taken into account: habitation, the existence of presses or kilns, and so on. We thus have to investigate the actual stratified excavations. If we obtain answers each time, we would be able to refine the number of inhabitants: do we really know that, for an equal surface area, the density of permanent inhabitants was the same in a villa of the Roman period where slaves worked, as in a hamlet of free peasants and farmers? This can only be verified by going beyond simple surveys. This is not often possible, which is why, rather than evincing disparagement, we should not hesitate to avail ourselves of the knowledge that demographic surveys can bring.

NOTES

¹ For other references, see Corvisier, (2001, pp. 105–106) and corresponding bibliography.

² Data in Corvisier (1991, pp. 23–28).

³ Below, see p. 36–37. This refers back to Corvisier and Suder (2000, pp. 21 and 27), which gives the sources. There to this should be added Cherry et al. (1996, 1991) on Keos; Renfrew-Wagstaff (1992) on Melos; Watrous (1982) on Lasithi; Watrous et al. (1993) on the Mesara; Haggis (1996) on Kavousi; Nixon et al. (1988) on Sphakia; Broodbank (1999) on Kythera; Whitley et al. (1999) on Praisos; Cavanagh et al. (2002) Laconia; Foley (1988) and Jameson et al. (1994) on the Argolid; Davies et al. (1997) on Pylos and Rizakis (1992) on Achaia.

- ⁴ Cf. Corvisier and Suder (2000, pp. 76–77).
- ⁵ Data in Cherry et al. (1996, 1991) and Whitelaw (1994).
- ⁶ Based on Renfrew-Wasgstaff (1992).
- ⁷ Based on Watrous (1982).
- ⁸ Based on Broodbank (1999).
- ⁹ Based on Jameson et al. (1994).
- ¹⁰ Based on Rizakis (1992).
- ¹¹ Based on Cavanagh et al. (2002).
- ¹² Fossey (1988), most of the data presented here is extracted from volume II, pp. 455–475.
- ¹³ Decourt (1992, pp. 15–48).
- ¹⁴ Fossey (1988, 1, pp. 43–99).
- ¹⁵ *Ibid.*, pp. 177–185.
- ¹⁶ *Ibid.*, pp. 167–175.
- ¹⁷ Based on Fossey (1986) and Typaldou-Fakiris (2004).
- ¹⁸ Based on Fossey (1990).
- ¹⁹ Van Effenterre and Gondicas (1999).
- ²⁰ See Corvisier (1996), discussions pp. 33–38.
- ²¹ POLYBE, XXXVI, 17; STRABON VIII, 4, 11; 6, 23; 8, 1; 8, 2 essentially.
- ²² Discussion sur la dépopulation dans Corvisier and Suder (2000, pp. 112–118).
- ²³ *Ibid.*, pp. 49–51, and 63–65.
- ²⁴ One will note however for the will of the fathers to marry their sons very early, which requires to maintain them, Demosthenes, Against *Boeotos II*, 12 (marriage at 18 years); Isaios, *Inheritance Ménéklès*, 18. In addition, in a case it true is muddled enough, the inheritance of Philoktemon, it seems that the adopted children (whatever the validity of this adoption *post mortem*, whose dispute is precisely the subject of the plea) of this one, deceased before his/her Euktemon father, were the alive one of this last already put in possession of agricultural plots of land in the family field, obviously still undivided since Euktémon was still alive (Isaios, VI, 36).
- ²⁵ For a recent example of demographic thinking within the framework of *the surveys*, Bintliff (1997a) the return to the demographic concern is also perceptible in Bintliff (1999).
- ²⁶ On the principal figures used at demographic ends, Corvisier (1980). One will add the 225 inhabitants/ha to it proposed by Jameson et al. (1994) for the only centres of population of the old habitats, accepted and used by Bintliff (1997b, pp. 235–235), but which oblige with an estimate of the part inhabited compared to the total surface of the site: 56% for Travlos. One thus arrives to 126 inhabitants/ha. One will bring this data closer to the figures also those mentioned low n.29.
- ²⁷ The followed method consists in adding the surface of the 16 Cities and 37 villages known to that, estimated, of the 15 hypothetical villages, that is to say 1172 ha, then to apply the 126 inhabitants/ha. mentioned above. But, to determine the importance of the rural population, the author starts from a preceding estimate of total population founded on the military quotas: 33 100 soldiers to multiply by 5 to reach) the total population. He arrives to 165 500 inhabitants, of which he deduces the 131 985 inhabitants from the urban sites, those of more than 10 ha, that is to say 1047,5 ha x 126). It is implicitly to consider that in the absence of survey general and systematic, one cannot manage to fix the rural population by archaeological ways.
- ²⁸ CATLING R.W. in Cavanagh et al. (2002, pp. 205–211).

- ²⁹ For example, 125 inhabitants./ha taken for base in Argolid, 150 in Koressos, 250 in Halieis, quoted by CATLING, *ibid.* n. 86 to 88.
- ³⁰ It is noted that this order of magnitude was already that to which P. Salmon arrived while being founded on the data of Glotz and Cavaignac (Salmon 1959) to which joined Corvisier and Suder (2000, pp. 32–35).
- ³¹ Thus, in the laconian example which has been just analyzed, R. W. Catlin notes very honestly that the figure to which it arrives appears quite low and comes from there to refer to the military data (but in the case of Sparta, one knows it, they are skewed because the Lacedemonian state largely used its allies) and with the population of the end of the 19th century, i.e. in fact, with a manner of perceiving the feeder possibilities of the area.
- ³² Corvisier (1980), in which the method is discussed and certain archaeological confirmations are indicated.
- ³³ Bintliff (1999).

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Chapter 3

ESTIMATION OF AN AGE DISTRIBUTION WITH ITS CONFIDENCE INTERVALS USING AN ITERATIVE BAYESIAN PROCEDURE AND A BOOTSTRAP SAMPLING APPROACH

Jean-Pierre BOCQUET-APPEL¹, Jean-Noël BACRO²

¹*CNRS, Paris, France*

²*Université de Montpellier, France*

Abstract: An iterative Bayesian estimation procedure is used in order to explore two classes of models pertaining to the universe of preindustrial demographic mortality. One model is for “attritional” mortality and the other for “catastrophic” mortality. The estimation procedure first extracts the model which best fits the data representing the distribution of age indicators in a cemetery. Then, using the anthropological reference sample of the age indicator, a bootstrap sampling technique determines the confidence interval for the estimation. Through simulations, we show that if the cemetery belongs to the class of the models explored, i.e. if the model is true, then the result is excellent for an age/indicator correlation level of about $r = 0.9$

INTRODUCTION

When the question of estimating age distribution in a skeleton sample was raised several years ago (Bocquet-Appel and Masset, 1982), the authors pointed out the amateurism that prevailed at the time and called for a change in methods. In the light of what became of this question, which has now become one of the major scientific issues in paleodemography, it would perhaps be cruel, now, to return to the reactions it caused and the condescending tone adopted by certain researchers to-day. To pursue, then, in our approach to the estimation of an age distribution of a skeleton sample, we have used an iterative Bayesian procedure in order to explore two classes of models pertaining to the universe of preindustrial demographic mortality.

Based on these two model classes that are formalised by a priori probabilities, one representing the current demographic mortality of a population (also called “attritional” mortality), and the other representing “catastrophic” mortality, the procedure extracts the model which best fits the observed distribution of age indicators in a cemetery. Then, using the anthropological reference sample of the age indicator, a bootstrap sampling technique is used to determine the confidence interval of the estimation.

FROM PAST TO PRESENT: ESTIMATING AGE DISTRIBUTION IN ADULT SKELETONS

In order to estimate the demographic parameters of age distribution in skeletons, two questions must first be solved. The first is how to obtain the age distribution itself, and the second is how to obtain its demographic parameters. In this article, we focus on the first question. When attributing ages to individual skeletons in a cemetery, the natural approach is to distribute them into demographic age groups and to create, discontinuously, a histogram of the distribution, for example by distributing the skeletons into classes such as 0–0.9 years, 1–4.9 years, 5–9.9 years, . . . , 20–29.9 years, 80 years and over. For immature individuals, taking into consideration the reservations concerning historical populations whose biological references would be preindustrial (Bocquet, 1977), this technique provides a good approximation of the age distribution. But for adults, we know that this age distribution does not arise from the distribution of individual age estimates into age classes. If this approach is used, the distribution of individual ages converges towards a different distribution: that of the sample of reference skeletons which was used to calibrate the age indicators (Bocquet-Appel and Masset, 1982, Figure 1: 322). Moreover, “*It is impossible to estimate skeleton age without bias, unless we know beforehand the age structure at death of the populations to which it belongs*” (Bocquet-Appel and Masset, 1985: 111). To estimate individual age, the distribution from which it is drawn needs to be known beforehand, and not vice versa. The reason for this, which was originally discovered by Masset (1974, 1973, 1971), has given rise to arguments in the literature (Bocquet-Appel and Masset, 1996; Konigsberg and Frankenberg, 1992; Bocquet-Appel, 1986; Buikstra and Konigsberg, 1985; Bocquet-Appel and Masset, 1985; Van Gerven and Armelagos, 1983; Bocquet-Appel and Masset, 1982). These seem to have been brought to a conclusion: in the words one of the main former polemicists, “*Bocquet-Appel and Masset’s assertion that estimated*

age-at-death population structure will be influenced by the nature of the reference sample and the statistical techniques used to generate standards for age estimation is valid" (Buikstra, 1997: 374).

Since 1982, in order to remove the influence of the reference sample, we have proposed iterative techniques drawn from the IPFP algorithm (Bocquet-Appel and Bacro, 1997; Bocquet-Appel and Masset, 1996). On the whole, IPFP techniques make it possible to obtain a fairly accurate estimation of the average age of an unknown distribution in adult skeletons. But even though their use has achieved some progress, by making it possible, on the one hand, to offer an alternative to the usual anthropological techniques that predetermine average ages and, on the other hand, to enter within a system of demographic model life-tables (see Séguy and al, in this volume), the result is not wholly satisfactory since an estimation of the entire age distribution for adults is still necessary. To estimate the distribution an iterative Bayesian procedure is used which proved to be an effective solution. Once we have a distribution of an age indicator for skeletons in a cemetery, i.e. observed data, the approach consists of sweeping a domain in the space of demographic mortality models, via prior probabilities of age-specific mortality, keeping these prior probabilities which minimize deviation from the data. Which domain in the models' space should be swept? Only two broad mortality classes were retained, corresponding to two classes of causes: demographic (or attritional) mortality and catastrophic mortality (see Margerison and Knüsel, 2002). Attritional mortality is random mortality that produces a known and predictable type of distribution, based on the rate of degradation, with age, of cellular duplication. For historical reasons, we targeted the space of *preindustrial* demographic mortality. Preindustrial mortality is determined, mainly, by diarrhoea during early childhood and epidemic infectious diseases. Attritional mortality represents current mortality in populations, which can be expressed either by data from historical life-tables, or by mathematical functions (see below). We preferred to use the latter expression, since it allowed us to sweep an assumed theoretical continuum of human experience in a regular manner, without the need for a contingent sample of historical life-tables, which bring in problems of discontinuity and sampling such as, in particular, the influence of growth rates experienced by historical populations, which bias the life-tables and which are never taken into account. The assumption, then, is that the archaeological cemetery is a natural demographic one.

Concerning catastrophic mortality, this class groups together the impacts of events having a random effect on the living population, such as an epidemic of plague, an ecological disaster or mortality from warfare.

Because the impacts of these evils are randomly distributed among individuals, i.e. they occur independently of age and gender, they effectively mimic the age distributions of the dead, which are similar to those of the age pyramids of the living populations affected (see, for example Signoli et al., 2002; for a summary, see Chamberlain, 2006).

Attritional mortality and catastrophic mortality are the two model classes on which we focus in this article. Mortality with non-demographic structures, tending towards the unforeseeable and chaotic, is therefore excluded, such as the result of mass executions due to purely cultural selection of certain age groups, where the age pyramid has no influence on the selection.

THE ITERATIVE BAYESIAN ALGORITHM

We know, from an anthropological reference collection, the joint distribution of age a and of a biological age indicator i , $f(a, i)$ and, in a cemetery, the distribution of the biological indicator $f(i)$. We now need to estimate the age distribution $f(a)$ in the cemetery. Age is a continuous variable. Therefore, various approximations of an age distribution in skeletons are possible, both continuous and discontinuous. In the discontinuous case presented here, the custom in demography is to summarise information by age classes divided into 5-year intervals, while in paleodemography, a 10-year interval is used for adults.

The joint age/indicator $f(a, i)$ distribution, where the values at the intersection of a row and a column in the table are the number of individuals n_{ia} ($= n_{ai}$) in the a -th age group and the i -th stage of the indicator, can be represented by a two-way table, also called a contingency table. This table has two marginal totals. The first (in columns) is the sum of each row, representing the distribution of the age indicator n_i ; the second (in rows) is the sum of each column, representing the distribution of the age n_a . The two distributions are unspecified but regular. The aim is to estimate the second marginal total representing the age distribution, using the two-way table on the one hand and the marginal total representing the distribution of the indicator of age on the other hand. The results obtained using the n_{ia} table, via an IPFP algorithm, thus appeared to be approximate. The reason is that a particular distribution of prior probabilities π_a is implicitly embedded in the algorithm and directs the result. But the user is not aware of this. This is the uniform distribution, in which the probability density is represented by the marginal row totals

(the sum of the columns) where each age class is equiprobable with an initial value $p_a = \sum_a p_{ai} = 1$. The uniform distribution was deliberately embedded to eliminate the influence of the anthropological reference sample, but this approach turned out to be counter-productive. From the outset, it removes a large number of possible archaeological situations that are not formalized by a uniform distribution of skeletons, and which can be grouped together in the two model categories of mortality described above. Instead of a single uniform distribution, the procedure will thus sweep the space covered by preindustrial demographic mortality classes, via the *a priori* probabilities π_a obtained by a mix of Gompertz-Makeham and extreme value laws as described further on. The Bayes formula has already been used for estimating age (Lucy et al., 2002; Hoppa and Vaupel, 2002; Lucy et al., 1996) and is convenient for this operation.

If we write p_{ia} and π_a , respectively the probability of the indicator of stage i given the age class a , and the *a priori* probability of the age class a , then the *a posteriori* probability of the age class is equal to: $p_{ai} = (p_{ia} \times \pi_a) / \sum_a (p_{ia} \times \pi_a)$. The algorithm given in Table 1 thus sweeps the *a priori* probabilities of a class of models, and retains those which minimise deviation from the data. It can be shown, by simulations, that although the procedure does not validly estimate the p_{ai} , it does select *a priori* probabilities that are

Table 1: Algorithm of the iterative Bayesian procedure used to estimate an age distribution

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1 DO: Bootstrapping a  $p_{ia}$  sample from the anthropological reference population for the age
indicator used
2 DO: Do vary the a priori probabilities  $p_a^\circ$  in the demographic class model! Repeat The
loop 1000 times
3 DO:
    3.1  $p_{ai} = (p_{ia} \times p_a^\circ) / \sum_a (p_{ia} \times p_a^\circ)$ 
    3.2  $p_i = \sum_a (p_{ia} \times p_a^\circ)$ 
    3.3  $p_a = \sum_i (p_{ai} \times p_i)$ 
    3.4  $\chi^2 = \sum_i n_i \times [(f_i - p_i)^2 / p_i]$ 
    3.5 IF  $\chi^2 > \chi^{2(t-1)}$  go to 4
    3.6 do stock  $p_a$ 
    3.7  $\chi^2 = \chi^{2(t-1)}$ 
END DO
4 IF  $\chi^{2(t-1)} < \chi^2 \min$  THEN  $\chi^2 \min = \chi^{2(t-1)}$ 
5 Estimation of the distribution:  $p_a^\circ$  corresponding to  $\chi^2 \min$ 
6 END DO
7 END DO
8 SORT the  $p_a^\circ$ -values stored in 3.6
9 Determines the bilateral confidence interval CI95% of the  $p_a$ 

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very close to the unknown target distribution. These selected probabilities are then considered to be the estimation of the unknown distribution. Assuming that the cemetery does indeed belong to the demographic model class swept, i.e. that the model is true, then a confidence interval for the distribution estimate is obtained at the 95% level (IC95%), via a bootstrap sampling procedure for p_{ia} applied to the anthropological reference population of the age indicator.

FORMALISATION OF THE ATTRITIONAL AND CATASTROPHIC MORTALITY MODELS

The space for attritional mortality was formalised via a mix of Gompertz-Makeham and extreme value distributions. The full set of extreme value distributions admits a parametric notation that is dependent on three parameters: location, scale and shape. The Gompertz distribution is a particular distribution of extreme values (Willekens, 2001), and the fact of considering the family of extreme laws as a whole makes it possible to broaden the set of distributions to be explored in order to model attritional mortality. The more or less pronounced mix with a Gompertz-Makeham law makes it possible to moderate the behaviours of the mortality distribution in the extreme age classes and, ultimately, to mimic a large number of distributions that are potentially representative of a given attritional or catastrophic mortality. Martigues' data (Signoli et al., 2002) were used to characterise the reference values of the parameters to be considered, and variation intervals of these parameters were determined so that a large number of cases of distribution of attritional or catastrophic mortality types could be covered. These reference values for the parameters were determined by maximum likelihood, by independently considering a Gompertz distribution (Makeham parameter of 0) and a distribution of the minimum. The various parameters were then varied in an embedded manner¹ (see Figures 1 and 2).

Each of the two models was expressed by 753 vectors of *a priori* probabilities, and respectively named the attritional and the catastrophic models. Attempts were made to introduce flexible functions into this algorithm, including the laws of Beta (α_1, α_2), Beta non-centred ($\lambda, \alpha_1, \alpha_2$), Weibull ($\lambda, \alpha_1, \alpha_2$) and Bi-Weibull (Bocquet-Appel, 2005), but none was able to reproduce the attritional model correctly.

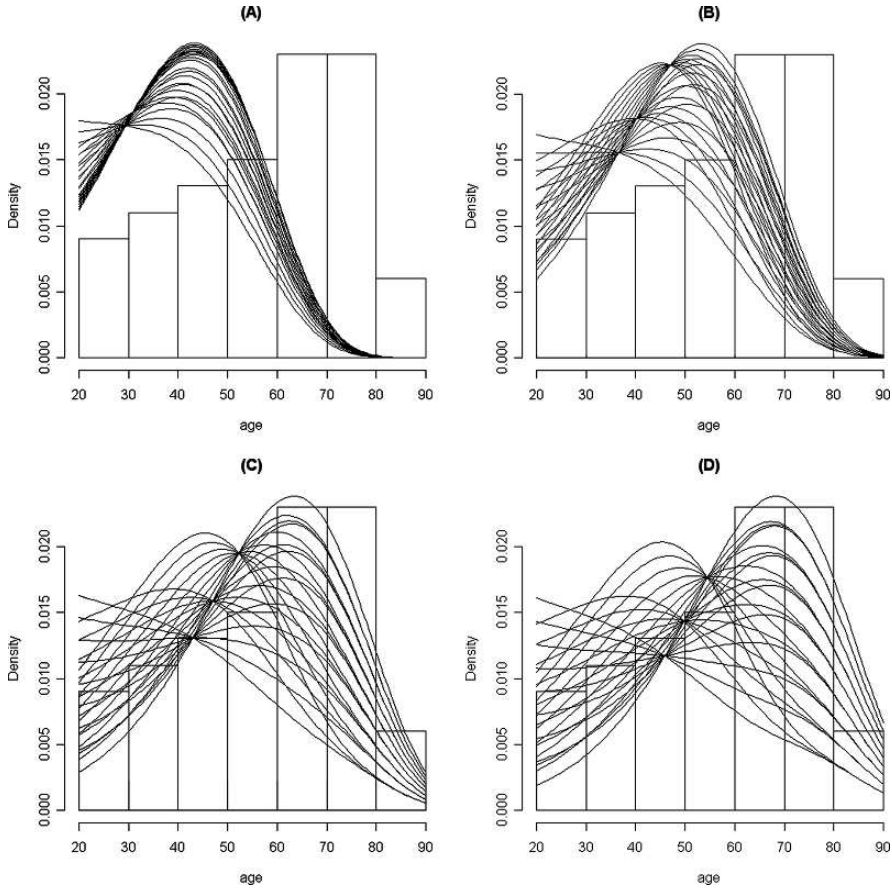


Figure 1: Examples of a priori laws concerning attritional mortality obtained from a mix of Gompertz-Makeham and minimum laws, according to various sets of parameters. The shape parameter of the minimum law is set at -0.1 and the position parameter has the values (A) 45, (B) 55, (B) 65, (B) 70. The other parameters vary as explained in the text above. The histogram represents the attritional empirical distribution of Martigues' data

RESULTS AND CONCLUSION

Figure 3 shows some of the results of the iterative Bayesian procedure obtained by random simulations. They give examples of estimations of a target distribution of attritional mortality and its confidence interval (CI95%) from the corresponding distribution of a hypothetical age indicator. The

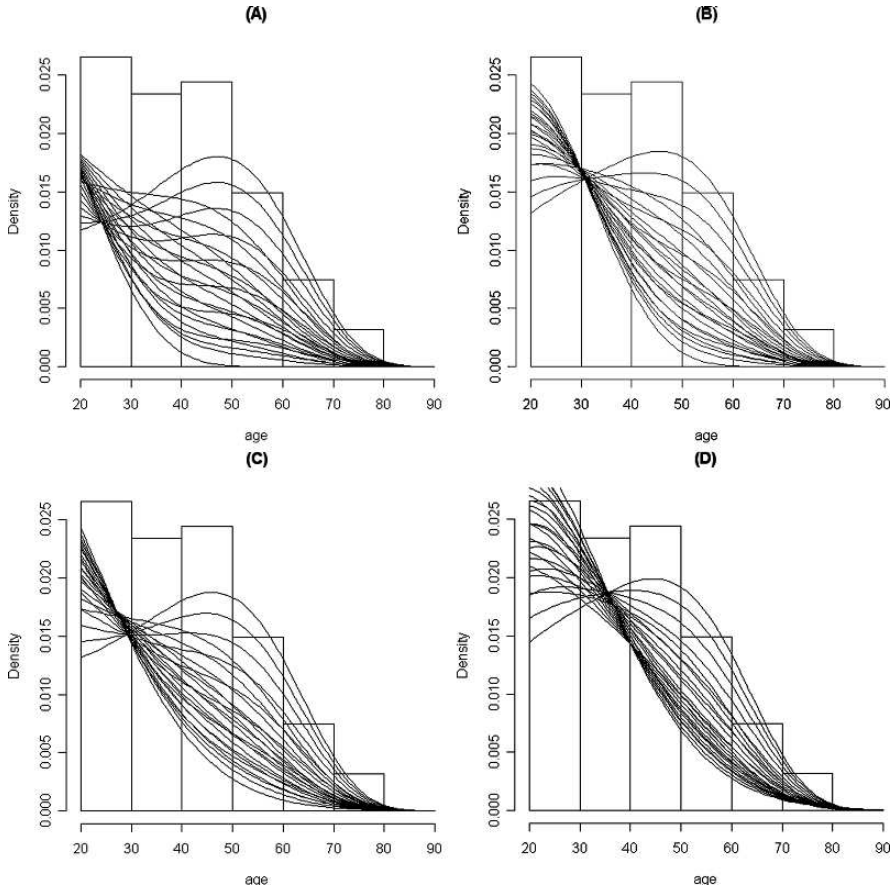


Figure 2: Examples of a priori laws concerning catastrophic mortality, obtained with a mix of Gompertz-Makeham and minimum laws, according to various sets of parameters. The shape and location parameters of the minimum law have the following values, respectively: (A) -0.2 and 10 , (B) -0.2 and 20 , (C) -0.6 and 20 , (D) -0.6 and 30 . The other parameters vary as explained in the text. The histogram represents the empirical “catastrophic” distribution of Martigues’ data

results take two correlation levels into account between the chronological age and the age indicator $r(a, i) = 0.7$ and 0.9 , representing the amount of biological variability with age, expressed by the p_{ia} values in the transition matrix. By visual inspection, it can be seen that the $r(a, i)$ correlation has no effect on the estimation of the target distribution (dotted line) but, as one would expect, it does have an effect on its CI95%, which is halved from one correlation level to the next. In passing, we should note that the influence

of the size of a p_{ia} table, here with 6 stages of an indicator and 7 age classes, i.e. comprising an unequal number of 6 lines \times 7 columns that ought to make the system ill-conditioned (Konigsberg and Frankenberg, 2002), has no foundation. The influence of this p_{ia} -table, with an extra column compared to the number of rows, is to increase the confidence interval. In short, when the target distribution comes from the same model as that

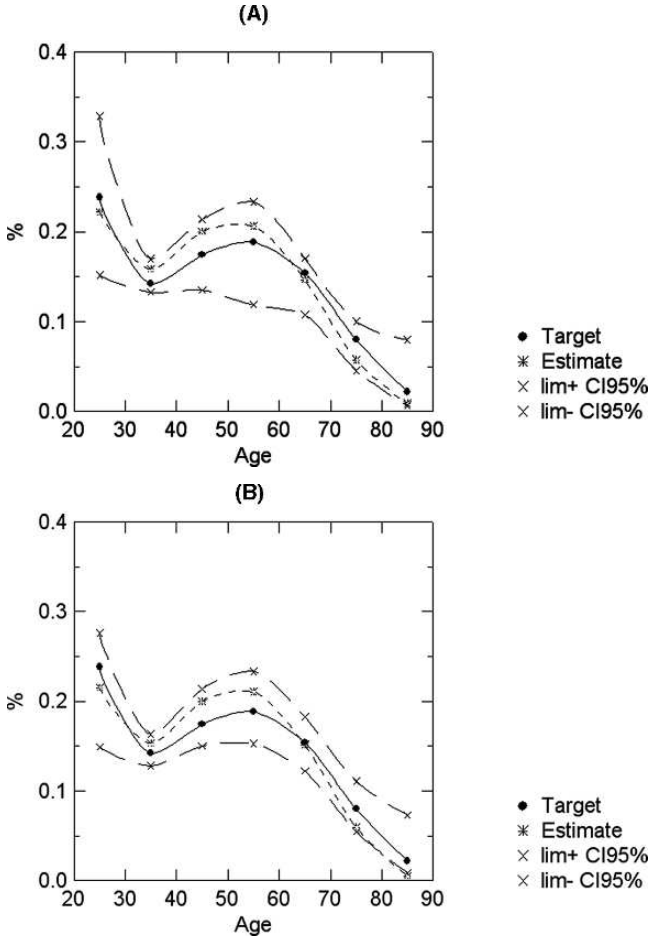


Figure 3: Estimations, using the iterative Bayesian procedure, of the same simulated target distribution, and their confidence intervals CI95% obtained by bootstrapping, for three age-indicator correlation levels $r(a,i)$. (A): $r(a,i) = 0.6$; (B): $r(a,i) = 0.7$. (C): The third distribution was estimated with ap_{ai} matrix: 6 stages \times 7 age groups. The influence of this 6×7 rectangular table on the estimation is negligible. (D): $r(a,i) = 0.9$, the simulated target distribution and its estimation coincide

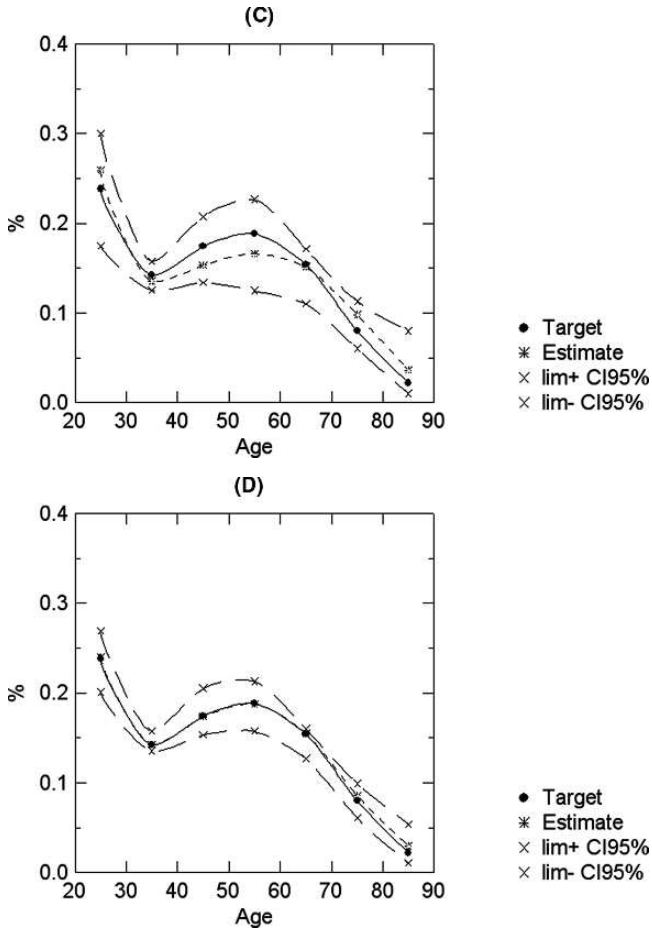


Figure 3: (Continued)

represented by the *a priori* probabilities, the result is good, even with a relatively poor correlation level of 0.7 between the age and the indicator.

What happens when the model represented by the *a priori* probability, once injected into the iterative Bayesian procedure, does not correspond to the model of the target? Figure 4 gives an example of attritional target distribution and its estimation using the *a priori* probability of the contrasting catastrophe model, for two correlation levels. In both cases of the example, the criterion for the best fit χ^2 is smaller when the injected model is the true one, with respectively 0.00804 (true) vs 0.10185 (false) and 0.01804 (true) vs 0.02790 (false). With 2500 simulations, for each of the two correlation

levels $r(i, a) = 0.7$ and 0.9 , the averages for the best χ^2 fit were 0.04945 (true) vs 0.14709 (false) and 0.05192 (true) vs 1.74070 (false), i.e. 3 and 33 times smaller when the injected model was the true one.

However, the two demographic models (attritional and catastrophic) were produced from a mix of the same families of laws (Gompertz-Makeham and Minimum). Depending on the values of the parameters generating the

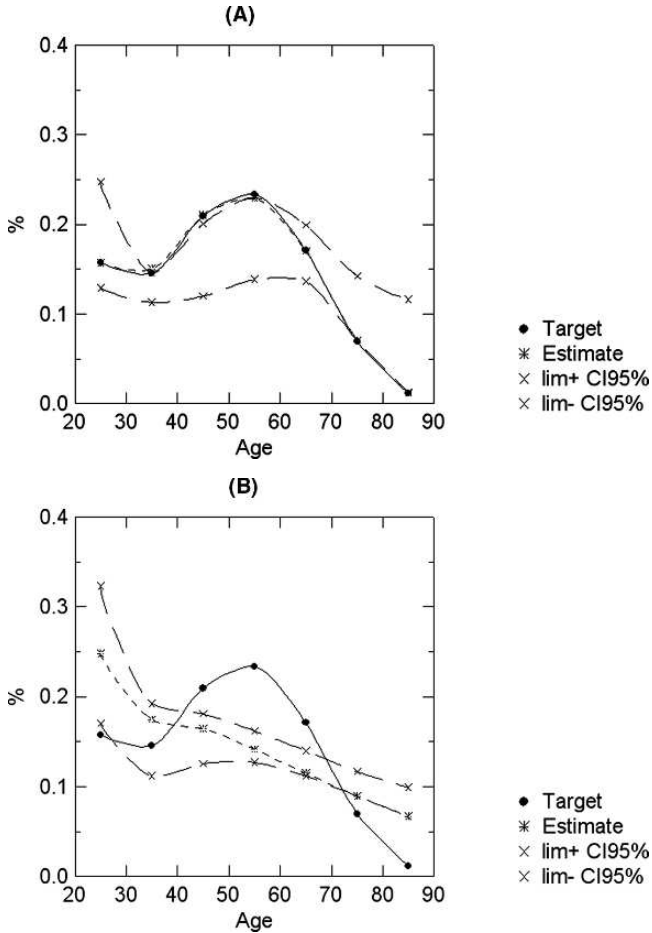


Figure 4: Estimations, using the iterative Bayesian procedure, of the same simulated target distribution, and their confidence intervals CI95% obtained by bootstrapping, for two levels of age-indicator correlation $r(a,i)$ (row: $r(a,i)=0.7$ and 0.9), with each of the two models of a priori probability. Column on the left: attritional simulated distributions with the a priori attritional model (best fit $\chi^2 = 0.00804$ and 0.05192); on the right, estimated distributions with the a priori catastrophic model (best fit $\chi^2 = 0.14709$ and 1.74070)

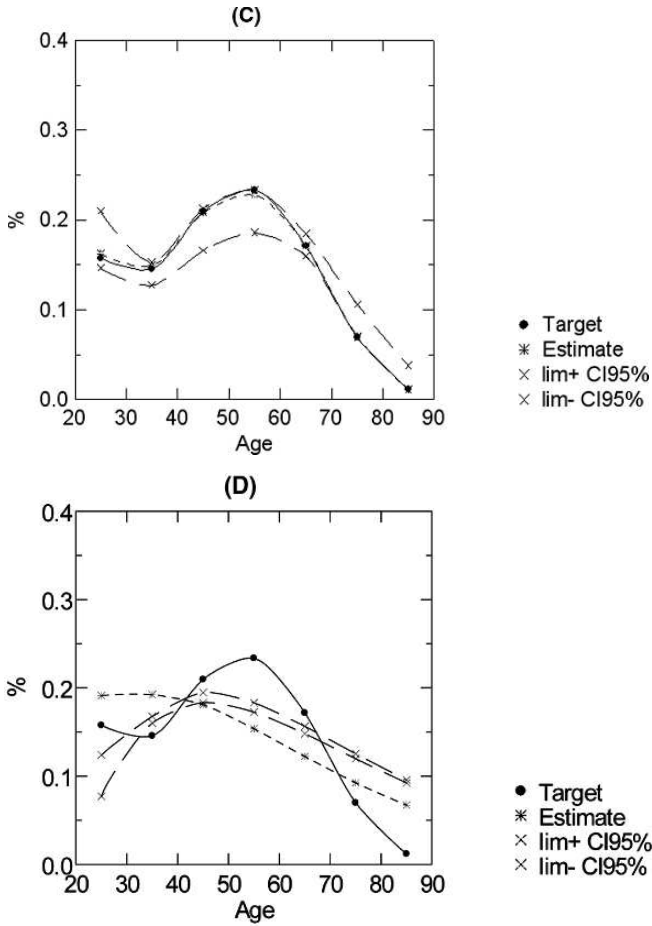


Figure 4: (Continued)

distributions, there are zones where they partially overlap. In these zones, and given the level of correlation between indicator and chronological age, the smallest χ^2 fit value can be obtained with the inadequate a priori probability model, as shown in Figure 5. If we reason within the general framework of the statistical inference to test the H_0 assumption that mortality is attritional, as opposed to the H_1 alternative that mortality is catastrophic, characterisation of the rejection zones assumes knowledge of the distribution of the values of the χ^2 fit under H_0 . This law depends not only on the level of indicator-age correlation (Figure 5), but also on the estimation of the transition matrix (see below and Figure 6). The law we are seeking is

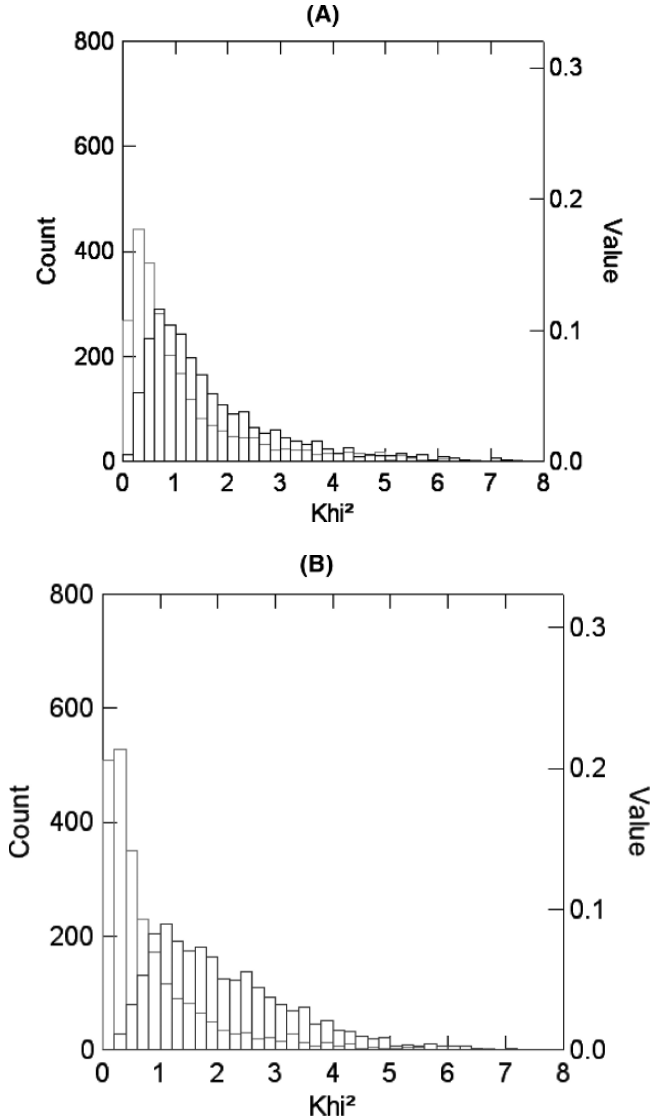


Figure 5: Distributions of the values for the best fit χ^2 from the iterative Bayesian procedure, obtained by random simulation, for 3 age-indicator correlation levels. From top to bottom: 0.7, 0.8 and 0.9. In each of the two figures, the hypothesis injected into the procedure, as represented by the a priori probabilities, is true on the left and false on the right. The risks α (risk of first kind, false positive: H_0 wrongly rejected) and β (risk of second kind, false negative: H_0 wrongly kept) depend on the level of age-indicator correlation

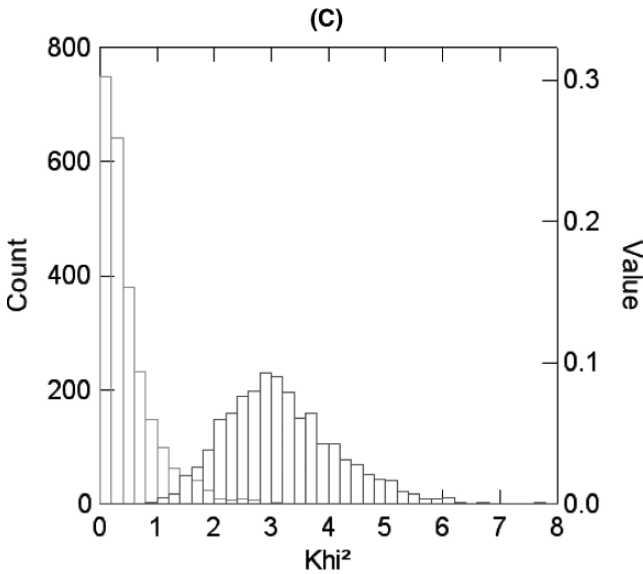


Figure 5: (Continued)

therefore difficult to characterise from a theoretical point of view, but its empirical version does produce information as to the errors of the first and second kinds that are linked to a particular study framework. For a fixed level of correlation and a given sample size of individuals, the empirical distributions of the χ^2 best-fit values under H0 or H1 can therefore provide an approximation of the underlying laws and allow an evaluation of the confidence thresholds for the tests performed. Figure 5 clearly shows that the risks α (risk of the first kind, false positive: H0 wrongly rejected) and β (risk of the second kind, false negative: H0 wrongly kept) depend on the level of age-indicator correlation. In particular, the discriminating power of the χ^2 best-fit values increases significantly with the age-indicator correlation. If we take the usual framework of a test at $\alpha = 5\%$, for $r(i, a) = 0.7$, the limiting value for the best fit χ^2 would be approximately 4.1 (Fig. 5A), which corresponds to a high β risk, at roughly 93–94%, whereas with $r(i, a) = 0.9$, the limiting value falls roughly at 1.64, with a β risk at 3–4% (Fig. 5C)! Furthermore, it should be remembered that the data, whether from the cemetery or from the anthropological reference population (p_{ia}), are only samples. Both sets are subject to random fluctuations that are proportional to $1 - r^2$, with r^2 the age-indicator correlation coefficient. What is the scale of the sampling effect on the estimations? Figure 6 shows the distribution of

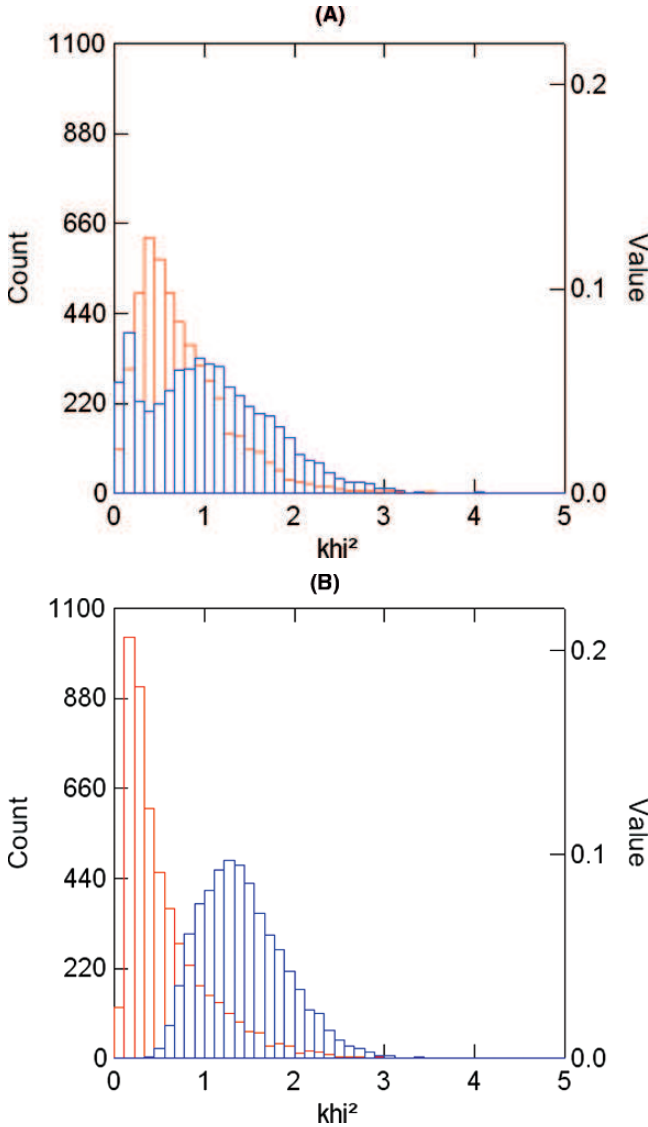


Figure 6: Distributions of the values for the best fit χ^2 from the iterative Bayesian procedure, obtained by random simulation, using the same target distribution ($N=100$). In each of the two graphs, the hypothesis injected into the procedure, represented by the a priori probabilities, is true on the left and false on the right. Sample of the p_{ai} – transition matrix with 7 age classes: top: $\times 50$ individuals = 350 individuals; bottom: $\times 100$ individuals = 700 individuals. The influence on the estimation of the random fluctuations in the p_{ai} – transition matrix, representing the reference population, is crucial. Age-indicator correlation = 0.9

the best fit χ^2 in the case where the model injected into the procedure is true, and where it is false, for a high level of correlation between age and indicator $r(i, a) = 0.9$, for the same target of size $N = 100$ and two transition matrices p_{ia} , one with a relatively small sample size ($N = 350$) and the other relatively high ($N = 700$). It is clear that it is the sampling of the transition matrix, i.e. the stability of its estimated frequencies, that is the determining element in the procedure. The matrix of the anthropological reference population, which was estimated with a relatively small sample size $N = 350$, does not produce discriminating χ^2 -values. As an indication, by taking $\alpha = 5\%$, the limiting value of the best fit χ^2 -value for $N = 350$ is 1.74, which corresponds to $\beta = 83\text{--}83\%$, whereas for $N = 700$, the limiting value is 1.57 and $\beta = 66\%$.

Where the Loisy en Brie skeletons are concerned, the estimation is made from the state of involution of the trabecular bone structure of 96 femoral heads, classified into the six Nemeskeri stages (Acsadi and Nemeskeri, 1970), distributed respectively as 2.0, 8.0, 31.5, 39.5, 13.0, 2.0, and of the anthropological reference population of Coimbra (see Table 2). Given the degree of maturity of the femoral bone, the distribution ranges from 23 to 89 years. Figure 7A shows the best estimate, which was produced by the ‘‘catastrophic’’ model ($\chi^2 = 0.001718$). However, a visual inspection shows that the estimation of distribution resulting from this model does not have the typical triangular pattern of a catastrophe, if the confidence interval omitted. The estimation, with fewer young and old people at either end of the distribution relative to the centre, tends to be rather uniform and seems to express an indeterminate rather than a precise pattern. The relatively low number of 96 femoral heads on the one hand, as well as a relatively weak age-indicator correlation $r(i, a) = 0.6$ on the other hand, are the causes of this estimation where there is little age differentiation. The technique

Table 2: Age distribution of femur heads from the Coimbra reference population

Femur	Age							Total
	23–29	30–39	40–49	50–59	60–69	70–79	80+	
1	8	2	0	0	0	0	0	10
2	21	16	6	1	0	0	0	44
3	35	42	27	26	8	5	2	145
4	9	28	26	36	27	27	7	160
5	1	2	4	16	10	9	8	50
6	0	0	1	0	0	5	3	9
Total	74	90	64	79	45	46	20	418

cannot tell more than the information available. The influence of the femur sample size on the estimation can be judged by simply multiplying the observed sample size by 3, to 288 femurs, with their frequency distribution by indicator stage left unchanged. A typical attritional distribution is then obtained (see Figure 7B).

In expectation of a solution that will eventually make it possible to obtain the age distribution, with no other information than that provided by the age indicator, i.e. with only biological data, the approach presented here provides a satisfactory approximation, for a correlation

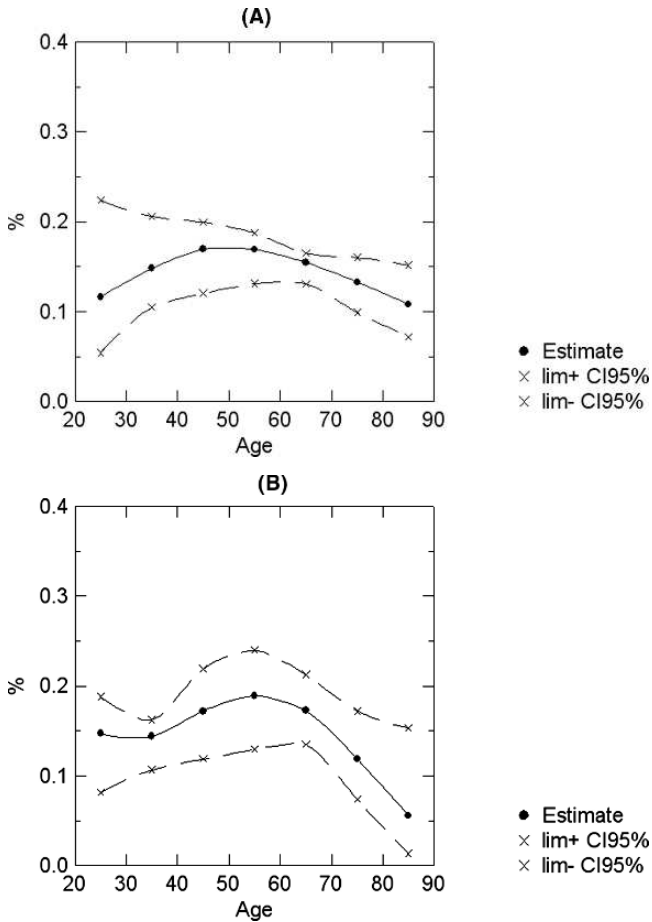


Figure 7: Estimation (23–89 years) and confidence intervals for the age distribution of the 96 femoral heads from the SOM Neolithic hypogee at Loisy-en-Brie (Haute Marne, France), using the 6 stages of involution of the trabecular structures of J Nemeskeri's femur heads

level of the indicator with age of about 0.9. It can be extended without difficulty to other classes of demographic models, such as epidemic mortality.

TECHNICAL NOTE

The Iterage FORTRAN program will estimate an age distribution and its confidence interval (CI95%) by means of an iterative Bayesian procedure, given: i) the distribution of an age indicator in a cemetery, ii) the distribution of the age indicator in an anthropological reference population, iii) the vectors of *a priori* probabilities representing a demographic model. The programme, in a non-compiled version, is downloadable on line at: <http://www.ivry.cnrs.fr/deh/bocquet/bocquet.htm>, together with a small command file.

Distribution of an age indicator in a cemetery: given as input data by the user, in an aggregated form in stages or ranks.

Distribution of the age indicator in an anthropological reference population: two distributions are proposed: i) 418 x-rayed femoral heads from the Coimbra anthropological collection (Bergot and Bocquet, 1976) and their graduations in Nemeskeri's system (Acsadi and Nemeskeri, op. cit.); ii) Nemeskeri's five anthropological indicators for 398 individuals from the Coimbra anthropological collection (Bocquet et al., 1979). Their overall predictive capacity is low. Users can introduce their own reference population for any age indicator.

Vectors of a priori probabilities representing a demographic model: Two models are proposed, as described above in this article: a model of preindustrial mortality, also called attritional, and a model of catastrophic mortality. Each of the two models is presented as 754 vectors of distribution, for 7 ten-year age classes from 20 to 89 years. Users can easily introduce additional models.

NOTE

¹ For a fixed value of the shape parameter (values -0.13 , -0.12 , -0.11 , -0.10 for attritional mortality and -0.2 , -0.4 , -0.6 , -0.7 for catastrophic mortality), a fixed value for the location parameter (variable with intervals of 5 from 45 to 75 for attritional mortality and from 10 to 40 for catastrophic mortality) and a fixed value for the Makeham parameter (from 0 to 0.02 with intervals of 0.01), variation of the proportion p attached to Gompertz-Makeham's law from 0 to 0.8 (with intervals of 0.1).

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Chapter 4

MODEL LIFE TABLES FOR PRE-INDUSTRIAL POPULATIONS: FIRST APPLICATION IN PALAEODEMOGRAPHY

Isabelle SÉGUY¹, Luc BUCHET², Arnaud BRINGÉ³

¹ INED/CEPAM, Nice, France

² CEPAM/INED, Nice, France

³ INED, Paris, France

With the collaboration of: Magali BELAIGUES-ROSSARD, Paul BEURNIER, Nadège COUVERT, Carole PERRAUT, INED, Paris, France

Abstract: Contemporary model life tables cannot accurately reconstruct the mortality patterns experienced by pre-industrial populations. It has thus become essential to develop mortality models that are adapted to the populations studied by paleodemographers, and that fulfil a threefold objective: to be based on a sufficiently large set of tables representing early mortality at diverse times and places; to use entries that can be easily obtained from reliable and well-established anthropological indicators; and to take the population growth rate into account, despite the problem of calculating it from bone remains.

Our models are based on linear regressions that link the logarithm of mortality probabilities to a demographic variable or to one of the paleodemographic indicators suggested by J.-P. Bocquet-Appel: the juvenility index, the *P* ratio (the deceased aged 5 to 19 years, over the deceased aged 5 years and over), and the mean age at death of adults, all of which are used as entries in the models constructed for men, women, and both sexes combined. Different growth rates are also used, for an interval from -0.01 to $+0.01$, by steps of 0.0025 . For each entry, the set of models represents 75 model life tables, making it possible to estimate mortality by age and, under certain assumptions, some of the demographic indicators associated with it.

If we assume that the demographic behaviour of archaeological populations closely resembles that of observed pre-industrial populations, we can propose an estimate of the demographic parameters of two ancient cemeteries in western France

Attempting to take a dynamic approach to reconstruct past populations, shaped by the rhythmic cycle of births, deaths and even migrations, with, at best, nothing at our disposal but the bone remains of those who have died; this is the challenge facing paleodemographic analysis.

It is important to recognize that paleodemographers cannot make use of even the most basic demographic measures. Except on rare occasions, they have no way of knowing the sex and age structure of the population under study, and are therefore unable to calculate either mortality rates¹ or life expectancy at birth, two classical entry parameters in demographic tables. Thus the numerator (number of deceased individuals between ages x and $x + a$) associated with the population model is always affected by a margin of error that makes any calculation impossible, especially for adults. Similarly, it is necessary to ensure that the denominator (individuals present at age x) adequately represents all the population components.

A number of proposals have been developed from population models (stationary, stable . . .) that make it possible to estimate the main demographic indicators of the population under study from incomplete or partial data. Studying the dynamics of archaeological populations nonetheless raises a number of problems.

MORTALITY MODELS AND PRE-INDUSTRIAL POPULATIONS

Stable population / stationary population

Since Acsádi and Nemeskéri, in 1970, most paleodemographers have accepted the hypothesis of a zero-growth population (termed a “stationary” population); they considered that, over long periods of cemetery use (several generations or even centuries), the mechanisms regulating traditional populations must have kept growth at close to zero, reflecting the balance between natality and mortality (Dupâquier, 1972; Bideau, 1983). In such circumstances, the sex and age distribution of the buried population would be identical to that of the living population. This makes it easy to calculate the different demographic parameters corresponding to the theoretical population associated with the life table.

In reality, however, this hypothesis is hard to defend, as it bears little relation to the conditions faced by pre-industrial populations, regularly hit by mortality crises that tested their powers of recuperation. J.-N. Biraben’s dynamic model (1969), of moderate growth sporadically shaken by mortality

crises, is certainly a closer reflection of the actual experience of earlier demographic regimes. To treat as stationary a population that is not, seriously skews the results.

It thus becomes imperative to construct models that take growth rates into account, despite the difficulties of estimating this parameter from reliable osteological indicators.

A mortality schedule for pre-industrial populations

As early as 1977, J.-P. Bocquet-Appel came to realise that the mortality models developed by demographers (ONU, 1956; Ledermann, 1969; Coale and Demeny, 1966, 1983) were unsuited to representing the specific features of mortality in pre-industrial populations².

Findings from studies in anthropological demography (Howell, 1979; Robert-Lamblin, 1983, 1986; Pison, 1989) and in historical demography (Woods, 1993; Wrigley et al., 1997) have confirmed it. Despite differences in lifestyle, all populations that are primarily agricultural and without access to modern medicine share similar demographic characteristics: high infant and juvenile mortality, life expectancy at birth that is low and similar to life expectancy at 20 years, fertility barely above replacement level – a precarious balance frequently under threat from mortality crises.

On the basis of this observation, J.-P. Bocquet and C. Masset selected only life tables fulfilling the selected criteria³ from those available in 1977. From their sample of forty tables, the authors established statistical correlations linking the juvenility index to certain demographic parameters: life expectancy at birth, infant mortality, and mortality probabilities at 0 and 5 years. Termed “paleodemographic estimators”, these regressions were published in 1977 (Bocquet-Appel and Masset, 1977), and subsequently refined: first in 1985, to take the regression margin of error into account (Masset and Parzys, 1985), and then in 1996, to combine two indicators, the juvenility index and adults’ average age at death, and to enlarge the sample to forty-five tables (Bocquet-Appel and Masset, 1996).

This model suffers from a number of weaknesses, due to the data available at that time: a limited number of observed tables (45), a restricted geographical field, a focus on Europe and South America (Asia was represented by only two tables), and a shortage of pre-1750 tables (15). It also fails to produce all the life table parameters⁴.

Other models have attempted to use non-contemporary data (Acsádi and Nemeskéri, 1970; Weiss, 1973). Constructed directly from anthropological data, these tables are nonetheless marred by serious errors linked to the

problem of determining the age and sex of skeletons. Using contemporary model tables assumes that there is continuity in demographic behaviour from prehistoric times to the present day and that contemporary model tables represent all possible mortality schedules through space and time. Our statistical analysis (*cf. infra*) has convinced us that this is not so, and that there is strong justification for creating model tables for pre-industrial populations. Inappropriate life tables can also lead to significant biases in the interpretation of results.

Models constructed with entry parameters available in paleodemography

In contrast with historical demography, which is based on pre-statistical written documents, we have already pointed out that the margin of uncertainty with biological evidence makes it impossible to obtain probabilities of dying from osteological data. It is therefore essential to create specific parameters for building mortality models in paleodemography; for the models to function correctly, these same entry parameters should also be the variables on which the linear regressions are based.

In addition, archaeological constants (the almost systematic under-representation of children under 5 years in the cemeteries), differences in the way age is established for children (biological growth phenomenon) or adults (biological aging phenomenon), and a clear distinction between the mortality curve for children and adults⁵, all make it necessary to take into account variables representing the two age groups. This means selecting variables that provide information about the under-twenties (excluding the 0–4 year age group, who are under-represented), on the one hand, and about adult ages (20 years and over), on the other. A certain number of indicators have already been suggested (Bocquet-Appel and Masset, 1977, 1996; Bocquet-Appel, 2002), and we have included them in this study.

NEW MODEL LIFE TABLES FOR PALEODEMOGRAPHERS

Prompted by C. Masset, we developed mortality models responding to a threefold objective:

- to be based on a substantial set of life tables (167), statistically representative of mortality in pre-industrial populations, and covering all regions of the world and the period from the sixteenth to the twentieth century;

- to suggest entry parameters easily obtained from historical or osteological sources, and on which a broad consensus exists;
- to take account of population growth or decline.

Creating the sample of observed tables

From an initial set of a thousand tables, collected from statistical yearbooks and demographic studies published up to 1997, we carefully selected a sample of 292 life tables⁶ that correspond to populations with the characteristics that define pre-industrial populations, in terms of both lifestyle (agricultural populations, little urbanisation, without modern medical services) and demography (high infant and juvenile mortality, high fertility).

We standardized the data presentation, estimated certain probabilities (generally the last ones) and tested the tables in order to identify and eliminate the incoherent ones. The tables remaining in the sample were then subjected to a statistical analysis⁷ in order to group together those with similar characteristics, with respect both to the level and structure of mortality, and to differential mortality⁸ (men/women). This last parameter meant that we created three separate samples: “men,” “women,” and “both sexes.”

The final sample used for the modelling process contained 167 “both sexes” tables⁹, 139 “female” tables and 147 “male” tables (for the “both sexes” sample, see the list of tables in the appendix).

The average picture emerging from our sample (Figure 1) differs substantially from that given by existing models. It resembles the *African Standard* values (Brass, 1975) more closely than those produced either by J.-P. Bocquet-Appel and C. Masset’s “forty tables” (1977), whose levels appear highly overestimated due to the table selection, or by S. Ledermann’s 154 tables (1969), 93 % of which are built on post-1890 data.

Choice of mathematical model

We applied multiple regressions to this sample, linking the whole set of estimated probabilities of dying to a given entry parameter and drawing on several mathematical models which connect the logarithm of probabilities of dying to a given variable (expressed either in its logarithmic form or as a simple value).

For calculations by the method of successive probabilities of dying, Ledermann’s (1969) model was used. It takes the form:

$$\log {}_a q_{(x+a)} = a_0 + a_1 \log {}_a q_x \quad (\pm 2\sigma)$$

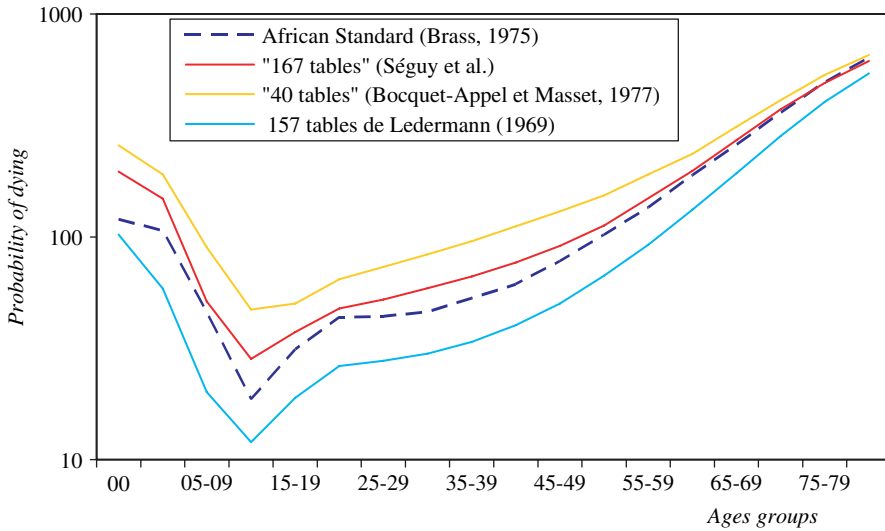


Figure 1: Comparing different mortality universes

with ${}_a q_x$, the probability for an individual aged x years to die in the age interval $(x, x + a)$, and σ , the residual standard deviation.

The method involves constructing a series of regression equations linking each probability to the preceding one, and thus avoids the bias associated with chain estimates (the entry probability only allows the correct estimation of the probability immediately following it; the correlation deteriorates rapidly for subsequent probabilities). As the quotients followed an approximately lognormal distribution, the regressions were estimated using the probability logarithms.

More specifically, for the first years of life, we suggest an inverse regression to estimate the preceding probability of dying:

$$\log {}_a q_{(x)} = a_0 + a_1 \log {}_a q_{(x+a)} \quad (\pm 2\sigma)$$

Another model links the logarithm of mortality probabilities to a given paleodemographic indicator (X), whose form is:

$$\log {}_a q_{(x+a)} = a_0 + a_1 \log X \quad (\pm 2\sigma)$$

or

$$\log {}_a q_{(x+a)} = a_0 + a_1 X \quad (\pm 2\sigma).$$

With these models, mortality levels can be estimated, for different ages x , with respect to data observed in other times and places (i.e. the 167 reference

tables); this implies accepting the hypothesis that populations analysed with this model share a pre-industrial mortality pattern.

Integrating the growth rate

To incorporate growth rates into our models in the absence of a sufficient number of published tables with known growth rates, we had to associate a series of different growth rates with each mortality table in the “both sexes”, “male” and “female” samples, generating a wide range of stable populations. This made it possible to measure the link between various demographic parameters, mortality laws, and population age structure. In this study, we introduced a range of growth rates within the interval -1% to $+1\%$, by steps of 0.25% ¹⁰.

Figure 2 shows variations in the distribution of deaths by age resulting from a fixed law of mortality and variable growth rates.

There are two possibilities for modelling the demographic parameters associated with a fixed mortality law and a selected growth rate: multiple linear regression of the type:

$$\log {}_a q_{(x)} = a_0 + a_1 X + a_2 r + \varepsilon$$

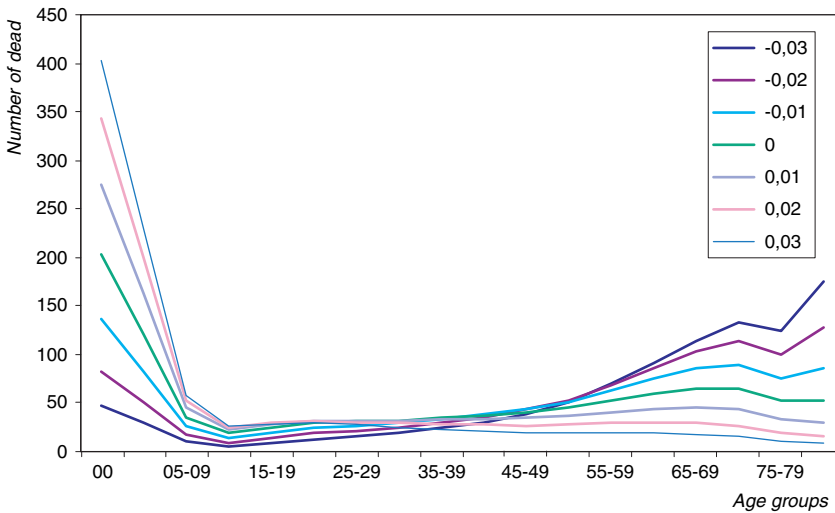


Figure 2: Proportional distribution of deaths by age, according to various values of r (The example is taken from the mean table of the “both sexes” sample)

where X denotes the paleodemographic variable and ε designates Gaussian white noise, and/or a network of model life tables constructed for each selected value of r . We develop this second approach in the present article, leaving the first for a subsequent publication.

Quality and presentation of the models

In order to obtain the best model, we analysed the studentised residuals and the adjusted R^2 value for each regression, before eliminating the most atypical tables. This procedure of elimination follows strict rules limiting the operator's subjectivity and permits the rerunning of the programme. The significance of the model's parameters was also tested automatically, in order to include only those with a *p-value* lower than 0.005.

Each estimate is also matched to the values of the residual standard deviation and the adjusted R^2 ; both help evaluate the quality of the proposed model.

To allow for the problem of determining children's sex, the models are designed for the treatment of the sexes together or separately. Here, we present only the "both sexes" models for the nine values of r used.

Estimating mortality probabilities with the preceding, or the following, probability

The preceding probability makes possible very precise estimates of adult mortality rates (with $R^2 > 0.9$), with the exception of ${}_5q_{20}$; for that age group, the quality of the regression is much lower, given the extreme diversity of observed situations and differential mortality. Always problematic, the infant and juvenile mortality rates estimated with this model are far from satisfactory (R^2 less than 0.8); specific entries have to be used for these young ages.

The preceding probability method does not make it possible to correct the first probability of dying ${}_1q_0$. The infant probability of dying, therefore, needs to be adjusted using the subsequent probability or probabilities (${}_4q_1$ or ${}_5q_5$), knowing that the best estimates are provided by ${}_5q_5$ and not ${}_4q_1$. This is due to variability in ${}_4q_1$ which may take on a value higher than that of ${}_1q_0$ ¹¹.

The estimation model for ${}_1q_0$ is thus:

$$\log_1 q_0 = a_0 + a_1 \log_5 q_5 + \varepsilon$$

and for ${}_4q_1$ is:

$$\log_4 q_1 = a_0 + a_1 \log_5 q_5 + \varepsilon$$

Although this model gives a better estimate of the first two probabilities than the preceding probability method, the best adjustments for young ages are reached using specific entries, the juvenility index in particular (see below).

The preceding probability and the following probability methods of estimation are of most interest to historical demographers, whose sources enable them, at the cost of certain assumptions, to calculate mortality rates by sex and age. They are also valuable when used to complement “paleodemographic” models, when regression quality deteriorates (see below, multiple-entry models).

Estimating probabilities of dying from specific variables (Appendix. Tables 1, 2, 3)

The preceding and following probability methods cannot be used directly with data from paleodemography, as the entry variables in the tables need to be compatible with reliable osteological indicators. Among these, we have selected:

- the juvenility index: $\frac{D(5-14)}{D_{20+}}$ and noted “*J*”,
- the ratio proposed by Bocquet-Appel (2002): $\frac{D(5-19)}{D_{5+}}$ noted “*P*”,
- the average age of death for adults¹²; noted “*a*₂₀”.

It is important not to regard the paleodemographic variable, calculated from bone indicators and used as a model entry, as identical to the demographic variable, estimated from life table data and used to calculate the various regressions, despite the fact that it is impossible to measure the difference between them (except in specific cases: Signoli et al., 2005; or under certain assumptions: Bocquet-Appel, 2005: 276 *et sq.*). We have therefore adopted a convention designating the paleodemographic variable as “estimated *J*” “estimated *P*,” or “estimated *a*₂₀”.

The adults’ average age at death (*a*₂₀) - (Appendix. Table 1).

The adults’ average age at death (*a*₂₀) shows a clear linear correlation with the probabilities of dying, for any given growth rate *r*. The linear association between adults’ average age at death (estimated) and the probability logarithms shows that we can introduce the variable directly.

The quality of adjustments is good, and this variable makes it possible to correctly explain the probabilities ${}_5q_{10}$ to ${}_5q_{65}$. The accuracy decreases substantially, however, for the last two probabilities (${}_5q_{70}$ and ${}_5q_{75}$). It is preferable therefore to use a different variable to estimate mortality rates for oldest age groups, as well as for infantile and juvenile mortality rates (${}_1q_0$, ${}_4q_1$, ${}_5q_5$), which generally are not well correlated with the mean age at death of adults.

Although ${}_5q_5$ estimates produce a satisfactory R^2 as long as r is positive, the quality of the estimate is offset by a very high standard deviation. Estimating ${}_5q_{15}$ remains problematic whatever the value of r : reaching the optimal model compelled us to eliminate a significant number of tables considered atypical. At this point, we have no other osteological indicator available that could be substituted for one of the three variables presented to estimate ${}_5q_{15}$.

The juvenility index (JI) and the P indicator (Appendix. Tables 2 and 3).

These indicators are strongly correlated with the growth rate. For a given growth rate, they offer good correlations essentially with the logarithms of the first probabilities. The use of logarithms is justified by the fact that values for the juvenility index are dispersed according to a lognormal law.

These two indicators are of particular interest for the first probabilities (${}_1q_0$ to ${}_5q_{10}$). However, whatever the value of r , the juvenility index provides better estimates for the first three probabilities than the P indicator. In contrast, in conditions of population increase ($r \geq 0$), the P indicator improves the estimation of ${}_5q_{10}$ and, at times, that of ${}_5q_5$, but at the cost of eliminating a higher number of tables. As the P indicator always gives mediocre estimates of ${}_4q_1$ ($R^2 < 0,8$), the juvenility index is preferable.

Although these two indicators are less strongly correlated with adult mortality, they make it possible to estimate certain mortality probabilities by age, on condition that we accept less accurate regressions ($0,7 > R^2 > 0,8$) and privilege situations of decreasing population ($r \leq 0$). In these conditions, the P indicator allows us to estimate ${}_5q_{30}$, ${}_5q_{40}$, ${}_5q_{45}$, ${}_5q_{50}$, and even ${}_5q_{55}$, whereas ${}_5q_{30}$ and ${}_5q_{50}$ can be estimated using the juvenility index.

As a paleodemographic indicator, the “ P estimate” has a double advantage over the juvenility index: its calculation is easier and takes account of all ages of the exhumed population, from age 5 onwards. Whether these advantages are sufficient to justify the choice of the “ P estimate” over the “ J estimate” needs to be assessed with historically documented series.

**Modelling using multiple entries for each growth rate
(Appendix. Table 1).**

As we observed, the variables selected provide relevant information for some age groups only. It is possible to improve mortality estimations at certain ages by combining the entries providing the best estimates for each probability. The first probabilities (${}_1q_0$ to ${}_5q_{10}$) are thus calculated with the model using the *JI* entry (or even the a_{20} entry for infant mortality, depending on the chosen growth rate); subsequent probabilities are based on the a_{20} entry (except for ${}_5q_{70}$ ¹³, where it is preferable to use the preceding probability whatever the value of r). The definition of a model's "quality" was established by comparing the adjusted R-squares, while taking the standard deviations into consideration. In principle, we selected models with the highest adjusted R² and the smallest standard deviations, with a preference for models that did not require the elimination of too many atypical tables.

**EVALUATION OF RESULTS USING
A TEST-SAMPLE, AND APPLICATION
TO ARCHAEOLOGICAL DATA FROM FRENCH
CEMETERIES OF THE ANCIENT AND MEDIEVAL
PERIODS****Testing with historical data**

For a given site, it is rare to have both osteological and contemporary textual data precise enough to calculate the law of mortality¹⁴. This is why we chose to test our model on demographic variables that could be obtained from written sources (parish registers, for instance).

We chose Quebec's 1801 life table (Bourbeau et al., 1997) to test the proposed indicators for the two-sex model. *A priori*, this population corresponds to the definition of a "pre-industrial" population and was not included in our sample of 167 tables. For instance, for $r = 0$, we compared the estimated mortality probabilities (φ) according to the various models proposed, against their observed value (y).

Overall, the results we got from the following and preceding probabilities are highly satisfactory (Tables 1 and 2, Figure 3). But, as previously mentioned, this method is not valid in paleodemography.

Table 1: Québec 1801, sexes combined. Estimation of mortality probabilities according to different models: - preceding probability; - adults' average age at death ($a_{20} = 60.32$ years); - multiple entries ($a_{20} = 60.32$ years, $JI = 0.073$ and $\log_5 q_{65}$)

Age groups	Observed q_x	Preceding q_x		Entry $a_{20} = 60.32$ ans		Multiple entries	
		<i>estimated</i> q_x	CI (95%)	Estimated q_x	CI (95%)	<i>estimated</i> q_x	CI (95%)
00–04	182			173	4.1	179	3.0
01–04	151	121	3.5	119	3.9	126	2.8
05–09	41	52	1.8	39	2.2	42	0.5
10–14	26	25	0.6	23	0.8	23	0.8
15–19	37	35	0.9	30	0.6	30	0.6
20–24	50	50	0.8	39	0.8	39	0.8
25–29	50	56	0.9	43	0.8	43	0.8
30–34	53	58	0.8	48	0.7	48	0.7
35–39	55	61	0.9	54	0.7	54	0.7
40–44	63	65	0.9	64	0.8	64	0.8
45–49	70	70	0.9	76	1.0	76	1.0
50–54	88	81	0.9	95	1.3	95	1.3
55–59	113	105	1.2	127	1.9	127	1.9
60–64	160	149	1.3	178	2.1	178	2.1
65–69	227	209	1.9	244	2.8	244	2.8
70–74	328	308	2.9	352	4.4	347	2.5
75–79	450	432	3.3	477	6.3	477	0.0
80+	590	750		750		750	

Table 2: Québec 1801, sexes combined. Estimation of juvenile mortality according to different models: - following probability; - juvenility index ($\frac{D(5-14)}{D_{20+}} = 0.073$); - P indicator ($\frac{D(5-19)}{D_{5+}} = 0.111$)

Age groups	observed q_x	Following q_x		Entry $JI = 0.073$		Entry $P = 0.111$	
		estimated q_x	CI (95%)	estimated q_x	CI (95%)	estimated q_x	CI (95%)
00-04	182	181	3.0	179	3.0		
01-04	151	127	2.5	126	2.8		
05-09	41			42	0.5	49	1.3
10-14	26			24	0.4	27	0.4

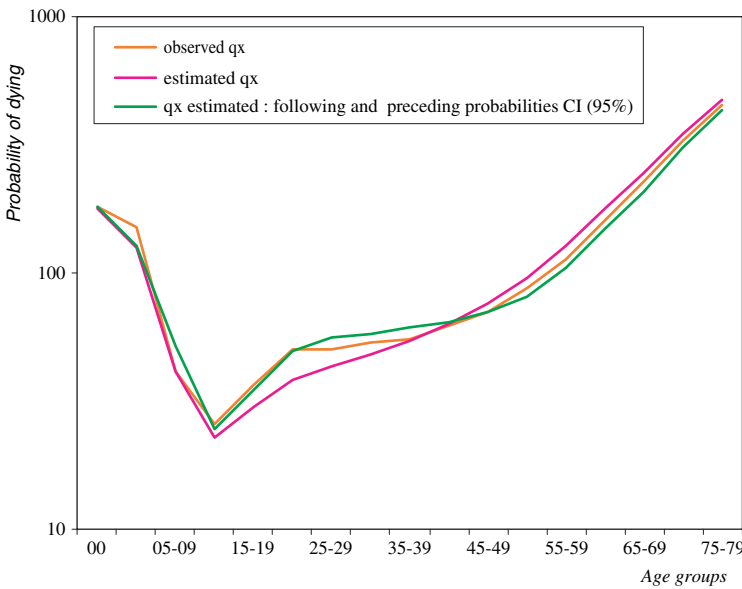


Figure 3: Québec 1801, sexes combined. Mortality probabilities observed and estimated using different models

As for the calculations based on the paleodemographic entries (JI , P and a_{20} , computed here from table parameters, and not from osteological data), juvenile mortality rates are relatively well approximated by the entries covering those ages (Table 2). As we have already noted, the P indicator does not provide better estimates than the juvenility index.

In all three models (Table 1 and Figure 3), the quality of estimation deteriorates over the age of 55, with a tendency to overestimate the probability

of dying at each age. Combining the entries with the best regressions only improve the computation of ${}_5q_{70}$ (due to the better adjustment obtained with the regression on the $\log_5 q_{65}$), which is effectively obtained in this example.

Examples of applications to archeological data

These model tables make it possible to revive the paleodemographic approach to buried populations and to probe further some recurrent questions in paleodemography: for example, the estimation for subjects under twenty years old and for children 0–4 years (skeletons of young children are under-represented or nonexistent in ancient cemeteries), or the within-site demographic evolution. These are possible once hypotheses concerning population growth or decline can be taken into account in the choice of model.

The units of skeletal material included are from two cemeteries excavated exhaustively, and subject to complete historical, archaeological and anthropological investigation. These contemporaneous sites are comparable, as the same research methods were used in each study: the same reference population, the same biological age indicators and the same method for estimating age at death.

One of them (Lisieux, Calvados) has been the object of earlier paleodemographic studies, based on the stationary population hypothesis (Séguy et al., 2001; Séguy et al., 2006). All that remained was to integrate population variation into the analyses.

Frénouville (Calvados, France, IIIrd -VIIth century AD)

The rural necropolis of Frénouville¹⁵ (Calvados, known as “Le Drouly”) covered an area of approximately one hectare. Of the 650 tombs dating from the end of the IIIrd to the end of the VIIth century excavated there, 163 tombs, on a north-south axis, belonged to the Lower Empire (IVth century); this is the sample analysed here.

Since the whole cemetery was excavated, it could be expected that all the deceased were buried there; as it is, only 26 graves contained immature subjects – approximately 15% of the whole population buried there. This figure is much lower than the expected percentage, given the high mortality of infants and young children in ancient populations. Using the a_{20} indicator (estimated at 57.9 years for the 137 adults) as the entry in the eponymous model, we selected a mortality curve by age and, assuming zero growth¹⁶, compute the demographic parameters associated with it (Table 3): ${}_5q_0 = 293$

Table 3: Frénouville, Lower Empire. Estimated life table. Entry a_{20} estimated (57.9 years), sexes combined, $r = 0$

Frénouville IVth c. AD (a_{20} -HF)	Estimated q_x	CI (95%)	Living (S_x)	Deaths (D_x)	Life expectancy at age x (E_x)
00	191	4.3	1000	191	37.8
01-04	126	4.0	809	102	45.6
05-09	47	2.9	707	33	47.9
10-14	26	1.0	674	18	45.1
15-19	35	0.7	656	23	41.3
20-24	46	0.9	633	29	37.7
25-29	51	1.1	604	31	34.4
30-34	57	1.0	573	33	31.1
35-39	65	0.9	540	35	27.9
40-44	76	1.1	505	38	24.6
45-49	89	1.3	467	42	21.4
50-54	112	1.7	425	48	18.3
55-59	147	2.4	378	56	15.3
60-64	198	2.4	322	64	12.5
65-69	266	3.0	258	69	9.9
70-74	378	4.7	189	72	7.6
75-79	497	6.8	118	59	5.8
80 +	750	—	59	59	4.0

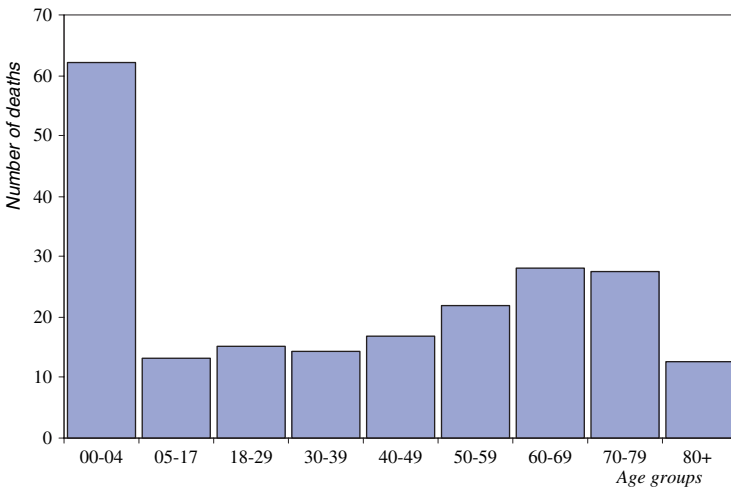


Figure 4: Estimation of the number of deaths by age group, given the estimated mortality at Frénouville and the number of adult skeletons exhumed (137)

per thousand; life expectancy at birth = 37.8 years; life expectancy at age 20 = 37.7 years; birth rate = death rate = 26.5 per thousand.

Assuming that the population was stationary and that Frénouville's demographic profile at the end of Antiquity was similar to that of "pre-industrial" populations, it is possible to estimate what the percentage of nonadults, of whom so few were exhumed (26), should have been.

According to the estimated mortality by age, the 137 adult skeletons exhumed correspond to a population at risk of dying (from 0 to ∞ years) of 212 individuals; of these 75 (35.6%) died before the age of 18, and 62 before the age of 5 years (Figure 4). In the absence of archaeological or osteological data (given the total lack of well-preserved child skeletons), it is difficult to assess whether or not the population varied in numbers during the fourth century. Even a very low growth rate, however, would produce a different number of nonadults.

Lisieux (Calvados, France, IVth century AD)

A large funeral zone was discovered by chance in the yard of the old Michelet school, 250 metres from the Lisieux castrum¹⁷, and was excavated thoroughly. More than 1150 skeletons were found, divided in two distinct sets dating from the Lower Empire and from the Higher Middle Ages, with no occupation in between. Its area (0.8 hectare) and the density of burials (up to six levels of well-identified graves) mean that the Lower Empire necropolis represents the site's most intensely-used phase. The first graves, characterized by their north-south orientation, were dug at the beginning of the fourth century, and the last ones at the very beginning of the fifth. The excavated graves have uncovered high-quality archaeological artefacts that demonstrate a certain level of wealth among some of the people exhumed (Paillard, 1994). The quantity of well-dated funeral artefacts has made it possible to classify the burials by 25-year periods.

We use this series of 793 individuals in this study.

CHARACTERISTICS OF THE BURIED POPULATION (TABLE 4).

In contrast with what is most frequently observed in rural cemeteries of Lower Normandy in the same period, immature individuals are relatively numerous (208 were identified, 26.2% of all buried individuals) and all age groups are represented, from perinatal to adolescent subjects. However, the percentage of nonadults did not remain constant over the whole period

Table 4: Lisieux-Michelet, IVth century AD. Distribution of adult and nonadult individuals by chronological phases, “masculinity ratio” and proportion of adults of unknown gender for each phase

Periods	Total of skeletons	Adults (AD)	Non adults (IM)	% IM/Total	Adults' sex ratio	Adults' unknown sex (%)
310–325	169	118	51	30.2	0.62	5.9
325–350	195	155	40	20.5	0.57	9.0
350–375	183	147	36	19.7	0.53	5.4
375–400	141	97	44	31.2	0.61	10.3
+/-400	60	41	19	31.7	0.44	4.9

of necropolis use, as we observe in the proportionally lower number of nonadults between the years 325 and 375.

Throughout the fourth century the proportion of men is higher than that of women at adult ages. Only in the early years of the fifth century is there an inversion of this tendency, with the number of women exceeding that of men.

The proportion of adult males is greatest at the beginning (62%), and during the last quarter of the fourth century (61%); during these periods funeral artefacts and traumatic pathology are suggestive of a military presence (Paillard et al., 2006).

ESTIMATING THE MEAN AGE AT DEATH OF ADULTS AND THE JUVENILITY INDEX, BY 25-YEAR PERIODS (TABLE 5).

Using models means accepting, for each quarter-century period, the hypothesis that all those who died over the age of 20 years were indeed buried in the cemetery. The mean age at death of the 585 adults exhumed

Table 5: Lisieux-Michelet, IVth century. Number of adults, mean age at death of adults (a_{20}) and juvenility index (JI) by quarter century

	±1st quarter 310–325	2nd quarter 325–350	3rd quarter 350–375	4th quarter 375– \approx 400
Number of years (a)	15	25	25	30
Number of adults	118	155	147	138
a_{20}	53.97	53.39	56.21	54.81
JI	0.203	0.110	0.075	0.138

was calculated with a method slightly different from the one used by J.-P. Bocquet-Appel and C. Masset 1996): the anthropological indicator remains the synostosis of cranial sutures, distributed in seven stages (Masset, 1982), but the population is distributed in five-year age groups (Séguy, et al., to be published).

The many children found on this site permit us to use our method to calculate a juvenility index (Buchet et al., 2006a); for the fourth century as a whole, its value is 0.127.

ESTIMATING GROWTH RATES FOR EACH QUARTER-CENTURY PERIOD (FIGURE 5).

The number of skeletons reveals substantial differences between the four quarter-century chronological phases of the fourth century (a growing number of burials until the mid-century, followed by a decline until the cemetery was abandoned).

We know that, at the beginning of the fourth century, the Michelet cemetery at Lisieux was set up following a radical reorganization of the urban fabric that must have led to population movement, at least at the regional level. A study of population health status shows that it must also have faced recurring crises of survival, possibly related to military events; these crises caused variations in fertility, and even forced some families to emigrate. As a result, any hypothesis of zero growth during all the phases of cemetery use must be set aside and, instead, mortality and population

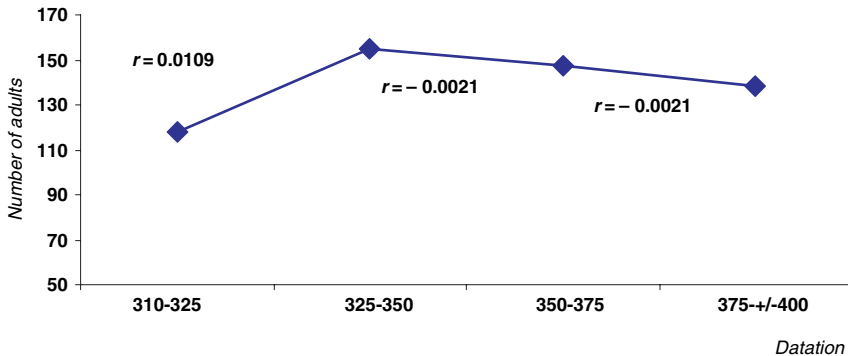


Figure 5: Lisieux-Michelet, IVth century. Reconstituting variations in the annual growth rate (r).

Table 6: Summary of the demographic parameters for the different chronological phases of Lisieux-Michelet, estimated using the multiple entry model a_{20} , JI and $\log_5 q_{65}$

	1st quarter 310–325	2nd quarter 325–350	3rd quarter 350–375	+/- 4th quarter 375 - +/- - 400	
<i>Number of years (a)</i>	15	25	25	30	<i>Anthropological data</i>
<i>N adultes</i>	118	155	147	138	
a_{20}	53,97	53,39	56,21	54,81	
<i>JI</i>	0,203	0,11	0,075	0,138	
<i>r</i>	0	0.0109	-0.0021	-0.0021	
e_0	26,3	37,6	35,6	29,4	<i>Demographical parameters (estimated)</i>
e_{20}	33,8	28,6	37,0	35,5	
${}_5q_0(\text{‰})$	438,4	275	300	387	
<i>D 0–17 ans (%)</i>	53,23	60,93	52,72	53,76	
<i>D 0–4 ans (%)</i>	43,84	31,5	25,7	26,4	
<i>Birth rate (‰)</i>	38.,03	26,60	28,06	34,00	
<i>Mortality rate (‰)</i>	38,03	15,69	30,18	36,11	

growth (positive or negative, by natural increase or migration) should be integrated concurrently, according to the following formula:

$$r = \frac{1}{a} \ln \frac{d(t+a)}{d(t)}$$

where d represents the number of adult skeletons exhumed, t the observation phase, and a its duration.

ESTIMATING DEMOGRAPHIC PARAMETERS FOR EVERY QUARTER OF A CENTURY (TABLE 6).

For each twenty-five-year period, it is possible to estimate several demographic parameters, taking into account the value of r , estimated according to archaeological facts, as well as values of a_{20} and of II , calculated from osteological indicators.

From the archaeological and paleo-pathological data, the inhabitants of the Lisieux castrum appear to have endured harsh living conditions at the beginning of the fourth century, not unlike those affecting the rural populations in the plains of Caen during the same period. Worse still, the second quarter of century represents a critical phase in the city's history, with serious troubles creating economic upheavals that resulted in mediocre living standards.

These events are less visible in the paleodemographic estimations; there, on the contrary, positive annual growth rates suggest an improvement in living standards (relatively high life expectancy at birth, very low infant and juvenile mortality, and a mortality level unusual among "pre-industrial" populations). This forces us to envisage a different scenario: the arrival of a substantial number of men, women and, to a lesser extent, children, possibly fleeing the insecurity and impoverishment of the countryside in this second quarter of the fourth century. In this case, the stable population model is inappropriate, and a theoretical model incorporating migrations would be preferable.

From 350 onward, the archaeological data display a notable improvement in health, also apparent in the increase in estimated life expectancy at age 20. This improvement was short-lived, however; as early as 375, the traumatic aftermath observed probably reflects the renewal of military activity in the region. According to our calculations, the demographic conditions in the last quarter of the fourth century closely resemble those observed in the first. Once again, does the fact of ignoring migratory flows mask a completely different reality? Archaeological evidence that the cemetery was not in use from the start of the Vth century to the VIIth century makes all the more

plausible the hypothesis that the city was progressively abandoned during the second half of the fourth century.

Where archaeologists would be tempted to interpret an increase in the number of burials as evidence of population growth, demographic laws bring to light probable scenarios and incoherent reconstructions.

CONCLUSION

Up to now, paleodemographers were faced with a dilemma. On the one hand, they could use contemporary models that make it possible to calculate the main demographic parameters at the expense of serial estimates (due to the impossibility of entering these models with osteological data). On the other, they might prefer the pre-industrial mortality pattern and be able to estimate certain demographic parameters on the basis of reliable anthropological indicators (*méthode des "estimateurs"*), but be satisfied with an approach to mortality between 0 and 5 years, and to life expectancy at birth, according to various hypotheses of population growth.

The models we propose provide an estimate of several demographic indicators: life expectancy at age x , mortality probabilities by age, number of individuals deceased and surviving by age. They have the additional advantages of being based on a large body of life tables representative of pre-industrial populations, of being accessible from anthropological indicators (juvility index and adults' mean age at death, in particular), of specifying the margin of error for every regression, and of proposing a series of growth rates that make it possible to introduce archaeological population dynamics.

The first applications of these models to archaeological sets from ancient times showed the extent of divergence between interpretations, depending on whether we look at archaeological data or at findings from paleodemographic studies (particularly for one of the chronological phases of the Lisieux site). This motivated us to go beyond the demographic parameters usually considered (fertility, mortality), and take into account migration, whose impact is often underestimated.

Historical populations were indeed obliged to migrate over short or long distances, and these forced migrations could act both as cause and consequence of serious crises of excess mortality. The models presented here are based on stable population theory, and imperfectly reflect these events. As a consequence, we need to refine them further in order to adhere more closely to historical realities.

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NOTES

- ¹ From a demographic perspective, mortality rates express the probability of dying between ages x and $x + a$: the number of deaths between ages x and $x + a$ divided by the number of people at risk of dying (individuals who reached age x). In this sense, they are not equivalent to the proportion of deceased of age x as estimated from the number of buried individuals (except under the stationary population hypothesis).
- ² In this sense, the notion of “pre-industrial” populations encompasses all populations – European or not – with similar demographic characteristics. These populations more or less correspond to pre-transition populations, or those just starting their demographic transition.
- ³ A ratio of deaths between 5 and 14 years to deaths at 20 years and above (juvility index, noted: $\frac{D(5-14)}{D_{20+}}$) higher than or equal to 0.100, and a ratio of deaths between 5 and 9 years to those between 10 and 14 years (noted: $\frac{D(5-9)}{D(10-14)}$) superior to 2.
- ⁴ Two of the authors (Buchet and Ségué, 2002) have published a supplement of estimators for ${}_5q_5$ and ${}_5q_{10}$.
- ⁵ Studies have shown that child and adult mortality could evolve independently of each other, in the past, and that, the higher the general level of mortality, the lower the correlation between adult and infant mortality (Woods, 1993; Wrigley et al., 1997).
- ⁶ The “both sexes” sample is made up of 292 life tables, the “male” sample of 290 tables, and the “female” sample of 286 tables.
- ⁷ To do this, two methods were mainly used: dynamic clustering algorithm and K-means classification. These discriminant analyses were based on a series of indicators specially defined to characterize the most “ancient” mortality tables, such as life expectancy at birth, at age 20, the juvility index and infant mortality rates.

- ⁸ Discriminant variables chosen to measure changes in the structure of mortality: $\frac{1q_0}{4q_1}$; $\frac{5q_5}{5q_{10}}$; $\frac{20q_{20}}{20q_{40}}$; $\frac{1q_0}{e_{20}}$; $\frac{e_{5-15}}{e_{20}}$; changes in levels: e_{5-15} , e_{20-40} , as well as the parameters highlighted by J.-P. Bocquet-Appel and C. Masset ($\frac{D(5-14)}{D_{20+}}$ and $\frac{D(5-9)}{D(10-14)}$, with D equal to the number of deceased in the table); infant mortality according to sex: $1q_0$; e_{20} ; e_{20-40} ; e_{40-60} .
- ⁹ Historical tables (from the seventeenth to the nineteenth centuries) from industrialised countries make up 70% of the sample, and recent tables (late nineteenth and twentieth centuries) from developing countries the other 30%, each selected according to the value of certain demographic indicators. No sub-group stands out: the mean mortality level in the selected developing countries is significantly very close to that observed in the historical tables of industrial countries (Student's T test: $T = 0.023$, with a threshold of 0.05), with the exception of three probabilities ($4q_1$, $5q_5$, $5q_{25}$).
- ¹⁰ This gives 1503 tables for the "both sexes" sample, 1323 for "men" and 1251 for "women", corresponding to 25 stable population for each table.
- ¹¹ If $1q_0 < 4q_1$: the results for the model parameters are very close to those found in the general model, with only slight improvements; If $1q_0 > 4q_1$: the modelling increases the precision (depending on the data at our disposal) but needs to be used cautiously, according to the tables studied and the associated rate of growth.
- ¹² Which we estimate using a different formula from the one suggested by J.-P. Bocquet-Appel and C. Masset in 1996 (Séguy, Buchet *et al.*, to be published.- *Manuel de paléodémographie*).
- ¹³ As a matter of convention, we set the value of the last probability $5q_{80}$ at 0.750.
- ¹⁴ The samples we studied are all specific: a cemetery of cloistered nuns with a very privileged life style, a burial site related to a plague epidemic, a military port at the end of the nineteenth century (Signoli *et al.*, 2005). These could not be used for these tests.
- ¹⁵ Frénouville (Calvados, France): directed by C. Pilet (CRAHM, Caen, France), (Pilet, 1980); anthropological study: L. Buchet (CEPAM, Valbonne, France), (Buchet, 1978).
- ¹⁶ The sample studied includes all individuals buried from the beginning to the end of the fourth century; it was not possible, however, to establish chronological subdivisions which would have permitted the measurement of potential variations in growth.
- ¹⁷ Lisieux-Michelet (Calvados, France): directed by D. Paillard (SDAC, Caen, France); anthropological study: A. Alduc-Le Bagousse (CRAHM, Caen, France); paleodemographic study: L. Buchet (CEPAM, Valbonne, France).

List of life tables included in the "both sexes" sample

Country	Region	Date	Number of tables	References
Germany	All regions	1740–1850	12	Imhof, 1990
Germany		1765	1	Sussmilch, 1776
Germany	Bavaria	1881–90	1	SGF, 1749–1905
Germany	Breslau	1694	1	Halley, 1693
England	English peerage	1600–1824	9	Hollingsworth, 1977
England		1650–1809	17	Wrigley <i>et al.</i> , 1997
England		1838–1900	3	SGF, 1749–1905

(Continued)

Country	Region	Date	Number of tables	References
England	Carlisle, Milne's table	1779–1787	1	Milne, 1837
England	Londres	1759–68	1	Süssmilch, 1776
England	Northampton	1735–1781	2	Price, 1783
England	Norwich	1741–69	1	Bocquet-Appel, 2002
Autria		1901–05	1	ONU, 1956
Autria		1880–1882	1	Bocquet-Appel, 2002
Bolivia		1900	1	Bocquet-Appel, 2002
Bulgaria		1899–1902	1	ONU, 1956
Cameroun	Bamileke Region	1965	1	OCDE, 1980
Canada		1841–1891	6	Bourbeau et al., 1997
Canada	Quebec	1841–1901	7	Bourbeau et al., 1997
Chili		1909–1920	2	Preston et al., 1972
Chili		1930–1940	2	ONU, 1956
Chili		1951–1953	1	OCDE, 1980
China	Hsiao-Shan	1725–1844	8	Liu, 1985
China	Taiwan	1936–1940	1	ONU, 1956
Ivory Coast	Bouake	1961–1962	1	OCDE, 1980
Spain		1900–1920	3	ONU, 1956
ex Czechoslovakia		1899	1	ONU, 1956
Finland		1751–1880	13	Turpeinen et al., 1997
Finland		1911–1920	1	ONU, 1956
France		1740–1789	5	Blayo, 1975
Guatemala		1939–1941	1	ONU, 1956
France	Demonferrand' Table	1817–1832	1	Demonferrand, 1838
France	pré de st-Maur's Table	1740–1749	1	Buffon, 1774
France	Reunion (Island)	1960–1963	1	OCDE, 1980
France	Paris Basin	1671–1720	1	Dupâquier, 1979
Greece		1920	1	ONU, 1956
Guatemala		1893	1	Bocquet-Appel, 2002
Guinea		1954–1955	1	OCDE, 1980
Guyana		1945–1947	1	ONU, 1956
Upper-Volta		1960–1961	1	OCDE, 1980
Hungaria		1920–1921	1	ONU, 1956
India		1891–1901	1	ONU, 1956
India	Madras	1888–1891	1	Lardinois, 1977
Italia	Padouan region	1766–1865	5	Rossi et al., 1996
Jamaica		1910–1922	2	ONU, 1956

Japon		1899–1936	4	Japan Statistical Year book, 1978
Japon	Shimomoriya	1716–1869	1	Tsuya et al., 1997
Japon	Fugito	1775–1804	1	Hanley, 1974
Japon	Ogen-ji	1776–1955	8	Bowman and Preston, 1991
Japon		1899–1936	5	ONU, 1956
Mauritius		1942–1946	1	ONU, 1956
Mauritius		1951–1953	1	OCDE, 1980
Mexico		1930–1940	2	ONU, 1956
Nicaragua		1920	1	Bocquet-Appel, 2002
New-Zeland		1881–1891	2	Preston et al., 1972
Panama		1930	1	Bocquet-Appel, 2002
Paraguay		1899	1	Bocquet-Appel, 2002
Portugal		1949–1952	1	ONU, 1956
République dominicaine		1935	1	Bocquet-Appel, 2002
Russia	European part	1896–1897	1	ONU, 1956
Sri-Lanka (ex Ceylan)		1920–1947	2	ONU, 1956
Sweden		1751–1860	6	Historisk Statistik, 1955
Sweden		1755	1	Wargentin, 1766
Switzerland	Geneva	1625–1684	3	Perrenoud, 1975
Switzerland	Geneva	1625–1649	1	Perrenoud, 1984
Trinidad-and-Tobago		1945–1947	1	ONU, 1984
Trinidad-and-Tobago		1950–1961	1	OCDE, 1980
Venezuela		1936	1	Bocquet-Appel, 2002

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Appendix 1: Main statistical parameters for estimating probabilities with the adults' average age at death (a_{20}).

$\log {}_a q_x$	Explicative variable	a_0	a_1	$R^2 adj$	$\sigma \log {}_a q_x$	Number of tables	Nota	r value
$\log {}_5 q_5$	a_{20}		-0.024	0.986	0.158	160		
$\log {}_5 q_{10}$	a_{20}		-0.029	0.996	0.098	153		
$\log {}_5 q_{15}$	a_{20}	0.141	-0.029	0.803	0.054	129		
$\log {}_5 q_{20}$	a_{20}	0.399	-0.032	0.858	0.048	146		
$\log {}_5 q_{25}$	a_{20}	0.549	-0.034	0.869	0.048	158		
$\log {}_5 q_{30}$	a_{20}	0.553	-0.033	0.910	0.038	161		
$\log {}_5 q_{35}$	a_{20}	0.630	-0.033	0.931	0.033	161		
$\log {}_5 q_{40}$	a_{20}	0.625	-0.032	0.912	0.036	158		+ 0.01
$\log {}_5 q_{45}$	a_{20}	0.636	-0.031	0.897	0.038	159		
$\log {}_5 q_{50}$	a_{20}	0.630	-0.029	0.874	0.040	154		
$\log {}_5 q_{55}$	a_{20}	0.555	-0.025	0.829	0.042	150		
$\log {}_5 q_{60}$	a_{20}	0.377	-0.020	0.849	0.032	131		
$\log {}_5 q_{65}$	a_{20}	0.230	-0.015	0.791	0.029	124		
$\log {}_5 q_{70}$	a_{20}	0.193	-0.011	0.539	0.037	137	(2)	
$\log {}_5 q_{75}$	a_{20}		-0.006	0.985	0.038	145		
$\log {}_5 q_5$	a_{20}		-0.024	0.986	0.158	160		
$\log {}_5 q_{10}$	a_{20}		-0.028	0.996	0.099	153		
$\log {}_5 q_{15}$	a_{20}		-0.026	0.999	0.053	127		
$\log {}_5 q_{20}$	a_{20}	0.399	-0.031	0.849	0.049	146		
$\log {}_5 q_{25}$	a_{20}	0.537	-0.033	0.864	0.049	156		
$\log {}_5 q_{30}$	a_{20}	0.553	-0.032	0.911	0.038	159		
$\log {}_5 q_{35}$	a_{20}	0.636	-0.033	0.929	0.033	161		
$\log {}_5 q_{40}$	a_{20}	0.633	-0.032	0.913	0.036	158		+ 0.0075
$\log {}_5 q_{45}$	a_{20}	0.649	-0.031	0.903	0.037	159		
$\log {}_5 q_{50}$	a_{20}	0.643	-0.029	0.881	0.039	154		
$\log {}_5 q_{55}$	a_{20}	0.590	-0.026	0.826	0.043	153		
$\log {}_5 q_{60}$	a_{20}	0.363	-0.019	0.818	0.034	138		
$\log {}_5 q_{65}$	a_{20}	0.267	-0.015	0.801	0.029	126		
$\log {}_5 q_{70}$	a_{20}	0.219	-0.012	0.564	0.037	138	(2)	
$\log {}_5 q_{75}$	a_{20}		-0.005	0.985	0.038	145	(4)	
$\log {}_5 q_5$	a_{20}		-0.024	0.986	0.158	160		
$\log {}_5 q_{10}$	a_{20}		-0.028	0.996	0.099	153		
$\log {}_5 q_{15}$	a_{20}	0.187	-0.029	0.721	0.068	145		
$\log {}_5 q_{20}$	a_{20}	0.402	-0.031	0.841	0.051	146		
$\log {}_5 q_{25}$	a_{20}	0.534	-0.032	0.852	0.051	156		
$\log {}_5 q_{30}$	a_{20}	0.555	-0.032	0.903	0.039	159		
$\log {}_5 q_{35}$	a_{20}	0.644	-0.033	0.926	0.034	161		
$\log {}_5 q_{40}$	a_{20}	0.643	-0.031	0.913	0.036	158		+ 0.005
$\log {}_5 q_{45}$	a_{20}	0.670	-0.031	0.905	0.037	160		
$\log {}_5 q_{50}$	a_{20}	0.656	-0.029	0.868	0.041	159		

Continued

Appendix I Continued

$\log_a q_x$	Explicative variable	a_0	a_1	$R^2 adj$	$\sigma \log_a q_x$	Number of tables	Nota	r value
$\log_5 q_{55}$	a_{20}	0.608	-0.026	0.837	0.042	153		
$\log_5 q_{60}$	a_{20}	0.383	-0.019	0.835	0.033	137		
$\log_5 q_{65}$	a_{20}	0.294	-0.015	0.804	0.030	129		
$\log_5 q_{70}$	a_{20}	0.240	-0.012	0.572	0.037	140	(2)	
$\log_5 q_{75}$	a_{20}		-0.005	0.985	0.038	145		
$\log_5 q_5$	a_{20}		-0.023	0.986	0.159	161		
$\log_5 q_{10}$	a_{20}		-0.028	0.996	0.099	153		
$\log_5 q_{15}$	a_{20}	0.177	-0.028	0.714	0.069	144	(3)	
$\log_5 q_{20}$	a_{20}	0.407	-0.031	0.832	0.052	146		
$\log_5 q_{25}$	a_{20}	0.525	-0.032	0.835	0.054	157		
$\log_5 q_{30}$	a_{20}	0.549	-0.031	0.891	0.042	160		
$\log_5 q_{35}$	a_{20}	0.631	-0.032	0.918	0.036	162		
$\log_5 q_{40}$	a_{20}	0.654	-0.031	0.912	0.036	158		+ 0.0025
$\log_5 q_{45}$	a_{20}	0.662	-0.030	0.901	0.037	162		
$\log_5 q_{50}$	a_{20}	0.675	-0.028	0.876	0.040	159		
$\log_5 q_{55}$	a_{20}	0.647	-0.026	0.833	0.043	157		
$\log_5 q_{60}$	a_{20}	0.404	-0.019	0.842	0.032	138		
$\log_5 q_{65}$	a_{20}	0.311	-0.016	0.823	0.029	127		
$\log_5 q_{70}$	a_{20}	0.268	-0.012	0.621	0.035	136	(2)	
$\log_5 q_{75}$	a_{20}	0.118	-0.007	0.357	0.037	143	(4)	
$\log_5 q_5$	a_{20}	0.456	-0.031	0.336	0.159	160	(1)	
$\log_5 q_{10}$	a_{20}		-0.027	0.996	0.101	155		
$\log_5 q_{15}$	a_{20}	0.216	-0.029	0.814	0.052	121		
$\log_5 q_{20}$	a_{20}	0.401	-0.030	0.828	0.052	145		0
$\log_5 q_{25}$	a_{20}	0.512	-0.031	0.821	0.055	158		
$\log_5 q_{30}$	a_{20}	0.558	-0.031	0.879	0.044	162		
$\log_5 q_{35}$	a_{20}	0.656	-0.032	0.911	0.038	163		
$\log_5 q_{40}$	a_{20}	0.680	-0.031	0.908	0.037	159		
$\log_5 q_{45}$	a_{20}	0.690	-0.030	0.903	0.037	163		
$\log_5 q_{50}$	a_{20}	0.701	-0.029	0.885	0.038	160		
$\log_5 q_{55}$	a_{20}	0.673	-0.026	0.846	0.042	158		
$\log_5 q_{60}$	a_{20}	0.427	-0.020	0.849	0.032	139		
$\log_5 q_{65}$	a_{20}	0.315	-0.015	0.807	0.030	133		
$\log_5 q_{70}$	a_{20}	0.329	-0.013	0.684	0.032	131	(2)	
$\log_5 q_{75}$	a_{20}	0.133	-0.008	0.381	0.036	143	(4)	
$\log_5 q_5$	a_{20}	0.390	-0.029	0.326	0.155	158	(1)	
$\log_5 q_{10}$	a_{20}		-0.027	0.996	0.102	155		
$\log_5 q_{15}$	a_{20}	0.147	-0.027	0.793	0.055	123		
$\log_5 q_{20}$	a_{20}	0.394	-0.030	0.803	0.056	147		
$\log_5 q_{25}$	a_{20}	0.531	-0.031	0.810	0.057	157		

$\log_a q_x$	Explicative variable	a_0	a_1	R^2adj	$\sigma \log_a q_x$	Number of tables	Nota	r value
$\log_5 q_{30}$	a_{20}	0.553	-0.031	0.871	0.045	160		
$\log_5 q_{35}$	a_{20}	0.653	-0.031	0.906	0.038	162		
$\log_5 q_{40}$	a_{20}	0.681	-0.031	0.907	0.037	158		- 0.0025
$\log_5 q_{45}$	a_{20}	0.700	-0.030	0.906	0.036	162		
$\log_5 q_{50}$	a_{20}	0.715	-0.028	0.893	0.037	158		
$\log_5 q_{55}$	a_{20}	0.685	-0.026	0.843	0.042	159		
$\log_5 q_{60}$	a_{20}	0.444	-0.019	0.812	0.036	149		
$\log_5 q_{65}$	a_{20}	0.331	-0.015	0.817	0.029	131		
$\log_5 q_{70}$	a_{20}	0.336	-0.013	0.689	0.032	130	(2)	
$\log_5 q_{75}$	a_{20}	0.137	-0.007	0.378	0.036	143	(4)	
$\log_5 q_{55}$	a_{20}	0.414	-0.029	0.327	0.155	158	(1)	
$\log_5 q_{10}$	a_{20}		-0.026	0.996	0.103	155		
$\log_5 q_{15}$	a_{20}	0.158	-0.027	0.786	0.056	123	(3)	
$\log_5 q_{20}$	a_{20}	0.430	-0.030	0.814	0.055	144		
$\log_5 q_{25}$	a_{20}	0.533	-0.031	0.847	0.050	146		
$\log_5 q_{30}$	a_{20}	0.562	-0.030	0.861	0.047	160		
$\log_5 q_{35}$	a_{20}	0.692	-0.032	0.911	0.037	159		
$\log_5 q_{40}$	a_{20}	0.703	-0.031	0.907	0.037	157		- 0.005
$\log_5 q_{45}$	a_{20}	0.722	-0.030	0.904	0.037	163		
$\log_5 q_{50}$	a_{20}	0.738	-0.028	0.899	0.036	158		
$\log_5 q_{55}$	a_{20}	0.755	-0.027	0.843	0.044	164		
$\log_5 q_{60}$	a_{20}	0.464	-0.020	0.823	0.035	149		
$\log_5 q_{65}$	a_{20}	0.351	-0.016	0.817	0.029	133		
$\log_5 q_{70}$	a_{20}	0.357	-0.013	0.699	0.031	131	(2)	
$\log_5 q_{75}$	a_{20}	0.148	-0.008	0.388	0.036	143	(4)	
$\log_5 q_{55}$	a_{20}	0.440	-0.029	0.329	0.155	158		
$\log_5 q_{10}$	a_{20}		-0.026	0.996	0.101	153		
$\log_5 q_{15}$	a_{20}		-0.024	0.998	0.069	139		
$\log_5 q_{20}$	a_{20}	0.431	-0.029	0.806	0.055	143		
$\log_5 q_{25}$	a_{20}	0.522	-0.030	0.837	0.051	145		
$\log_5 q_{30}$	a_{20}	0.573	-0.030	0.850	0.048	160		
$\log_5 q_{35}$	a_{20}	0.685	-0.031	0.900	0.040	160		
$\log_5 q_{40}$	a_{20}	0.720	-0.030	0.902	0.038	157		- 0.0075
$\log_5 q_{45}$	a_{20}	0.746	-0.030	0.904	0.037	163		
$\log_5 q_{50}$	a_{20}	0.763	-0.028	0.903	0.035	158		
$\log_5 q_{55}$	a_{20}	0.785	-0.027	0.852	0.042	164		
$\log_5 q_{60}$	a_{20}	0.480	-0.020	0.827	0.034	150		
$\log_5 q_{65}$	a_{20}	0.364	-0.016	0.801	0.030	138		
$\log_5 q_{70}$	a_{20}	0.372	-0.013	0.710	0.031	131	(2)	
$\log_5 q_{75}$	a_{20}	0.159	-0.008	0.398	0.035	143	(4)	
$\log_5 q_{55}$	a_{20}	0.468	-0.029	0.334	0.155	158	(1)	

Continued

Appendix 1 Continued

$\log_a q_x$	Explicative variable	a_0	a_1	$R^2 adj$	$\sigma \log_a q_x$	Number of tables	Notes	r value
$\log_5 q_{10}$	a_{20}		-0.026	0.996	0.103	154		
$\log_5 q_{15}$	a_{20}		-0.024	0.997	0.079	150		
$\log_5 q_{20}$	a_{20}	0.453	-0.029	0.814	0.055	140		
$\log_5 q_{25}$	a_{20}	0.543	-0.030	0.819	0.054	147		
$\log_5 q_{30}$	a_{20}	0.586	-0.030	0.840	0.050	160		
$\log_5 q_{35}$	a_{20}	0.717	-0.031	0.903	0.039	157		
$\log_5 q_{40}$	a_{20}	0.718	-0.030	0.886	0.041	160		- 0.01
$\log_5 q_{45}$	a_{20}	0.770	-0.030	0.905	0.037	163		
$\log_5 q_{50}$	a_{20}	0.790	-0.028	0.907	0.035	158		
$\log_5 q_{55}$	a_{20}	0.793	-0.027	0.860	0.040	163		
$\log_5 q_{60}$	a_{20}	0.495	-0.020	0.836	0.033	150		
$\log_5 q_{65}$	a_{20}	0.390	-0.016	0.822	0.029	136		
$\log_5 q_{70}$	a_{20}	0.388	-0.013	0.723	0.030	131	(2)	
$\log_5 q_{75}$	a_{20}	0.171	-0.008	0.412	0.035	143	(4)	

- (1) Replace with the J entry for a better estimate.
- (2) Replace with the $\log_5 q_{65}$ entry for a better estimate.
- (3) No better entry.
- (4) To be estimated, if necessary, from the preceding estimation.

Appendix 2. Main statistical parameters for estimating probabilities with the juvenility index (JI).

$\log {}_a q_x$	Explicative variable	a_0	a_1	$R^2 adj$	$\sigma \log {}_a q_x$	Number of tables	r value
$\log {}_1 q_0$	log JI	-0.335	0.441	0.823	0.042	129	+0.01
$\log {}_1 q_4$	log JI	-0.365	0.573	0.808	0.054	128	
$\log {}_5 q_5$	log JI	-0.387	1.065	0.979	0.030	163	
$\log {}_5 q_{10}$	log JI	-0.879	0.787	0.886	0.054	163	
$\log {}_1 q_0$	log JI	-0.318	0.437	0.822	0.042	129	+0.0075
$\log {}_1 q_4$	log JI	-0.327	0.580	0.803	0.056	131	
$\log {}_5 q_5$	log JI	-0.346	1.052	0.977	0.032	164	
$\log {}_5 q_{10}$	log JI	-0.846	0.780	0.895	0.052	162	
$\log {}_1 q_0$	log JI	-0.310	0.423	0.808	0.042	129	+0.005
$\log {}_1 q_4$	log JI	-0.316	0.565	0.804	0.055	129	
$\log {}_5 q_5$	log JI	-0.303	1.043	0.974	0.034	165	
$\log {}_5 q_{10}$	log JI	-0.811	0.777	0.904	0.050	161	
$\log {}_1 q_0$	log JI	-0.285	0.427	0.810	0.043	131	+0.0025
$\log {}_1 q_4$	log JI	-0.294	0.557	0.801	0.055	129	
$\log {}_5 q_5$	log JI	-0.264	1.029	0.970	0.036	166	
$\log {}_5 q_{10}$	log JI	-0.779	0.770	0.901	0.051	163	
$\log {}_1 q_0$	log JI	-0.272	0.419	0.809	0.043	132	0
$\log {}_1 q_4$	log JI	-0.253	0.568	0.806	0.057	132	
$\log {}_5 q_5$	log JI	-0.222	1.019	0.968	0.037	167	
$\log {}_5 q_{10}$	log JI	-0.750	0.758	0.913	0.048	163	
$\log {}_1 q_0$	log JI	-0.252	0.416	0.807	0.043	131	-0.0025
$\log {}_1 q_4$	log JI	-0.272	0.529	0.804	0.053	125	
$\log {}_5 q_5$	log JI	-0.185	1.004	0.964	0.039	166	
$\log {}_5 q_{10}$	log JI	-0.714	0.754	0.914	0.047	162	
$\log {}_1 q_0$	log JI	-0.243	0.403	0.818	0.040	126	-0.005
$\log {}_1 q_4$	log JI	-0.263	0.513	0.805	0.052	123	
$\log {}_5 q_5$	log JI	-0.146	0.991	0.961	0.041	166	
$\log {}_5 q_{10}$	log JI	-0.679	0.750	0.922	0.045	161	
$\log {}_1 q_0$	log JI	-0.229	0.398	0.810	0.041	127	-0.0075
$\log {}_1 q_4$	log JI	-0.245	0.505	0.801	0.052	123	
$\log {}_5 q_5$	log JI	-0.107	0.978	0.957	0.043	166	
$\log {}_5 q_{10}$	log JI	-0.646	0.744	0.929	0.043	160	
$\log {}_1 q_0$	log JI	-0.211	0.394	0.825	0.040	124	-0.01
$\log {}_1 q_4$	log JI	-0.227	0.497	0.799	0.053	123	
$\log {}_5 q_5$	log JI	-0.070	0.965	0.953	0.045	166	
$\log {}_5 q_{10}$	log JI	-0.614	0.736	0.931	0.042	160	

^a (When $R^2 < 0.8$, the quality of the regression equation is not good, replace with JI entry for a better estimate.)

Appendix 3. Main statistical parameters for estimating probabilities with the indicator P.

$\log_a q_x$	Explicative variable	a_0	A_1	$R^2 adj$	$\sigma \log_a q_x$	Number of tables	r value
$\log_1 q_0$	log P	-0.211	0.637	0.808	0.044	127	+0.01
$\log_1 q_4$	log P	-0.268	0.748	0.763	0.057	120	
$\log_5 q_5$	log P	-0.139	1.479	0.908	0.063	162	
$\log_5 q_{10}$	log P	-0.641	1.164	0.909	0.048	162	
$\log_5 q_{30}$	log P	-0.907	0.469	0.807	0.030	93	
$\log_1 q_0$	log P	-0.193	0.627	0.817	0.043	125	+0.0075
$\log_1 q_4$	log P	-0.260	0.724	0.759	0.057	120	
$\log_5 q_5$	log P	-0.119	1.432	0.906	0.064	161	
$\log_5 q_{10}$	log P	-0.622	1.132	0.912	0.047	162	
$\log_5 q_{30}$	log P	-0.896	0.459	0.811	0.030	93	
$\log_1 q_0$	log P	-0.185	0.608	0.808	0.044	126	+0.005
$\log_1 q_4$	log P	-0.251	0.700	0.754	0.058	120	
$\log_5 q_5$	log P	-0.100	1.387	0.903	0.065	160	
$\log_5 q_{10}$	log P	-0.603	1.101	0.914	0.046	162	
$\log_1 q_0$	log P	-0.186	0.576	0.805	0.042	123	+0.0025
$\log_1 q_4$	log P	-0.271	0.651	0.708	0.062	125	
$\log_5 q_5$	log P	-0.080	1.344	0.900	0.066	159	
$\log_5 q_{10}$	log P	-0.599	1.054	0.914	0.047	163	
$\log_1 q_0$	log P	-0.205	0.539	0.733	0.051	139	0
$\log_1 q_4$	log P	-0.251	0.649	0.679	0.068	131	
$\log_5 q_5$	log P		1.370	0.997	0.073	164	
$\log_5 q_{10}$	log P	-0.576	1.032	0.917	0.046	164	
$\log_1 q_0$	log P	-0.182	0.531	0.776	0.045	127	-0.0025
$\log_1 q_4$	log P	-0.204	0.653	0.635	0.077	141	
$\log_5 q_5$	log P	-0.561	1.000	0.915	0.047	163	
$\log_5 q_{10}$	log P	-0.806	0.644	0.680	0.070	143	
$\log_1 q_0$	log P	-0.166	0.519	0.800	0.043	122	-0.005
$\log_1 q_4$	log P	-0.259	0.584	0.649	0.069	131	
$\log_5 q_5$	log P		1.248	0.997	0.072	160	
$\log_5 q_{10}$	log P	-0.541	0.975	0.914	0.047	163	
$\log_1 q_0$	log P	-0.165	0.497	0.800	0.042	120	-0.0075
$\log_1 q_4$	log P	-0.251	0.566	0.643	0.069	131	
$\log_5 q_5$	log P		1.194	0.997	0.074	160	
$\log_5 q_9$	log P	-0.521	0.951	0.913	0.047	163	
$\log_5 q_{50}$	log P	-0.289	0.605	0.813	0.045	121	
$\log_1 q_0$	log P	-0.181	0.470	0.720	0.050	133	-0.01
$\log_1 q_4$	log P	-0.242	0.550	0.636	0.070	131	

$\log_a q_x$	Explicative variable	a_0	A_1	$R^2 adj$	$\sigma \log_a q_x$	Number of tables	r value
$\log_5 q_5$	log P		1.145	0.997	0.078	161	
$\log_5 q_9$	log P	-0.501	0.927	0.911	0.048	163	
$\log_5 q_{50}$	log P	-0.305	0.568	0.802	0.046	124	

^a (When $R^2 < 0.8$, the quality of the regression equation is not good, replace with JI entry for a better estimate.)

Chapter 5

THE HALLEY BAND FOR PALEODEMOGRAPHIC MORTALITY ANALYSIS

Marc A. LUY¹, Ursula WITTEW-BAKOFEN²

¹ *University of Rostock, Germany*

² *University Clinics Freiburg, Germany*

Abstract: This paper suggests a computer aided procedure for the direct transformation of an age at death distribution into a stationary Halley type life table, which can be used for the mortality analysis of skeletal populations. It is based on demographic methods and takes into consideration the uncertainty given by the wide age ranges estimated for each of the individual skeletons. The main difficulty connected with the mortality analysis of a prehistoric graveyard is the wide age range of the age estimations based on morphological age traits in the skeleton, whose width for each of the skeletons within a population depends on the state of preservation and the applied methods for age estimation. The method developed here is based on the idea of the Monte Carlo simulation in extracting a random age at death out of the given age range for each skeleton in order to construct a stationary life table population. If this procedure is repeated for a sufficient number of extractions, this will lead to a relatively narrow bundle of Halley type life tables, characterizing the specific mortality pattern of the observed skeletal population and including the uncertainty resulting from the individual age estimations. The limits of the final Halley band can be defined by including only the inmost 95% of age-specific $l(x)$ values for the single Halley type life tables. A number of test simulations show that this method provides robust and informative results for paleodemographic mortality analysis

INTRODUCTION

The reconstruction of survival conditions is one of the major goals of the study of historical graveyards, for which no written data of registered deaths exist. In paleodemography this is mainly reached by first of all estimating the individual age at death of each skeleton and then matching

them in order to get information on the mortality pattern of the whole skeletal population. Basically, the chances of processing and interpreting paleodemographic data are limited, as their quality does not compare to the data based on an official registration of a population. Thus, not even the question, whether the information gained is suitable to describe the demographic situation of a past population, can be answered adequately. It is not just a trivial statement that demographic calculations are possible for only that number of persons, which is fixed in the number of the skeletons (Dinkel et al., 2000). It has already been shown that several sources of errors in the basic data itself, as well as in the methods applied, prevent us from regarding a skeletal population as a sample representative for the underlying population itself (Acsadi and Nemeskeri, 1970; Wittwer-Backofen, 1988a,b; Milner et al., 2000). We shall however not be dealing with this question (see here Grupe et al., 2004).

In this paper we deal with the question, which methods are suitable for reconstructing the mortality pattern given the specific characteristics of a skeletal population, following several authors who recently started to intensify paleodemographic research again (Bocquet-Appel, 1994; Konigsberg and Frankenberg, 2002). The basic idea behind our approach is to transform an age at death distribution directly into a stationary Halley type life table. The method we propose takes the uncertainty of skeletal data into account and uses the basic idea of a Monte Carlo simulation. The suggested technique is based on former studies on life table construction in a paleodemographic context (Dinkel et al., 2000; Luy et al., 2001) where the idea of applying Monte Carlo respective bootstrap techniques according to Efron (1979, 1981, 1988) and Akritas (1986) has already been formulated. The final realization, however, is different from the approach presented in this paper (see in more detail Luy and Wittwer-Backofen, 2005). Our approach nor intends to construct a life table in the modern sense neither to produce confidence intervals for the classic life table parameters. To emphasize these specifications we designate the results of our method a “Halley band” in order to describe the mortality pattern of a skeletal population under the assumption of a stationary population.

The most successful way of a demographic mortality analysis is the construction of a life table, as this provides the most complete statistical description of the mortality conditions of a population (Pressat, 1972). On the basis of observed deaths the life table in general illustrates the development of a constructed hypothetical population over its lifetime experiencing the age-specific mortality rates of a specific time period. Because of these specific features a life table with its standardized parameters is a useful

basis for the comparison of mortality characteristics of different populations or of one specific population at different periods of time. Note, however, the application of the life table concept in anthropology is problematic. In paleodemography it has been demonstrated generally (Weiss, 1976; Sattenspiel and Harpending, 1983) how misleading interpretations of life tables may be, if fertility and population growth are not considered. This has been exemplified for the interpretation of the demographic transition to agriculture (Johansson and Horowitz, 1986). Nevertheless, we will show that under specific assumptions and preconditions the logic of a life table can be useful in order to describe the mortality pattern of a skeletal population.

The major input for a life table is the age at death of the members of the analyzed population. However, even this basic data causes problems for paleodemographic mortality analysis. For several years now, the question of age estimation has been asked by anthropologists, who developed different single trait and multi trait methods for estimating the age at death of a skeleton (see Buikstra and Ubelaker, 1994; Kemkes-Grottenthaler, 2002). The “complex method”, suggested by Nemeskeri et al. (1960), is one of the most frequently applied methods in Europe, since a group of European anthropologists provided tables for the age estimation from the trait stages (N.N., 1980). Several new techniques for estimating age at death as precise as possible have been added to this multi-trait method (Buckberry and Chamberlain, 2002; Boldsen et al., 2002; Wittwer-Backofen et al., 2004). Even though the Nemeskeri method is criticized by its use of modern Hungarian autopsy cadavers and its effect of an attraction to the middle (Kemkes-Grottenthaler, 1996, 2002; Jackes, 2000), it has recently been shown in double-blind evaluation studies of different internationally applied aging methods to an known age sample and a historical skeletal population, that age estimations derived from the “complex method” are within the same error ranges compared to alternative methods (Max Planck Gesellschaft, 2004, 2006; Wittwer-Backofen et al., in prep.). However, an exact age estimation is almost impossible, due to the unknown correlation of chronological and biological age of the individual, a question, which was addressed in intensive discussions (Bocquet-Appel and Masset, 1996; Jackes, 2000, 2003; Konigsberg and Frankenberg, 2002 and several more). The use of modern reference samples for the development of methods to be applied for historical skeletons has been criticized in detail and led to tests showing an a priori probability of the resulting age distribution which mirrors the age composition of the reference sample (Bocquet-Appel and Masset, 1982; Langenscheidt, 1985, see an overview in Usher, 2002). This fact led to critical discussions in anthropology even demanding to

reject the whole concept of paleodemographic research (Bocquet-Appel and Masset, 1982; Van Gerven and Armelagos, 1983; Konigsberg and Frankenberg, 2002).

Usually age at death estimation is only possible within a certain age range leading to intervals of different length. Under the worst circumstances human remains may be in a state of preservation, that barely allows distinguishing a child from an adult and sometimes not even that¹. It has been suggested to calculate the *probability* of a skeleton belonging to a particular age using Baye's theorem instead of fixing it into an age class with the same statistical probability of all distinct ages (Hoppa and Vaupel, 2002; Lucy et al., 2002). But in spite of this discussion about the method of calculation, the resulting age is not a concrete age, but is given in a certain interval of years. This also has to be taken into consideration when constructing a paleodemographic life table.

The method we suggest in this paper will be demonstrated on the basis of a specific dataset of a skeletal sample which was excavated in the Black Sea Coast region of Turkey near Samsun. The site named Ikiztepe (twin hill) hosted an early Bronze Age II and III graveyard (2nd half of the 3rd millennium BC). The skeletons come from single graves in stretched position and are extremely well preserved due to specific conditions of the soil. The graveyard is almost completely excavated and the buried population contained 673 individuals. The large amount of grave goods suggests that Ikiztepe was a trading settlement which achieved a certain degree of prosperity. Compared to other skeletal populations Ikiztepe is characterized by a relatively high proportion of infants and other subadults below the age of 20 (48% of all individuals). However, a certain amount of individuals below the age of 5 years are still missing, compared to modern populations under pre-industrial living conditions. Therefore, we limit the analysis of mortality to adulthood, even though in principal the method can be applied to all age classes.

Ikiztepe provides some of the most important materials of the early bronze age, because of its size, the good state of preservation and its completeness (see Wittwer-Backofen, 1985, 1987; Alkim et al., 2003), and it is therefore particularly suitable for the application of the method suggested here. The proportion of males to females is almost balanced, showing a slight male surplus. Individual age estimation was carried out according to the multi-trait "complex method" (N.N., 1980). As an effect of the relatively high amount of infants and children, which can be estimated almost without errors, the mean interval of the age at death of this population is 11.59 years. By leaving out the subadults below an age of 20, the mean of the individual age at death interval covers 19.89 years.

THE BASIC IDEA FOR THE CONSTRUCTION OF A HALLEY BAND

The basic problem of individually varying age intervals as resulting from the anthropological age estimation is demonstrated in table 1 for six individuals out of the Ikiztepe skeletal collection. It describes a typical situation as seen for skeleton No 1 which just indicates the person as having been an adult while for others like skeletons No 3, 672 or 673 it was possible to estimate the ages at death more precisely. As a basic starting point, the maximum age for the Ikiztepe skeletal population has been limited to 80 years, because a more exact estimation within the senile age group usually cannot be obtained while a maximum limit has to be defined to apply the life table technique. However, the defined maximum age limit has specific implications to the results obtained with the proposed method, as will be shown in a subsequent chapter.

The questions we deal with in this paper are: “How can we gain demographic information on the mortality conditions of the observed skeletal population out of such data?” and “How can the mortality pattern of the analyzed population be reconstructed with such individual age intervals?” Using only one specific age out of the anthropologically estimated range obviously would neglect the fact, that each age within the range has a certain probability regardless of the method chosen for age estimation. The example of skeleton1 in table 1 shows that it is impossible to represent the knowledge about the age at death of this individual with one single value. Each of the

Table 1: Age-estimated skeletons with different age-at-death intervals and extraction of exact ages at death out of the given age intervals by a random generator assuming equally distributed probabilities for the same skeletons

Skeleton No.	1	2	3	...	671	672	673
Age at death, lower limit	25	4	31	...	60	13	50
Age at death, upper limit	60	8	40	...	80	14	56
Age in drawing 1	44	6	35	...	78	13	55
Age in drawing 2	56	4	31	...	63	14	56
Age in drawing 3	57	8	40	...	76	14	52
Age in drawing 4	37	8	40	...	62	14	54
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
Age in drawing 497	45	5	33	...	80	14	56
Age in drawing 498	59	7	40	...	61	14	51
Age in drawing 499	36	5	35	...	68	13	53
Age in drawing 500	60	4	34	...	62	13	50

36 different possible ages at death might be true (we look at completed ages at death only rather than at exact ages in years, months, and days, what, however, could be done, too). Consequently, it is impossible that one single characteristic life table can be constructed for such a skeletal population. The task of paleodemographic mortality analysis should rather be to use the whole range of possible age at death distributions in order to derive a somehow estimated area, in which the “true” life table of the skeletal population is located with a certain probability. The width of this area of possible life tables must be determined by the individual age ranges and thus representing the basic uncertainties about the ages at death of each skeleton.

Every life table by definition represents a stationary population since the number of births (or individuals alive at the starting point of observation) is identical with the final number of deaths. This does not imply that the real population behind the life table must also be stationary and it does not imply that stationary conditions have to be assumed for this population. In modern demography the age-specific probabilities of dying are derived from the number of deaths and the risk population behind these deaths. However, in paleodemography information about the latter is usually not available. Only the number of deaths is known in combination with some information regarding the age at death distribution. In principle, the only possibility to construct a life table is to sum up all deaths and to treat them directly as a life table population. This is equivalent to the way most life tables of the 18th and 19th century have been constructed. In the demographic literature, this method of constructing a life table from ages at death only is referred to Halley 1693 known as “Halley method” (c.f. Moser, 1839, Shryock and Siegel, 1971). Since any paleodemographic analysis can only be based on deaths we call the area including the possible life tables derived from the given range of possible age at death distributions that results from our proposed method a “*Halley band*”. It works in the way that a skeletal population with on average more narrow individual age ranges results in a narrower Halley band with higher precision, compared to a population with broad individual age ranges. Note that the use of the given age at death distribution as a direct stationary life table population is not a restrictive necessity of the proposed method. If any information exist about the growth rate of the population observed than this information can be used for constructing a Halley band based on the corresponding stable growth rate (for a more detailed description of the connection between stationary and stable populations see Preston et al., 2001 or Keyfitz and Caswell, 2005).

We start our considerations with the fact that the “true” life table of a skeletal population must range within the limits defined by the lowest and highest possible ages for the observed individuals. In order to define this range

we have to construct two Halley type life tables in which first of all for each person the lowest age limit and then the highest age limit is used (Figure 1). Both curves start with a standardized $l(x)$ value (=“living persons at age x ”) of 10,000 living persons at age 20, which then decreases successively to the age of 75. For constructing these curves we preferred the demographic life table logic with a standardized number of individuals at age 20 to the real number from skeletal data because of a methodological reason. If we start with the 673 Ikiztepe individuals and subtract the number of deaths in ages 0, 1, 2, etc. we got 370 survivors at age 20 according to the maximum and 320 survivors at age 20 according to the minimum age at death distribution. Consequently, there would be an interval for the number of survivors in age 20. Since we intend to skip the pre-adult ages and thus start our analysis with age 20 we consider only individuals living at age 20. Thus, both curves have to start with the same number of survivors at age 20.

Obviously the curves could likewise start with any other number of survivors at age 20, e.g. 673, 370, or 320. Neither the shape of the curves presented in Figure 1 nor the resulting average age at death would be affected. Standardizing the survivorship curves to an initial value of 1, 100, 10,000, or 100,000 however allows the direct interpretation of $l(x)$ values as probabilities. For instance, the number of 7,500 survivors at age 25 according to the life table resulting from the minimum age at death distribution means that the probability to reach age 25 when being alive

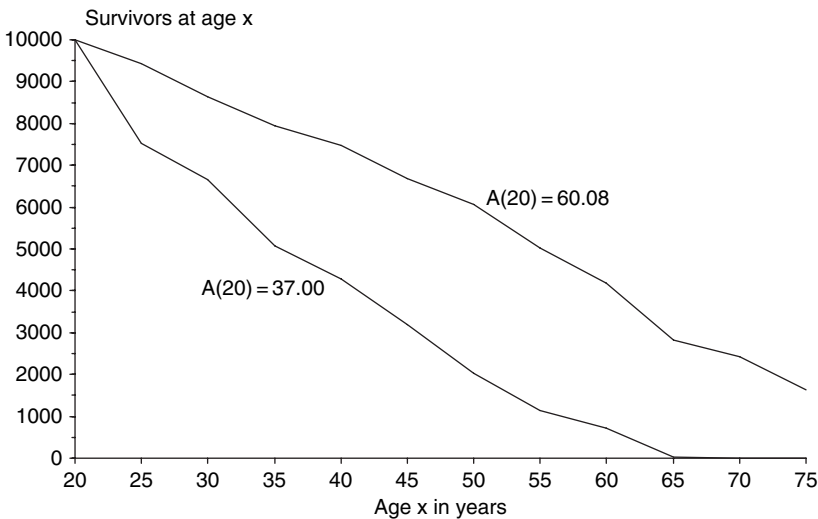


Figure 1: Halley type life tables from age 20 for the Ikiztepe skeletal population using the upper and lower limits of the individual age intervals

at age 20 is 75 percent. This characteristic of a life table shows again the necessity of both curves starting with the same number of survivors. Finally, such survivorship curves enable to determine the average age at death of individuals being alive at age 20. In the case of a stationary population the average number of years lived until death is identical to the well known life table parameter “life expectancy at age 20”, symbolized by $e(20)$. As already described, a paleodemographic life table can only be calculated from a certain number of deaths. With the intention of stressing this decisive difference to modern demographic life tables we refrain from using the parameter “life expectancy at age x ” and use instead the parameter “average age at death from age 20”, symbolized by $A(x)$. While $e(x)$ represents the average number of years lived by people being alive at age x until their death, $A(x)$ represents the average age at death of individuals being alive at age x . Thus, $A(x)$ can easily be derived by

$$A(x) = e(x) + x. \quad (1)$$

If the analysis starts at birth the average age at death $A(0)$ can be calculated directly from the single ages at death (and is identical to $e(0)$). If the analysis starts at a higher age x (like it is the case in this paper) the ages at death have to be transformed into a Halley type life table.

The two survivorship curves presented in Figure 1 can be interpreted as minimum and maximum limits for the stationary life table resulting from the given uncertainties in the age at death distribution of the analyzed skeletal population. For the Ikiztepe case, the corresponding maximum uncertainty in the average age at death from age 20 $A(20)$ lies between 37 years and 60 years (with $A(20) = e(20) + 20$). This high range shows that these extreme limits cannot be used in order to gain useful demographic information, even if, as in the case of the Ikiztepe population, they are more precise than in most other skeletal populations of that time. On the one hand the resulting variation is obviously too high and on the other hand the probability, that all of the individuals died in fact at the lowest or highest age given in the intervals, is nearly zero. But what is the most probable life table for this population resulting from the given age at death distribution?

The basic idea of the solution we propose in this paper is that each single age within the given age range is treated as a possible true age at death. The decisive question is whether these numbers of theoretically possible ages at death are to be treated with the same probability or if certain ages are more probable than others. Analyzing the Ikiztepe skeletal population we assume that each age lying within the age range has the same probability of being

the true age at death. However, the application of any other distribution function is also possible. The method we propose allows choosing any other alternative probability function within the age ranges as is demanded in the Rostock agreement mentioned before².

Using the equal probability distribution over the individual age ranges, we randomly determine for each skeleton an estimate for a specific point within the age range. From this age for each skeleton results a specific age at death distribution that can be transformed into a Halley type life table as has been done in Figure 1 with the lower and upper limits of the individual age ranges. The now resulting life table provides one possible outcome that must be located between the two minimum and maximum survivorship curves, depending on the specific random sampling. The procedure results in a life table closer to the maximum border curve, if for a greater number of individuals ages close to the upper individual age range are drawn and vice versa. However, also the life table constructed from a random drawn age at death distribution in the described way cannot be interpreted as being representative for the observed skeletal population, as it represents just one of an infinite number of possible solutions like the minimum and maximum survivorship curves from Figure 1 do. The decisive idea to overcome this problem with the method proposed here is to have frequent random draws (e.g. 500 times) and to calculate as many age at death distributions and corresponding life tables as draws have been made. It can be seen from the results gained, to which extent the resulting survivorship curves vary and whether their distributions are bundled in specific areas or not. If out of all gained $l(x)$ values (number of survivors at age x according to the applied life table logic) the lowest and highest 2,5% are cut off, the 95% borders of survivorship curves out of all 500 Halley type life tables can be determined. On condition that this procedure yields robust results, the resulting Halley band provides an area including possible and most probable life tables resulting from all possible age at death distributions and representing the mortality pattern of the observed 673 individuals with a probability of 95%.

THE CONSTRUCTION OF A HALLEY BAND FOR THE IKIZTEPE SKELETAL POPULATION

The proposed procedure will be illustrated in the following, based on the Ikiztepe data set. Figure 2 documents the distribution of 500 random drawings for exact ages at death of a skeleton with an estimated age range of 31 to 40 years. According to the basic assumption of equal probability, the

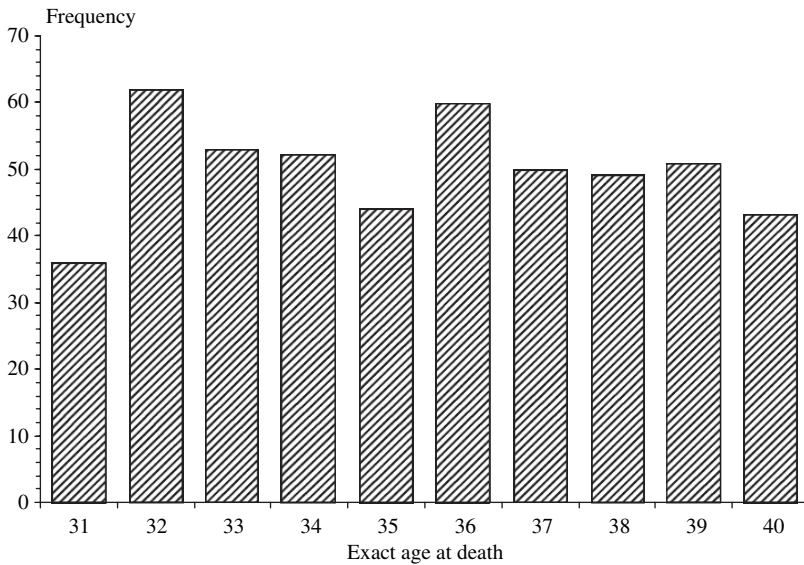


Figure 2: Distribution of 500 randomly extracted exact ages for a skeleton with the age range of 31–40 when equal probabilities are assumed for single age-at-death

500 drawn ages for this individual are approximately equally distributed. As can be seen in table 1, each run of random drawings results in 673 (number of skeletons in the population) exact ages at death and Halley type life tables based on the resulting age at death distributions can be constructed as described in the previous chapter. Thus, the simulation run no 1, based on the randomly drawn age at death for each skeleton, leads to age at death distribution 1, the simulation run no 2 leads to age at death distribution 2, and so on. Figure 3 shows for age 55 that the resulting $l(x)$ values of the Halley type life tables do not follow an equal random distribution, but show a normal distribution. This is a result of the fact that it is unlikely that all individuals died at ages close to the lower or upper limit of their specific age ranges. For some individuals the random generator draws ages close to the upper limit, for others ages close to the lower limit, and for the rest ages somewhere in between (see in more detail Luy and Wittwer-Backofen, 2005).

In the next step the highest and lowest 2,5% of the $l(x)$ distributions are removed from the sample, resulting in an empirically determined 95% Halley band, whose shape and size is based on the given age span of the 673 individuals exclusively (Figure 4). Comparing the results with the survivorship curves derived from the upper and lower limit age at death

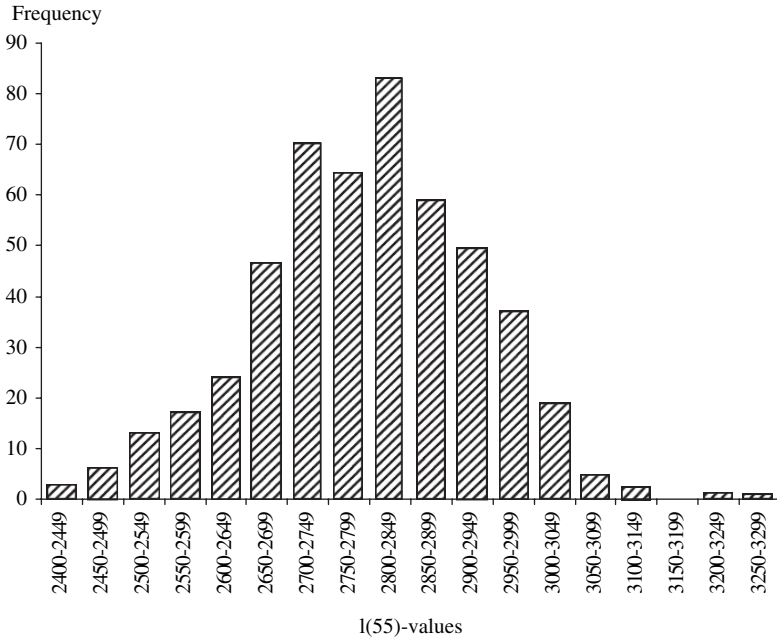


Figure 3: Distribution of $l(55)$ -values for the Halley type life table for the Ikiztepe skeletal population resulting from 500 random draws (for a simulation with 10,000 survivors at age 20)

distributions, it becomes obvious, that in spite of considering all uncertainties, the results bundle within a surprisingly narrow area. The reason for this can be found in Figure 3, showing the almost normal distribution of the resulting $l(x)$ values. According to the Halley band the average age at death from age 20 ranges between 44.55 years and 46.41 years. Thus, the remaining uncertainty is less than two years (compared to 23 years when using the upper and lower age range limits). Compared to the basic situation, in which there was no statement on survival conditions possible, with the proposed method we now are able to achieve information that can be used to describe a mortality pattern characterizing the skeletal population in a very distinct way.

Note, however, that this procedure does not provide confidence intervals for each of the $l(x)$ values or for the whole survivorship curve. The task of a confidence interval (respective confidence band) is to gain information on the unknown basic population on the basis of a sample (for life table analysis see Luy, 2004). However, in the case of a skeletal population this is basically impossible since the analysis is based on deaths

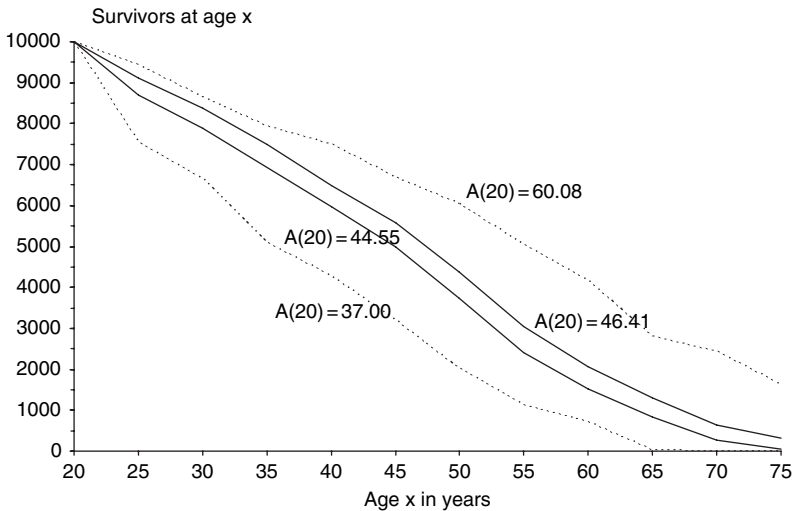


Figure 4: (95%-) Halley band from age 20 for the Ikiztepe skeletal population using 500 random draws (solid lines) in comparison to the Halley type life tables resulting from the upper and lower limits of the age range (dotted lines)

of the particular population only. Accordingly, the Halley band does not describe the life table of an unknown basis population, but describes the survivorship curve derived from the age at death distribution of the given stationary skeletal population. The width of the band expresses exclusively the anthropological uncertainty of the individual age estimations. In the example presented here the Halley band provides the 95% range of uncertainty for the survivorship curve of the 673 individuals of the Ikiztepe graveyard.

THE HALLEY BAND IN COMPARISON TO ALTERNATIVE ESTIMATIONS FOR THE SURVIVORSHIP CURVE

A comparison of the Halley band gained by the proposed method with the survivorship curves derived from the upper or lower range limits as done in the previous chapter provides no useful information about the functionality of the Halley band method. Therefore a better starting point for testing its analytical power is a Halley type life table resulting from the mean age at death within each individual age range (a). An

alternative solution applied more frequently in anthropology is the so called “*proportional method*” (b). Following this concept the individuals are split up with equal probability into their individual age intervals. In this method, a skeleton with an estimated age at death of 20 to 30 years is split into each of the age groups 20–25 and 25–30 with the probability of 0.5. A skeleton with an estimated age at death between 38 and 50 years is put to 2/13 into the age interval 35–40, to 5/13 into the age interval 40–45, to 5/13 into the age interval 45–50 and to 1/13 into the age interval 50–55 (for the mathematical description of the procedure see Boldsen, 1988). Another approach favoured by Boldsen (1988), is the “*Maximum-Likelihood-Method*” (c). Basically it claims a variation in the probability distribution of each single age class within the individual age at death intervals according to their weight with other overlapping age intervals. Therefore it constructs a dependency between the observations in the reconstructed mortality regime. The concept of weight functions is as well used in an approach starting from a given skeletal age-at-death, the probability of assigning a skeleton into a specific stage is estimated, followed by the construction of a sample-based age profile, with the individual age estimation as a last step (Müller et al., 2002).

- (a) The approach of using the *mean age at death* for the so constructed survivorship curve would lead to distorted results. The reason for this is that in this situation all individuals of limited preservation which led to age estimates ranging from 20 to 80 years automatically receive an age at death of about 50 years. The outcome of the corresponding life table thus shows a much too low mortality in young adult ages because many individuals actually did survive up to the age of 50. Above the age of 50 the life table keeps too low, because of the high number of deaths in the age group of 45 to 55 years. Consequently, a survivorship curve based on the assumption of mean ages describes a pattern far away from a realistic mortality pattern for human populations (Figure 5).
- (b) According to the “*proportional method*” an age at death distribution is constructed, which represents one possible outcome based on the given age at death ranges. The corresponding life table is expected to lie inside the proposed Halley band, although it has not necessarily to lie exactly in the middle. This comparison can be seen in Figure 6. Although the proportional method seems to be a useful solution, it does not account for the uncertainty of the basic data as does the Halley band. Hence this procedure provides one possible Halley type

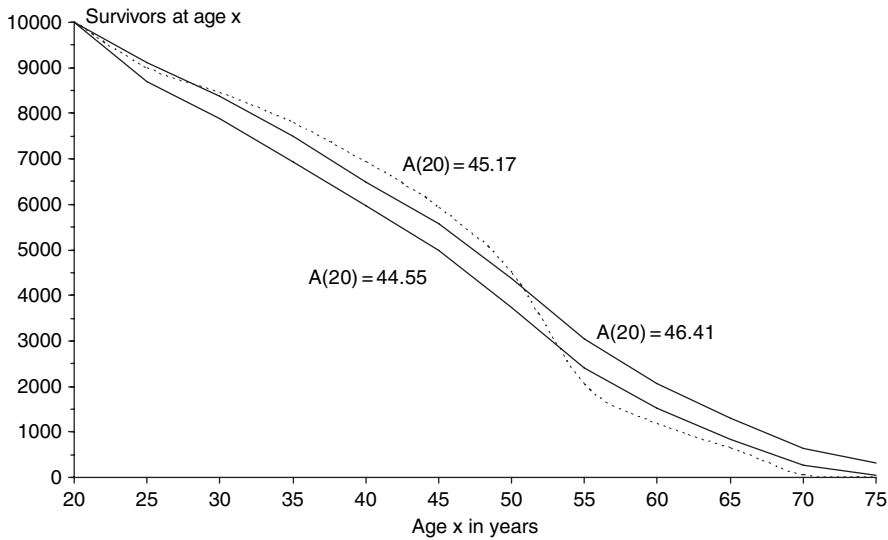


Figure 5: (95%-) Halley band from age 20 for the Ikiztepe skeletal population using 500 random draws (solid lines) in comparison to the Halley type life table corresponding to the means of the intervals for ages at death (dotted line)

life table which by no means is more likely than any other single survivorship curve within the constructed Halley band. Consequently, the proportional method does not represent a reasonable alternative to the Halley band, which therefore should be preferred in order to reach the specific aims of paleodemography. Since both alternatives to the Halley band (mean of age range and proportional method) presented here characterize the mean of all age at death intervals (but by different approaches) the resulting average age at death of the skeletal population must be identical. This is the case, since the value for $A(20)$ is 45.17 years in both cases (see Figures 5, 6).

- (c) The “*Maximum-Likelihood-Method*” leads to the fact that the persons do not enter the analysis with the same weight, but each person with a different weight. This is, however, not compatible to the logic of the demographical idea of life table construction. Moreover, it leads (like the other discussed alternatives) to a single age at death distribution with corresponding survivorship curve which additionally does not reflect the true information in the given data. Due to these reasons none of the traditional anthropological procedures can be regarded as reasonable alternative to the idea of the Halley band.

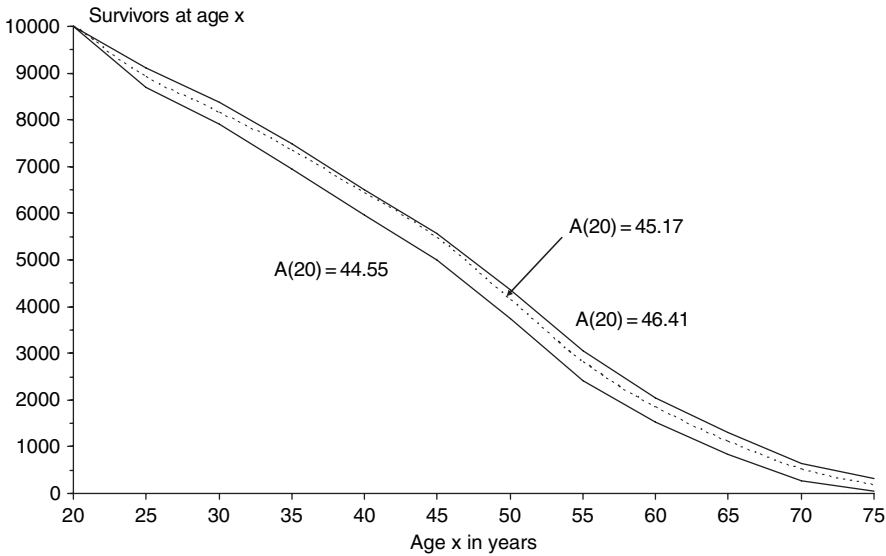


Figure 6: (95%-) Halley band from age 20 for the Ikiztepe skeletal population using 500 random draws (solid lines) in comparison to the Halley type life table corresponding to the proportional method (dotted line)

THE ROBUSTNESS OF THE HALLEY BAND WITH VARIATIONS OF THE AGE AT DEATH INTERVALS

In order to introduce the construction of Halley bands into the demographic analysis of anthropological data this procedure has to undergo a variety of test simulations. In this chapter we are going to vary the given age intervals of the Ikiztepe skeletal population in a way that specific results are to be expected if the method leads to reasonable and correct results. For this purpose the method will be tested in four different test simulations which are demonstrated in Figure 7. In a first test (a) all individual age ranges are reduced by raising the low limit half the span between low limit and mean of age. For the example given in Figure 7 follows that the age span of the individual with the original estimate of 30 to 50 years will be changed to 35 to 50 years. For each person the lower half of the age span is reduced by 50% and thus the uncertainty about the age at death is reduced also. In the given example the uncertainty is lowered from 20 to 15 years. In the second test (b) the same procedure is applied but decreasing the upper limit by half of the span between mean and upper limit. The lower limit

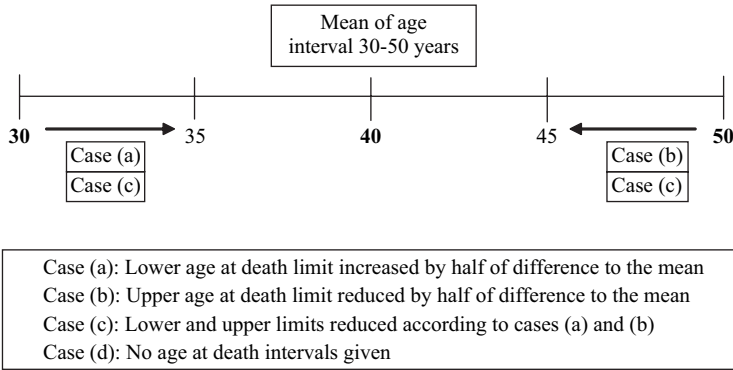


Figure 7: Variations in the given age-at-death intervals for testing the Halley band

holds the original value. Here, the test person in Figure 7 receives the age span of 30 to 45 years. The third test (c) combines both previous conditions, reducing the upper as well as the lower age limit, so that the test person receives a new age span of 35 to 45 years. Finally, the last test (d) simulates a situation presuming that no specific age range is known for all of the individuals. Thus, all individuals enter the simulation with an age at death interval of 0 to 80 years, which is defined as the highest possible age.

What is the expected outcome of these model simulations? Which results does an accurate and reasonable method have to provide? In comparison to the basic situation in case (a) two relevant variations occur: the age spans become narrower and the means of the age ranges increase. Consequently, higher $l(x)$ values for the Halley band are expected, combined with an accordingly higher average age at death from age 20, $A(20)$, and additionally the confidence area, i.e. the width of the band, will become smaller compared to the original analysis. The latter is also expected even for test case (b) in which lower $l(x)$ values together with lower values for $A(20)$ should result. Compared to these situations conclusions concerning the combined test simulation (c) cannot easily be formulated a priori. Certainly, the bandwidth will be reduced further compared to the test simulations (a) and (b). Similarly, the result of case (d) cannot be foreseen clearly. The Halley band should include the line between $l(20)$ and $l(80)$ but the width of the band cannot be predicted. However, we can expect an uncertainty area of maximum width that enables one to evaluate the Halley band applied to the data of the Ikiztepe skeletal population.

The results of these test simulations can be found in the Figures 8a–8d. The test simulations (a) and (b) provide exactly the results expected

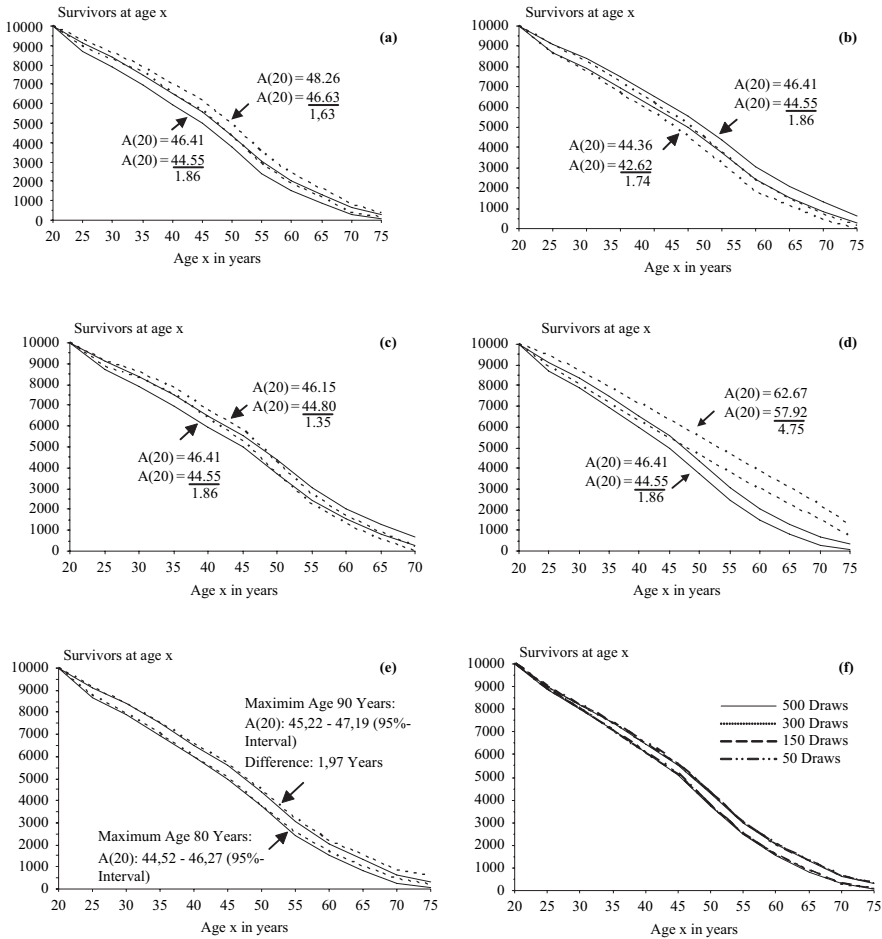


Figure 8: (95%-) Halley band from age 20 with highest possible age 80 for the Ikiztepe skeletal population using 500 random draws (solid lines) in comparison to test simulation (a) reduction of lower limit for ages at death; dotted lines; (b) reduction of upper limit for ages at death; dotted lines; (c) reduction of lower and upper limit for ages at death; dotted lines; (d) no information about ages at death; dotted lines; (e) a Halley band with highest possible age 90 (dotted lines); (f) Halley bands resulting from 300,150, and 50 random draws

according to the amount of $A(20)$ as well as to the reduction of the bandwidth (Figure 8a and 8b). The interval for the average age at death $A(20)$ reduces from 1.86 years (basic data) to 1.63 years (a) and 1.74 years (b). From the latter it becomes evident, that the width of the Halley band in fact is reduced, even though this does not become visually apparent from the graphs. According to what we expected, in test simulation (c) the bandwidth

is additionally reduced to 1.35 years. The Halley band starts between the age of 20 and 45 years above the Halley band for the original data and declines with higher ages below the original band (Figure 8c). At first sight this might be a puzzling result. It can be explained if we consider the Halley type life table resulting from the assumption of mean ages at death in all intervals (Figure 5). From Figure 8c it becomes obvious that the result from test simulation (c) approximates to these characteristics. Thus, the result is logical and correct when considering the fact, that due to the reduction of upper and lower limit the data are changed towards the mean of the age range. For the fact that the Halley band in the beginning lies above and for a higher age lies below the one of the basic data, the same reason as in the already described case of the “mean distribution” can be stressed.

The result of test simulation (d) is surprising. The lack of any knowledge about the individual ages at death is resulting in an unexpected narrow Halley band covering the diagonal in the diagram (Figure 8d). The uncertainty area for the average at death from age 20 $A(20)$ is 4.75 years and thus about 3 years broader than the Halley band for the original data. This is much less than expected. The pattern of the Halley band for test case (d) however, differs considerably with increasing ages to higher $l(x)$ values as compared to the Halley band for the Ikiztepe skeletal population. The unexpected similarity of the uncertainty between the Halley band with unknown ages to the one with the anthropological age at death estimates can be interpreted in the way that the individual age estimates for the Ikiztepe skeletons are in fact closer to the unknown situation as compared to precise ages at death. When having a closer look on the Ikiztepe sample, it becomes obvious that a large amount of skeletons have indeed rather broad age spans. This becomes evident when taking the average size of age at death intervals described in the introduction into consideration.

MODIFICATIONS OF THE HALLEY BAND BY VARIATION OF THE HIGHEST POSSIBLE AGE AT DEATH AND THE NUMBER OF RANDOM DRAWINGS

After the implications of individual age span variations have been simulated, we finally examine the influence of general methodological effects. It has to be tested, which impact on the Halley band is connected

with the decision of the highest possible age, which in the case of the Ikiztepe skeletal population has been set to the limit of 80 years. What effect does it have on the Halley band, if this limit varies using the same individual data? In principal defining such a limit does not automatically mean that a higher age at death can be completely excluded. The definition of such a limit results from the fundamental idea of the maximum life span in the past (Angel, 1947; Sacher, 1975; Hoppa and Vaupel, 2002).

In the case that all individuals, whose highest age at death cannot be fixed by anthropological methods, are defined with their maximum age span to the age of 90 years, reasonable Halley bands result, with a slightly higher degree of uncertainty, as the age span of the affected individuals is increased (see Figure 8e). The limits of variation for the average age at death from age 20 $A(20)$ is now 1.97 years. However, we hope that with the improvement of the methods used for individual age estimation (Wittwer-Backofen et al., 2004; Boldsen et al., 2002) these limits will be fixed better in the near future and thus will not remain objects of constant testing.

Finally it has to be looked at whether the Halley band based on random drawings is able to provide robust results. If this is the case, no influence on the results may occur starting from a specific number of drawings. To explore this, the Halley band method was applied to the basic Ikiztepe data with 50, 150 and 300 drawings (Figure 8f). None of these simulations differ significantly from the basic procedure which applied 500 drawings. This means, that the suggested number of drawings are absolutely sufficient to yield robust results. Additionally it shows that the method itself provides stable results. How large the number needs to be at least, depending from the number of individuals included in the analysis, has to be tested by further simulations. But it can be stated, that 300 or 500 drawings seem to be sufficient.

CONCLUSIONS

After the test simulations have been performed as described above, it can be concluded that the Halley band suggested in this paper leads to a robust description of the most likely Halley type life table resulting from all possible age at death distributions of a skeletal population. This method is compatible to demographic methods and provides results which can be interpreted in a significant and meaningful way. Compared to other methods, the Halley band provides a characteristic mortality pattern without weighting

those individuals with smaller age ranges higher than those with broader age ranges, as it is performed with the “Maximum Likelihood Method”. Thus, in spite of a high degree of uncertainty, important demographic information can be extracted. This shows that the proposed Halley band is able to provide anthropologically relevant information on the specific mortality conditions of the observed population.

As described, the equal probability distribution adopted here is in line with traditional anthropological techniques. However, this assumption is a matter of intensive discussion in anthropology and can be adjusted to any other distribution function. Instead of the traditional methods, especially data, the Bayes’s theorem is applied to (Hoppa and Vaupel, 2002; Lucy et al., 2002) should be used in the future. It is possible that the pattern described by the Halley band as well as the amount of uncertainty will differ from those resulting from the assumption of equal probability.

Finally it has to be emphasized that the method proposed here does neither provide a new method of age estimation nor a technique for the estimation of confidence intervals or confidence bands in a statistical meaning. To account for this, we tried to abstain from using these statistically well defined terms. In order to define such confidence intervals, specific procedures need to be developed which start from the Halley band suggested here. The width of the Halley bands accounts for the uncertainty in the anthropological age estimations and does not refer to the basic population in a statistical sense. Whether at all such a trial makes sense remains doubtful considering the question of representativeness of a skeletal sample. The suggested procedure of constructing Halley bands adds to the anthropological investigation and refers to the demographic analysis of the available data. For this purpose the Halley band seems to be a more useful method compared to other common methods as it accounts for the inevitable uncertainty given in the data itself. All other restrictions of paleodemographic research cannot be corrected by demographic methods and must be kept in mind while interpreting data of ancient populations.

NOTES

¹ It might not even be possible to determine the sex of those skeletons with sufficient probability. Since in this paper we do not carry out a sex-specific analysis this problem is not an issue in the application of the method introduced here.

² In order to apply another probability function, another specific mathematical algorithm has to replace the assumption of equal probability.

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Chapter 6

MODELING PALEOLITHIC PREDATOR-PREY DYNAMICS AND THE EFFECTS OF HUNTING PRESSURE ON PREY ‘CHOICE’

Mary C. STINER¹, Joseph E. BEAVER¹, Natalie D. MUNRO² and Todd A. SUROVELL³

¹*University of Arizona, USA*

²*University of Connecticut, USA*

³*University of Wyoming, USA*

Abstract: Working from archaeofaunal trends in the Mediterranean Basin and modern wildlife data, we present a demographic interpretation of Paleolithic prey “choice” with the aid of computer simulation modeling. Archaeological indications of expanding dietary breadth with the onset of the Upper Paleolithic period associate with increasing exploitation of highly productive small animals and smaller ungulate species, despite the higher procurement costs of some of these prey types. The study of small game exploitation capitalizes upon the extreme differences in behavioral and reproductive ecology of the prey species with similar body sizes. Predator-prey simulation modeling of large hoofed animals (artiodactyls) was also undertaken, since these animals constituted the bulk of meat acquired by Paleolithic foragers, but the simulation results for the ungulate taxa do not provide the same crispness in the test implications needed for addressing questions about demography, diet breadth, and possible predator pressure over the course of the Paleolithic. The sustainable yields for the small ungulates are not definitively higher than those for the large ungulates, and thus the shift down the ungulate body-size spectrum that we see in the Mediterranean data is not in itself solid evidence of human demographic growth. Given demographic growth as shown by other, better evidence (small game data), we nonetheless can attribute the shift to smaller ungulates as being the result of the population growth. Increasing dependence upon high producers, even if total volume of meat acquired remains the same, could have meant a significant reduction in the composite (cooperatively pooled) variance in foraging success, albeit at the price of greater hunting effort

Zooarchaeological data from several world regions indicate that the collective human “footprint” on terrestrial ecosystems changed dramatically from the Late Pleistocene through Holocene periods, often in connection with increases in human population density. It is likely, as well, that directional shifts in human predator-prey relationships occurred and, further, that these changes played a significant role in the reorganization of subsistence labor in human societies. However, establishing connections between the archaeological patterns, demographic, and ecological processes is as challenging as it is interesting. Certain fundamental essays link changes in human trophic level, foraging efficiency, and demography, and these have been important for modeling predator-prey interactions that involve omnivorous foragers such as humans (e.g. Harpending and Bertram, 1975; Winterhalder and Goland, 1993). Other insights come from anomalies identified by zooarchaeological studies of Paleolithic human diet breadth.

Working from a base of archaeofaunal trends in the Mediterranean Basin (Figure 1) and modern wildlife data, we develop a demographic interpretation of prey “choice” with the aid of computer simulation modeling. This study began with a focus on small game exploitation that capitalized upon the extreme differences in behavioral and reproductive ecology of the prey species with similar body sizes. Differences in prey body size must also have been important from the predator’s point of view, as body size affects food yield. The second phase of study therefore focused on predator-prey simulation modeling involving large hoofed animals (mainly artiodactyls). Large mammals do not provide the same crispness in the test implications needed for addressing questions about demography, diet breadth, and possible predator pressure, despite their obvious importance in Paleolithic economics. Complete presentations of modeling mechanics and archaeological correlates appear in Stiner (2005), Stiner et al. (2000), and Beaver (2007).

The presentation has three major parts. The first is an introduction to the archaeological patterns that precipitated our attempts to model the relations between predator prey relationships and dietary breadth. The second part presents key aspects and results of the small-game modeling project. The third part summarizes the more recent modeling work on large game animals (Beaver 2007). The presentation ends with a discussion of properties of the modeling studies and research design that we believe were critical for providing lasting insights on Paleolithic diet, demography, and human behavioral evolution.

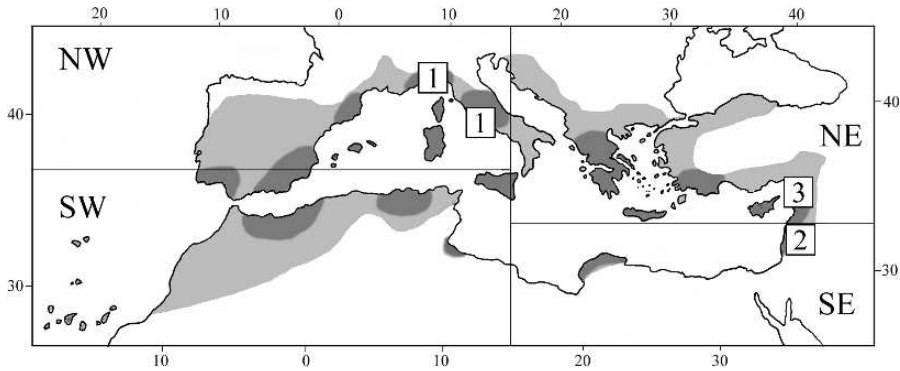


Figure 1: Geographical origins of the three Mediterranean faunal series: (1) western coast of Italy, with 16 assemblages; (2) Wadi Meged, inland Galilee of Israel, with 9 assemblages; and (3) Hatay coast of south-central Turkey, with 7 assemblages. Each faunal series originated in a distinct Mediterranean quadrant defined by somewhat distinct arrays of endemic species and environments. (Base map after Blondel and Aronson, 1999:8.) (Reproduced from Stiner, 2005.)

ARCHAEOLOGICAL BACKGROUND

Middle Paleolithic populations living between 250,000 and 35,000 years before present were quite carnivorous, more so perhaps than most human populations of later periods, and they relied most heavily on large hoofed game animals for meat. This fact placed these early foragers (including the Neandertals) at the top of the food chain. It therefore is not surprising that human populations of the period tended to be very small per unit land area (Stiner, 2005). It was only after the Last Glacial Maximum, and particularly after 13,000 years ago, that human hunting pressure on some ungulate populations led to unsustainable distortions in the structures of ungulate populations, as indicated by mortality patterns in archaeological sites and increasing reliance on high-turnover species. All of these shifts are in one way or another indicators of permanent expansions in human dietary breadth.

The breadth of forager diets can vary both within and between adaptations, depending upon the availability of high quality, high-yield foods (Pianka, 1978; Stephens and Krebs, 1986). Diet diversification is especially likely to occur when and where foragers put excessive pressure on preferred (a.k.a. highly ranked) resources, which in turn may force these resources into decline. A reduction in the predator population may occur as a result, or, rarely, changes in adaptation may occur instead.

The earliest indications of increasing dietary breadth in humans generally coincide with the transition from the Middle to Upper Paleolithic culture periods in the eastern Mediterranean Basin (Stiner 2001, 2003). Expansions in dietary breadth are most apparent from the relative emphasis Paleolithic people placed on a variety of quick versus slow-moving small animals, such as birds and lagomorphs as opposed to tortoises and shellfish. The most sensitive of the small prey populations in the Mediterranean Basin were tortoises (*Testudo* spp.) and certain marine shellfish such as limpets (*Patella* spp.). These prey animals can be abundant in some habitats yet represent the proverbial “canaries in the coal mine” for studying shifting human predator-prey interactions of the Pleistocene because of slow population growth rates (Stiner, 2001). No trend is apparent for the relative proportions (number of identified specimens, NISP) of ungulates and small game in most study areas (Figure 2). However, great changes took place in the *types* of small game emphasized by human foragers over 200,000 years, due mainly to the significant addition of birds and hares to Upper Paleolithic forager diets.

The classic models of prey choice and diet breadth assume that resources can be ranked in the energetic terms of the predator, according to the amount of nutritional return they yield relative to the cost of procuring them (Pianka, 1978; Stephens and Krebs, 1986). Broadly speaking, prey rank in the sense of relative nutritional payoff is directly related to some combination of body size and search and handling costs. Ethnographic and experimental evidence suggest that human hunting of large animals provides returns on effort that are several times those from smaller animals, and an order of magnitude larger than many vegetable foods (Kelly, 1995; Kuhn and Stiner, 2001). Holding body size constant, the most important key to Paleolithic rankings of prey in Mediterranean environments proves to be handling costs; quick running or flying animals, such as hares and partridges, have similar body weights to tortoises or several shellfish, but they are far more difficult to collect without the aid of tools and thus would be lower ranked in the absence of special capture devices. Simple differences in the ease of capture among the two broad groups of small animals in the Mediterranean Basin happens to correspond to great differences in prey population resilience, the latter governed mainly by the rates at which individual prey animals mature (Stiner et al., 2000). Tortoises and certain shellfish are especially susceptible to over-harvesting, because they require several years to reach reproductive age. In contrast, rabbits and some ground birds are notorious for their ability to reproduce rapidly and the resilience of their populations.

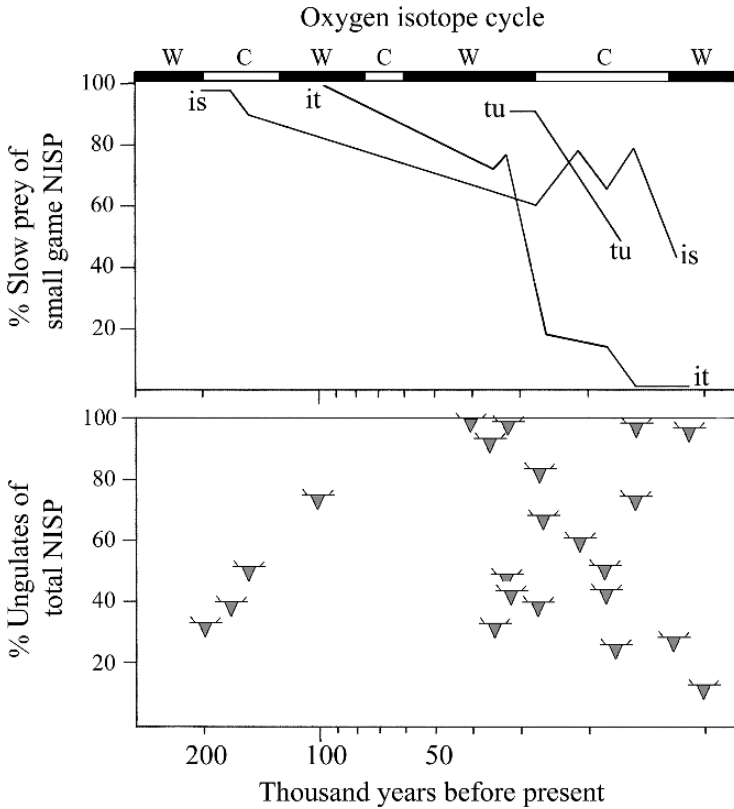


Figure 2: Trends in the percentages of slow small prey (lines) in the small game fraction of each assemblage from Israel (is), Italy (it), and Turkey (tu), together with ungulate remains (inverted triangles) in the total count of each assemblage. Time is expressed on a logged scale, as are oxygen isotope climate cycles (following Martinson et al., 1987; Shackleton and Opdyke, 1973). C denotes a cold stage, and W, a warm stage. (Reproduced from Stiner, 2001.)

It is significant that Middle Paleolithic foragers seldom pursued small prey except for those sessile or slow-moving animals (tortoises and shellfish) that could be collected with little effort. The situation changed around 45–50,000 years ago in the eastern end of the Mediterranean Basin, eventually spreading into adjacent regions of Eurasia. The proportional contribution in biomass of small game to Paleolithic diets is constant at about 3% until the late Epi-Paleolithic (after 15,000 years ago), when it rose to 17% or greater. The mix of small prey nonetheless was quite distinct from the early Upper Paleolithic onward (Munro, 2004; Stiner, 2001, 2005; Stiner and Munro, 2002). Given higher pursuit and handling costs of game birds

and small mammal prey, Paleolithic humans' incentives to switch to quick-moving types would have to have been strong. Prolonged scarcity of easily collected small prey ultimately would also increase the selective advantage of any technology that reduced the cost of capturing quick, agile animals. Importantly, the changes in small game use occurred in the context of relatively stable biotic communities, especially during the Late Pleistocene, when the greatest changes occurred in Paleolithic diets (Stiner, 1994:68–77; Tchernov, 1981, 1992).

Of course the amount of food obtained from one or two individuals of a large species greatly outweighs the total food obtained from many individuals of a smaller species. Another means for comparing patterns of game use employs estimates of meat plus bone—biomass—yields by time period, or number of individual animals multiplied by the estimated average carcass weight for each taxon. Biomass variation in the prey spectrum of Paleolithic hunters (Figure 3) reveals a tendency towards a decline in the ungulate sizes most commonly hunted; this pattern precedes somewhat the rising dependence on small game biomass. Towards the end of the Upper Paleolithic, after the Last Glacial Maximum about 20,000 years ago, biomass of hoofed animals was obtained primarily from medium and small artiodactyl ungulates, and eventually from small ungulates alone.

Hunters' emphasis on faster-reproducing species rises with time, and this is apparent across the entire prey body size spectrum (gazelles and roe deer, game birds, lagomorphs). While the proportional contribution of small game animals to Paleolithic diets was constant at 3% until the Epi-Paleolithic, there was a continuous downward shift in prey size overall, and correspondingly greater hunting of the more biologically productive ungulate taxa (see Figure 3). Though the most obvious changes in subsistence ecology occurred after 15,000 years ago, the trend appears to begin in the early part of the Upper Paleolithic. Thus we must look to this time range if we are to understand the roots of fundamental changes in human predatory adaptations and socioeconomic patterns.

How do the data on small game exploitation stand up in a formal analysis of prey diversity and dietary breadth following the predictions of classic foraging theory? Evidence of increasing dietary breadth is expected to take the form of more species in the diet and/or greater proportional evenness between high-ranked and low-ranked prey items in response to the declining availability of preferred types. A predator can afford to ignore lower-quality prey at little cost if the chance of finding a superior type in the near future is high, fostering a narrower diet that emphasizes a favored type disproportionately to its availability in the environment (condition 1 in

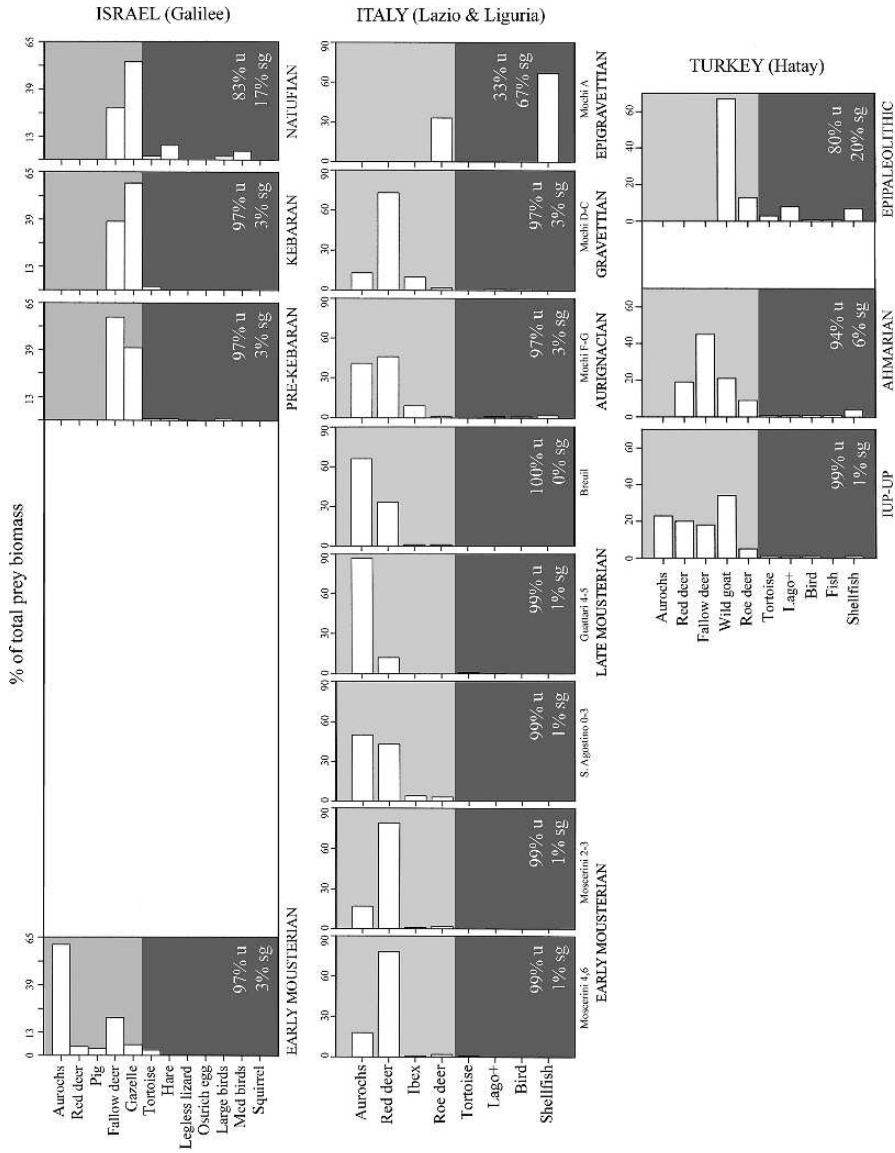


Figure 3: Percentages of total prey biomass obtained by Paleolithic hunters across periods for size-ordered prey species in three Mediterranean faunal series from Israel, Italy, and Turkey. Key: (u) total ungulate percentage; (sg) total small game percentage. Mochi A in the Italian series represents an extreme situation but is still fairly typical of coastal occupations for the period. (Reproduced from Stiner, 2005.)

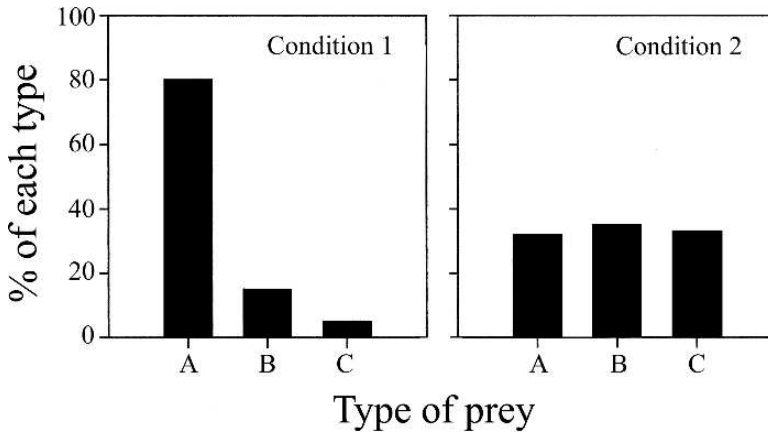


Figure 4: Predicted differences in evenness among three hypothetical types of prey taken by predators under distinct foraging conditions. Condition 1 is high availability of the highest-ranked prey types; condition 2 is declining availability of the highest-ranked types such that predator choice diversifies to include more of the lower-ranked types. (Reproduced from Stiner, 2005.)

Figure 4). As the supply of preferred prey dwindles, broadening the diet to include common but lower-yield prey types maximizes a predator's returns per unit of expenditure by reducing search time (Pianka, 1978). This second set of conditions therefore encourages a more diverse diet in the sense that the predator's emphasis is spread more evenly between two or more prey types that occur in the environment (condition 2).

Variation within the small game fraction of each Mediterranean faunal series tends toward more even dependence on high-ranked and low-ranked small prey overall (Figure 5), confirmation of expanding dietary breadth during the later part of the Mediterranean Paleolithic based on a significant correlation between time and the Inverse of Simpson's index ($n = 18$, $r = 0.606$, $p = .01$). Much of the dietary expansion took place during a cold climate stage (OIS 2). This is the opposite of what is usually expected to result from climate-driven changes in animal community composition, because the number of small animal species tends to be higher in warmer environments (Blondel and Aronson, 1999; Pianka, 1978). The evidence indicates a categorical, or stepwise, change in the way humans interacted with small animal populations as early as 40–50,000 years ago in some areas.

Differences in the relative productivity of prey species are a key to understanding the implications of the economic trends for Paleolithic demography, and rising human population densities in particular. An important

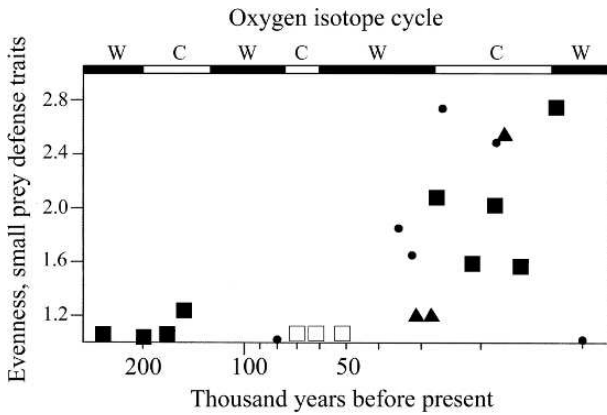


Figure 5: Evenness among three prey categories within the small game fraction only, based on prey defense mechanisms—slow game, quick-running terrestrial mammals, and quick-flying birds—using the Reciprocal of Simpson’s Index (3 = most even). Filled circles represent cases from coastal Italy; filled triangles represent cases from coastal Turkey (Hatay region); filled squares represent assemblages from the Wadi Meged faunal sequence (Hayonim Cave and Meged Rockshelter); open squares are estimates for the late Mousterian of Kebara Cave (Speth and Tchernov 2002); other symbols as in Figure 2. (Reproduced from Stiner, 2001.)

quality of small prey animals that reproduce quickly is their greater potential reliability as a food source. Large mammals are less productive than many small species as a rule, but some productivity gradient must exist within the large species as well, since they vary in body weight. One goal of the large mammal prey simulation study is to understand better the potentially variable yields and the possible signatures of diet breadth expansion. The second goal is to integrate the findings on large and small game exploitation.

SIMULATIONS OF PREDATOR EFFECTS ON SMALL PREY

Differences in prey population resilience and the work of capture should have constrained Paleolithic people’s uses of small game in predictable ways. *Resilience* here refers to a prey population’s ability to withstand heavy, cyclical predation. It is linked most directly to individual maturation rate. Slow-growing small taxa dominate the earlier portions of each Paleolithic sequence and fast-growing types become important later, thus the periodicity or intensity of predation relative to prey maturation rates must have been

Table 1: Summary of life history and predator defense characteristics of the common small prey types in the Mediterranean Paleolithic faunas

Prey	Offspring production rate	Maturation rate	Predator defense mechanisms
Shellfish	high	slow-moderate	safety in numbers, armor, cryptic
Tortoises	moderate	slow	freezing, hiding, armor
Lagomorphs	moderate	fast	hiding, bolting & rapid running
game birds	moderate	fast	hiding, bolting & rapid flight

important. Ground birds, lagomorphs, tortoises, and most shellfish may produce many young per year (Table 1). However, Mediterranean tortoises require roughly a decade to mature (Hailey, 1988). Lagomorphs and game birds such as partridges reach reproductive age within a single year and their populations turn over rapidly. It is clear that prey birth rates alone cannot explain the differences in prey population turnover rates or the trends in small game use of the later Paleolithic.

Work of capture is determined by a prey animal's defense and escape mechanisms and therefore also influences prey rank. Work of capture in this sense may represent the cost of searching for prey, investment in technological aids, or the energetics of a true chase. It may also include processing costs, although in the study areas under consideration people used fire to do much of the processing work for them. In the Mediterranean Basin, we have two broad categories of small prey—those that are easily caught by hand and those that are not. Even with the aid of harvesting tools, the work-of-capture costs may be significantly higher for quick animals. The attractiveness of tortoises to humans is their ease of collection in combination with (in many cases) relatively low processing costs. Also significant is the fact that modern tortoises (and shellfish) can exist at very high densities in the absence of human disturbance, because of their low metabolic rates, high sub-adult and adult survival rates, and potentially long life spans (e.g. Hailey, 1988; Shine and Iverson, 1995).

The contrasting life history strategies of tortoises, lagomorphs, and game birds suggest that low-turnover prey species should respond quite differently to human predation than high-turnover species. Of great interest to us is the magnitude of difference in productivity among the subject prey animals. We assume that hunting intensity increases with the population density of predators on a landscape. The Monte Carlo simulation models were designed to address two questions: First, what is the maximum annual "yield" that predators can take from a subject prey population without surpassing the

threshold for a stable (sustainable) predator-prey relationship? Second, how much more resilient are hare and partridge populations than tortoises to similar increases in predator density?

Model design: High and low growth conditions

The parameters for the simulations were taken from a variety of modern wildlife studies, preferably but not exclusively for the species identified in the Mediterranean archaeofaunas. Table 2 summarizes model structure and Table 3 the life history parameters used for tortoises (*Testudo*), hares (*Lepus*), and partridges (*Alectoris* and *Perdix*); the sources of data in Table 3 are many and will not be repeated here (see instead Stiner et al., 2000). Data from long-term studies of viable populations, with good control over birth rates, mortality rates, and their causes, were favored for modeling purposes.

To investigate the interplay of life history traits in predator-prey systems, we modeled two extremes of population growth for each kind of small prey animal—a high growth model (HGM) and a low growth model (LGM).

Table 2: Predator-prey simulation model structure and variables (from Stiner et al., 2000)

Individual variables by sex:

MALE

Age

Mass (tortoises only)

FEMALE

Age

Mass (tortoises only)

Next age of reproduction

Litter size

Fertility parameters:

Female minimum age of reproduction

Birth interval (spacing)

Minimum number of offspring

Maximum number of offspring

Natural (non-human) mortality parameters:

Maximum potential life span

Age of onset of adult mortality rate

Annual adult mortality rate

Juvenile mortality rate

Hunting parameters:

Minimum age/size to hunt

Annual kill percentage

Because prehistoric prey and predator densities cannot be known absolutely, our strategy was to compare the relative resiliencies of tortoise, hare, and partridge populations under favorable and lean conditions for prey reproduction and growth. Truly average conditions are rare in the life of any individual, and most or all years in that individual's lifetime will likely fall between the curves defined by our high and low growth models. The simulations were written by T. A. Surovell as Visual Basic macros in Microsoft Excel 7.0 (Figure 6). Populations were modeled as sets of actual individuals, each characterized by age, sex, and, in tortoises, body mass. Additionally, females were assigned values for next age of reproduction and annual litter size. Individual age increased by a fixed value per unit of time elapsed.

Fertility was controlled by three parameters in the model: female minimum reproductive age and the minimum and maximum number of offspring per annum. When a female was born, her next age of reproduction was set to the minimum age at which she could begin reproducing and to normal birth spacing thereafter. A predetermined number of offspring, between the minimum and maximum values in Table 3, was added to the population each year (except for LGM tortoises, as we discuss shortly). An even sex ratio at birth was maintained on the basis of empirical evidence.

Table 3: Assigned fertility and mortality parameter values for tortoises, hares, and partridges in the High Growth (HGM) and Low Growth Models (LGM) (from Stiner et al., 2000).

Parameter type	Tortoises		Hares		Partridges	
	HGM	LGM	HGM	LGM	HGM	LGM
Fertility:						
female age at first reproduction (years)	8	12	0.75	1.0	0.75	1.0
birth interval (days)	365	730	365	365	365	365
maximum number of offspring per annum	14	14	11	9	13	11
Mortality:						
maximum potential lifespan (years)	60	60	12	12	8	8
age of adult-level mortality onset (years)	1	1	0.5	0.5	0.2	0.2
annual adult-level mortality rate	0.053	0.093	0.4	0.5	0.5	0.6
annual (base-level) juvenile mortality	0.70	0.85	0.6	0.7	0.42	0.6

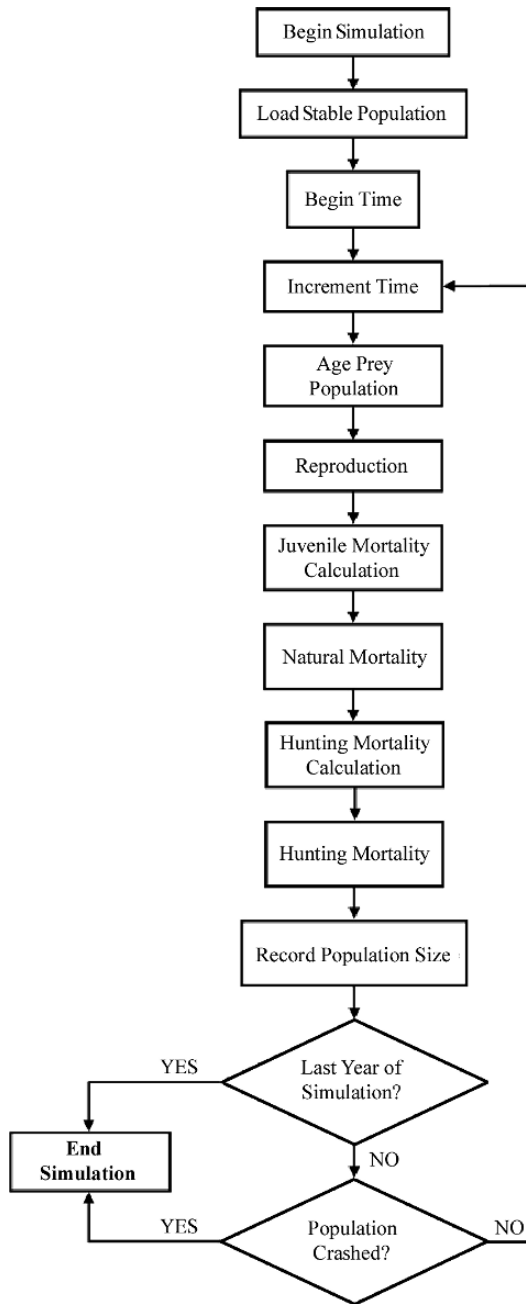


Figure 6: Model structure for simulations of predator-prey dynamics involving humans and small prey animals

Mortality was controlled by four parameters in the model: maximum potential lifespan, annual juvenile mortality, annual adult mortality, and age of onset of adult-level mortality. Mortality effects were divided between only two age groups, juveniles (including newborns) and adults, an approach justified by available wildlife data. Adult mortality randomly removed a fixed percentage of adults from the population each year, in addition to removing any individuals lucky enough to have exceeded the maximum potential lifespan. Density-dependent mortality from nonhuman causes affected only juveniles, because young animals are most likely to suffer under conditions of high prey population density. Thus, juvenile mortality was allowed to vary as a linear function of population density:

$$m_{jt} = m_{jb} + [(pop_t/pop_k)(1 - m_{jb})]$$

where m_{jt} is juvenile mortality at time t ; m_{jb} is base-level juvenile mortality; and pop_t/pop_k is population density at time t . Therefore, $m_{jt} = m_{jb}$ when $pop_t = 0$, and $m_{jt} = 1$ when the population is at environmental carrying capacity.

Hunting by humans was controlled by two constants in any given run—minimum age (or size) to hunt (a selectivity factor) and annual kill percentage. So long as individual prey above a given age or body size threshold was available, it is assumed that humans would be attracted to them. If individuals above the threshold were no longer available, then humans would target the oldest available individuals below that age threshold.

Parameter development—the example of tortoises

The process of parameter research was quite involved and is described elsewhere for each type of prey (Stiner et al., 2000). It is useful, however, to provide one example in order to illuminate important decisions in parameter development from empirical data. *Testudo*, the common genus of tortoise in the archaeofaunal series, provides an ideal standard for comparing small game use in the Mediterranean Paleolithic. Apart from a study by Doak et al. (1994), little modeling work has been done on tortoises, making it necessary to begin from scratch. In doing so, we note several important insights from wildlife studies of modern *Testudo graeca* and *T. hermanni* in the Mediterranean Basin. First, the illegal pet trade, which favors large specimens for international markets, has rapidly

driven down mean individual size in affected tortoise populations in North Africa (Lambert, 1982; Stubbs, 1989) and Spain (Blasco et al., 1986–1987). Second, immature tortoises generally are much more difficult to find than are adults in Mediterranean habitats (Lambert, 1982). Third, adult female tortoises tend to be larger than males of the same age (Blasco et al., 1986–1987; Lambert, 1982), making the reproductive core of the population that much more vulnerable to size-dependent predation by humans. Our model takes into account the steeper growth curve of females relative to males, because size-biased collecting should affect females and males somewhat differently. Tortoises over about 0.3 kg were considered adults, on the basis of curve fitting, corresponding to 10 years of age for females and 12 years of age for males.

Testudo graeca and *T. hermanni* populations can be modeled as one taxon for our purposes. Information on the population dynamics of Mediterranean and other tortoises is scarce. Fortunately, tortoises differ little in terms of the variables employed here, especially if compared with most mammals and birds. Tortoise life histories are characterized by high hatchling mortality but very low subadult and adult mortality, in addition to long life spans and delayed reproductive maturation (Hailey, 1988; Shine and Iverson, 1995; Wilbur and Morin, 1988).

Adult mortality in *Testudo* varies among populations and across years, but composite study results show that survival tends to be continuously high after the first year of life (Hailey, 1988; Lambert, 1982; Meek, 1989). Although tortoises are far from mature at this stage, the age of onset of adult-level mortality was set at one year in both models. We set hatchling mortality (i.e. for the first year of life) at 70% in the HGM (females produce 2.1 to 4.2 yearlings per annum) and at 85% in the LGM (0.7 to 1.4 yearlings produced per annum), partly on the basis of estimates by Doak et al. (1994) for hatchling survival in desert tortoises (*Gopherus*). High adult survivorship is essential to the health of tortoise populations, whereas hatchling survival rates can vary much more without detracting from the long-term fate of those populations (Doak et al., 1994; Heppel et al., 1996a; Heppel et al., 1996b); these observed characteristics are reflected in our models. Because egg production depends partly on female body size (Hailey and Loumbourdis, 1988), the number of offspring (eggs) produced per annum was allowed to vary linearly with body mass within the specified range. Because wild individuals of the genus *Testudo* seldom live beyond 60 years (Lambert, 1982), this value served as the maximum potential lifespan. It allowed 53.5 and 48.0 years of reproductive activity in the HGM and LGM, respectively.

A strong negative correlation exists between age at sexual maturity and the adult mortality rate in turtles and tortoises and in reptiles in general (Shine and Iverson, 1995). We used the regression line associated with this correlation to control the covariance of these parameters. To account for published variation in age at first reproduction (cf. Blasco et al., 1986–1987; Castanet and Cheylan, 1979; Hailey, 1990), values for *T. graeca* and *T. hermanni* were set at 12 years in the HGM and at 8 years in the LGM. These correspond to adult mortality values of 5.3% and 9.3%, respectively, well within the range documented for modern wild populations (Hailey, 1988, 1990; Lambert, 1982; Meek, 1989). Annual egg production for *T. graeca* varies between 7 and 14, according to Hailey and Loubourdis (1988). Birth spacing was set to 365 days in the HGM but at 730 days in the LGM, on grounds that as few as half the adult females in a tortoise population might reproduce in a given year (Wilbur and Morin, 1988).

Simulation results for tortoises, partridges and hares

Figure 7 presents the simulated outcomes of incremental increases in predation on tortoises and on partridges over 200 years under high growth (HGM) and low growth (LGM) conditions. Adult tortoises were assumed to be preferred wherever available to the predators. It is clear from this exercise that tortoise populations cannot tolerate annual losses of more than 4 to 7% (LGM and HGM respectively) of reproductively mature individuals without crashing. In comparison with hares and birds, tortoise populations are exceptionally sensitive to predation and are easily destroyed. Sustainable harvesting is possible only below these thresholds. The same may have been true for certain shellfish (e.g. limpets, *Thais*) that Paleolithic humans in the Mediterranean area depended upon for food, although they are not modeled in this study.

The partridge simulations are based on wildlife data on chukars (*Alectoris chukar*) and gray partridges (*Perdix perdix*), species that are widely distributed in the Mediterranean area. The simulated outcomes of incremental increases in predation on partridge populations over 200 years under high growth (HGM) and low growth (LGM) conditions show that partridges are very resilient to sustained heavy predation. Their populations are difficult to destroy, even where off-take is consistently high. The simulated partridge populations can tolerate up to about 65% annual losses of adults in the HGM, and about 22% in the LGM. Similar results were obtained for Old and New World hare and rabbit species.

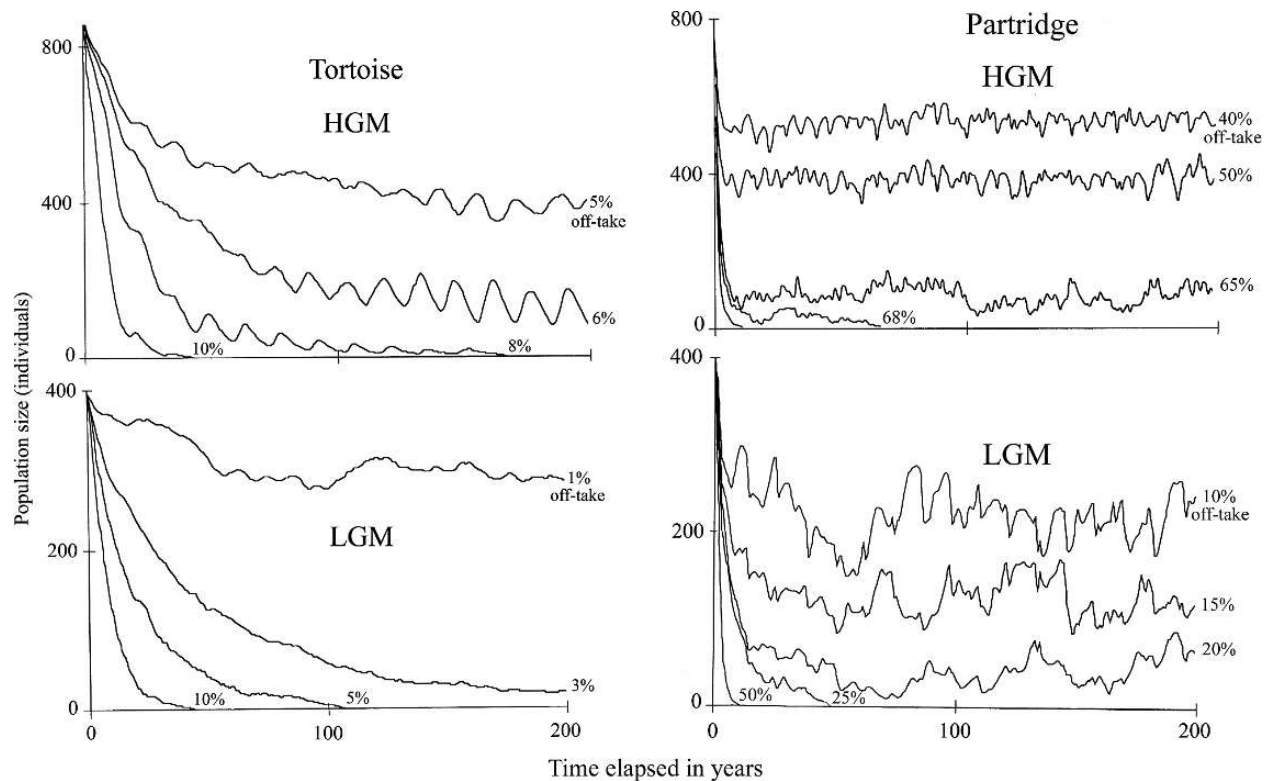


Figure 7: Simulated predation on tortoise populations (*Testudo*) and on partridge populations (*Alectoris*, *Perdix*) under high growth (HGM) and low growth (LGM) conditions. Percentages refer to annual off-take (mortality) from the total population, with adults weighing more than 0.3 kg taken preferentially. The undulations (chattering) in some of the HGM curves are due to alternating focuses on male and female prey, a product of model design. (Reproduced from Stiner et al., 2000.)

Folk wisdom tells us that lagomorphs are exceptionally productive. What it does not tell us is how game birds and tortoises compare with them. Figures 8 and 9 compare the areas and ranges of the high and low growth curves for tortoises and hares in our simulations of population growth. The area enclosed by the HGM and LGM curves for tortoises does not overlap at all with that for hares (or partridges) during the years of population growth, despite our rather puritanical limits on hare productivity. In our simulations, hare populations reached equilibrium between about 7 (HGM) and 25 (LGM) years, whereas tortoise populations reached equilibrium between about 50 (HGM) and 125 (LGM) years.

The simulations confirm the existence of major differences in the scale at which humans could possibly hope to depend on tortoises, hares, and partridge-like birds for meat. Other things being equal, hare populations can support proportionally 7 times greater off-take by predators than tortoises can support, and partridges can support 10 times greater off-take than tortoises. This means that humans' reliance on tortoises is sustainable only if human population densities are very low. Humans' reliance on partridges and hares is sustainable in both low- and high-density conditions.

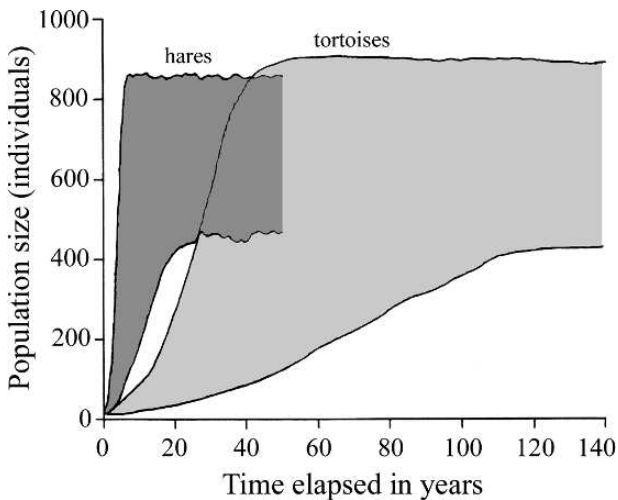


Figure 8: Comparison of areas between the high and low growth curves for simulated tortoise and hare populations. The upper line represents the high growth model (HGM) and the lower line the low growth model (LGM) for each kind of prey. Initial population size was 10 individuals. Carrying capacity was set at 1,000 for tortoises and 1,250 for hares in order to render population sizes comparable in the graph. (Reproduced from Stiner et al., 2000.)

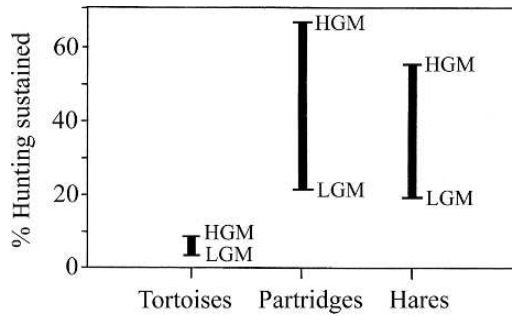


Figure 9: Comparison of hunting tolerance thresholds for tortoise (4–7%), partridge (22–66%), and hare (18–53%) populations under high (HGM) and low (LGM) growth conditions. Upper horizontal bars represent thresholds above which predators' dependence on the designated prey type is no longer sustainable. Vertical bars represent natural variation in population resilience as defined by the LGM and HGM. (Reproduced from Stiner et al., 2000.)

Differences in small animal productivity make greater economic sense of Upper Paleolithic and Epipaleolithic humans' increasing use of birds and hares when large tortoises were in short supply. One can also argue that partridges and hares represented more stable or reliable sources of small meat packages as human population densities increased. However, the high-turnover prey species in the two Mediterranean study areas are also quick and thus more difficult to catch by hand. It is for this reason that they may have been ranked lower in Middle Paleolithic foraging systems, and humans overcame the disadvantages of these prey items only with greater technological investment in the Upper Paleolithic.

Links between predator pressure and population density

Small animal species vary tremendously in predator defense mechanisms and population resilience, in contrast to the ungulates that were commonly hunted by prehistoric humans. In addition, small animal species vary less in body weight relative to humans than do large game animals. It is for these reasons that data on small game exploitation can reflect subtle changes in Paleolithic demography. Heavy harvesting of tortoises or any other sensitive prey species reduces the viability of that population and, soon, the frequency with which foragers can find suitably large individuals of the affected species (Botkin, 1980; Broughton, 1997; Christenson, 1980; Earle, 1980; Mithen, 1993; Pianka, 1978).

It therefore is remarkable that up to about half of all identifiable animal remains (NISP) in some early Middle Paleolithic assemblages of Hayonim

Cave are from a reptile that is exceptionally sensitive to predation. What is more, the sizes of the individual tortoises taken during the Mousterian were larger on average than those of the later Paleolithic periods (Stiner, 2005; Stiner et al., 2000). High archaeological frequencies of a low-resilience prey species, along with large individual body sizes, imply that the early human populations that depended upon the species were small and highly dispersed. Middle Paleolithic populations may simply not have experienced the sorts of stresses that would have made agile, fast-growing small animals attractive.

Predator-prey simulation of small animals modeling illustrates how rising human population density and associated predator pressure may alter prey abundances and thereby select for changes in the prey types that were emphasized by foragers. More surprising is the evidence that resource intensification began so early in the story of subsistence revolution in Eurasia. The results suggest a notable expansion in dietary breadth with the onset of the early Upper Paleolithic and an even greater expansion during the later Upper Paleolithic and Epipaleolithic.

SIMULATIONS OF PREDATOR EFFECTS ON ARTIODACTYL UNGULATES

The small game simulation study is advantaged by the extreme differences in the reproductive ecology and predator avoidance behaviors of birds, small mammals and reptiles, all of which are similar in body size (at least relative to the body sizes of humans). However it was the large mammals that formed the bulk of animal biomass consumed by foragers prior to the end of the Paleolithic in the Mediterranean Basin (Figure 10), and in many other world regions as well. Simulation modeling of predator-prey interactions involving large mammals would therefore seem necessary. This endeavor involves some distinct challenges, because ungulate species are much more similar to one another with respect to reproductive rates and predator avoidance characteristics. Unlike the situation with small game animals, ungulates also differ also greatly in body weight.

The archaeological observations nonetheless indicate that the earlier faunas contained more large ungulates and the later faunas more small ungulates. The potential explanations for the decline in mean ungulate body sizes acquired by hunters include hunting pressure and climate-induced changes in natural community structure; in the Mediterranean case, however, these changes co-occur in time with the small game trends, which are

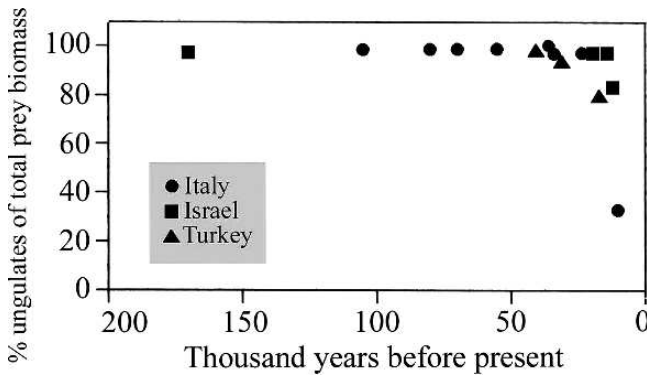


Figure 10: Percentages of total ungulate biomass obtained by Paleolithic hunters across periods in each of the three Mediterranean faunal series from Israel, Italy, and Turkey. (Reproduced from Stiner, 2005.)

attributable in large part to human effects (Stiner, 2005). Body size in ungulates generally correlates inversely with the rate of reproductive output and population turnover rate, and presumably prey population resilience. Small ungulate species, such as gazelles and roe deer, mature in a much shorter time than do larger deer (about 2 yrs for fallow deer, 2–3 yrs for red deer), and all of these species mature faster than do large ungulates such as aurochs (Table 4). In addition, larger ungulates occur in fewer numbers on a given landscape overall, and encounters with them may more sporadic and less predictable.

One goal of the large mammal prey simulation study is to understand the potentially variable yields among large mammals and to look for reliable signatures of diet breadth expansion. The second goal is to integrate the findings on large game exploitation to those for small game animals. The simulation model attempts to capture the essential population dynamics of each species, while remaining simple enough to avoid model-specific behaviors.

Model structure

The model for the ungulate predator-prey simulations is descended from that employed in the small game study, but with two modifications (Beaver 2007). First, both “natural” (non-anthropogenic) and human-caused mortality occur multiple times per year, rather than once a year. The similarities in the reproductive characteristics of ungulate species in comparison with tortoises, partridge, and hares makes a more fine-grained

Table 4: Simulation model parameters for ungulate species, based on wildlife data sources (Beaver 2007)

Species	Model	Pregnancy Rate	Mean Number of Offspring	Female Age of First Reproduction	Age of Onset of Adult Mortality	Maximum Age	Base Rate of Natural Juvenile Mortality		Adult Natural Mortality Rate	
							Female	Male	Female	Male
Aurochs	LGM	0.3	1.0	4	3	16	0.11	0.13	0.05	0.08
	HGM	0.5	1.0	4	3	18	0.1	0.1	0.04	0.06
Fallow Deer	LGM	0.8	1.0	2	2	12	0.21	0.21	0.11	0.12
	HGM	0.9	1.0	2	2	14	0.15	0.15	0.07	0.08
Gazelle	LGM	0.9	1.0	1	1	12	0.4	0.4	0.2	0.2
	HGM	1.0	1.2	1	1	12	0.25	0.25	0.15	0.15
Goat	LGM	0.6	1.5	2	1	12	0.25	0.25	0.15	0.15
	HGM	0.7	1.7	2	1	12	0.15	0.15	0.1	0.1
Ibex	LGM	0.7	1.0	2	2	12	0.2	0.2	0.12	0.12
	HGM	0.8	1.1	2	2	12	0.12	0.12	0.08	0.08
Red Deer	LGM	0.5	1.0	3	2	14	0.15	0.19	0.06	0.11
	HGM	0.7	1.0	3	2	14	0.12	0.15	0.04	0.07
Roe Deer	LGM	0.8	1.8	2	1	10	0.3	0.3	0.15	0.15
	HGM	0.9	2.0	2	1	12	0.2	0.2	0.1	0.1

model desirable, and spreading the two sources of mortality through the model year significantly reduces the effect of scheduling decisions on which type of mortality should occur first. Second, hunting levels are determined in the model relative to the initial, stable population size, rather than in terms of each year's population size. This approach holds the food yield constant as the prey population is exploited. Yield is of greater importance in examining ungulate species exploitation if human population sizes are also an issue. This is because the different types of small game populations vary so much in inherent resilience yet are more similar than ungulates are in body size, whereas ungulate population resilience increases as body size decreases. An approach that can be used to compare sustainable yields among species is thus more important with large game (Figure 11).

Ungulate model results

Ungulate population responses to human predation are modeled for seven Artiodactyl species that occurred in and around the Mediterranean Basin during the Paleolithic: aurochs (*Bos primigenius*), fallow deer (*Dama dama/mesopotamica*), gazelle (*Gazella gazella*), ibex (*Capra ibex*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild goat (*Capra aegagrus*). High (HGM) and Low Growth Model (LGM) sets of population parameters were derived for each species from the ecological and wildlife management literature (Table 4), using substitute species where necessary (e.g. *Bison bison*, *B. bonasus*, and *Syncerus caffer* for the extinct aurochs). The maximum sustainable hunting rates for the modeled species range from 0.26% (aurochs, LGM) to 11.3% (roe deer, HGM) of the initial population, with the LGM-HGM range for each species overlapping with that for at least one other species. The maximum sustainable hunting rate is the most important difference in ungulate population responses to continuous human predation; hunting rates considered as a fraction of the species model's maximum sustainable rate have essentially indistinguishable effects, regardless of species (Figure 12, Table 5). For example, a hunting rate half of the maximum sustainable rate depresses any ungulate population by about 14%, and a hunting rate that is 90% of the maximum sustainable rate depresses the population by approximately 30%.

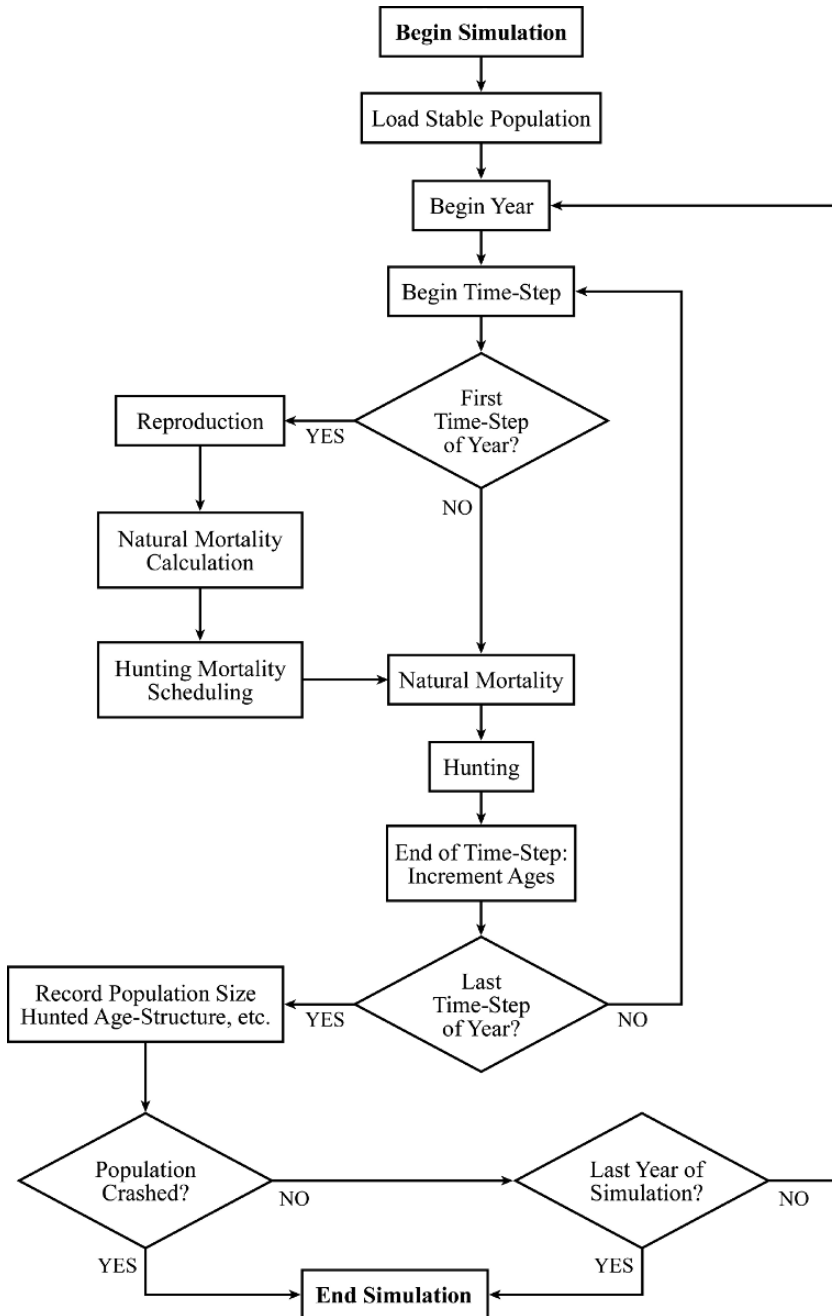


Figure 11: Model structure for simulations of predator-prey dynamics involving humans and ungulates (from Beaver 2007)

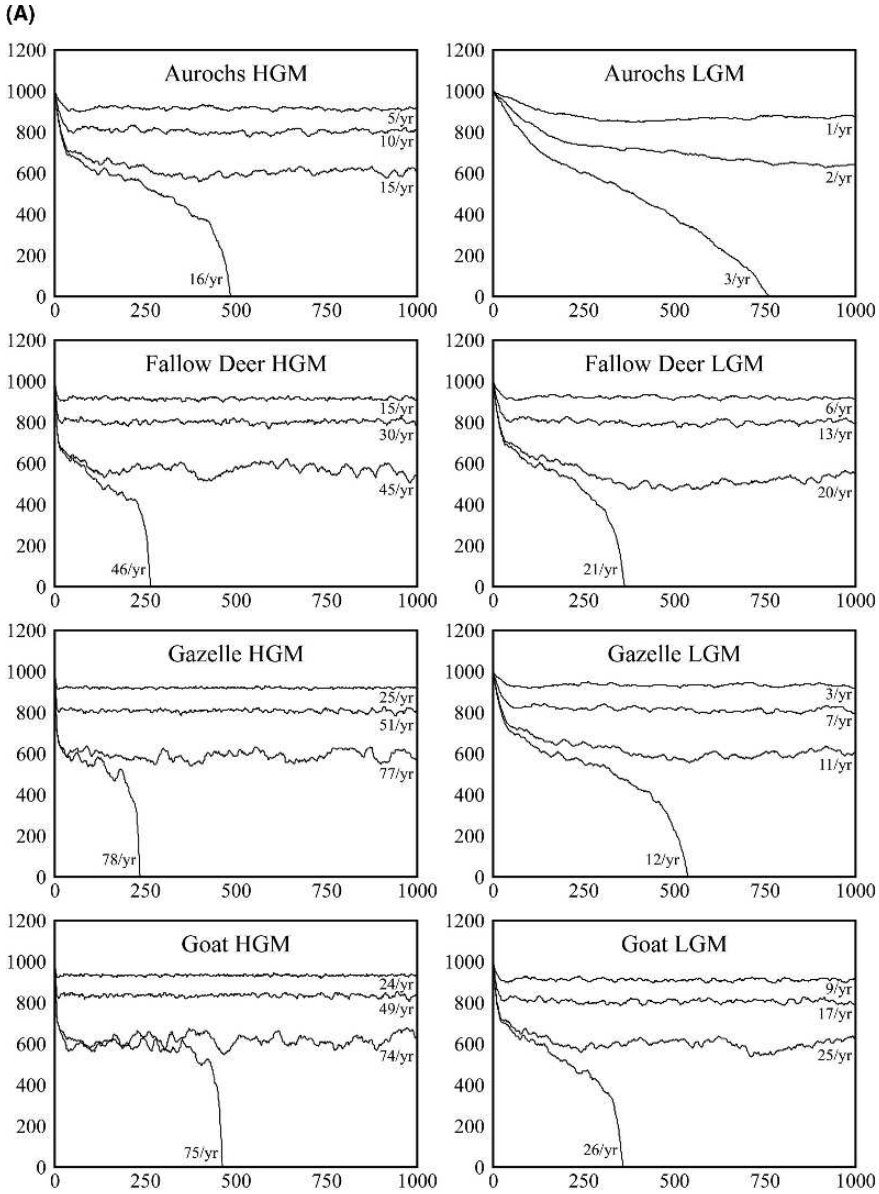


Figure 12: Ungulate population responses by species to human hunting of the indicated number of individual animals per year. The x-axis represents time in years; the y-axis represents prey population size

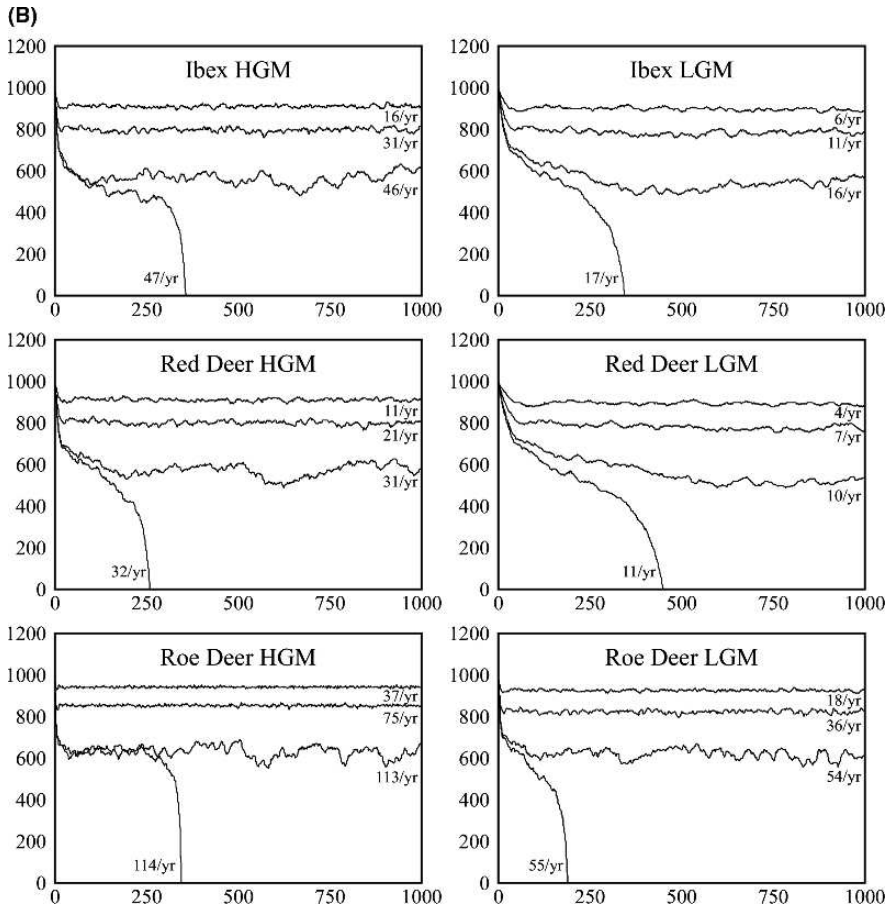


Figure 12: (Continued)

Ungulate results compared to those for small game

There are several factors that make ungulate exploitation a less profitable analytical focus than small game for paleodemographic research. Stiner et al.'s (2000) discussion of small game emphasized the importance of the differences in hunting technology and human behaviors required to hunt different types of small game. In that case, substantially greater technological and/or energetic investment is required to exploit substantially more resilient, but also very similarly sized, animals. In the case of ungulates, very similar technological/energetic investment may allow the exploitation of

Table 5: Mean maximum hunting rates that can be sustained by the modeled populations under low growth (LGM) and high growth (HGM) conditions (Beaver 2007)

Species	Sustainable Percentage	
	LGM	HGM
Aurochs (<i>Bos taurus</i>)	0.260	1.513
Fallow Deer (<i>Dama dama</i>)	1.989	4.529
Gazelle (<i>Gazella gazella</i>)	1.102	7.727
Goat (<i>Capra aegagrus</i>)	2.524	7.393
Ibex (<i>Capra Ibex</i>)	1.598	4.584
Red Deer (<i>Cervus elaphus</i>)	0.999	3.102
Roe Deer (<i>Capreolus capreolus</i>)	5.397	11.277

similarly resilient but very differently sized ungulates. It is the convergence of all three factors—exploitation cost differentials, population resiliency differentials, and body size similarities—that favors demographic interpretations of trends in small game use.

Even the total potential yield of different ungulate species is difficult to apply to problems of human demography. The maximum sustainable hunting rates obtained for ungulate species models correlate strongly and negatively with body size, following a power-law relationship; $h = .307m^{-.526}$, where h is the mean of the maximum hunting rates sustainable by the high and low growth models for each species and m is the estimated mean adult body mass for that species; $r^2 = .886$, $p = .002$. A human population can hunt many more roe deer than red deer without crashing the population, but humans *must* do so in order to acquire the same amount of food, making the relative population densities of the different ungulate species an important consideration. This situation contrasts strongly with that for the three types of small game modeled by Stiner et al. (2000), whose maximum sustainable hunting rates are not closely related to body size.

Because prey population density is negatively correlated with body size, the population densities of smaller animals are higher than those of larger animals, and especially within closely related groups of species (e.g. among the Artiodactyla). This relationship is on average one where population density increases more slowly than body size decreases (e.g. Damuth, 1981, 1987; Peters and Wassenberg, 1983). Thus the sustainable yields for the smaller ungulates are not definitively higher than those for the larger ungulates (compare Figures 13–15).

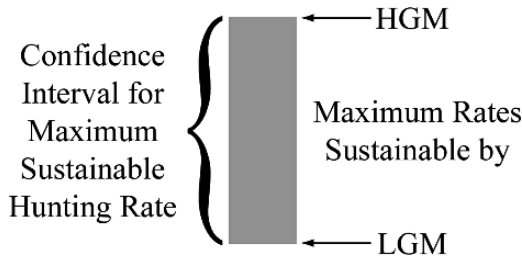


Figure 13: Definition confidence interval based on the HGM and LGM maximum sustainable hunting rates

The picture is complicated further by the question of just what was happening with the human population increases in the Paleolithic. It is clear that human populations in the Middle Paleolithic were small and spread sparsely around the Old World. When these populations increased, did group sizes (and thus local exploitation levels) increase while groups remained equally scattered and equally mobile? Or did more or larger groups form, filling up more territory but with similar local exploitation levels? In the latter case, were areas exploited more often or for longer periods? It seems likely that all of these conditions occurred at various times and places. Sustainable hunting rates and food yields were also examined under different durations of exploitation (from one-year to century-long episodes) and different rates of reoccupation (leaving the prey populations unexploited from 50% to 95% of the time). These simulations indicate that, while the smallest ungulate species can sustain higher yields under some patterns of local occupation or reoccupation, under other patterns it is the largest species that can do so. Under yet other conditions, the species of intermediate size are most capable of supporting the highest yield! A careful consideration of ungulate species exploitation alongside other data may eventually allow us to better understand how human population growth in the Paleolithic manifested, but such data are difficult to use to identify faunal changes caused by demographic increases.

DISCUSSION

The archaeological record of small game hunting during the Mediterranean Middle Paleolithic indicates nearly exclusive use of sessile or slow-moving prey. This is followed in the early Upper Paleolithic by major proportional increases in quick-flying common game birds and, by the

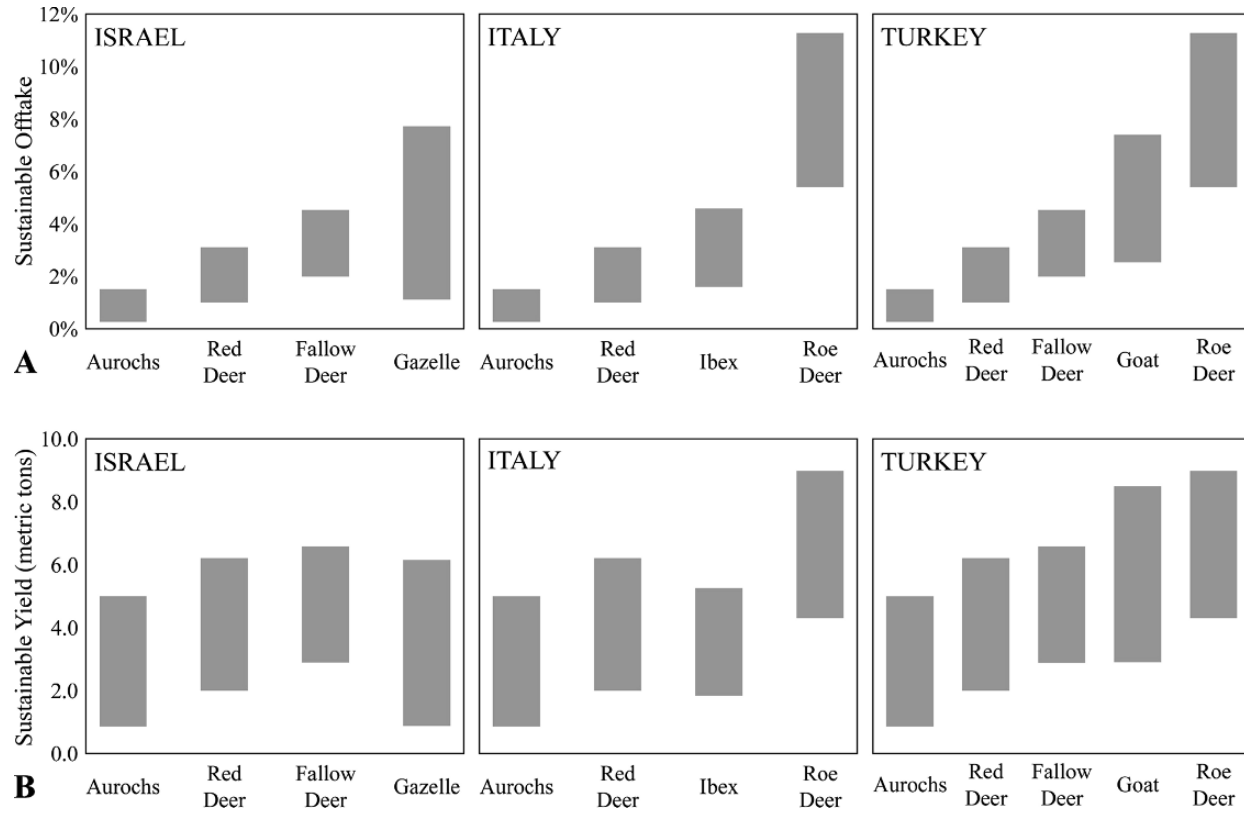


Figure 14: Comparisons of sustainable annual off-take rates for ungulate species in each Mediterranean data set (A) as percentages of the initial unhunted population and (B) as biomass yields from populations 'ecologically equivalent' to a population of 1000 red deer. Bars represent confidence range for maximum sustainable off-take rates from low growth to high growth model values.

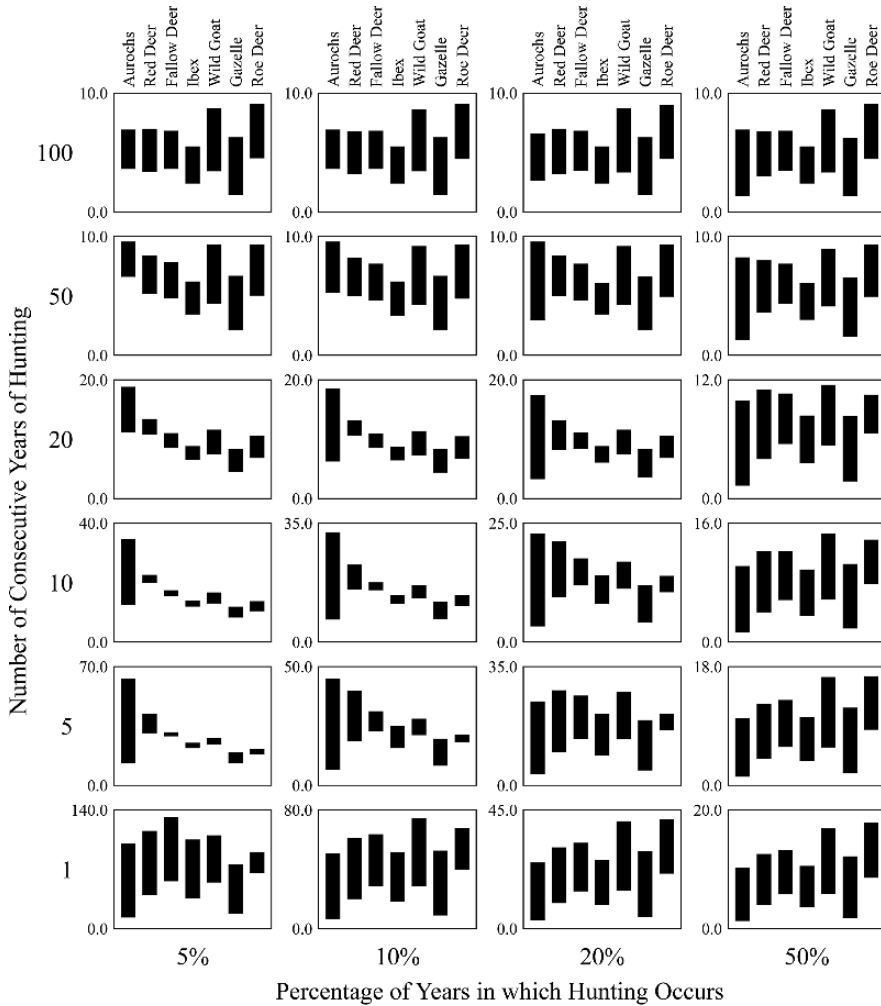


Figure 15: Comparison of biomass yields sustainable by modeled ungulate populations at varying durations and intervals of exploitation. Y-axes of graphs are biomass yield in metric tons per year during periods of exploitation. Bars represent confidence range for maximum sustainable yield from low growth to high growth model values

Epi-paleolithic, in fast-running lagomorphs as well. Highly ranked prey animals, as defined by Middle Paleolithic exploitation, were the slow-moving tortoises and shellfish. Use of these animals continued through the Upper Paleolithic and Epipaleolithic, but agile types supplemented the diet in greater proportions, despite their lower ranking on grounds that

their capture costs were higher. More significant than any expansion of the taxonomic spectrum in Paleolithic human diets was a rising emphasis on a few highly productive taxa that were less easily caught by hand. We also see an increase in small, fast-reproducing ungulate species in Paleolithic diets with time. However, the sustainable yields for the smaller ungulates are not definitively higher than those for the larger ungulates. The shift down the body-size spectrum that we see in your Mediterranean data through the Upper Paleolithic is not in itself solid evidence of demographic growth. However, given demographic growth as shown by other, better evidence (like the small game), we can attribute the shift to smaller ungulates as being the result of the population growth. Put another way, smaller ungulate prey are not sufficient for a conclusion of predator population growth, but significant predator population growth is sufficient (in the absence of a good environmental cause) for a focus on smaller ungulate prey. We suggest that an increasing dependence upon high producers, even if total volume of meat acquired remains the same, could mean a reduction in the composite (cooperatively pooled) variance in foraging success, albeit at the price of greater hunting effort.

For the bulk of prehistory, mobility has been humans' primary solution to local resource scarcity. With increasing population, humans in some regions seem to have had fewer options for solving problems of resource availability through mobility, beginning sometime in the Upper Paleolithic, and the situation deteriorated further in the Epipaleolithic (*sensu* Bar-Yosef, 1981; Binford, 1968, 1999; Cohen, 1977, 1985; Flannery, 1969; Tchernov, 1993, 1998). Increasing dependence on a variety of more biologically "productive" or resilient prey populations over time might have allowed people to obtain a greater volume of meat per unit of habitat area. Perhaps more important is that prey population resilience could have substantially increased the reliability (i.e. reduced the variance) and diversity of meat sources to which a population had access, especially as the costs of acquisition or processing were controlled through technology. A more reliable supply of animal protein and fats has significant implications for child survivorship.

Middle Paleolithic humans in the Mediterranean region maintained remarkably narrow diets across a wide range of latitudes. The evidence indicates that human populations were exceptionally small throughout the Mediterranean Middle Paleolithic. A categorical shift in human predator-prey dynamics accompanied by demographic expansion seems to demarcate the Middle to Upper Paleolithic cultural boundary. There seems to have been a lack of pressure or economic incentive for these clever, mobile hunters to squeeze more out of their traditional food supplies—that is, there was little

selection, if any, for greater foraging efficiency. More difficult to explain are the downward shifts in trophic level so characteristic of later humans. These shifts took the form of subsistence diversification via the inclusion of lower-ranked foodstuffs associated with greater processing costs, and they coincided more than once with increases in human population densities. Low human population densities during the early Middle Paleolithic also imply small social groups and networks, certainly limiting the numeric scope of individual interactions. Under these conditions, the possibilities for evolution of complex sharing and exchange behavior as a way to counter the effects of unpredictable resource supplies would also have been limited. Larger social networks for spreading risk might also have appeared in conjunction with expanding diets, possibly setting some Upper Paleolithic populations at an advantage.

Subsistence behaviors that enhance the predictability of supplies of critical nutrients can improve childhood survivorship and thereby help a population grow without a change in birthrate. Changes in the character and regularity of meat acquisition also hold social implications: the small-large dichotomy in prey body size and the slow-quick dichotomy in small prey may correspond to the emergence of significant divisions within labor networks among modern hunter-gatherer cultures. Immobile or sluggish small animals are essentially gatherable resources and thus directly accessible to both sexes and all age groups in human societies. Fresh meat from large game animals generally must be obtained by hunting—normally the job of grown men. Quick small animals present other challenges: they are most efficiently caught with special tools and, in some cases, a substantial measure of vigilance. Although access to small quick game is limited by technical skills, these often are learned in late childhood. The price of these activities was higher labor investment in tool preparation and maintenance or direct inputs of cooperative labor to capture small animals in quantity. In western Asia, demographic pressure preceded rather than followed the earliest technological innovations of the Upper Paleolithic and Epipaleolithic periods.

To date, most information on human population history has been obtained from studies of modern human genetic diversity, which on the whole suggest several demographic pulses originating from western Asia, Africa, or both that ultimately affected peripheral populations of Europe and elsewhere (e.g. Ammerman and Cavalli-Sforza, 1984; Barbujani and Bertorelle, 2001; Hewitt, 2000; Reich and Goldstein, 1998; Relethford, 1998, among others). Time is the most difficult variable to control for in these studies: biological clocks inferred from gene mutation rates are notoriously inaccurate, and

so there is a dismaying variety in their interpretation. In contrast to the situation for the genetic data, demographic pulses evidenced by the archaeological record of human subsistence and human cemetery data (Bocquet-Appel, 2002) can be dated by radiometric techniques over geographical gradients, permitting independent tests of prehistoric human population dynamics and population history. In our zooarchaeological case, a close look at the Middle Paleolithic record relative to the records of later periods revealed an appropriate way to test the hypothesis of expanding dietary breadth in response to human population pressure. The Mediterranean spur-thighed tortoise, a species long ignored in zooarchaeological research in the Levant, provided new insights into the nature of Mousterian subsistence and demography. The small animal remains found in archaeological sites are attributable to Paleolithic human activities and hold the unique power to clarify the timing and geographic centers of rapid population growth suggested by research on human molecular phylogenetics, as well as to clarify some of the factors that contributed to the earliest forager-producer transition.

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Chapter 7

THE DEMOGRAPHY OF PREHISTORIC FISHING/HUNTING PEOPLE: A CASE STUDY OF THE UPPER COLUMBIA AREA

Nathan B. GOODALE¹, Ian KUIJT² and Anna M. PRENTISS³

¹ *Hamilton College, USA*

² *Notre Dame University, USA*

³ *University of Montana, USA*

Abstract: The calibrated radiocarbon evidence reveals a bimodal distribution indicating aggregated and dispersed occupations in the Upper Columbia region of North America. Through examining changes in settlement and subsistence in conjunction with dating sequences, we propose a model of population dynamics and their changing amplitude through time. The correlated lines of evidence suggest that population levels show a relationship to changing economic systems as well as social structures. In this paper we map these changes from forager to collector type economic systems as well as generalized to more complex forms of hunter-gatherer socio-systems

INTRODUCTION

A number of recent reflections on the field of paleodemography (Bocquet-Appel and Masset, 1982, 1996; Meindl and Russell 1998) have pointed out that while issues of mortality and fertility of archaeological populations continues to be a central area of concentration in paleodemography, alternative research has focused on methodological developments, as well as topical subjects such as the migration, distribution, density and age composition of prehistoric peoples. One important methodological challenge relates to how researchers reconstruct paleodemography in prehistoric cases where there is a paucity or absence of burial evidence.

Documenting prehistoric population shifts within the Plateau region of western North America are critical for understanding the emergence of pre-contact social complexity, patterns of population growth and migration in the past, and the impact of Old World illnesses during the historic period. This

research has proven highly complex as prehistoric burial practices generally occurred off site, and as such, there is a scarcity of human remains for archaeologists to reconstruct human health or develop a detailed understanding of demographic changes at the settlement or regional level. Drawing upon radiocarbon dating and site history from several case studies, this paper reflects an exploration of population dynamics from the Upper Columbia area of the Canadian Plateau between 4000 and 500 years ago. We illustrate how the identification of long-term population histories can be accomplished using archaeological research methods to reconstruct the occupational history of residential structures, changing settlement and subsistence strategies, and periods of regional population growth and abandonment.

Results of this study offer interesting implications for our understanding of the relationship between population growth and culture change. Most fundamentally we address the long debated issue (e.g. Cohen, 1981; Croes and Hackenberger 1988; Rosenberg, 1998) of whether population growth, in a sense, forces change in fundamental subsistence strategies and consequently in other elements of culture. Our results suggest that some simplistic notions need to be reconsidered.

THE UPPER COLUMBIA AREA OF THE CANADIAN PLATEAU: REGIONAL BACKGROUND

The Upper Columbia River drainage extends from Kettle Falls in the south to the Upper Arrow Lake in the North. This includes the Lower Kootenai and Slocan River drainages (Figure 1). The Upper Columbia drainage contrasts significantly with that of the Middle and Lower Columbia in several ways. First, from an environmental standpoint, this landscape features substantially forested contexts including a substantial interior rainforest. Second, human adaptations in this area were often quite different from those in nearby regions of the Plateau. Ethnographic research documents a complex hunter-gatherer society (Lakes Salish or Sinixt) whose primary subsistence resources included not just salmon and roots, but a high investment in larger game including mountain goat, bighorn sheep, and elk. No other Eastern Plateau society exhibited the same degree of cultural complexity as that of the Sinixt. As this study demonstrates, densely aggregated communities appear to have emerged in this area more than once implying cycles of aggregation and possible socio-economic complexity. The following analysis seeks to review current cultural chronologies developed for the Kettle Falls, Arrow Lakes, and Slocan areas and then

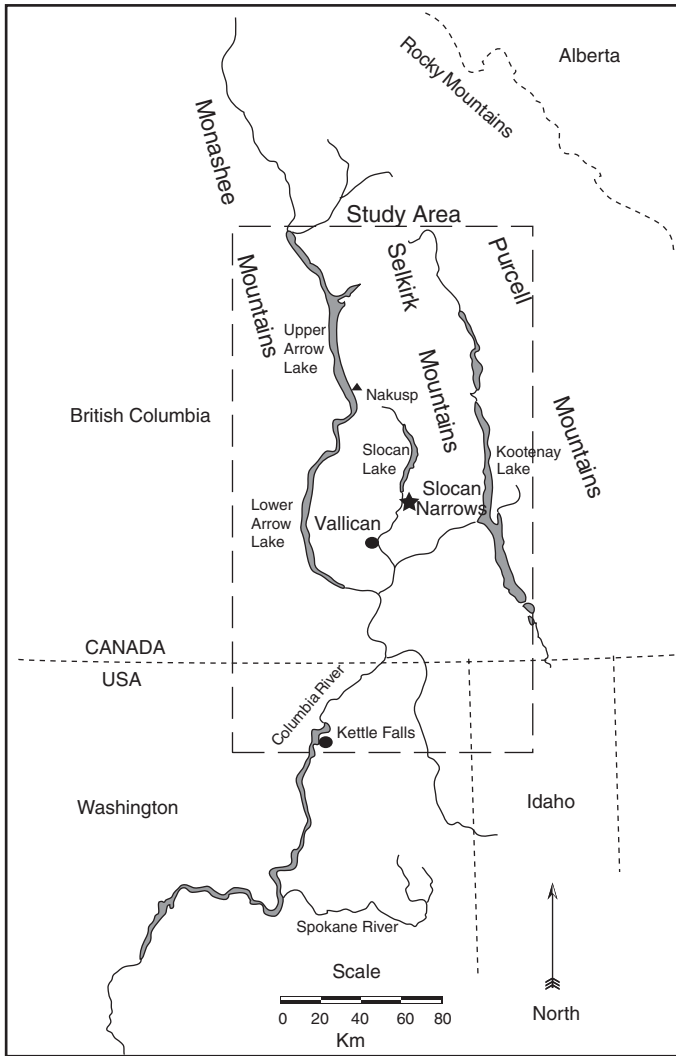


Figure 1: Map of the Upper Columbia area, British Columbia Canada and the Northwest US

to develop a comprehensive understanding of demographic change for the region based upon archaeological data primarily reflecting settlement and subsistence behavior, but also considering limited indicators of variability in social organization.

Archaeological research in the Kettle Falls area provides a relatively well-understood cultural sequence for the prehistoric past (Chance and

Chance 1977, 1979, 1982, 1985). Other research has resulted in an understanding of the cultural historical framework for the Upper Columbia Drainage and Arrow Lakes area (Turnbull, 1977; Mohs, 1982; Rousseau, 1982, 2004; Eldridge, 1984; Goodale et al., 2004). Cultural historic frameworks for the area have been constructed based on stylistic changes in artifacts, pithouse morphologies and their arrangement on the landscape. This section presents the Arrow Lakes chronology from Turnbull (1977), the Slocan Valley variants of Mohs (1982), Rousseau (1982), and Eldridge (1984), and recent additions by Prentiss et al. (2001) and Goodale (2001).

The first substantial evidence of settlement in the Arrow Lakes Region has been assigned the Deer Park phase (Turnbull, 1977) or the Winlaw phase (Mohs, 1982; Eldridge, 1984) and dates to 3500–2450 BP. This represents the first period in the area when people started to live in semi-subterranean dwellings known as pithouses. These houses were built by excavating a circular area, building a support framework of large and small timbers, and eventually covering it with smaller timbers radiating from the center. Lastly, the builders covered the wood sections with soil, hides and matting (Figure 2). The housepits contained in this phase follow a distinct distribution along the immediate river and lake-shores in a linear fashion. The housepits excavated by Turnbull and Mohs assigned to this phase are small in size ranging from 7–10 meters in diameter. However, the Slocan Narrows Site (DkQi 1) has revealed two large houses that measure 16 meters and 22 meters in diameter which date to this time period (Prentiss et al., 2001).



Figure 2: Artist reconstruction of a plan view of pithouse

The housepits found in the Upper Columbia dating to this time period are circular to oval in plan and Mohs (1982) describes them lacking raised earth rims. This may only be a characteristic of small sized housepits because the large house at DkQi 1 has an obvious raised rim. Mohs (1982) also notes that the Deer Park/Winlaw cultural phase is not well represented at the Vallican site. As is outlined later, the early occupation at the Slocan Narrows site provides the best example of pithouse architecture from this early phase. The Slocan Narrows site contains over 40 housepits, featuring two clusters of exceptionally large houses, many of which could date to this early time frame.

The lithic tool assemblage of the Deer Park/Winlaw phase is marked by the presence of medium-sized stemmed and shouldered projectile points that are similar to Shuswap horizon points of the Fraser-Thompson Plateau area (Richards and Rousseau 1987; Rousseau, 2004). The most frequently recovered raw materials include Kootenay argillaceous chert, siltstone, schistose, mica-quartzite, and basalt. The lithic assemblage at the Slocan Narrows site associated with this cultural phase is very limited. Faunal remains are limited to unidentifiable mammal with fish and shell completely absent. This is primarily due to acidic soils.

The next cultural phase in the Upper Columbia region is the Vallican phase dating to 2450–1250 BP. Housepits average 11 meters in diameter from the Vallican site (Mohs, 1982). No housepits associated with this time period have been discovered at the Slocan Narrows site or in the Turnbull (1977) excavations. Diagnostic lithic artifacts include corner and basal notched points and crescent or key-shaped scrapers/perforators. This stylistic variation in the lithic technology is similar to the later Takumakst and early Sinaikst periods at Kettle Falls, the Okanagan Chilikwist phase (Grabert, 1974), and the Plateau horizon of the Fraser-Thompson region (Richards and Rousseau 1987; Rousseau, 2004). Vallican phase artifacts differ from the Takumakst in quality of stone working. The Takumakst period in the Kettle Falls Region contains hastily made lithic tools whereas the Vallican phase features high quality tools and exotic goods such as nephrite adzes. Although no housepits dating to this time period were found at the Slocan Narrows site, numerous (relative to the lithic assemblage size) Plateau horizon style projectile points were recovered in addition to one key-shaped scraper. Faunal remains are rare for reasons discussed previously. However, when they are recovered, assemblages include mammal bones and the shells of freshwater mussels (Mohs, 1982).

The final cultural phase that was defined by Mohs (1982) and Turnbull (1977) is termed the Slocan Phase and dates from 1250 BP to

Contact. The housepits that date to this time period have been excavated at the Slocan Narrows and Vallican sites. The houses excavated at the Vallican site average 8.7 meters in diameter. However, there is variability with medium and small sized pithouses occurring together. This average was determined by the data set provided by Mohs (1982) and only includes those cultural depressions with a diameter greater than 5.0 meters. The second occupational phase of Housepit 1 at the Slocan Narrows site (DkQi 1) dates to this time period suggesting that very large houses (e.g. 16 meters in diameter) do date to this phase. This phase employs a wide variety of pithouse styles including circular, oval, and rectangular outlines with top and side entrances. Cache pits are also used during this time and are external to the housepits along with extramural hearths and activity areas.

Lithic artifacts of the Slocan phase include small side-notched points, occasional Columbia corner-notched points, and frequent groundstone items (Eldridge, 1984; Mohs, 1982; Rousseau, 1982). These points are characteristic of the Kamloops horizon on the Canadian Plateau (Rousseau this volume). However, the Kamloops multi-notched variety has remained undiscovered in the Slocan Valley and Upper Columbia Region. The material culture during this time also closely resembles materials recovered in the Kettle Falls area.

METHODS FOR TRACING PREHISTORIC REGIONAL DEMOGRAPHY: CONSIDERING ADAPTIVE PATTERNS

Expanding upon existing regional chronologies, in this section we consider how a detailed consideration of broader adaptive patterns helps researchers understand regional and local demographic cycles. The following analysis provides a first step towards defining temporal variability in human adaptations in the Upper Columbia, similar to that undertaken by Chatters (1995) for the middle and lower portions of the Columbia and Snake River basins. The data used in this analysis are derived from 116 ¹⁴C dates from the published and unpublished literature for the area (see Goodale, 2001; Goodale et al., 2004 for more detailed consideration). These dates are representative of pithouse occupations, root processing ovens, cultural earthworks, storage features, hearths associated with non-residential sites, and dated faunal assemblages. Each date was calibrated via CALIB 5.0.1 and then plotted with respect to the date's mean age by a series of graphs presented below. A strict review of provenience was conducted in order to assess which dates were appropriate for this data set. Dates that

were not used either lacked adequate provenience data or were considered to be associated with other unrelated cultural or non-cultural events (i.e. rim dates from pithouses). As originally defined by Stryd (1973:76), we grouped pithouses based on size where small houses are < 10m, medium houses are > 10–< 15m, and large houses are > 15m in diameter.

We employ the calibrated dates to examine changes in patterns of socio-economic change and demographic cycles of the prehistoric inhabitants of the Upper Columbia. Needless to say, any reconstructions of paleodemography balance fine-grained analysis aimed at investigating local and regional variation in the tempo of life-ways (see Crombé and Van Strydonck 2004; Gkiasta et al., 2003; Steele et al., 2004 for one example of this debate). Depending upon the interests of researchers, attention is often split between consideration of demographic tempos vs. the methods employed in reconstructing them. In this essay we look at the distribution of ¹⁴C dates from multiple site and feature contexts and we have developed preliminary proxy measurements of settlement and subsistence behavior and population densities. This analysis helps us trace regional processes of population growth, aggregation, and dispersal through six distinct phases.

DATA PATTERNS

Pithouses (N = 24)

In the Upper Columbia Region the first housepits appear ca. 3400–3200 cal BP. (Figure 3). The early houses, dating between 3400 and 1800 cal BP, range in size from small to large. The Slocan Narrows site contains 16 and 22 meter diameter houses, dating prior to 2700 cal BP, which are the largest housepits recorded on the Plateau at this early date. Between 1200 and 200 cal BP the greatest concentration of occupations occur as small, medium, and large housepits. In this region, small housepits occur between 3400 and 600 cal BP, medium housepits occur between 3400 and 200 cal BP, and large housepits occur between 2800 and 600 cal BP.

Root processing (N = 65)

In the Upper Columbia Region the root processing record begins at ca. 6200 cal BP. The dated root processing ovens were obtained entirely from sites in the southern part of the study area at Kettle Falls and in the Calispell Valley (see Andrefsky et al., 2000). The interval from 6200 to 3800 cal BP

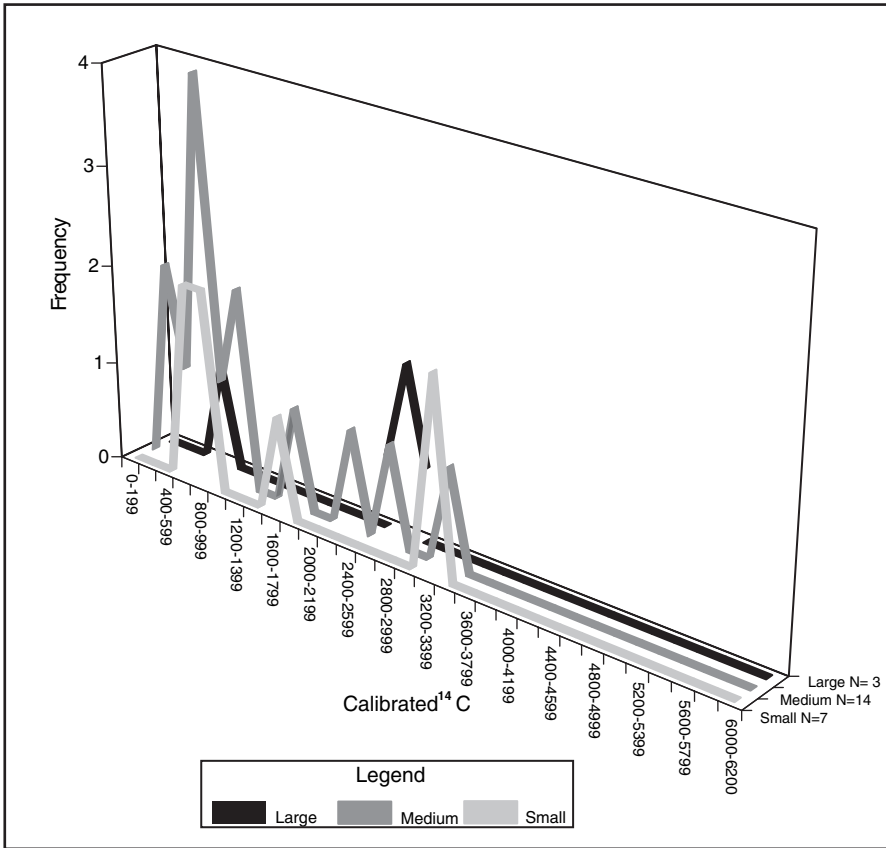


Figure 3: Pithouse occupation by mean of calibrated date

is characterized by limited use of root processing ovens (Figure 4). Two periods of intense root processing appear to correlate with increasing use of pithouses after ca. 3800 cal BP. The first peak in oven frequencies occurs at ca. 3800 cal BP and continues until 2400 cal BP, and the second occurs between 1200 and 600 cal BP.

Storage pits (N = 5)

The calibrated data for the use of storage pits in the Upper Columbia is very limited. The storage pit features that have been dated for this region may have been used for storing edible plants such as camas, but much further research is needed to fully understand variability in storage technologies in this area. All

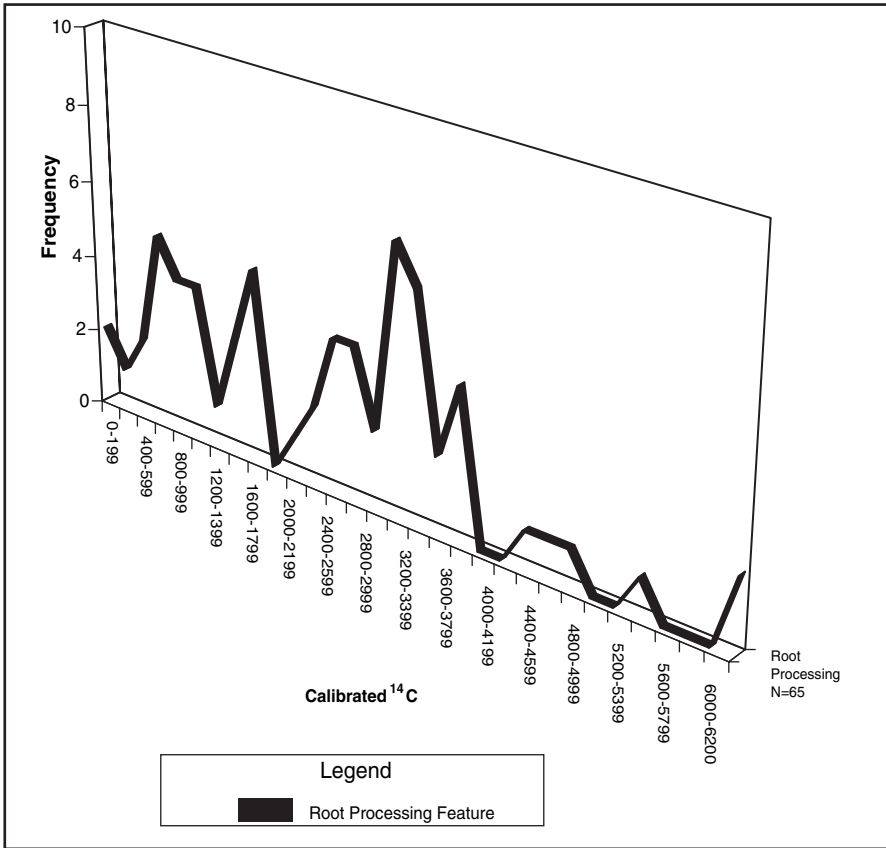


Figure 4: Root processing use by mean of calibrated radiocarbon date

dates come from sites in the Kettle Falls and Calispell Valley areas. Storage pit features occur during the same intervals as that of the most frequent indicators of root processing. Pit features contain a variety of stone tool artifacts, mammal bone and some camas root remains (Andrefsky et al., 2000).

Cultural earthworks

Cultural earthworks have been identified at the Slocan Narrows and Vallican sites in southeastern British Columbia (N = 4). Cultural earthworks appear in the late prehistoric during 800 to 0 cal BP. These dates bracket the earliest and latest times for possible construction of these features. Earthwork functions are not well understood. A 60 m earthwork at the Slocan Narrows

site (Prentiss et al., 2001) may have been used for defensive purposes. Platforms at the Vallican site may have had defensive functions as well, though other functions, such as house platforms, are also possible. It should be noted that the appearance of these features corresponds with changes in aspects of environment and behavior corresponding to onset of the “Little Ice Age” and a decline in root processing activity.

Non-residential sites (N = 17)

The dates of hearths from contexts inferred to be non-residential (not from pithouse sites) in nature show a bimodal distribution (Figure 5). The first peak occurs between 3600 and 2200 cal BP and the second occurs

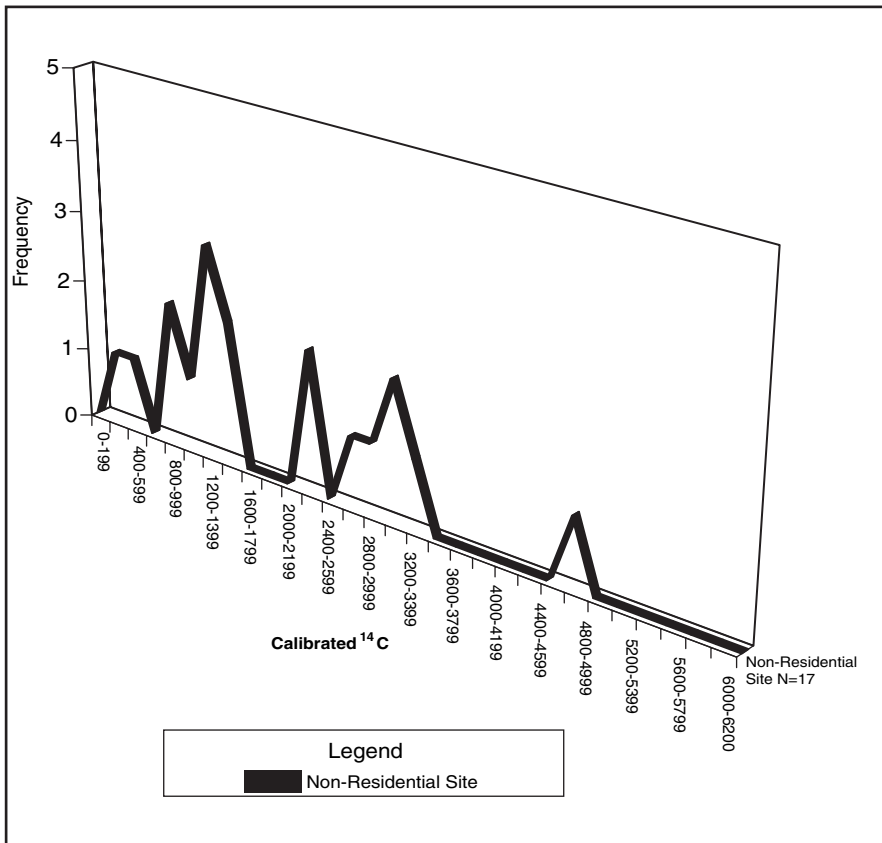


Figure 5: Non-residential site use by mean of calibrated radiocarbon date

between 1600 and 0 cal BP. These intervals correspond to a temporal peak in pithouses, storage pits, and root processing ovens.

PREHISTORIC DEMOGRAPHIC CYCLES IN THE UPPER COLUMBIA

The calibrated evidence provides evidence for shifting paleodemographic patterns among prehistoric hunter-gatherer-fisher groups living in the Upper Columbia Region. Six intervals appear to be evident during the past 6200 years of occupation (Figures 6 and 7, Table 1). Most obvious

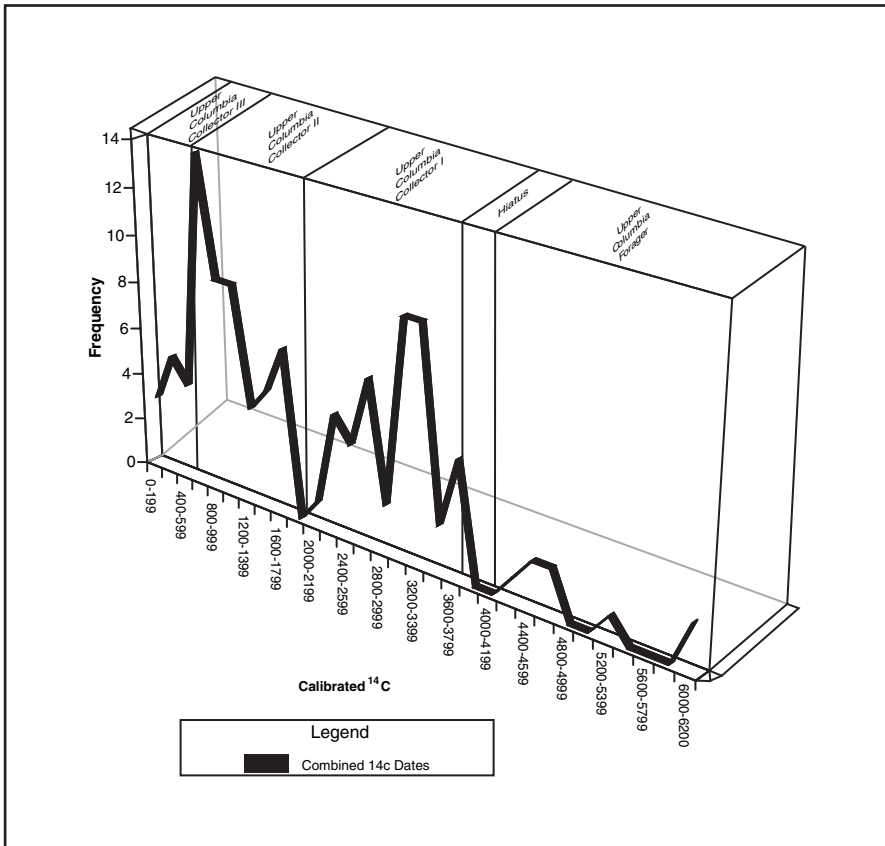


Figure 6: Combined calibrated radiocarbon data incorporating housepits, root roasting features, non-residential sites, storage pits and cultural earthworks

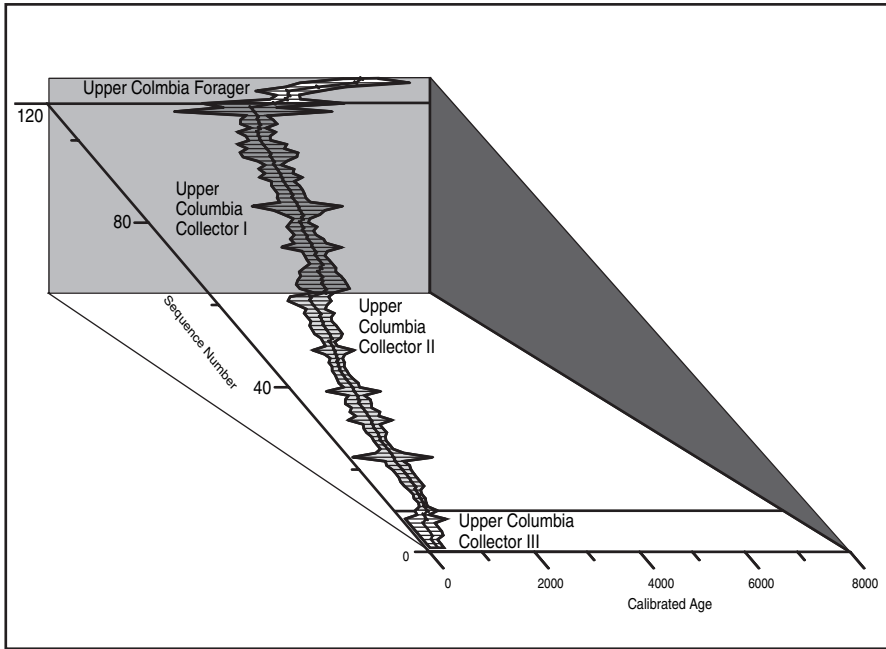


Figure 7: Dates by calibrated means for the Upper Columbia sequence. Each Date is represented by a mean (black dot) with the two sigma range (line). Note the comparison to Figure 6 where the start and end of each phase is also highlighted in this graph by large deviations of the means with breaks between Forager to Collector I, Collector I to Collector II and Collector II to Collector III

are the two periods of increased sedentism and population growth, illustrated by increased pithouse construction and root intensification (see also Thoms, 1989), followed in each case by indicators of population dispersal and possible subsistence extensification (e.g. Morrison, 1994).

Table 1: Adaptive interval and site density in the Upper Columbia

Adaptation	Total Time in Years	# of Sites	% of Sites	Site:Year
Forager	2000	4	9.5%	1:500
Hiatus	400	0	0%	0
Collector I	2000	15	35.7%	1:133.3
Collector II	1200	15	35.7%	1:93.3
Collector III	500	8	19.0%	1:62.5
Total	6100	42	100%	42:6100

In describing these processes, we employ Binford's (1980) terminology (collectors and foragers) throughout this discussion as a means of conveying our understanding of the most likely and frequent mobility and subsistence strategies employed by hunter-gatherers of each phase. Briefly, foragers harvest a broad range of food for immediate use but employ very little to no food storage. In most ethnographic cases their residential groups are small and movements on the landscape are frequent. Archaeological indicators include small camps with impermanent residences and resource procurement locations (hunting/butchering sites for example). The Pithouse I phase on the Mid-Columbia, however, is an exception to the high mobility assumption since they appear to have been sedentary foragers using small pithouses (Chatters, 1995; Chatters and Prentiss 2005). In contrast, collectors target specific species of plants and animals (e.g. salmon) for mass harvest and rely heavily on food storage. They tend to be less residentially mobile, but often employ high degrees of logistical mobility or special task group movement associated with targeted resources. Their archaeological signatures include camps and villages that are occupied for longer periods (e.g. winter villages on the Plateau), logistical camps, caches, and resource procurement locations.

Prentiss et al. (2006) have argued that a variant of the collector strategy, termed "complex collectors," developed exceptionally large houses co-residentially occupied by multiple family units (corporate groups per Hayden and Cannon 1982). This strategy, originating on the central Northwest Coast and perhaps elsewhere, may have offered advantages to larger human groups in areas of very patchily abundant food resources (e.g. Kettle Falls, Slocan Narrows) via the ability of house groups to simultaneously harvest multiple food resources while guarding access to those most critical such as fishing sites. It is within the complex collector strategy that we see the highest degrees of socio-economic complexity across the Pacific Northwest region.

Initial peopling and adaptation—the upper Columbia Forager (6200–4200 cal BP)

The Upper Columbia Forager represents a high mobility forager adaptation that is suggested by the lack of evidence for any permanent residential structures. This period contains dates for the first use of root processing in the Upper Columbia Region and is represented by six dates in the Calispell Valley: five dates from 45PO139 and one date from 45PO141. Roots seem to have been a fairly stable resource base during this time and were probably used in a limited manner. The Upper Columbia Forager

period also contains one date from the Fishery site in the Kettle Falls area that is in association with a non-residential site. This period represents a “forager” adaptation similar to the Middle Holocene Nesikep tradition of the Canadian Plateau and the Cascade phase in the Columbia Plateau (Chatters, 1995; Prentiss and Chatters 2003a; Stryd and Rousseau 1996).

Regional and local abandonment—“Hiatus” (4199–3800 cal BP)

Available radiocarbon evidence indicates that there was a brief occupational gap between earlier forager and later collector adaptations. This hiatus temporally corresponds to a similar pattern throughout the Canadian and Columbia Plateaus (Chatters, 1995; Prentiss and Kuijt 2004; Rousseau, 2004). While some of this can be partially explained by the presence of a “flat place” on the radiocarbon curve at 3950–4050 cal BP (Stuiver et al., 1998), the abandonment period is spread across a wider time span and the pattern is seen across the entire Plateau region. Thus, it appears that there was an occupational hiatus of several hundred years shortly after ca. 4200 cal BP.

Renewed population growth and sedentism—the upper Columbia Collector I (3799–2000 cal BP)

The Upper Columbia Collector I represents the first of two peak occupational horizons and the advent of the collector-type system in the Upper Columbia. The first semi-subterranean pithouses were established and occupied during this interval and vary in size from small to large. Housepits dating to this time are found in single or low density clusters in the Upper Columbia landscape and is generally representative of a dispersed collector adaptation. The Slocan Narrows site may provide an exception to this pattern since it contains two clusters of extremely large houses, two of which now date to this time frame (Prentiss et al., 2001). Further research could demonstrate an early aggregated community in this context. The first indicators of intensified camas root processing occur in conjunction with an expansion in the frequency of storage pits. Faunal and floral data are still lacking at this point, but given the presence of dispersed and possibly occasional aggregated pithouse communities in optimal fishing locations, evidence for camas intensification, and the use of storage tactics, this period likely marks the beginning of the dispersed generalized collector adaptation in the Upper Columbia. It is, moreover, concurrent to similar behaviors at

the advent of Pithouse II (Chatters, 1995, 2004) and the Shuswap horizon (Richards and Rousseau 1987; Rousseau, 2004).

Shifting systems—“Hiatus” or transition?

Between the Collector I and Collector II adaptations there is a decline in frequencies of radiocarbon dates. Although this could be explained, at least in part, by sampling bias, a similar pattern has been recognized by Chatters (1995) for the entire Columbia Plateau. This suggests the possibility of short-term population decline and/or significant alteration of basic residential mobility patterns reducing group visibility in the region prior to the advent of the next broad adaptive period. Clearly further research is required into this important but little understood period.

Aggregate villages and social complexity—the upper Columbia Collector II (1999–600 cal BP)

The Upper Columbia Collector II corresponds to a second high-density occupation of the Upper Columbia. Archaeological evidence exists for the emergence of aggregated housepit villages by ca. 1200–600 cal BP. Large sites, such as Vallican, Slocan Narrows, and Ilthkoyape, feature the highest density clusters of houses in all size ranges. Unusually large houses within large villages may reflect the appearance of the complex collector strategy. This period also corresponds to the late peak in root processing and storage pits. Hearths associated with non-residential sites also peak at this time. Some of these could be the consequence of logistical or task group mobility strategies. Specialized sites such as the Fishery at Kettle Falls (45ST94) clearly reflect specialized resource harvesting strategies, typical of collectors (Chance and Chance 1977). Intensified harvesting of shellfish is also known from the Vallican site (Mohs, 1982). Faunal remains from 45PO137 in the Calispell Valley, demonstrate continuous use of both fish and mammalian resources during this time with a relatively more intensive use of mammals over fish.

Dispersal and decline—the upper Columbia Collector III (599–100 Cal BP)

The beginning of this interval corresponds to the start of the Little Ice Age (Pielou, 1991) and marks the expansion of glaciers in high altitude contexts of the Rocky Mountains and Cascade Range. This interval is characterized

by a decline in the frequency of radiocarbon dates. Housepit occupations are, however, still present and medium sized structures dominate the record. The use of root processing ovens appears to decline and may be consequent to the onset of the “Little Ice Age” and the associated effects on the availability of resources in some areas (Prentiss and Kuijt, 2004). During this time, cultural earthworks appear in the archaeological record. If these features do reflect heightened attention to territorial defense it could be linked to an increasingly patchy environment brought on by cooler conditions. Interestingly, warfare increases in many other areas of western North American during the final several hundred years of the prehistoric period and into historic times (Chatters, 2004). Burials from the Vallican site highlight the distinct presence of complex social organization. Burial two for example, included an infant and a fetus, wrapped in animal skins, interred with 2102 glass trade beads, 138 rolled copper tube beads, 595 dentalia shell beads and pendants, 59 drilled elk-tooth pendants, 16 perforated copper slate pendants, 9 copper alloy buttons, 3 copper alloy rings, one iron pendant, one coiled copper tube bead, and various other small items (Mohs, 1982). Clearly this reflects a high degree of material investment in the status of children. Overall, these data highlight a generally reduced or at least more dispersed population, yet increased attention to marking of territory and social status, particularly during the early historic period.

PALEODEMOGRAPHIC CYCLES OF THE PLATEAU: TESTING THE DEMOGRAPHIC MODEL

In conjunction with other synthetic studies from other regions (most notably Andrefsky, 2004; Chatters, 1995; Rousseau, 2004) the data presented above have allowed us to reconstruct cycles of demographic change. First, populations appear to have strongly increased and declined twice in the past 4000 years. This pattern appears to correlate with the emergence and decline of aggregated pithouse communities and various markers of socio-economic complexity. It must be made clear, however, that the radiocarbon record may reflect actual population dynamics as well as a sampling bias due to researchers focusing on the most archaeologically visible sites. If the data do reflect population dynamics, then this has some interesting implications for our explanations of cultural variability as well as corresponding changes in socioeconomic systems. Second, it is now clear that at some periods select local and regional areas were abandoned. Chatters (1995), Prentiss and Chatters (2003a), and Prentiss and Kuijt (2004)

assert that near to total abandonment of many parts of the Plateau occurred at ca. 4000 cal BP. These researchers argue that abandonment was associated with climate change and cultural maladaptation and may have opened the region to an influx of populations from the Northwest Coast with new adaptations (namely the collector system). Data presented in this study support arguments for abandonment at this period and, to a lesser degree, ca. 1800–2000 cal BP as a period of low population. We test these ideas with three additional analyses now emphasizing site frequencies, patterning in 2 sigma calibrated radiocarbon date ranges, and growth of a specific village.

Population dynamics

The percentage of radiocarbon dated sites is roughly equal to the percentage of sites occupied for each given adaptive interval. We assume, based on evidence presented in Goodale (2001), that higher site frequency reflect higher population densities. The highest density of occupied sites is seen with the Upper Columbia Collector I and II, with relatively lower densities during the Collector III adaptation, and even lower during the Forager adaptation. Interestingly the site density for the Collector I and II are roughly the same. However, merely counting the frequencies of sites in each interval is an insufficient test. A more accurate approach is to consider the relationship between total time span in each interval and frequencies of sites (Table 1). The data from this analysis suggest generally low populations during the Forager and Collector I periods, followed by a substantial increase during Collector II and III. Further, despite seemingly reduced frequencies of aggregated pithouse villages and root-roasting and storage pits, these data suggest that Collector III may have not have featured significant population reduction, but merely a more even pattern of dispersal on the landscape.

Abandonment and change in the Upper Columbia: Analysis of calibrated dates

Another way to understand regional demographic changes is to assess patterning in calibrated dates at two-sigma (95% confidence interval) error ranges. Points where major adaptive change occurred which were accompanied by breaks in occupation sequences should be recognizable as significant disjunctions in the radiocarbon record. Figure 7 illustrates the full range of calibrated dates ($N = 116$), plotted and coded by cultural interval. This picture reveals a fairly continuous distribution spanning 7,200 to 0 cal

BP. This is especially evident during the Collector I, II and III intervals where the centroids (means) overlap in many instances. A couple of exceptions occur. First, between the Forager and Collector I adaptations, the high two-sigma range of the youngest Forager date and oldest Collector I date explain the overlap. Although this may be partially explained by variability in the calibrated radiocarbon curve, comparisons with data from other areas of the Plateau (Chatters, 1995; Prentiss and Kuijt 2004) still support the possibility that a significant population reduction or even full abandonment occurred during the period of 4,200–3,800 cal BP. Second, there is another break during the transition from Collector I to Collector II. This would be a major disjunction if not for the presence of a single date from a root-roasting pit considered for purposes of this study to be the final event in the Collector I sequence. The time period from 2,200 to 1,800 cal BP appears to represent some form of cultural transition, perhaps associated with a brief population dispersal. However, the radiocarbon record does not appear to reflect abandonment. Chatters (1995) recognizes a similar pattern on the Middle Columbia and Lower Snake. Finally, there is a continuous overlap of dates associated with the transition from Collector II to Collector III. This supports the argument that no major population disjunction occurred between Collector II and III. It appears likely that there was little cultural change between these intervals other than in the scale and frequency of large group aggregation in pithouse communities.

Aggregate villages: scale of communities as seen at Slocan Narrows

To really understand paleodemographic patterns on the Canadian Plateau, as well develop insights into the process behind these changes, it is important to consider the settlement and cultural context within which the radiocarbon data were recovered. This is especially important in understanding the emergence and reuse of large aggregate villages at select points of prehistory. To contextualize the radiocarbon analysis results we want to briefly turn to excavation data from the Slocan Narrows site, located in south-central British Columbia, Canada. While there is considerable regional variation, the broad demographic pattern observed at this site is generally representative of other local sequences, and provides insight into regional shifts.

The Slocan Narrows site represents the largest and most northern aggregate pithouse village site in southeastern British Columbia (Figure 8). There are over 40 pithouses located in a spatially restricted area. Excavations conducted in 2000 on multiple pithouses along the Slocan Narrows illustrates

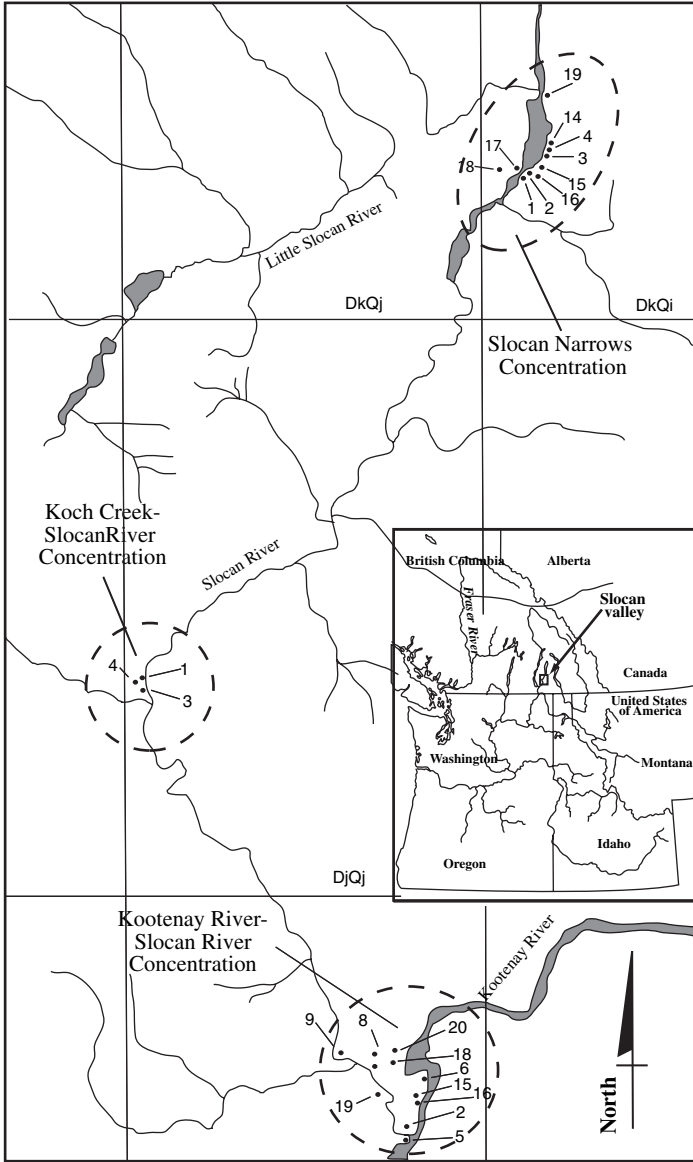


Figure 8: Map of Slokan Valley and clustering of known archaeological sites at select choke points

that this area was among the earliest hunter-gatherer-fishing occupations of the Canadian Plateau (Prentiss et al., 2001; Goodale et al., 2004). Radiocarbon and stratigraphic evidence, moreover, illustrates that the site was occupied in multiple prehistoric periods. For example, Housepit 1, a large pithouse on the southern edge of the site was originally constructed and occupied at 2,650+/-70. Similarly, a radiocarbon date for the Housepit 2 floor of 2,724+/-48 indicates that this large pithouse was occupied at approximately the same period. If representative of the entire site, this suggests that the first occupation at Slocan Narrows consisted of large pithouses, and by extension, required considerable labor of large social groups. It appears that many of the pithouses were then reoccupied at later points. While broader sampling is needed to understand the details of the regional sequence, preliminary results indicate that between 700–850 years ago there was a second phase of significant population aggregation in this area. For example, the upper cultural B horizon of Housepit 1 is dated to 710+/-70. Housepit 2 and 5 contain a complex sequence of sediments, which includes the cultural B horizon within Housepit 5, redeposited terrace material within the Housepit 5 rim, floor materials within both houses and sub floor terrace gravels and sand. A burned post from the floor of Housepit 5 was dated to 830+/-70, providing further evidence for the reuse of these pithouses and settlement location.

It is when one considers local and regional archaeological patterning, and when one adopts a landscape approach, that we gain a real understanding of the pulses of prehistoric demographic change over the last three thousand years. First, it appears that the transition to winter sedentary villages was focused on select key fishing/resource locations. This is seen in the clustering of residential sites near Slocan Lake, mid way down the Slocan River, and at the confluence of the Slocan River and Kooeteney River (Figure 9). While there are a few isolated pithouses between these locations, these are quite rare and usually smaller. Thus, we can see a clear and deliberate focus on specific landscape locations, those that served as fishing check-points along major transportation corridors.

The control of these locations must have been of considerable importance to families and communities, and suggests that ownership and access to seasonal salmon runs must have become a critical issues with the emergence of larger pithouse villages. In the case of Slocan Narrows, the pithouses were located at a critical location where the river became constricted so as to facilitate salmon fishing (Figure 10). It is also the last area before the river becomes quite broad, with seasonal flooding, and at the same time, the first accessible area that would allow for people to build pithouses near the

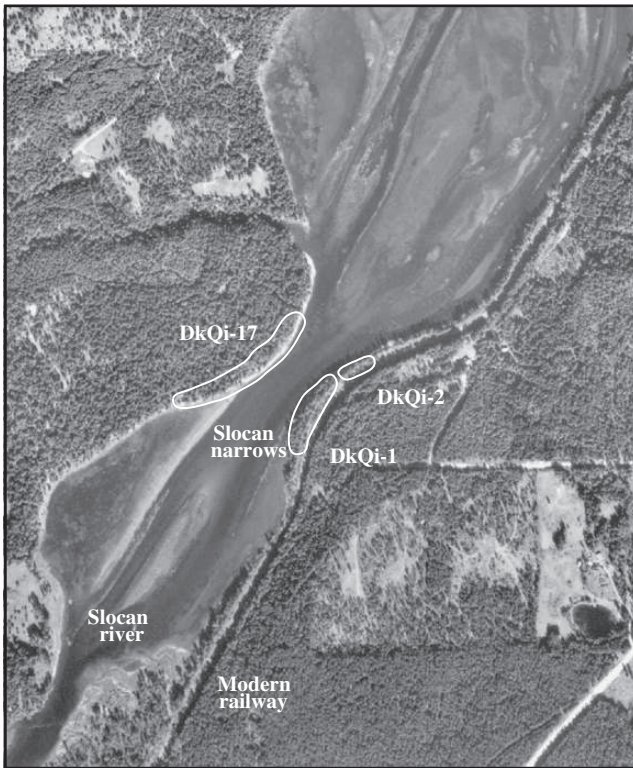


Figure 9: Air photograph of Slocan Narrows area of the Slocan River. Note the clustering of winter aggregation pithouse villages along the two sides of the river. Community members living at these settlements would have been able to control access by people living further to the south, as well as utilize this location to catch salmon migrating up stream for spawning in the fall

river. Presumably those families, households and clans that were successful in controlling such fishing rights in the long-term were able to out compete other local groups and consolidate fishing rights and access to key fishing areas through marriage and conflict.

While it is tempting to assume that the different occupations at the Slocan Narrows site represents new levels of sedentism and population growth, it is probably more accurate to view this as regional shifts in settlement systems and population aggregation. In light of the sporadic and discontinuous occupational history at the site, we believe that the Slocan Narrows site reflects the movement of people into this region from other areas. These villages would have been seasonally occupied, with the highest population levels being seen in winter and with people being dispersed across the landscape

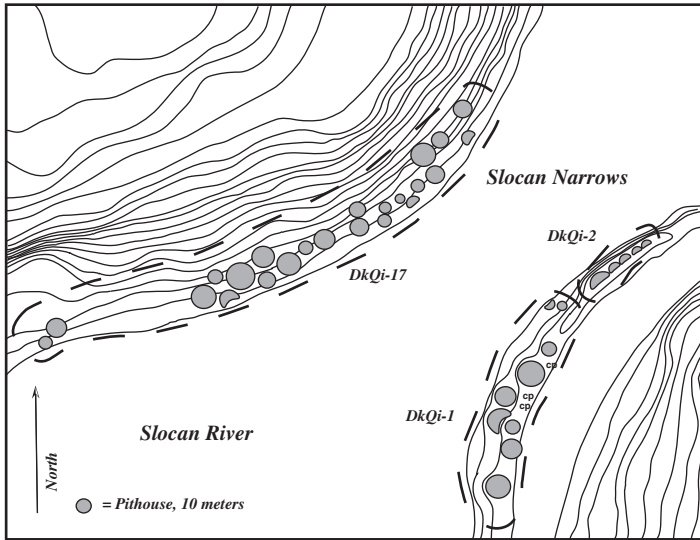


Figure 10: Location of pithouses in archaeological sites DkQi-1, 2 and 17, Slokan River, British Columbia, Canada. As with other aggregate pithouse villages, the construction of many of these structures would have required considerable effort, and were likely to have been reused several times

in other seasonal task groups to collect a range of plant and animal food resources. The existence of similar earlier pithouse occupations to the south (ca. 3500–3000 and 1000–1300 cal BP), and absence of such large pithouse villages to the north, illustrates that Slokan Narrows represents at least two demographic pulses of people into the Upper Columbia River area. This was at least partially related to the fact that the Slokan Narrows site is situated very close to the end of salmon spawning areas. It is not clear why this demographic expansion occurred when it did, nor why these villages were abandoned at later points. Researchers have yet to determine, moreover, if these patterns represent repeated transitions from local general hunter-gatherers adaptations to specialized fishing economies, and back again, or if we are witnessing episodes of human movement into underutilized areas at select points of the past.

DISCUSSION

This research presents a number of implications for understanding the demographic change among the complex hunter-gatherer-fishing societies of the Upper Columbia. First, this research provides another indicator of dramatic cultural change and population growth after ca. 4200–3800 cal

BP (Figure 11). A small-scale mobile society appears to have existed in the Upper Columbia prior to the onset of the full Neoglacial climatic period. Rapid cooling at 4200 cal BP and vegetative changes may have prompted population reduction until at least 3800 cal BP, after which point people with collector and fishing adaptations moved into this area. We argue that this process was not one of simple social change, but a whole-scale transformation of the basic socio-economy. Similarly, Prentiss and Chatters (2003a,b) propose that the interior Plateau collector system emerged on the Northwest Coast at a much earlier date, spreading into the former region after the climate change had largely emptied the area.

Second, it would appear that aggregated pithouse communities emerged and declined twice in portions of the Upper Columbia. The village at Slocan Narrows featured the largest early pithouses on the entire Canadian Plateau (Prentiss et al., 2001). Although only two of the large houses have been radiocarbon dated, it is likely that the two clusters of these houses will reveal numerous other early dates. These houses are equivalent in size to the largest houses found at sites such as Keatley Creek in the Mid-Fraser Canyon (Hayden, 1997). They are large enough to have housed groups potentially as large as 30 to 40 people per house (cf. Hayden et al., 1996). Management of groups this large may have necessitated at least some form of achievement-based ranking (Ames, 1985; Binford, 2001). Researchers now need to look for additional data to explore this issue and to ask how and why this occurred. The radiocarbon record suggests a rapid and relatively short-lived process of aggregation in this locale. This probably started elsewhere with small houses, but very quickly was replaced by construction of the unusually large houses at Slocan Narrows. The larger scale process of aggregation occurred late in the Collector II period, producing major villages at Slocan Narrows, Vallican, Ilthkoyape, and probably, many other locations now destroyed by development.

Even if some details of subsistence strategies remain to be defined, data from the Upper Columbia region appear to have strong implications understanding population and culture relations. A number of Pacific Northwest archaeologists have argued that it was steadily rising population since 4000 B.P. that affected the rise of new forms of subsistence and gradually, large villages and even socio-economic inequality (Cohen, 1981; Croes and Hackenberger 1988; Lohse and Sammons-Lohse 1986). Examining data from the Lower Snake and Middle Columbia Valleys, Chatters (1995) in contrast, argued that the major changes in Plateau cultures appear to have come about in times of exceptionally low human numbers. The Upper Columbia data demonstrate similar patterns to those suggested by Chatters.

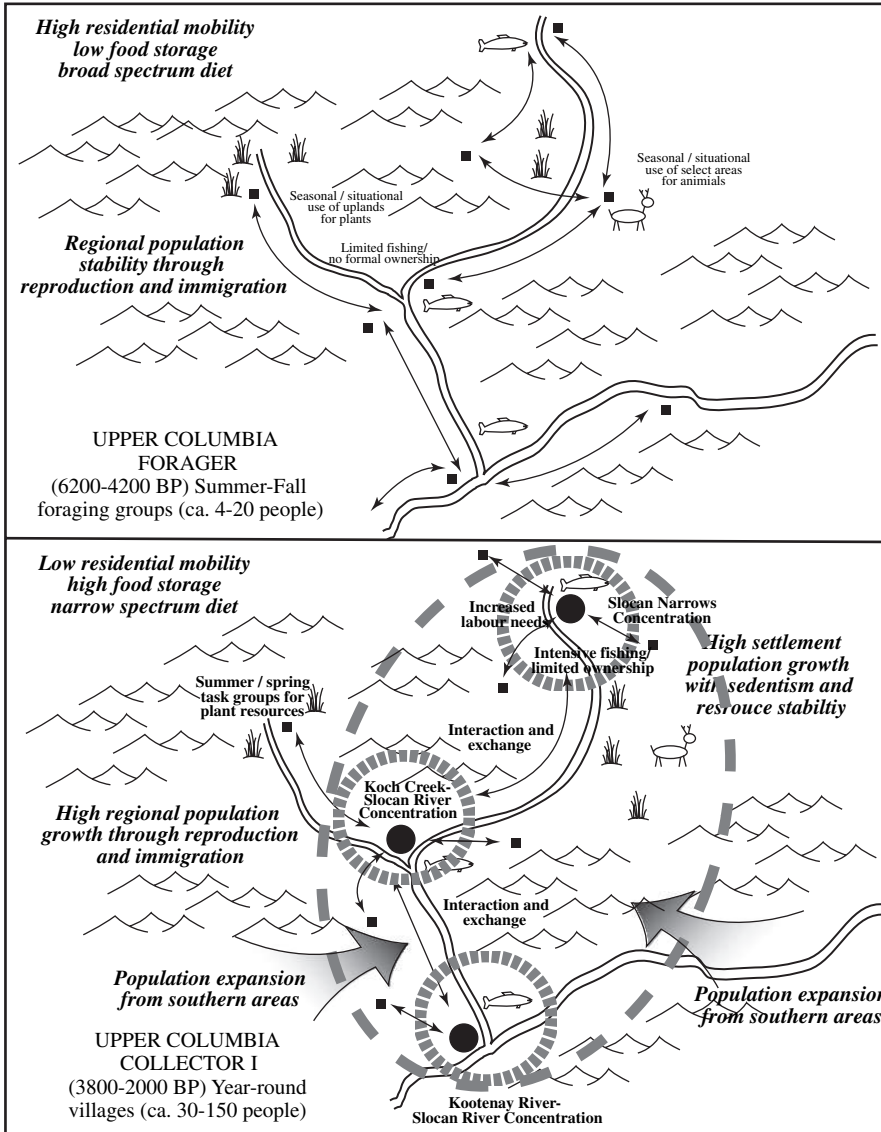


Figure 11: Demographic, settlement and subsistence changes from the Upper Columbia Forager system (ca. 6,200 to 4,200 BP) to the Upper Columbia Collector I system (ca. 3,800 to 2,000 BP)

Two major changes occurred in middle to later Holocene prehistory. The collector strategy appeared shortly after ca. 3800–4200 cal BP and the complex collectors after ca. 1400–2200 cal BP. In both cases, populations were at regional lows suggesting that radical changes in socio-economic organization could only occur under low population conditions (e.g. Prentiss and Chatters 2003b). Populations only rose after the advent of the new strategies, later to decline and be replaced by new variants. The ultimate implication is that the traditional population pressure models (e.g. Boserup, 1966; Malthus, 1976) employed by archaeologists are not valid for understanding major transformations in the organization of settlement, social relations and food acquisition and processing. It is more likely however, that these types of models are useful in understanding cycles of subsistence intensification, particularly those that result in maladaptive declines in labor efficiency (Broughton, 1994).

This study also has implications for understanding the process of community decline and abandonment on the Plateau. Debate between Hayden and Ryder (1991) and Kuijt (2001) have directed new attention to the processes and scale of demographic collapse and reorganization of large-scale interior Plateau communities. Local factors such as landslides and temporary damming, as well as larger scale processes including climatic change and regionally altered resource conditions, need to be considered. Decline of the Slocan Narrows and Vallican site villages coincides with similar processes in the Fraser-Thompson drainages (Hayden and Ryder 1991; Kuijt, 2001) and to the south on the Middle Columbia and lower Snake Rivers (Chatters, 2004). These studies support Kuijt's (2001) argument that there was a regional reduction in population at this point, and that such wide-scale abandonment was probably related to paleoclimatic changes and subsistence resource shifts.

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Chapter 8

THE PALEODEMOGRAPHY OF CENTRAL PORTUGAL AND THE MESOLITHIC-NEOLITHIC TRANSITION

Mary JACKES¹, Christopher MEIKLEJOHN²

¹ *University of Waterloo, Canada*

² *University of Winnipeg, Canada*

Abstract: Newly available information on the excavation of the Portuguese Mesolithic shell middens, Cabeço da Arruda and Moita do Sebastião, has allowed reassessment of the paleodemography of the sites. Following the restudy of Arruda and an examination of Moita site structure, we now discuss the problem of arriving at a minimum number of individuals (MNI) for Moita and use the age distribution of the dead to estimate the total fertility rate (TFR). We confirm the difference between Moita and Arruda and note their divergence from the Neolithic site of Casa da Moura. Our method of estimating TFR, deriving from the use of West model tables, is explained and is tested by reference to historical data sets and by calculation of equivalent demographic values using the Brass relational table approach. Our focus is the Mesolithic-Neolithic transition and we establish the context of demographic change in the late Mesolithic and early Neolithic of central Portugal by reference to changing environmental, nutritional and disease conditions. The low level of population growth at Moita would have increased during the occupation of Arruda. However, subsequent changes in climate and sea levels led to unfavorable conditions and we hypothesize that the Tagus lowlands were abandoned in favor of healthier uplands where there was a rebound and an increase in population growth in response to changed lifeways

INTRODUCTION

This paper continues work that has interested us for over twenty years, the interpretation of the demography of the Mesolithic and Neolithic of central Portugal, which falls within the much broader sphere of the interpretation of demographic variables in human populations during the late Pleistocene and Holocene. The continuing debate over what Deevey (1960) called the

demographic transition (but see Schulze and Mealy, 2001) is the focus of our interest. Here we will concentrate on the interpretation of the Portuguese mid-Holocene record and touch on other areas only to clarify our concerns about the assessment of population samples and the difficulties of global interpretation.

We begin with a brief introduction to certain aspects of paleodemographic data and methods, followed by a mention of our earlier work on European Mesolithic and Neolithic demography, in order to explain our interest in the Portuguese data. We introduce and discuss the skeletal sample from Moita do Sebastião that is central to this paper. Methods allowing us to estimate the relative fertility levels of the key Portuguese sites are detailed and evaluated. Finally, we place the sites within the general context of the demographic aspects of the transition to agriculture in Portugal.

Paleodemographic reconstruction

The potential uses of demographic data in bioarcheological interpretation have undergone a revolution over the past thirty years. When Peterson wrote his critical review of paleodemography (1975) his concerns were with the accuracy of sex and age determination, and with sample bias. His conclusion was that paleodemography was founded in quicksand and unlikely to yield meaningful results.

While Peterson's concerns have not been fully answered, the focus of the enquiry has changed and matured, following upon the work of Bocquet-Appel and Masset (1977). Our work has centred upon an examination of what the age profile tells us about population growth (or decline) and fertility.

However, there are three critical aspects that need examination if paleodemographic age at death distributions are to be interpreted accurately. The first is that there must be accurate age assessment of the osteological sample. This has been extensively reviewed (e.g. Jackes, 1992). Very careful assessment of possible sample bias is also necessary. A further concern is the structure of the age profile to be used. For reasons discussed elsewhere (Jackes, 1986, 1992, 2000; Jackes et al., 2001a) we believe an age profile that divides the sample into five year categories for the period from birth to 24 years, and groups all adults aged 25 and over, provides the most satisfactory results. In this way, errors in adult age assessment are largely avoided with minimal loss of explanatory power.

The second aspect concerns the completeness of the sample. Are we dealing with a full collection as excavated? What is the relationship of the

excavated sample to the site as a whole? This is an aspect that has especially concerned us in our examination of the Portuguese data since excavation has been ongoing since the mid 19th century.

The third aspect has to do with the issue of which demographic values can be considered representative of the original biological population. We plot the ratio of subadults to adults, as first proposed by Angel (1969, 1971) and the mean probability of death during childhood (Jackes, 1986). These serve as summary values that will allow us to make comparisons among sites, to interpret the data by setting site values within a wider context in order to make sure that the data are valid and biologically possible and in order to provide an interpretation.

Paleodemographic research and the shift to food production

The transition from food gathering to food production (in Europe the Mesolithic-Neolithic transition) has produced an extensive literature. The demography of the transition, first discussed by Deevey (1960), was subsequently elaborated by, for example, Spooner (1972) and Cohen (1977). The central question asked was whether or not population growth could be seen as a cause or a consequence of the transition.

We stress that paleodemographic exploration of the transition requires a good deal of self-discipline on the part of the researcher because there are clear pitfalls in such analysis. Data must be from sites which are stringently chosen. Firstly, they must be from the appropriate time period. Secondly, we cannot ignore strictures levelled against the use of data from sites with enormous time spans and tiny samples, sites that were incompletely excavated, sites in which only a percentage of burials were used to develop the life tables, sites with clear biases introduced by the burial patterns (e.g. Jackes, 1992). If the basic data, the number and age distribution of the skeletons, are biased or flawed, the conclusions rest on shifting sand.

We also suggest that global modelling of transitions such as that from food gathering to food production is a questionable exercise because it assumes that the transitions are similar in different parts of the world. Clearly the transition in the Near East, where it is earliest, differs from that found in Europe where there is debate over its very nature. What parts of Europe may have undergone colonization by farmers from the Near East (see e.g. Scarre, 2003; Zvelebil, 2003; Di Giacomo et al., 2004 cf. Semino et al., 2004)? To what extent were there real changes in subsistence? What was the effect, if any, on the social organization and settlement patterns of the

immigrant and/or the indigenous populations? Answers to these questions will have major influence on the interpretation of demographic changes.

Earlier attempts to explore transitions in North American contexts (Jackes and Lubell n.d.; Jackes, 1986; Jackes, 1993) were problematic. Many recent papers focus on the difficulty of identifying a clear transition to horticulture in the Americas (B. Smith, 1989, 1995, 1998, 2001a; Chapdelaine, 1993; D. Smith in prep.; O'Shea, 2003): the most trenchant statement is that by Bruce Smith as he fulminates against the "reductionist, essentialist, and dichotomous world view that societies are either hunter-gatherer-foragers or farmers" (Smith, 2001b:4). Even more recently Bellwood, in a general summary, has characterized the shift to agriculture in Central and North America as "diffuse" (2005: 155, 177).

Our attempts to identify and analyze transitions other than in Europe and North America have also been problematic. We unsuccessfully sought suitable East Asian samples (Jackes, 2004; Jackes and Gao, n.d.). The North African Maghreb, sometimes used in analyses which include the circum-Mediterranean Basin, shows a set of very specific problems (Lubell, 2001, 2005; Rahmani, 2003, 2004). Included in these are the demonstration of change within the Epipaleolithic, the analogue but probably not homologue of the European Mesolithic, the late introduction of the Neolithic into the Maghreb, and the long time period represented by the sites. One core site sometimes seen as analogous to the European Mesolithic is Tavoralt. This site falls completely within the Iberomaurusian period but probably represents a 10,000 year time span. It also involves two cemeteries, only one of which is directly dated (one date at ca. 13,730 calBP), perhaps 7,000 years before the Neolithic of Capsian Tradition appears. Use of such a site to model the demographic situation for the pre-Neolithic is problematic. There is very limited evidence for subsistence change until the Neolithic of Capsian Tradition, and even then the long-established Epipaleolithic pattern continues.

Our work on the Near East (Jackes et al., in prep. b, contra Eshed et al., 2004) suggests that it is an over-simplification to assume there was a clear-cut Mesolithic-Neolithic transition directly associated with a demographic transition (see also Davis, 2005).

Paleodemography of the shift to food production in Europe

We began studying paleodemographic changes at the shift to agriculture in Europe by analyzing the human skeletal remains recovered from the Mesolithic shell middens of the Muge estuary in central Portugal (see Lubell

et al., 1989). Our initial reconstruction of the demographic profiles of two Mesolithic sites and one Neolithic site (Jackes, 1988: see further below) suggested firstly that rates of growth and apparent fertility were higher in the Neolithic than in the Mesolithic, and secondly that the two Mesolithic sites were different from each other.

Since our initial publication of these data we have been involved in two further preliminary studies of demographic profiles in the European Mesolithic and early Neolithic (Meiklejohn et al., 1997; Jackes et al., in press), the first centered on samples from Northern Europe, the second on collections from Djerdap (Iron Gates Gorge). The results are congruent with the findings of Jackes (1988), but the samples are not satisfactory. Some samples are small, some incomplete, some biased, some are agglomerated samples from more than one site, and there are uncertainties about the archeology and archeological provenance in some. Few of the individual samples stand up to close scrutiny, and therefore we cannot consider these a solid basis for interpretation of the agricultural transition.

We are convinced that central Portugal is one of the only geographical regions in which we can examine the transition with some degree of assurance that the data are sufficiently robust. We began work here in 1983 (Lubell et al., 1989), focusing our attention on radiometric dates and stable isotope analyses, and attempting to gain a fuller understanding of the sites (e.g. Jackes and Lubell, 1999a,b; Lubell et al., 1994). We have looked at metric and non-metric indicators of group relationships, and whether or not the groups were homogeneous over space and time. We have concluded that there was no large influx of population at the time of the subsistence transition (e.g. Jackes et al., 2001b). However, our work on the extraction and analysis of ancient DNA is continuing and may provide further information (e.g. Bamforth et al., 2003).

Most recently we have been examining means of assessing the population structure of those sites we believe can provide the most reliable data for assessment of the transition. We have been working in great detail on questions of numbers of individuals in the sites and their age profile, and enquiring how representative the burials are of the original group.

Unfortunately, we can work only with what the archeological record makes available to us, so there can never be the rigor we would desire in the selection of samples suitable for reaching definitive answers. However, central Portugal provides us with the numbers, the sites, and a long history of archeological exploration so that we can at least approximate a reasonable research methodology. This is not to gainsay that further archeological research in central Portugal may provide evidence of a “fuzzy” transition,

and we very briefly touch upon this below. Archeologists may well discover that there are as many questions in central Portugal about the nature and timing of the transition as there are elsewhere (Oosterbeek, 2004), but our ongoing work on dating and stable isotope analyses provides a fair measure of certainty about the suitability of the sites we will discuss and their relation to a subsistence transition. We are using sites that appear to fall on either side of a subsistence divide as demonstrated by stable isotope analyses and which represent a fairly limited time period on either side of that divide (see Jackes and Meiklejohn, 2004 for information on stable isotopes and radiocarbon dates, with details on methods of calibrating the dates).

The samples available to us are from two Mesolithic sites and one Neolithic site. The Mesolithic sites (Cabeço da Arruda and Moita do Sebastião) come from a restricted area along the Muge, a southern tributary of the Tagus River. The Neolithic material is from a cave (Casa da Moura) in a karstic limestone area to the north of the Tagus (Figure 1). Casa da Moura is the earliest among a complex of such ossuary cave sites which includes others we have studied, Furninha, Feteira and Fontainhas. It is unfortunate that we do not have Neolithic material which is geographically closer to the Mesolithic sites, but suitable material is not available from Portuguese sites south of the Tagus. Only the completely inadequate sample from Melides Lagares is of the right time period¹. For Escoural, also south of the Tagus in the northern Alentejo, the excavation history and a summary of what we know (Cauwe, 1996) would suggest that the MNI, while over 34, is insufficient. Furthermore, the dating, based on human bone fragments from Galleries 4 and 12 (Gilot, 1996), is at least 1,500 years after the end of the Muge occupation. Escoural is quite certainly younger than 5500 calBP and therefore ca 1,000 years after the transition.

A full discussion of the sample from Cabeço da Arruda has been published (Jackes and Meiklejohn, 2004) and does not require reiteration. Casa da Moura has been the subject of re-excavation and analysis (Straus et al., 1988) as well as discussion on the methods of dealing with the human sample (Jackes, 1992; Jackes and Lubell, 1996). Examination of documentary evidence on Moita do Sebastião and its excavation has begun (Jackes and Alvim, 2006, Alvim et al., in prep.; Jackes et al., in prep. a), and it is appropriate to undertake a complete re-evaluation of the Moita sample, so that we have a firmer basis for our discussions of Muge paleodemography. The publication of Veiga Ferreira's field notes and sketches from the excavations at Moita do Sebastião between 1952 and 1954 (Cardoso and Rolão, 1999/2000) allows this complete re-evaluation of the site and the human skeletons found there. This newly published material is supported by

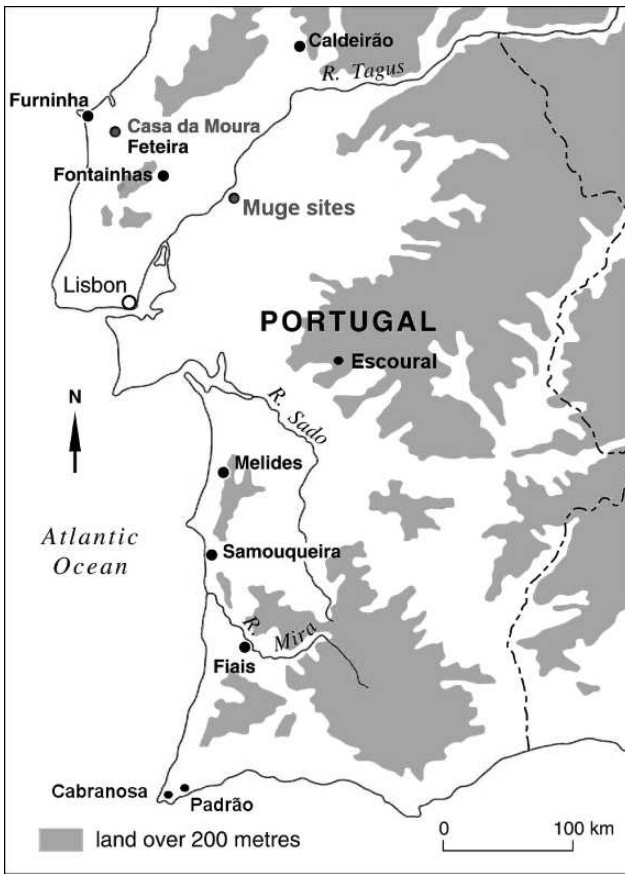


Figure 1: Map showing locations of sites mentioned in text

new evidence on the skeletons excavated in 1954 (Jackes et al., in prep. a). Together with archival material from the 19th century, the evidence from the 1950s allows us to re-examine Moita do Sebastião as a whole.

MUGE AND MOITA DO SEBASTIÃO – THE BACKGROUND TO THE PALEODEMOGRAPHY

The Cabeço da Arruda and Moita do Sebastião shell middens are located on terraces of the Muge River which flows into the upper estuary of the Tagus from the east. Other middens were present, including the largest still

in existence, the less well known site of Cabeço da Amoreira². A number of factors must be considered in order to provide the context for the occupation of the Muge valley, which was extensive in the Mesolithic and apparently largely absent in the succeeding Neolithic.

The occupation of the three Muge sites appears to have lasted from shortly after 8000 years calBP to sometime prior to 6500 years calBP (see Figure 2). Moita was the earliest, and was occupied for about 700 years. Arruda was first occupied a few hundred years later and the occupation lasted for almost a millennium. Amoreira, the least known of the three, appears to be roughly contemporaneous with Arruda but perhaps beginning a century or so later and lasting a century or so longer.

Figure 2 provides a composite image which places the Muge human burials within their maximal probability ranges (at least 95.4%) using calibrated dates adjusted for a reservoir effect of 253 ± 29^3 . Those burials for which we have both stable isotope values and radiocarbon dates provide the date range for each site. Amoreira is least well documented, only two human bone collagen dates being definitively available⁴. The “whiskers” show the maximum range for the use of this site, derived from recent dates on faunal material (Roksandič pers.com.). Charcoal dates on basal levels at

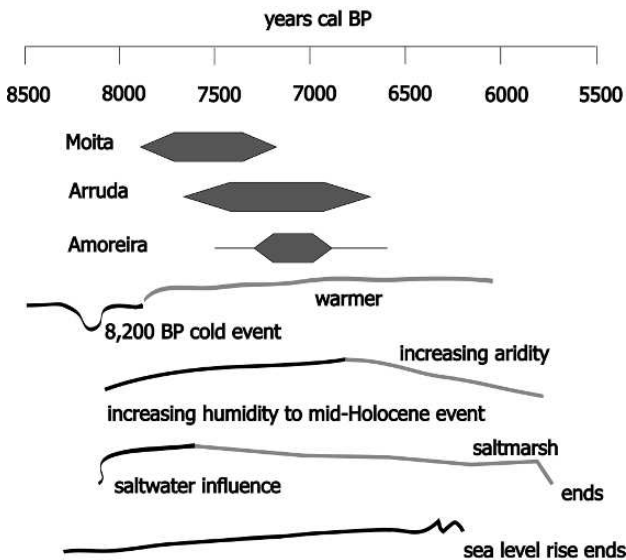


Figure 2: Diagrammatic summary of changes in the Muge valley at the Mesolithic-Neolithic transition

Moita and Amoreira (see Jackes, 2004: Figure 8) seem to confirm the age ranges suggested here for the burial levels.

The work of van der Schriek (2004; van der Schriek et al., 2003) allows us a more fine-grained look at conditions within the Muge valley, particularly based on Core MDS6N (20) between Moita and Arruda. This is well dated and shows the start of saltwater influence at ~8100 calBP, dated on plant material associated with foraminifera and fine-grained sedimentation. A foraminiferal peak indicates the maximum tidal influence at 7500 calBP, after which pine pollen begins to decrease and the assemblage indicates intensification of the salt marsh flora. The peak of salt marsh vegetation was reached by 6000 calBP and all salt water indications disappear within a few hundred years of this date.

These data suggest that the primary occupation at Muge occurred within the last 1,500 years or so of sea level rise in this region. The end of the postglacial rise in sea-level along the Portuguese coast is dated by lagoons which formed behind sand barriers. The sea was no longer rising by 6200–6300 calBP (dated on wood; Freitas et al., 2003). Up until that time, the sea had risen at an average rate of 85 cm per 100 years (Boski et al., 2002; but see also Long, 2000 and Psuty and Moreira, 2000 with regard to variations or oscillations).

A primary reason for occupying the Muge valley during the late Mesolithic would have been the abundant estuarine molluscs found in the salt marshes. The major species in the archeological deposits are *Scrobicularia plana* (peppery furrow shell) and *Cerastoderma edule* (cockle) (Lentacker, 1991). *C. edule* will tolerate a range of salinity (Tyler-Walters, 2003); *S. plana* can survive in settings with very low salinity (Pizzolla, 2002), such as would have occurred when the terrestrial sources of moisture were greatest, just after 7000 calBP. *S. plana* is found in mud flats and salt marsh creeks (Costa et al., 2001). It is “detritivorous”, feeding on the detritus by sucking it from the mud surface using an inhalant siphon when the tide is in. High densities can be supported, as suggested by the faunal remains from the Muge sites which include huge numbers of *S. plana*. *C. edule* which is both detritivorous and suspensivorous, burrowing less deeply into the mud and able to tolerate a wide range of salinity, may have been able to survive more of the changes that occurred towards the end of the Mesolithic occupation of the Muge. Figure 2 suggests that, with increasing temperatures and aridity, the Muge salt marshes could have become too saline for *S. plana*. It is perhaps relevant that Mendes Corrêa (1932) reports that *S. plana* is less abundant at Amoreira than at Arruda, *C. edule* being more frequent in the deposits at Amoreira than at Arruda. Finally, the tides

would have ceased to reach the Muge and estuarine species would have disappeared completely. Thus, the abundant bivalve molluscs which drew the Mesolithic population to the Muge are likely to have found the fluctuations in conditions intolerable and disappeared.

Besides shellfish, the salt marshes would have provided another resource. Chenopodiaceae pollens are dominant in the area of Moita and Arruda during the period of occupation (van der Schriek et al., 2003, Figure 5). Chenopods provide easily gathered and extremely nutritious food derived from both their green tips and from their seeds (e.g. glassworts or marsh samphires which are succulent halophytes, able to live in salt marsh habitats). Liguliflorae and Poaceae come second and a more distant third in the pollen frequency counts. While the latter grasses (e.g. *Spartina* spp.) would have provided useful materials for daily life, it is likely that the former daisy-type plants provided food in the form of golden samphire (a type of aster adapted to saline conditions). Chenopods would have reduced in number as the frequency of tidal inundation decreased, to be replaced by grasses.

The importance of the marsh swamp species to the people of Moita is stressed by the findings of Roche and Veiga-Ferreira (Roche, 1972) during the excavations of the early 1950s to be described below. Six Moita skeletons were buried with shells of *Neritina fluviatilis*, a gastropod species (= *Theodoxus fluviatilis*) which can tolerate salinity. Lentacker (1991) found a large number of these shells in the collections from Arruda and Amoreira. Moita skeleton No. 3 was buried on a bed of unopened *Tapes decussata* (a bivalve mollusc).

Because it is at the interface of terrestrial, marine and freshwater environments, an estuary has outstanding richness of resources. But with the changes through time indicated in Figure 2, there is likely to have been pressure on the population to move away from the Muge into the uplands where the reduced resource diversity would have encouraged changing to Neolithic life-ways, as happened elsewhere in Iberia (Straus et al., 2000:14).

With a warm, more arid, climate and lower tidal activity, the possibility of toxicity increases: diarrhetic shellfish poisoning (DSP) is most likely to occur with low rainfall and high salinity during the summer (Vale and Sampayo, 2003). Furthermore, the combination of lower tides, higher temperatures and greater aridity would have increased the possibility of other diseases.

The Tagus valley with its marshes and rice growing areas, established over many hundreds of years, was an area of high malaria incidence until after World War II (Bruce-Chwatt and de Zulueta, 1977; Bruce-Chwatt, 1988; Howorth, 1988). That, of course, does not mean

that malaria was present prior to European contact with tropical regions and the importation of *Plasmodium falciparum*. Iberia is considered to have historical evidence of malaria by the 11th century AD (Bruce-Chwatt, 1988:12). There is, however, a growing body of evidence for the historical presence of indigenous European malaria, even in the northern parts of the continent and in the British Isles, irrespective of contact with imported tropical diseases. The existence of indigenous European malaria has been documented (e.g. Hackett, 1937:201–231; Bruce-Chwatt, 1988: 12–16; Huldén et al., 2005) and has been studied in great detail in the salt marsh regions of south eastern England (Dobson, 1997). Estuarine stagnant waters were the major factor in increased death rates in these areas. *Anopheles atroparvus* breeds in such areas (Reiter, 2000) and serves as the vector for the transmission of *Plasmodium vivax* (but is not susceptible to *P. falciparum*, see also Bruce-Chwatt and de Zulueta, 1977 and Bruce-Chwatt, 1980:99). Steadily warm temperatures, such as those which occurred during the Mesolithic occupation of the Muge are an essential factor: “. . . as temperatures climb so will the rate at which mosquitoes develop, adult mosquitoes will feed more frequently on blood (and so pick up and pass on the infection faster) and malaria parasites will develop quicker in the mosquito” (Lindsay and Joyce, 2000). Historical records demonstrate that summers with low rainfall led to autumns in which “the ague” was most prevalent in the estuarine swamp areas of England (Dobson, 1997:323). Relapse and latent primary infections could also cause spring deaths (op cit. 325, see also Paul et al., 2004). As documented by Dobson, clearly described periodic tertian fevers occurred in the spring and autumn, intermittent illnesses which are consistent with infection by *Plasmodium vivax*, which causes fever, chills, headache, weakness, vomiting and diarrhea. *P. vivax* is milder than *P. falciparum* malaria (though still capable of causing anemia⁵): nevertheless, the documented differential death rates between areas of estuarine swamp and the uplands in historical England is extremely significant.

While the most severe form of malaria (caused by *P. falciparum*) is likely to have been absent in Europe until around 2500 years ago (Tishkoff et al., 2001), it is no more than a guess that milder forms of malaria did not enter Europe until domestic animals were present. Indeed, the absence of domesticated mammals is very likely to increase malaria rates in human beings, since *A. atroparvus* is zoophilic, i.e. would bite animals in preference to human beings (see e.g. Hackett, 1937: 230; Bruce-Chwatt, 1980:110 and passim.; Kuhn et al., 2003). However, if Mesolithic groups constructed some form of shelters and used fire to warm themselves during the

winters (as seems likely from evidence at Moita), then, in the absence of domestic animals, they are likely to have been subjected to the attention of *A. atroparvus*. Bruce-Chwatt (1980:125–126) states that *A. atroparvus* is common in Portugal and the basic Iberian vector, indicating that Iberian malaria was not, in fact, necessarily caused by *P. falciparum* throughout history.

Changing conditions, dwindling resources as the salt marshes disappeared, and increased possibility of disease would have decreased health and fertility and made the Muge valley unattractive to Mesolithic groups who were no doubt already knowledgeable about the attractions of neighboring regions: the lower estuary of the Tagus or the Sado, the sea coast, the adjacent uplands. The depopulation of the Muge at the end of the Mesolithic was predictable. But where did they go? Calado (2002) has suggested a connection between the Tagus tributaries and Sado estuarine Mesolithic midden sites and the uplands of the central Alentejo which were more or less empty of people at the time when occupation of Moita began.

Across the Tagus, to the north, elements of a Neolithic lifeway were already becoming established in Portugal. Despite limited evidence, this is documented by the data from the isolated inland cave of Caldeirão where a date of over 7000 calBP overlaps the younger Muge dates, and Casa da Moura, for which the oldest date overlaps the youngest Arruda date. In the Upper Alentejo there are very early dates possibly associated with megalithic monuments (Oliveira, 2000). The most conservative date (6210 ± 50 bp) would place these at 7000–7200 calBP – a little younger than the oldest Caldeirão Neolithic date. But, as pointed out by Jorge (2000:59), these dates must be treated with caution. Further south, there are sites which indicate coastal and estuarine occupation with continuing “Mesolithic” activities at the same time as the youngest Arruda date (Lubell et al., 2007), for example, one of the two human burials at Samouqueira and a well-provenanced mammal bone at Fiais dated at ~ 7100 calBP. Gonçalves (2003) provides us with many instances of newly excavated or dated Early Neolithic sites throughout Portugal. For example, at Cabranosa and Padrão (Cardoso and Carvalho, 2003), in the extreme south west of Portugal, we find Neolithic sites with Cardial ware dated on shell to between 6540 and 6870 calBP⁶, again contemporaneous with Samouqueira and the latest Arruda date (both calibrated with the reservoir effect for a diet very heavily based on marine resources).

In other words, it appears likely that Portugal at around 7000 calBP was a mosaic of different late Mesolithic/Early Neolithic influences.

Oosterbeek (2004) has pointed out that even along the immediate drainage of the one river (the Tagus) within the one period/culture (the Mesolithic during the time of the first burials at Moita), there is variation. How much more likely, then, that during the late Mesolithic and early Neolithic, groups were doing different things in different places. We have previously emphasized Neolithic and Mesolithic physical heterogeneity (Jackes et al., 1997; Jackes and Lubell, 1999b). Those populations living along the Muge seem to have found it necessary to disperse, for reasons which we have suggested above. Those living further upriver along the Tagus stayed and began to display some Neolithic cultural elements (Oosterbeek, 2004): the difference between the two areas may well relate to the particular circumstances of the Muge salt marsh alterations. A simple unilineal approach to this most important and complex period of human history has never been less acceptable.

It is likely then that we can only guess whether our samples from central Portugal do actually tell the full story about the Mesolithic-Neolithic transition in Portugal. At best, the picture will be incomplete. We have seen that it is likely that the Mesolithic resources of central Portugal during the Mesolithic could sustain a reasonably high and probably increasing level of fertility. What do the human skeletons tell us?

The site of Moita

Moita do Sebastião was excavated first in the 1880s and then, as a rescue excavation, from 1952 to 1954. In the earlier campaign, skeletons were excavated in 1880 and again in 1885: Jackes and Alvim (2006) have discussed the documentary evidence on the 19th century excavations. The 1950s excavations by the Abbé J. Roche and O. da Veiga Ferreira came after bulldozing and construction had revealed additional human skeletons.

Jackes and Alvim (2006) have reconstructed the relationship of the various excavations to each other and to the original topography of the mound. The location of the 1880 excavation has been pinpointed to the centre of the northern margin of the conical mound which rose to an estimated height of 24.5 m ASL on the south bank of the marshy course of the Muge. The excavation lay within encircling paths leading from the high point of the mound down across the river flats to the Amoreira bridge over a drainage ditch into the Muge. The paths no doubt detoured around some feature, which we can speculate was the location of post-Mesolithic disturbance. Roche (1972) described the mound surface before it was bulldozed

as much disturbed. In 1880, Roque plotted a quarry pit on the south of the mound (Jackes and Alvim, 2006) and Paula e Oliveira (1889) noted that a concentration of post-Mesolithic pottery was found – no doubt in a large depression – in the surface layers in 1884.

In 1885, the excavations were continued along the north east face of the mound and this trench was redefined in 1954 by Roche and Veiga Ferreira. The reconciling of the 19th century and 20th century records with aerial and satellite images has allowed the “reconstruction” of the mound and the placement of the excavations (Jackes and Alvim, 2006), thus making it possible to assess whether the entire burial area was excavated and whether skeletons were lost to bulldozing in the early 1950s during the removal of the mound summit. The conclusion must be that, by the end of the excavations in 1954, the mound was completely searched to the level of the bottom of the midden deposits and that little in the way of human material would have been lost, although the faunal evidence is no doubt compromised by the removal of the layers which would have overlain those in which – in general – the skeletons lay. It seems that we are justified in stating that we have something close to the totality of skeletons originally buried at Moita.

The 1880 skeletons lay at the base of the archeological deposits and this was also true of the 1950 skeletons, which were found at the level of the basal sands. The same pattern probably held for most of the skeletons excavated at Arruda in the 19th century, and for all those excavated at Arruda in the mid-20th century (Jackes and Meiklejohn, 2004). This, however, is not true of one Arruda skeleton from a recent exploratory excavation (Roksandič and Rolão pers. comm.). Nevertheless, most of the evidence from Arruda, and from Moita, is that the skeletons lay at the same general lower level rather than being randomly scattered throughout the midden deposits. At Moita, that level was at about 21 m ASL.

Furthermore, the horizontal as well as the vertical placement may have been patterned. The Moita skeletons lay in clusters arranged in a rough semi-circle to the north, east and south of the mound centre (Jackes and Alvim, 2006), and the clusters formed a horseshoe shape opening towards a series of features which Roche (e.g. 1989) interpreted as a domestic structure. This interpretation can be questioned, especially as the skeletons would have been placed at the general level of the structure and in close proximity around it. The majority of the youngest children lay in pits placed to the south west of, and adjacent to, the structure. However the “structure” is to be interpreted, there is no doubt that a complex array of post holes, pits, shaped pebble concentrations and hearths was found in association with the Moita burials (Roche, 1972).

Material from the excavations of the 1950s

In dealing with Moita, the easiest part should be assessment of the skeletons from the 1952–54 excavations. Much information has recently become available. The publication of Veiga Ferreira's notebooks and sketches, together with photographs not included in Roche's publications, has been a very important addition to our knowledge (Cardoso and Rolão, 1999/2000). Newly discovered unpublished photographs (Jackes et al., in prep. a) have added a good deal of information on the skeletons excavated in 1954. The majority of the Moita material excavated by Veiga Ferreira and Roche was deposited in Porto at the Mendes Corrêa Institute of Anthropology, but six skulls remain stored in Lisbon in the Geological Services Museum.

An inventory of the 1950s material has been drawn up for this paper, derived from photographs and sketches made during excavation and from the Roche material still in Lisbon, together with the records made by Ferembach (1974) and by Meiklejohn in 1969 (numbers 1–18 only are in the CM Porto inventory), as well as a record made by Jackes and Huet Baçelar in 1984 when a search was undertaken to locate all the Muge material and labels that had been salvaged from a 1974 fire in Porto. Further work is being undertaken by Eugénia Cunha at the University of Coimbra to which all the Porto material has now been moved. In this paper, we are deriving our numbers of individuals from the original records up until 1984 and from Jackes et al. (in prep. b). However, even this well-recorded material furnishes us with difficulties, as discussed in Appendix I.

Material from the excavations of the 1880s

In trying to gain an accurate assessment of the Moita material from the 1880s, we meet greater problems. No full study of the skeletal material was attempted until the work of Ferembach who published a cursory inventory (1974). Added to that are complexities of the labeling and identification. The material is labeled from 1 to 60, A to Z and I to XLI, but in no case is the series complete. The Roman numerals are meant to designate the skulls, but this does not seem to have been true in the 1920s, since Vallois (1930) used Arabic numerals for skulls.

The skulls are meant to be associated with burials, but there is no consistency in the pattern of numbering. Vallois (1930) noted that most skeletons were accompanied by a card specifying the associated skull. However, he stated that in every case but one there was a discordance with the card

on the skull specifying the associated skeleton: the exception was Skull 16/Skeleton 8 (Vallois, 1930:365). The confusion was exacerbated by the fact that, in a number of cases, there were elements of several skeletons stored together under the same number. The problems we faced in 1969 (CM) and later in the 1980s (CM and MJ) were already patently evident by the time Vallois examined the collection in the late 1920s.

The problems are similar to those we described for Arruda (Jackes and Meiklejohn, 2004). The situation is perhaps less acute, but nevertheless includes difficulties deriving from burial practices, from curation around the time of excavation, and from the subsequent history of the collection. Naturally the situation with the material deriving from the excavations in 1880 and 1885 is more problematic than that from the early 1950s. Vallois (1930) noted that the death of Paula e Oliveira no doubt led to a loss of information on the 19th century material. In fact, Ribeiro and Roque, the original excavators of Moita in 1880, both died before the second period of excavation in 1885 was undertaken by Paula e Oliveira (Jackes and Alvim, 2006): as a result there was a double loss of continuity. Using archival material, Jackes and Alvim (2006) provide new evidence of the conditions under which the 1880 excavations were undertaken. In 1880, at least 16 skeletons were found heaped together, so that the excavator had no idea how to approach the problem. The 1880 problems were such that although Arruda was photographed, published (e.g. Ribeiro, 1880) and proudly displayed to prehistorians attending the International Congress for Prehistoric Anthropology and Archeology (CIAAP) in Lisbon that year, details of the Moita excavations have remained unknown until recently (Jackes and Alvim, 2006).

There are some published descriptions of Moita material from the 19th and earlier 20th century, mostly focusing on supposed differing Muge skull types and recording disagreements as to whether the differences are real or simply the result of post-depositional distortion and inaccurate reconstruction. Illustrations of some of the skulls under discussion were provided by Paula e Oliveira (1884), Cartailhac (1886), Vallois (1930) and Ferembach (1965) allowing us to identify most as being from Arruda (see Jackes and Meiklejohn, 2004). Of present interest in these publications is passing mention of the nature of the collections and their curation. For example, two Moita skeletons had no skulls (Paula e Oliveira, 1881:10 ftn 1; Cartailhac, 1886:314–315); 25 Moita skulls were catalogued in the Geological Services of Portugal Museum in Lisbon in the 1920s but there might have been about five more (Vallois, 1930:356–7) some of which Ferembach (1965:269) reconstructed herself. Vallois stated (1930:357) that

it was actually impossible to determine the number of Moita skulls present in Lisbon. He recorded that skulls were lost, or had no numbers, or did not have the numbers by which they had been previously described in Mendes Corrêa's publications. Mendes Corrêa (1923) even doubted whether one Moita skull was Mesolithic and noted that museum employees were unable to prove to him that other material was verifiably from Muge⁷.

Thus, previous publications on the 19th century Moita collection have not provided us with much assistance in trying to assess the number of individuals excavated from Moita. The most complete description we have of the 19th century material is of crania (Vallois, 1930)⁸.

The majority of problems no doubt arise from the simple moving of pieces from one individual to another within the collection. Drawers containing individuals usually had a paper label lying with the bones, but most individual bones were not specifically numbered. As a simple example, a child accompanied by the label "No. 47" had two right mandibular rami in the 1980s – one appears to be the same age as the isolated left mandibular ramus of the child identified as No. 46.

Many of the problems are more complex and unfortunately involve the very youngest individuals, who appear to be under-represented within the samples from both the 1880s and the 1950s. Appendix II discusses some of these problems and the rationale for decisions we have made when trying to count the number of young children.

The question of whether there was selective burial of children in one area of the site is very important for paleodemography. There is no indication whatsoever in the 19th century accounts of Moita and Arruda that there were concentrations of juvenile burials. Indeed, Cartailhac (1886) recorded a mother and baby buried together at Arruda and an 1880 sketch map of Arruda showed that just one child lay fairly close to a general area of scattered adult burials (Alvim et al., in prep.). At Moita, children were found among adults by Roche: No. 6 was a 2 year old, according to Ferembach (1974), and a small infant was found with No. 7, while Skeleton No. 13 was accompanied by fragments of two children, 12 years and 3 years. And yet, Roche excavated an area at Moita which was obviously dedicated to child burials: the juvenile skeletons Nos. 22, 23, 24, 25, 26 and 27 all lay together in an area of the site some way removed from the main concentrations (Jackes and Alvim, 2006). Ferembach gave these ages of 2 years, 10 months, 18 months, around 12 months, around 3 years and circa 7 months. The skulls of 23 and 24 were still on open display in Lisbon until sometime in the 1990s and they were studied both by Ferembach (1969) and by Meiklejohn

(although they were no longer labelled with those numbers by the 1980s – one was given another number and one had no number).

While Roche recorded an area for juvenile burial at Moita, the sites were obviously mixed to some extent. This is an important point with regard to Arruda which has been incompletely excavated: could there be an area of Arruda child burials yet to be discovered? In fact, we have found that the Arruda fertility level is higher than that of Moita (Jackes and Meiklejohn, 2004), meaning that the ratio of juveniles to adults is higher among the Arruda skeletons, but there is no evidence whatsoever that this is the result of the excavation of an area in which many children were selectively buried.

It is clear that we have too few young children and that they are the most problematic individuals in our attempt to count the Moita dead with accuracy. However, by including or excluding individuals under 5 years of age we will not be altering our conclusions, in that our method acknowledges the frequent under-representation of young children and excludes them from the analysis. However, it is important to know whether we have a full representation of older children and of adults. And a major issue here is related to burial practices and to the completeness of excavation rather than to taphonomy or post-excavation curation. Both Moita and Arruda have problems in this regard and we have attempted to describe and confront these problems (Jackes and Meiklejohn, 2004; Jackes and Alvim, 2006) in order to justify our method of the age at death counts for paleodemographic reconstruction of Mesolithic populations at Muge. However, excavation and post-excavation history both add to the problems and have led to our choice of counting the dead through detailed examination of the mandibles. It is, of course, also dictated by the necessity of undertaking *absolutely comparable analyses* of the Mesolithic sites with the material from the Neolithic ossuary cave at Casa da Moura.

The method chosen for establishing the numbers of individuals has been outlined and justified fully, most recently with regard to our complete reassessment of Arruda paleodemography (Jackes and Meiklejohn, 2004). Seriation of mandibles with particular emphasis on the cheek teeth ensures that the skeletal elements with the highest probability of preservation, careful excavation, retention and identification in museum collections are used for a count of individuals in cases where there is a chance that skeletons were mixed, disturbed, or partially discarded.

Our re-examination of the historical records on the excavation and subsequent curation of Arruda confirms that some skeletal material excavated from the 1860s to the 1880s was indeed mixed within the deposits and some

was discarded upon excavation. We can expect that the Moita skeletons underwent the same fate, especially because the burials excavated at Moita in 1880 were heaped together much more closely than were those at Arruda. By concentrating on the mandibular elements, we are using material which is least likely to be discarded and also taphonomically and diagenetically most likely to survive.

Furthermore, mandibles provide the most detailed approach to the problem of coming to the best estimate of the number of individuals in a site – an estimate higher than that provided by, for example, right distal humeri. The reason for this is that one does not have to restrict oneself to the single most frequent side, but can use detailed fragment comparisons based on attrition, pathology and metric and non-metric morphology.

TRANSLATING THE NUMBERS OF DEAD INTO DEMOGRAPHIC VALUES

What was the fertility rate in Central Portugal between 6,000 and 8,000 years ago?

Information on the age distribution of the mandibular dentitions used for the present analysis is shown in Table 1. The distributions for Arruda and Casa da Moura are the same as those published in Jackes and Meiklejohn (2004), but that for Moita has been altered based on the complete reassessment of the material, especially of the material excavated by Roche and Veiga Ferreira, because additional information on the excavations is now available, as discussed above.

Why do we use these age categories? Standard five year age categories are desirable so that comparisons can be made with model and

Table 1: Age distribution of the dead

	Moita	Arruda	Casa da Moura
<i>age</i>	<i>n.</i>	<i>n.</i>	<i>n.</i>
0–4	11	17	42
5–9	7	9	31
10–14	1	5	33
15–19	2	4	18
20–25	10	8	64
25–x	54	62	152
Total	85	105	340

historical data. As mentioned above, we cannot calculate infant mortality since the under-representation of infants, especially in Neolithic sites, is extreme – because of taphonomic reasons, because of differential burial and/or because of poor excavation or curatorial methods. We are likely to have an under-representation of children up to age 5, in fact, but by that age we have sufficient and well-preserved dentitions to be able to make a reasonable estimate of age (we use radiographs in most cases). It would be preferable to have complete skeletons in order to examine diaphyseal lengths of long bones and development of epiphyses, but it will be clear that this is not possible in Neolithic cave ossuaries such as Casa da Moura, and is unlikely in the Muge sites under the conditions of excavation and curation that prevailed in the 19th century.

Figure 3 shows that the Neolithic site, Casa da Moura, differs from the two Mesolithic sites in the distribution of the dead. The under-representation of the very youngest age category is obvious. Since loose teeth make up part of the sample, there is a possibility of some errors of attribution at age category margins and this may explain why the Casa da Moura juvenile mortality curve does not have the shape that we might expect. The use of summary values in making comparisons (e.g. the mean of childhood mortality values calculated from the age at death distribution and the ratio of children to adults in a cemetery sample) allows us to avoid such finer-grained but error-prone detail. More problematically, Casa da Moura older adults are likely to be under-represented in the loose dental sample (see below). Since the Casa da Moura sample size is very adequate, in archeological terms, we will assume that the Neolithic data bears some relation to reality.

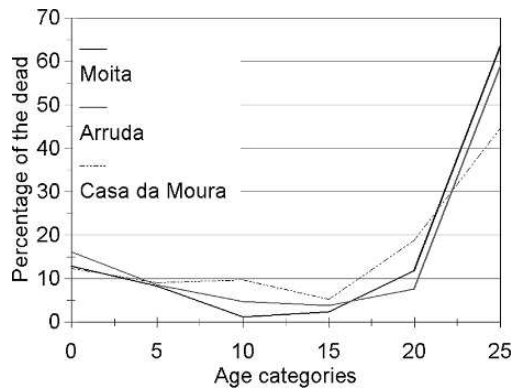


Figure 3: Age at death distributions across standard 5 year age categories, with all adults 25 and over grouped, for three Portuguese archaeological sites

However, it must be understood that there are many unknown factors regarding cemetery populations: excavation, curation, taphonomical factors, osteological methods, cultural variations deriving from the distant past, burial practices – all these introduce such uncertainty to our subject that we must beware of ascribing precision to our results. Since we have stressed in the past (e.g. Jackes and Meiklejohn, 2004), and again make clear, that our samples have many sources of error, it is worthwhile asking whether they are sufficiently robust for us to be sure that the age at death distributions are actually different from each other. The Index of Dissimilarity⁹ and Kolmogorov-Smirnov two tailed exact significance in Table 2 demonstrate the similarity of the age distributions of the two Mesolithic samples and their difference from Casa da Moura (the difference is more extreme in the case of Moita and Casa da Moura). The differences among the samples are therefore robust. This is particularly important because Moita has a sample size of only 85. Subadult:adult ratios, which we will use below, have been shown to be ineffective analytical tools when sample sizes are below 100 (Paine and Harpending, 1996:153). MJ has, since 1984, developed a data base of nearly 200 archeological and historical standardized age at death distribution tables with sample sizes of 100 or more. This has given us a very clear picture of the valid range of our demographic estimators (subadult:adult ratios), of their relationship to each other, and of the nature of those very few cases which fall far beyond the normal range. Since Moita falls well within the expected range, and all the characteristics of the distribution (for example, the shape of the mortality quotient curve) appear normal for archeological material, we have chosen to use the site in our analysis.

How can we translate our rough approximation of age at death distributions, derived from dentitions, into demographic terms? We need to put it into a format that will allow us to compare among the sites and – above all – assess whether the data make sense in biological terms. We need to be able to translate this into fertility estimates and assess their validity. The technique which we will use allows us, for example, to verify that the small

*Table 2: Testing differences among age at death distributions**

	Moita	Arruda	Casa da Moura
Moita	–	0.086	0.194
Arruda	0.395	–	0.182
Casa da Moura	0.004	0.019	–

*Index of Dissimilarity (above the diagonal) and Kolmogorov-Smirnov two tailed exact significance (below the diagonal)

and incomplete Melides sample mentioned above, which comprises burials in two caves of apparently differing phases during the Neolithic, should be ignored. It shows us that the 95% confidence limits of the estimates for total fertility (TF) using two methods would range from 18 to 22. This would mean that the *average* Melides woman during her reproductive period would have around 20 children, clearly beyond the bounds of biological probability (as discussed in Appendix III).

The technique used has been described in detail elsewhere (e.g. Jackes and Meiklejohn, 2004 and Jackes et al., in press). Our method has been to use the index of juvenility (the juvenile adult ratio or J:A – the ratio of juveniles aged 5–14.99 years to adults aged 20 and above) first proposed by Bocquet-Appel and Masset (1977, 1982) against the mean of the apparent mortality quotients for the three age categories from 5 to 19.9 years (MCM or mean childhood mortality quotient; Jackes and Lubell, n.d.; Jackes, 1986). We have a reasonable idea of the relationship of these two values, which we use as demographic estimators, based on our archeological and historical samples discussed above. Our next step is to find their relationship to fertility. Briefly, total fertility rates (TFR) are derived from the model data of Coale and Demeny (1983: 51 tables) and the United Nations (1982: 3 tables) While the use of model tables is not ideal, there is no appropriate large body of actual data on the relationship between juvenile to adult ratios and the total fertility rate. The Coale and Demeny tables were based on empirical data strictly assessed for accuracy and our use of them is restricted to the proportion of subadults to adults. It should be reemphasized that we are not directly using any Coale and Demeny fertility estimate, but have calculated estimates from the pooled sex model life tables, adjusted for the male/female ratios. While the thrust of the argument here is the *relative* fertility among the sites, and this can be accommodated by the use of estimates derived from model data, there is some assurance that our estimates of fertility levels are plausible (see below).

The juvenile adult ratios and mean childhood mortality values for these model data are used to generate fertility estimates by prediction (fit for both TF with J:A and for TF with MCM from SPSS 12.0 curvefit quadratic) as described in Jackes et al. (2006).

Recently, Bocquet-Appel (2002) has proposed the use of P (5–19/5+), which avoids many of the problems of age assessment of juveniles and subadults. It is basically the equivalent of MCM. Why would we wish to retain values that are subject to age assessment errors? In fact, the use of the age categories around age 20 gives the anthropologist an incentive to be extremely careful in checking the data. We often assume that we can tell a 19 year old

from a 20 year old, and yet this is a very problematic age range. The need for great care lies in the fact that paleodemographic reconstructions have often had a very large number of people supposedly dying in their late teens or their early twenties. This was believed to be characteristic of archeological populations, since Weiss (1973) published model tables which he had developed from 50 sets of data, all but 14 of which were archeological. Figure 4 shows the variations of Weiss's age at death distributions from age 15 onwards (ages 0 to 14 varied according to a separate but comparable pattern). It is surprising that such age at death distributions were accepted without question. We can only assume that the real reason for the appearance of such curves in the paleodemographic literature is that there must be mis-aging at category margins. The implications of this sort of mis-aging for demographic values will be further discussed below.

Figure 5 shows the relationship of total fertility to our demographic estimators, using the limits of those estimators derived from our data base of samples of 100 and more (see above). The correlation coefficient is very slightly higher with MCM ($R^2 = .99$) than with J:A ($R^2 = .987$), but they are basically equivalent. MCM is more dispersed than J:A in our large comparative data set of archeological age at death distributions and we would choose to emphasize the TF estimations from J:A simply because MCM may be more error-prone. MCM is more dispersed than J:A in the comparative data set because it tends to fall too high in some archeological, but not in the historical, samples. In other words, MCM is too high for J:A in some of the archeological samples, and the samples in which this discrepancy occurs are those with excessively high late adolescent mortality. An extreme example

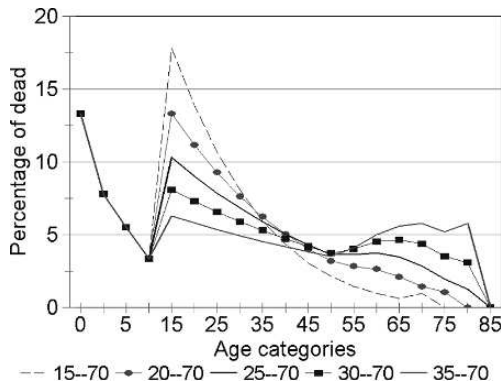


Figure 4: Range of adult age at death distributions for Weiss model tables demonstrated by the use of five selected tables (Weiss, 1973)

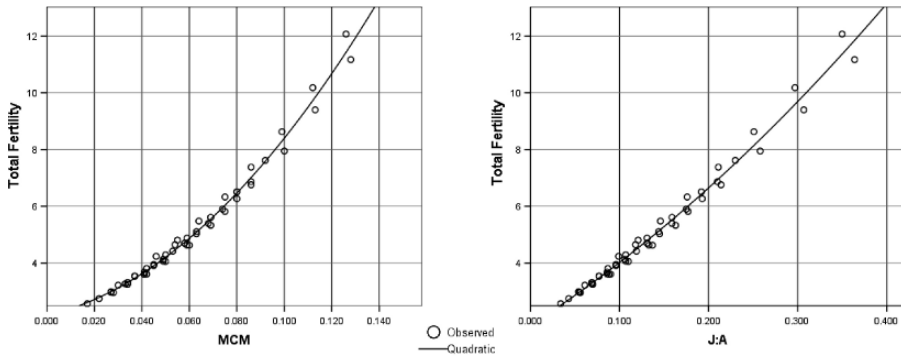


Figure 5: Total fertility derived by calculation from 51 West model tables (Coale and Demeny, 1983): total fertility and mean childhood mortality and total fertility and the juvenile adult ratio

of this would be provided by the Weiss model table 15–70 (MCM = .124; J : A = .171) (see Figure 4). At J : A = .170 one would expect the MCM to be much lower, under .100. The significance of the discrepancy can be shown by pointing out that from J:A, the Weiss 15–70 estimate is that the average woman would have many fewer children (TF = 5.4–6.4, 95% CL) compared with the estimate from MCM (TF = 10.7–11.7, 95% CL). The full life table TFR is 5.87.

Table 3 presents fertility estimates for the Portuguese archeological samples using both estimators, together with the 95% CL range of the predictions. But do the TFR range estimates provide adequate proof that there is no overlap between Mesolithic and Neolithic fertility? Greenwood’s formula for the standard error of the survival function was employed to test this. The last two columns of Table 3 give TFR estimates calculated from the survival function error range derived from Greenwood’s formula and

Table 3: Ranges estimated for total fertility rates from 95% CL of predicted values and using Greenwood’s formula for the survival function standard error

Site	TFR range predicted from 51 West model tables 95% CL		Range for TFR predicted from the SE of the survival function using 51 West model tables	
	MCM	J:A	MCM	J:A
Moita	3.6–4.5	4.1–5.1	3.6–4.4	4.2–5.2
Arruda	5.4–6.3	6.1–7.2	5.3–6.6	6.0–7.5
Casa da Moura	8.2–9.1	9.0–10.1	8.0–9.3	8.9–10.4

indicate that the ranges provided by the 95% confidence limits of the Coale and Demeny predictions are adequate. It is possible to go further, giving the 95% confidence limits of this standard error range: once again there is no overlap between the Mesolithic and Neolithic TFR estimates, and the overlap between Moita and Arruda is minimal.

It must be understood that the figures provided in Table 3 are presented as indications of relative rather than absolute fertility. TF may overestimate fertility (Terrisse, 1986, but there is no real substitute, Bongaarts and Feeney, 1998); the true sex ratio is unknown, so we are simply assuming a 1:1 sex ratio. A very important point is that Casa da Moura, with an MNI estimated directly on loose teeth in some cases, must present an age at death distribution which has an inbuilt error, one that is likely to increase the estimate of fertility. The reason for this error, as mentioned above, is that it is certain that adults of advanced age must be under-represented in the loose dental sample.

Discussion on fertility estimates

Upon what should we base our estimates of unknown factors of the distant past, basic factors such as fertility levels? We may choose historical data, but these may represent locations in which the population structure is altered by immigration. This would be true, not only of European settlements in the New World, but of cities like London and Geneva¹⁰. The effect of rural-urban immigration has long been debated (see e.g. Sharlin, 1978, 1981; Finlay, 1981) but the use of data from outside major cities is obviously preferable. Historical data deriving from small rural centers in which there is no underreporting of infant deaths and no out-migration of younger adults, so that every individual born in the community is recorded by age of death, would be an ideal, but unrealistic, expectation. The historical data which we will use below is, in fact, from a region of emigration. The absence of sufficient historical data, expressing all human mortality and fertility experience accurately, is, of course, the reason for the development by demographers of model tables.

We have chosen to use Coale and Demeny West model tables to generate fertility estimates. However, this choice could be criticized. As Brass (1971:88, 90) noted of Coale and Demeny tables, “extreme schedules... are extrapolations to a greater or lesser extent... [and] the schedules constructed for very high mortality levels extend well beyond the range of the observed life tables...”¹¹. We have therefore generated relational (logit) model tables (Brass, 1971) in order to test the comparability

of our fertility estimates with those derived from an alternative method (see Appendix III). Paine and Harpending have previously tested tables developed using the Brass approach against Coale and Demeny model West tables and found that there is “little or no difference” (1996:152; 1998:235), but they stated that the Crude Birth Rate may be underestimated by around 5% by Coale and Demeny tables (Paine and Harpending, 1998:238).

It is worth repeating a point made clear in Appendix III, that it has long been recognized that there may be discrepant results in relational tables with regard to child mortality, requiring the use of a very specific standard (Zaba, 1979:81). *And we have no idea what standard should be used with archeological data.* As stated in Appendix III, we are using an historical French sample, Tourouvre, as a standard from which to generate relational tables because it represents the midpoint of our historical samples.

As shown in Appendix III, Coale and Demeny West model tables will provide fertility predictions that are comparable to those which can be generated by relational tables, using an historical sample, Tourouvre, as a standard (cf. Figure 5 and Figure 6). We cannot, of course, claim pinpoint accuracy: for example, both the formula used to calculate ${}_1L_0$ and the actual sex ratio of adults 15–44.99 are problematic under the best of conditions. The general accuracy of the approach by which Coale and Demeny West model tables are used to predict the TFR in archeological samples has, however, been tested in several ways. The basis of testing is 1) to see whether TFR predictions accord with table TF values, 2) to see whether there is independent evidence of those fertility levels, or 3) to consider independent evidence of relative fertility levels derived from the predictions.

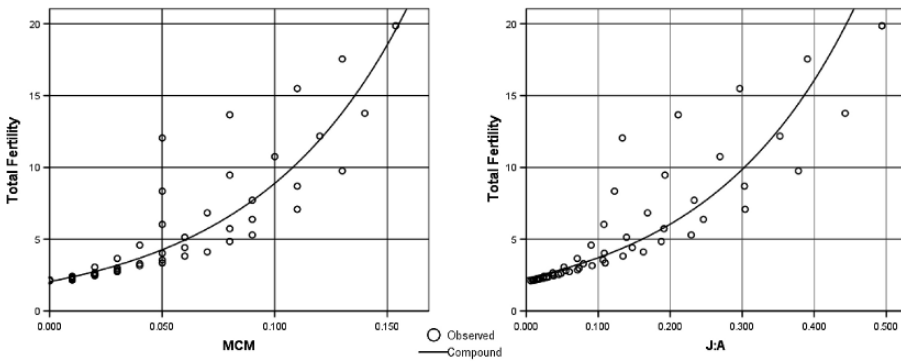


Figure 6: The relationship of TFR and MCM in 55 tables generated from the Tourouvre standard, $R^2 = .842$; the relationship of TFR and J:A in 55 tables generated from the Tourouvre standard, $R^2 = .831$

Firstly, we can use the three UN tables (General, Far East, South Asia) to test the tabled lower end of the range for the 51 Coale and Demeny tables. Secondly, we have used data from the !Dobe Kung (Howell, 1979), with a TF estimate of around four children derived from the J:A of the age at death distribution. In fact, the upper confidence limit accords with Howell's estimate of 4.3 for the period from 1963–1973. Low fertility has also been tested by use of US census data for the period 1901–1910 (the data was for white individuals resident in the original registration states; Glover, 1921:66–67, 72–73) and the results are consistent with other estimates of fertility derived from these data, especially for urbanized north-eastern whites (Haines, 1989). Thirdly, the middle range has been examined in very broad terms by considering ethnohistorical evidence on Iroquoian aborigines compared with historical records for French Canadian and northern French Europeans (for an early attempt at this, see Jackes, 1994; also Landry, 1993) with consonant results, given the many uncertainties. Finally, the upper end of the range has been checked by reference to American Hutterites of the period 1941–1950 (Eaton and Mayer, 1953:238, ages redistributed into standard age units). Summing the age specific fertility rates of all Hutterite women of reproductive age between 1936 and 1940 gives a TFR of 9.4, and for those of reproductive age between 1946 and 1950 the TF value was 8.1 (Eaton and Mayer, 1953:227). It is then very reasonable to estimate ~8.8 as the correct TF value to associate with those who died between 1941 and 1950.

Table 4 lists the TFR predictions from quadratic regression based on our 51 Coale and Demeny West model tables for the Portuguese age at death distributions. We compare these with the result predicted from our estimators by compound regression from relational tables derived from the Tourouvre historical standard, first using the full set of 55 tables and then a set of 50 tables in which the TFR is below 13. We choose the compound/growth regression methods which give equivalent results and provide the highest R^2 value. Based on the Hutterite data, the most accurately recorded historical data for high fertility, Table 4 shows that our general level of total fertility is estimated with some degree of reliability. Table 4 also demonstrates that relational tables can provide widely divergent results and must be used with caution. Thus we have chosen to emphasize results from West model tables.

Finally, Table 4 makes the point that our hypothesis of increased fertility in the late Mesolithic (an increase in the TFR of 2) and a greater level of increase in the Neolithic (perhaps 2.5–3) is proven to the degree that two quite separate methods of prediction agree on this.

Table 4: Comparison of archeological total fertility rates derived from two independent sources (model tables and relational tables), with an historical sample included as a control

	Prediction from 51 West model tables MCM	Prediction from 51 West model tables J:A	Prediction from 55 tables using Tourouvre standard MCM	Prediction from 55 tables using Tourouvre standard J:A	Prediction from 50 tables using Tourouvre standard MCM	Prediction from 50 tables using Tourouvre standard J:A	Prediction from 55 tables using Brass global standard MCM	Prediction from 55 tables using Brass global standard J:A
Moita TFR	4.0	4.6	4.1	4.2	4.0	4.1	4.4	5.4
Arruda TFR	5.9	6.6	6.0	6.0	5.7	6.0	6.7	9.6
Casa da Moura TFR	8.6	9.6	9.2	9.7	8.4	9.6	10.7	20.0
Hutterites 1941– 1950 TFR	7.7	9.0	8.0	8.8	7.4	8.7	9.3	17.3

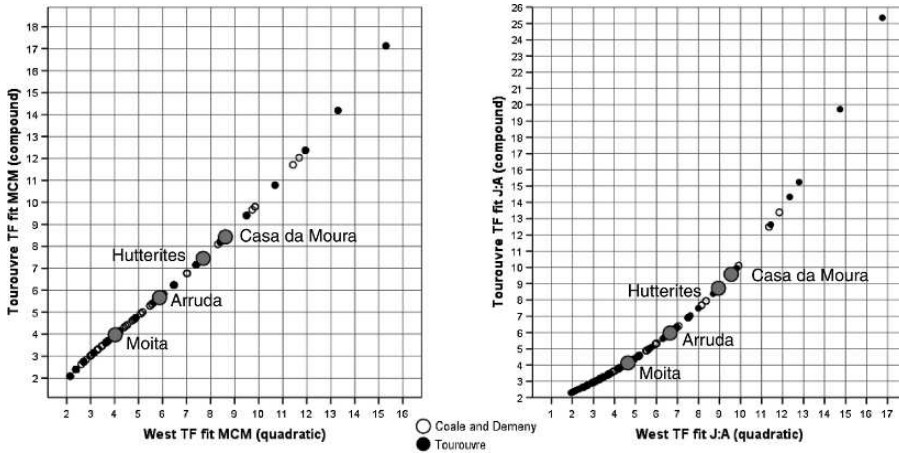


Figure 7: Comparison of fits for TFR from estimators, MCM and J:A, between West model tables ($n = 51$) and relational tables derived from the Tourouvre standard (the predictions were based on $n = 50$, $TFR < 13$, the results shown are the predictions for 55 tables)

Figure 7 gives us assurance that our general levels of fertility are likely to approximate reality since two different estimation techniques have arrived at very similar conclusions.

In fact, Figures 5, 6 and 7 indicate the likely limits of our estimators: by both methods J:A ~ 300 will predict an average fertility of ten children¹². This limit surpasses that of our historical samples and is close to the upper limit of all those archeological samples in our large data base which have sufficient sample size and appear to be unbiased.

DISCUSSION, SUMMARY AND CONCLUSIONS

Can we be completely certain we know how to interpret the Muge sites? The answer is no, in that they seem to be both special purpose and occupation sites. In fact, we have limited knowledge of them.

Moita appears to be the first of the sites in which human burials were placed. This occurred at a time when the saltwater influence on the Muge was established and increasing and while the climate was warming and becoming more humid. Pine pollen was decreasing, so the environs were becoming more open.

The burials at Moita (of which there were at least 85) all seem to occur at the same level – about 21m above the present sea level. They lay on basal sands and were mostly covered by a heavy breccia. In general, they appear

to have been primary in-flesh burials, but with disturbance of earlier by later inhumations. They occurred in groups in a horse-shoe shaped formation opening onto some type of arrangement of pits and posts to the west of the burials. Burials were often accompanied by shells of one sort or another; pits of unopened *Scrobicularia plana* occurred in association with the pit and post features, and close to an area in which many very young children were buried, isolated from the other interments.

It is likely that the mass of the Moita faunal material, terrestrial and estuarine, occurred in the levels above the burials, but a great deal of this was destroyed when the deposits above the burials were removed by bulldozers in the winter of 1951–52. These deposits also included very disturbed post-Mesolithic layers.

It seems likely that many of the Arruda burials post-date those at Moita. Arruda has been only partly excavated and some of the excavated material has been lost, so the number of individuals excavated (more than 105, perhaps in excess of 150) is both estimated and incomplete. The burials so far known come from the south-east to centre section of the portion of the mound which faces the Muge. Again, the burials were generally at the level of the basal sands, though a few are known to have occurred at a slightly higher level. The burials were supine and in-flesh, although at least one child's skeleton must have been bundled. Again, 20th century excavations made it clear that earlier burials were disturbed by later burials, so that human skeletons may be found in various states of incompleteness or disarticulation.

Amoreira has also been partially excavated and a few burials were found there (Newell et al., 1979; Cunha and Cardoso, 2001). New work now underway has yielded several more (Roksandič, 2006). The site appears to have been used for inhumations in the last half of the period during which people were buried at Arruda, but further excavation may change this interpretation¹³.

There were changes in the environmental conditions during the period of intensive use of the three excavated Muge middens as burial locations. After a peak of humidity, there seems to have been an increase in aridity and, at the same time, a diminishing tidal influence, probably accompanied by higher salinity levels in the marshes. We suggest that the later environment was less well tolerated by the estuarine molluscan species which formed an important dietary resource for the Muge population. Furthermore, an important source of vegetable food would have disappeared as the marshes matured into a vegetation zone more dominated by grasses and reeds. The possibility of shellfish toxicity would have increased in the hotter and drier

salt marshes. At the same time, there is an increased possibility of disease from mosquitoes breeding in the brackish standing water.

This concatenation of circumstances could explain why the Muge population apparently disappears and why evidence of the early Neolithic is found only in the adjacent uplands, around 80km to the south (Calado, 2002: Figure 2.2), predating the earliest Neolithic monuments of the Upper Alentejo (which appear ca. 6500 bp; Jorge, 2000:59)¹⁴.

The Moita and Arruda burials provide us with some basis upon which to make estimates of the demography of the central Portuguese Mesolithic. The samples are not ideal, but they are reasonably large and they do not appear to be biased. From the demography, and from other biological anthropological evidence (as diverse as from mean stable isotope values, to dental pathology and wear, to femoral geometry), we postulate changes between Moita and Arruda, so that the Mesolithic of that time and place could not have been a static, unchanging period. Indeed, we do not see the environment as unchanging, so concomitant changes in the human population would be likely.

The paleodemographic evidence suggests that fertility rose during the late Mesolithic. But population increase could have been truncated – both by a worsening environment for the important estuarine species and by fertility-reducing fevers and higher infant mortality.

Caldwell and Caldwell introduce an unsupported contention (2003:210 – no prior discussion appears in the paper) that violence – apparently in addition to infanticide – served as a method of population control amongst hunter-gatherers. Could we be seeing an under-representation of adults resulting from deaths due to violence away from the normal burial grounds (cf. Jackes, 2004)? In fact, the under-representation of adults would serve to increase apparent fertility levels by our method of TF estimation. However, we see no osteological evidence of increasing violence in response to increasing fertility (Jackes, 2004). One Moita skull, Moita 20 from the 1950s excavations, appears to have depressed fractures (Antunes and Santinho Cunha, 1993 speculate on other Muge skeletal material), but proof of systemic violence requires a great deal more patterned evidence (Jackes, 2004) and the slight evidence available shows no increase from Moita to Arruda.

Caldwell and Caldwell (2003) argue that the upper limit of “natural” TF can be expected to be 7.5 (perhaps following Wilson and Airey, 1999), but that hunter-gatherer women raised an average of four children each, the differential apparently being explained by infanticide. We do not accept Caldwell and Caldwell’s lack of emphasis on behavioral or biological

restraints upon fertility (of the type discussed in Jackes, 1994). Nor is there evidence, if the population did not increase markedly, that there must have been infanticide or high childhood mortality. It is worth noting that excellent evidence on archeological fertility suggests that some horticulturalists were able to maintain a low birth rate with neither internal violence nor infanticide (Jackes, 1994; Jackes, 2004).

Since we are examining only those children over four years of age, we are not concerned with the numbers of infants and young children. There can be no doubt that there is infant and early childhood under-representation at the Muge sites. Whether this results from burial patterns, preservation factors (Bello et al., 2002), excavation or curatorial factors (cf. Jackes and Meiklejohn, 2004) cannot be determined. The representation is so low that we could not adduce low fertility as the reason for low infant mortality. On the other hand, infant mortality generally leads to a very limited increase in total fertility rates (Palloni and Rafalimanana, 1999). Infant mortality is an incomplete explanation for the relative numbers of juveniles and adults among the dead but we can avoid discussion of infant under-representation because we are examining only those children who survive beyond four years of age. What we can say is that children above four years of age are represented among the dead in such numbers (relative to adults) that the average Muge woman who completed her reproductive period would have had four to six children. Thus we propose a TF above the postulated four per hunter-gatherer woman and a slight increase in population. We see a Mesolithic population in which the diet was diversifying, the dental pathology was decreasing, and where there was perhaps a change in the level of sedentism (Lubell et al., 1994; Jackes and Lubell, 1999b). We have suggested, based on osteological evidence, that there was probably a reduction in the birth interval concomitant with increased sedentism and dietary change (Jackes et al., 1997). Supplementing the diet of nursing infants would reduce the period of lactational amenorrhea. While this would apply with most force to the Neolithic population, there could definitely have been a reduction in birth spacing during the late Mesolithic Muge occupation. We note the excellent food resources of the Muge saltmarshes, resources that were suitable as weaning foods.

It is important to emphasize here that we can discuss only the period of the Moita and Arruda burials – the situation may well have changed for the worse after 7000 calBP. In fact, we see the possibility of decreasing fertility caused by, for example, dwindling food resources and an increased likelihood of marsh fevers (the suggestion being of recurrent intermittent fevers with spring and autumn peaks) with the eventual abandonment of the

Muge valley. It is interesting that our most recent Muge radiocarbon date is for an individual from Arruda who has stable isotope values suggesting that he was, in fact, eating a marine rather than a mixed estuarine/terrestrial diet. The possibility is, then, that the later Muge people became less sedentary and ranged further across central Portugal. Migration into an empty land following a period of crisis might well have induced a rebound and some increase in fertility, an effect difficult to differentiate from that caused by increased sedentism and a change of diet (see e.g. Heuveline, 2003). But we can make no claim that Casa da Moura people had any relationship at all with the Muge – indeed, it is very unlikely, since the two groups would have been separated by a formidable geographical boundary (the Tagus River). Nevertheless, we have no alternative but to use Casa da Moura as our Neolithic exemplar – the sample size is good even though the identification of individuals from loose teeth is, of course, less than ideal. But the important fact is that the earliest date we have for Casa da Moura Neolithic skeletons overlaps the latest date from the Muge burials.

We have a generally clear differentiation into Mesolithic and Neolithic lifeways based on the stable isotopes, we have well-dated and adequate (though not ideal) samples. We can, once again, affirm that central Portugal provides us with the best evidence for an increase in fertility after the introduction of the Neolithic, but that it is important to understand that fertility could and apparently did increase within the late Mesolithic. Furthermore, the exact cause of the fertility increase in the Portuguese Neolithic is not clear: we suggest that it is accompanied by a reduction in birth spacing (Jackes et al., 1997). Many other factors could be involved as sedentism will lead to alterations in social and economic lifeways, which would affect sexual behaviour and pregnancy outcomes.

We can only guess whether our samples from central Portugal do actually provide the complete picture of the Mesolithic-Neolithic transition in Portugal. We can guess at increased fertility but we cannot prove it. We have seen that it is likely that the Mesolithic resources of central Portugal during the Mesolithic could sustain a reasonably high and probably increasing level of fertility. An increasing population and an unfavorable change in the Muge environment would suggest movement into other areas, areas previously empty and available for settlement. It is thus reasonable to assume that, once Neolithic elements were incorporated, especially the increasing sedentism, this increase would have been maintained, just as is suggested by the Casa da Moura human remains.

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APPENDIX I

A central issue concerns the consistency of the record with regard to the 1950s excavations. In this we are dependent on the information of the two excavators, the descriptive work on the collection by Ferembach, and the independent inventories we have both made. Problems are obvious from the period during and immediately after the excavation. The information provided by Roche and Veiga Ferreira is sometimes contradictory. For example, Skeleton No. 14 is sketched by Veiga Ferreira with a skull, but was photographed and described by Roche as lacking all of the cranium except part of the mandible. Inventories of Ferembach, Meiklejohn and Jackes all confirm the lack of a skull. Similarly, No. 10 had a crushed skull according to Veiga Ferreira, but no skull was ever recorded in the Mendes Corrêa Institute in Porto. However, Roche mentions a mandibular fragment, so we can at least record the presence of a mandible.

Roche (1972) says Skeleton No. 2 was an isolated skull, but that was not true at excavation according to Veiga Ferreira, and this is clear from his sketch. Ferembach's publication on Moita (1974) suggested that the material labelled No. 2 might have been mixed during transport between Muge and the Mendes Corrêa Institute in Porto. Eventually parts of four individuals were mixed under the label of No. 2. By 1984, No. 2 certainly consisted of the postcrania of several individuals, both male and female, but neither skull nor mandible. However, a mandible and an unmineralized skull, the skull oddly discordant with other Muge material, were stored with Skeleton No. 1. This skull was labelled "2". Another skull labelled "83" was also present with No. 1. Neither of these skulls was stored with either skeleton in 1969 when Meiklejohn inventoried No. 2. Ferembach, however, noted a damaged mandible that had a label saying "A2" and Meiklejohn's record of a mandible with No. 1 in 1969 is likely to be the same one. Thus we record a mandible present for No. 2.

There is also a contradiction between Veiga Ferreira and Roche with regard to No. 4, but it is clear that this individual never consisted of more than a few postcranial fragments, at best. Ferembach (1974) actually refers to it as unidentifiable fragments.

Beyond the above we have material that comprised more than one individual at excavation. Those burials recognized as containing mixed bones at the time of excavation were Nos. 1, 7, 13, 18 and 20 according to Ferembach (1974); for example, No. 13 consisted of parts of two adults and two children. Roche noted that No. 1 had parts of two individuals, and No. 7 of three individuals, that Nos. 8 and 11 could be the same person, and that

No. 13 was made up of several people. Further, Veiga Ferreira suggested that individuals Nos. 8 and 11 were in fact parts of the same person. Added to this, we have material which consisted of indeterminable bone debris (Nos. 28, 29), and were certainly nothing which even the excavators could be certain should be recorded as human burials (Jackes et al., in prep. a). Ferembach also says that No. 20 consisted of two people, but it is possible that Nos. 20 and 21 were mixed after excavation, since she did not find No. 21 in Porto. Veiga Ferreira's sketch dated 15/5/1953 of Skeleton Nos. 20 and 21, as well as the photograph of them (Roche, 1972 plate vii.1), makes it clear that this is the most likely explanation.

The excavations of 1952–54 followed upon the bulldozing of the site in the winter of 1951–52: it is worth asking whether the fragmentation and mixing of some skeletons was a result of the bulldozing. However, it is clear that this was not so. The greatest number of mixed and incomplete skeletons (i.e. Skeleton Nos 1, 2, 7, 8 and 13) lay at or near the intersection of the two test trenches dug in 1952. Veiga Ferreira described this as the “centre of the mound”: at that point there lay a concentration of skeletons in a central location with regard to the mound as a whole (Jackes and Alvim, 2006) and, in fact, potentially a focal point of ritual importance (Alvim, in prep.). It seems to have been Roche's opinion (1972) that a series of burials in the same small area caused disruption and fragmentation of the earlier skeletons. Certainly, we cannot argue that the bulldozer drivers destroyed skeletons, since photographs (Cardoso and Rolão, 1999/2000, Figure 28) make it clear that the skeletons in this area – for example, Skeleton No. 2 – lay below the surface left by the bulldozers. The common loss of the knee area in some skeletons (e.g. Skeleton No. 33; Jackes et al., in prep. a) appears to give an indication of the level reached by the bulldozers. In the central location under discussion, Skeletons No. 5, 3 and 2, although also buried with knees tightly flexed on upright thighs, sustained minimal damage, suggesting that the bulldozers barely scraped the top of the skeleton level. Because the skeletons were covered by a hard breccia, and it was this breccia that stopped the bulldozer drivers from removing the lowest archeological levels, it is logical that the only damage was to the flexed and upright knees.

Since the mixed and incomplete state of some of the skeletons cannot be ascribed to bulldozer damage, it is clear that assessment of the number of individuals would require close study even were all the material in perfect condition. Unfortunately, post-excavation events have further complicated the matter. The majority of the material was transported to the Mendes

Corrêa Institute in Porto and there suffered during a fire and subsequent flood caused by the fire hoses in 1974. We have concluded that it is best to say that the Roche excavations uncovered 33 individuals. In this, we are accepting Ferembach's assertion that a three year old and a 12 year old were included with Skeleton No. 13. There were no doubt fragments of children present. Our more recent survey of the material was rapid and followed the disruption of the fire, so although we did not fully agree with Ferembach's interpretation of the material, we cannot insist on our conclusions.

APPENDIX II

Juveniles among the skeletons from the 19th century Moita excavations present particular problems. Ferembach (1974) records the fragmentary skull of a ?newborn infant numbered No. 38 and the skull of an adult female, No. 37. In 1969, Meiklejohn did not see skull No. 38 nor was it present in 1984. However, No. 37 was made up of numerous fragments, some of them of a child, and by 1984 the fragments numbered No. 37 included a juvenile tooth, but clearly not that of a newborn.

Meiklejohn's various inventories (1969, 1984, 1985-86) indicate that both adult and juvenile material was also migrating in and out of the group of bones labelled No. 39. Ferembach describes No. 39 as a three year old represented by a mandible. This was not present in 1969, and by 1984 No. 39 was represented by the fragmentary maxilla of a small child, associated with an adult mandible. The adult mandible now labelled No. 39 must, in fact, have had another association originally. We will accept No. 39 as representing a child for whom the mandible is no longer present, since there are loose mandibular teeth recorded amongst the materials discussed. An age of three years is acceptable for this individual.

Among the material mentioned above none appears to suggest a newborn, and we might therefore question whether to include one here. A young child, under three years, now without a number, has a left mandibular horizontal ramus, and there is also a full mandible, now called No. 45. In fact, No. 45 now consists of post-cranial fragments of three children, two of them under one year. Examination of the long bones present in the collection thus becomes necessary to our attempt to establish the number of infants. The juvenile long bones in the entire Moita collection do not suggest the presence of very young children other than those indicated by the dentitions, except infant bones labelled No. 7 and those now included in No. 45. We

can say, without being certain of it, that Ferembach's mention of No. 38 as a newborn and our records of Nos. 7 and 45 suggest that at least one or two children present in this collection are under one year. And we can say with more confidence that there are three older children who are under five years. But this still does not, of course, provide a full representation of the expected number of children under five. There may have been more excavated: Ferembach mentions others, for example No. 41, a skull which was not present under that number in 1969 or in the 1980s. But we have absolutely no way of knowing whether No. 41 of Ferembach is associated with No. 45 of the 1980s. Ferembach (1974:23) records that 11 children (including all the problematic cases discussed here) were originally kept together in the same drawer in the museum of the Geological Services of Portugal.

APPENDIX III

We generated a random set of relational model tables (Brass, 1971), within the values of $\alpha = -1.5$ to $+1$, $\beta = .5$ to 1.5 (Zaba, 1979), but widened to the extreme of $\beta = 1.6$ to accommodate the tables generated by Brass himself (1971: 79–81). Our first set of relational tables uses Brass's global standard as the starting point and includes Brass's own 12 tables. The second set uses Tourouvre-au-Perche (a northern French village, 1670–1719; Charbonneau, 1970:194) as seed data with the same α , β values as used with the Brass global standard. The Tourouvre age at death distribution was chosen because it occupies a central position in a cloud of 32 historical samples, directly on the line expressing the relationship of our two demographic estimators in the historical samples. There is no claim here that northwestern European historical demographic values are representative of global fertility experience (they are apparently not, though long established ideas on internal homogeneity and bimodality of western and eastern European fertility patterns in the past are being challenged e.g. Lynch, 1991; Wetherell and Plakans, 1997). Social and environmental determinants of fertility (Jackes, 1994) make it very unlikely that we can rely on one specific standard. Nevertheless, we do have some idea of *biological* constraints which will allow us to set reasonable upper limits.

Deviations in both directions from biologically feasible levels of mortality at the lowest and highest ages are immediately obvious in the relational tables. There have been a number of attempts to modify

Brass's approach, most recently that of Murray et al. (2003), especially in order to deal with aberrant results at the lowest and highest ends of the age at death distributions. This is very marked for infants, but in fact the improbability of results is much greater for the final five year age category (with extraordinary coefficients of variation ranging from 212–256 in our tests on two different sets of 55 such tables – see below). The problem of such aberrant results constitutes a major flaw, and in many of our generated tables the demographic values at the youngest and oldest age categories are markedly outside biological probability. For example, virtually the highest known infant mortality (Liberian migrant extreme mortality, ${}_1q_0 = .747$, McDaniel, 1992) is exceeded or approached in a number of the relational tables, while in others, infant mortality values are well below those of ${}_4q_1$. Since our estimates of fertility derive from the infant C values, divided by the sum of the C values for women aged 15 to 44.9, any aberrance in infant values will lead to unreliable fertility estimates.

We have excluded from analysis the standard tables and also those six Tourouvre and three Brass global standard derived tables in which ${}_1q_0$ exceeds .800. We have further removed one Tourouvre table in which the TFR would be 21, that being an unrealistic average for fertility since that would imply – for the *average* woman – one child every $9 + 6 = 15$ months for 26 years, with no fetal wastage, no illness, no food shortages, requiring 26 full years of continuous sexual activity, no spousal death, no sterility, no anovulatory cycling, no celibacy, no pregnancy complications, no age-dependent changes in fecundity, and relatively early weaning. The effect of infant mortality will not overcome the biological improbability of such a high average fertility. The fact that we have included tables in our analyses which imply that the *average* woman had over ten children might lead to criticism from medical experts (K.M. Richardson, pers. com.). The effects of great grand multiparity (ten or more children) are difficult to assess since it is rare, and studies lack access to women without modern health care. The most recent review of information (Aliyu et al., 2005) certainly points to macrosomia, medical complications and placental pathologies under the best conditions.

We are left with 39 Brass standard and 36 Tourouvre standard tables to study. Appendix III Table 1 shows us that the standard chosen is crucial in determining the fertility levels. But Appendix III Table 1 provides further information. In order to test whether the α and β values chosen for use with the standard are also likely to be crucial, we generated a further set of 54 completely different tables (values for β ranging from .5 to 1.5 in

Table 1: Descriptive statistics for life table total fertility rates and infant mortality quotient coefficient of variation, show differences among sets of relational (logit) tables

	TFR mean	sd	min.	max.	$_{1q_0}CV$
Brass global standard: 39 tables	3.572	1.858	2.06	8.17	85.83
Brass global standard: 55 tables	3.257	1.559	2.04	7.93	109.24
Tourouvre as standard: 36 tables	4.744	3.450	2.10	15.50	75.29
Tourouvre as standard: 55 tables	5.509	4.352	2.10	19.86	89.34
Tourouvre as standard: 50 tables	4.454	2.790	2.10	12.18	93.52

steps of .5, while each β level has α values from -1.5 to $+1$ in .25 steps) from the Tourouvre standard (which will be included as $\alpha = 0$, $\beta = 1$ for a total of 55 tables). The question of biological unlikelihood was initially ignored, but the Tourouvre set was then reduced to 50 tables by removing all those in which $TFR > 13$. We also generated 55 equivalent tables using the Brass global standard to retest the effect of the standard versus the levels chosen.

The Tourouvre ($n = 55$) TFR standard deviation shown in Appendix III Table 1 is large. This is partly a result of the fact that the infant mortality quotient ($_{1q_0}$) coefficient of variation is extremely high, there being several outliers among the values (cf. West tables, footnote 11 above). In fact, the relational tables' coefficients of variation for the estimators themselves are unacceptably high and Appendix III Table 2 shows that the Brass global standard and our various sets of Tourouvre tables have demographic estimator values far more dispersed than our sample of historical life tables (world-wide, though biased towards Europe or populations of European origin).

Table 2: Coefficients of variation show differences among data sets in dispersal of estimators

	MCM CV	J:A CV
Historical data: 32 life tables	26.063	29.120
Coale and Demeny: 51 West tables	44.435	54.951
Brass global standard: 39 tables	96.828	106.165
Brass global standard: 55 tables	95.424	102.860
Tourouvre standard: 36 tables	87.713	86.636
Tourouvre standard: 55 tables	80.719	93.453
Tourouvre standard: 50 tables	79.925	89.904

The relationship between the various estimates is not simple. While the differences between the TFR predictions for West ($n = 51$) and Tourouvre ($n = 55$ or 50) do not diverge strongly at low levels of MCM and J:A, the differences plotted against the estimators inscribe curves and so it is not possible to make blanket statements about whether one method or the other over- or under-estimates TFR. However, the 95% confidence limits for the Tourouvre tables are so broad that the differences are non-significant for much of the range: extremely discordant results between the methods accumulate markedly when estimator values exceed certain levels (MCM $\sim .100$ and J:A $\sim .300$), precisely those levels at which biological feasibility becomes questionable. The Brass global standard predictions are different. The UN tables from which the global standard was derived are closer to the West model tables than to the Tourouvre standard in terms of the relationship between the estimators: thus, the major divergence of the global standard is from Tourouvre generated TF values.

This is not an appropriate place to expand on the complex relationship among the estimators, the choice of standards for relational tables, the α and β levels and the West model predictions. It is sufficient to say that the Tourouvre ($n = 55/50$) predicted TFR and the West ($n = 51$) predicted TFR generally accord unless the tables are beyond the range of biological likelihood.

It is clear that both the standard and the exact details of how those tables are generated will determine predictions of fertility levels when relational tables are used. The relational table method cannot be used without some external check on results and this we have provided.

NOTES

¹ The Melides Zambujal sample is small, about 51, and is too late in time. Melides Lagares provides a smaller sample of about 29 for which, curiously, there are no dentitions retained (see also Nogueira, 1927–1930).

² Hereafter called Moita, Arruda and Amoreira. The sites are sometimes referred to collectively as Muge.

³ This is the regional mean ΔR for Portugal published at <http://radiocarbon.pa.qub.ac.uk/marine/> and based on Monge Soares (1993). Correction for ΔR follows procedures recommended in <http://radiocarbon.pa.qub.ac.uk/calib/manual/chapter2.html#MARINEHELP>.

⁴ Cunha and Cardoso (2001) give a date of 6850 ± 40 for an Amoreira burial originally stored in Porto. The date, using the mixed marine/terrestrial curve, adjusted for a 50% marine diet on the basis of a $\Delta^{13}\text{C}$ value of -16.5‰ , would be 7410–7450 calBP. Meiklejohn in 1969

and Jackes in 1984 both inventoried the material held in the Mendes Corrêa Institute of Anthropology in Porto and noted very few skeletons positively identified as excavated from Amoreira.

- ⁵ Anemia has often been associated with cribra orbitalia or porotic hyperostosis. We found no cases of the conditions in either the Moita or Arruda samples.
- ⁶ Zilhão (2001) used a different reservoir effect value and incorrectly calculated these dates in such a way as to make them 500 years earlier.
- ⁷ When we started working on the human remains from Portugal, the Mesolithic provenance of the material excavated in 1952–54 was not in doubt. However the earlier material was far less secure (see discussion in Newell et al., 1979). Our first radiocarbon, stable isotope and SEM analyses were designed to examine whether variations in matrix and degree of mineralization were reason enough to question the Mesolithic provenance of some Moita skeletons.
- ⁸ Vallois described eleven skulls using Arabic numerals and those skulls seem to accord with the skulls now designated by the equivalent Roman numerals. His only Moita photograph was of Moita 19, which is demonstrably Skull xix, though between 1929 and 1984 it had sustained marked damage. The skulls he described still bear the same numbers: vii, xvi, xvii, xviii (now lacking a mandible), xix, xxiii, xxix, xxx, xxxiv (which by 1984 had a mandible not present according to Vallois), xxxv (it is possible that this skull was reshaped subsequent to Vallois' description), xxxvi (not recorded by either Meiklejohn or Ferembach in the 1960s).
- ⁹ Expressing the sum of the absolute differences between two distributions.
- ¹⁰ E.g. Dobson (1997) in passing provides much evidence on internal migration in England; Monter (1979) gives information on reasons for migration to Geneva. In data from later in Genevan history (from Perrenoud, 1978), the relationship between our demographic estimators lies slightly outside the scatter of our other historical data sets.
- ¹¹ The 129 tables from which West mortality schedules were drawn up are post-1870 and are generally from Europe or areas colonized by Europeans, apart from nine tables from Japan and Taiwan. West tables are regarded as no more than an indication of generalized demographic values. Our 51 West model tables comprise 15 decreasing, 28 increasing and 8 stationary tables. Our basic non-stationary tables cover $r = -.01, -.005, .005, .01, .015$. Included are levels 1 (8 tables up to $r = .025$), 2, 3, 4, 6 and 8 (6 tables each), 5 (10 tables up to $r = .035$), and 10 (3 tables at $r = .01, 0$ and $.01$). All TFR values are below 13. Infant mortality quotients are below .630, even when West 1 and 2 are extended to $r = .05$ (on 56 tables up to West level 8, ${}_1q_0CV = .33$).
- ¹² $TFR = 10$ would be predicted by the Tourouvre method from $MCM \sim .110$, and from $MCM \sim .114$ using the Coale and Demeny method.
- ¹³ Carvalho (2002:239) summarizes Roche's view of the contemporaneity of Moita and Arruda and the later date of Amoreira, based on tool type percentages.
- ¹⁴ This time frame occurs during a particularly broad plateau in the intcal04 calibration curve, making interpretation problematic. Nevertheless, there is a reasonable possibility of dating these structures to soon after 7300 calBP.
- A new publication gives emphasis to the close association between the Mesolithic Muge sites and estuarine conditions: see van der Schriek, T., Passmore, D.G., Stevenson, A.C., Rolão, J., 2007. The palaeogeography of Mesolithic settlement-subsistence and shell midden formation in the Muge valley, Lower Tagus Basin, Portugal. *The Holocene* 17, 369–385.

Chapter 9

THE LIBBEN SITE: A HUNTING, FISHING, AND GATHERING VILLAGE FROM THE EASTERN LATE WOODLANDS OF NORTH AMERICA. ANALYSIS AND IMPLICATIONS FOR PALAEODEMOGRAPHY AND HUMAN ORIGINS

Richard S. MEINDL¹, Robert P. MENSFORTH² and C. Owen LOVEJOY³

¹*Kent State University, Ohio, USA*

²*Cleveland State University, Ohio, USA*

³*Kent State University, Ohio, USA*

Abstract: The demographic reconstruction of extinct societies from archaeological sites is a complex problem. A variety of variables affect the adequacy of the cemetery census, especially aboriginal burial practices, post-mortem preservation, excavation techniques, and estimation of demographic variables by investigators. Most important of all is the need to adjust life table values by typically high human rates of intrinsic growth. The number of populations that meet all these stringencies is unfortunately few, but one is the Libben Site, located in the Great Black Swamp of Northern Ohio. Dating from late first millennium, it is the largest single-occupation archaeological skeletal series from the Eastern Woodlands of the United States. Drawing from auricular-based skeletal ages and modern ethnographic estimates of fertility, we present the paleodemography of this important site, including growth-adjusted mortality profiles and age structures. These carry important implications for all phases of human evolution

The demographic reconstruction of extinct societies begins with a sampling process that involves several potential sources of error. Aboriginal burial practices, soil conditions, disturbances of the skeletons, and the skill of excavators may all affect how well a cemetery mirrors the population that used it (White, 1991). As Weiss (1973) reminds us, if an unbiased representative sample cannot be assumed, further demographic analysis is not likely to be productive. This chapter describes the census of one

of the largest and most homogeneous skeletal populations yet recovered in prehistoric North America and its general implications for paleodemographic analysis. Following this, we then discuss some issues with respect to how the population's age distribution was determined (including the results of a recent reassessment based on modified criteria), and review how assumptions that must be made in palaeodemography about fertility measures impact our understanding of demographic evolution in earlier human populations. We conclude with a brief discussion of the importance of demographic rates to the natural history of humans as a species.

LIFE IN THE GREAT BLACK SWAMP: THE SKELETAL BIOLOGY OF THE LIBBEN SITE

The Libben site is located on the north bank of the Portage River in Ottawa County, northern Ohio, USA (Lovejoy et al., 1977). Radiocarbon dates indicate an occupation from the 8th to the 11th centuries AD. At this time the locality was situated within a dense elm-ash, swamp forest, covering freshwater marshes and streams with abundant fish and mammal resources. As in many riverine Late Woodland sites cultivated maize and small amounts of shellfish were present, but the people at Libben relied extensively on a trap-and-weir economy. They captured small game from the marshes and great quantities of fish from the river, streams, and lakes. Muskrat was especially prized. Refuse pits contained migratory waterfowl, mammals and fish. These included White-tailed deer, the abundance of which was seasonal. Quantitative analysis of pit contents (by weight) revealed proportions of meat resources: for every kilogram of dressed poultry, there were four kilograms of venison and muskrat meat, and more than twenty kilograms of edible fish.

The primary goal of the Libben project has been the elucidation of human demographic evolution, and this site has provided a unique opportunity to estimate the mortality and age composition of a prehistoric, pre-contact population. Excavation of the cemetery (which was also a living site) proceeded with the skeletal sample as its primary objective. Each skeleton was fully exposed, and then drawn, mapped, and photographed by a senior excavator. Preliminary age, sex, and pathology were noted before each burial was removed for further analysis. The postcrania of subadults were carefully monitored for all possible secondary centers of ossification, as were all juvenile dentitions for their completeness. All bulkheads separating excavation squares were systematically excavated. These procedures yielded

a number of embryonic and fetal skeletons, the earliest being from the first trimester. More systematic examinations of these skeletal remains have been carried out over many years post-excavation.

Libben was a permanent fishing village with clear evidence of long-term, year-round habitation. It was situated on a sandy knoll, and surrounded by river and marsh. There was a defensive stockade on the marsh side that may have been replaced or repaired as many as three times during the site's occupation. The largest dimension of this two-acre site [c. 0.80 hectares] is east-to-west, with the greatest density of burials near its center. About 1300 articulated burials were recovered from Libben. Almost all were extended, there being only a very small number of bundles and cremations. Most were oriented north-to-south, but no relationships to age, sex, or artifacts have been uncovered despite extensive systematic attempts to do so (Schick, n.d.). Burials were found throughout the habitation site, and unlike many other Ohio Woodland sites—or modern Christian, Islamic, and Jewish cultures for that matter—there was no segregation of living and burial space. At Libben there was continuity from life to death.

Libben's continuous habitation resulted in one of the richest skeletal assemblages yet recovered in North American prehistory. It includes extensive lithic and ceramic artifacts, as well as a variety of personal effects including columella, bone and shell beads, and gorgettes, as well as extensive faunal remains (Lovejoy et al., 1977). Pottery was primarily coiled and grit tempered, relatively thick, breakable, utilitarian, and only minimally decorated. No association between type and/or characteristic of artifacts with locality or depth within the site has been demonstrated. It is clear that the site is essentially homogeneous, with a stable occupation that appears to have spanned roughly ten generations; a time period that represents about half of the Late Woodland phase of northern Ohio.

Archaeological and systematic analysis of the entire population has revealed almost no evidence of violent conflict between other villages or within the population itself (Lovejoy and Heiple 1981). The site precedes the first ethnographic accounts of Algonquian-speakers (who staunchly defended tracts of hunting land) by some 700 years. While long bone fractures were numerous, almost all were caused by accident, and there was a strong association with age, most fractures occurring either during adolescence or old age. Only two cases of blunt trauma to the cranium were observed in the entire population. Projectiles imbedded in skeletons were rare and no battered individuals, as are sometimes recovered from other sites, were found. Detailed analysis of fracture patterns showed that most were associated with general activity and were not defensive injuries; for

examples, Colle's fractures (distal radius) were frequent but there were only two "parry" fractures (ulnar midshaft) in the entire cemetery. There is no evidence of any kind of child skeletal fractures or blunt trauma. There was, however, as in cases of the first sedentary populations from the Kentucky Late Archaic (see Meindl et al., 2001; Mensforth, 2001), a depression of adult male survivorship compared to that of females.

There are several additional instances at Libben for which an obviously natural cause of death was readily diagnosed. These included various neoplasms and several obstetric pathologies, including a shoulder dystocia, a transverse lie, and a tubal pregnancy, each a likely source of fatal hemorrhage. A few graves contained multiple, obviously contemporary burials, suggesting possibly brief episodes of acute infectious disease. Several Late Archaic and Woodland archaeological sites have also revealed evidence of sedentism in the eastern woodlands (Meindl et al., 2001), and like these, Libben manifests high frequencies of incipient periostitis, sometimes having clearly advanced to systemic osteomyelitis. Patterns of porotic hyperostosis at Libben suggest an auto-induced iron deficiency anemia as a probable defense mechanism against common infections (Mensforth et al., 1978).

It is important to note the few cases of true chronic immobility which were recovered, and that systematic analysis of fracture healing also indicates a lack of any significant migratory activity on the part of the population. In recent years it has become popular to cite various long bone injuries and suggest that these indicate "caring" on the part of other society members, and that such individuals could not have survived without a strong social network. However, similar injuries have been reported for many non-human primates, which obviously lack such a network (see Schultz, 1939; Buikstra, 1975; Bramblett, 1967). In addition, there is indirect evidence of essentially the opposite, viz., that attention and immobility were sufficiently prized as "patient care" attributes that some injuries *unlike* those seen in other primates are recovered. In this regard, one adult Libben burial of substantial age exhibited profound lower limb atrophy typical of congenital spastic paraplegia, which testifies to a complete absence of any possible mobility. Moreover, the pattern of fracture healing in the population was quite remarkable, with very high levels of proper alignment and only minimal loss of long-term mobility. These suggest enlightened, true instances of social care and numerous instances of long-term immobilization for proper fracture healing (Lovejoy and Heiple 1981). These data strongly suggest an absence of seasonal mobility and are in full accord with the analysis of vegetal and mammal remains (suggesting continuous, year-round occupation of the site), the abundance and variety of local resources, and the elaborate protective palisade.

Libben was an egalitarian society, and death and burial were important rites of passage for all of its members. Only two kinds of non-articulated burials were included in the demographic sample (see earlier). These included a handful of bundle burials composed only of skulls and major long bones, indicating a general effort a thousand years ago to return at least the essential remains of kinsmen back to the home burial ground. A second exception to the “articulation rule” for demographic inclusion was the recovery of patently fetal or infant long bones, which might have been broken or scattered over as much as a square yard or more by the action of plant roots, reptiles, rodents, cryoturbation, and other agents. Such cases were enumerated in the census, but care was taken not to double-count them (i.e. they became part of the demographic cohort so long as no other associable remains of the same age were found within a six-foot radius of the fetal bone—usually a femur, tibia, or humerus).

METHODS OF AGE DETERMINATION FOR THE LIBBEN POPULATION

Libben subadults were aged by standard methods, primarily by analysis of their dentitions, each of which was scored for both crown and root development—eruption data were only rarely employed. Epiphyseal closure, long bone and basicranial dimensions were used for burials less than one year of age and in rare cases where dentitions were not recovered. All burials with unfused root apices and/or partially calcified crowns were systematically seriated within the entire population of subadults (Lovejoy et al., 1985a). Long bone information confirmed or adjusted their placements within this series. Nearly 18% of the Libben burials are infants, and a large proportion of these are neonates.

Adults were originally aged using a variety of standard procedures (reviewed in Lovejoy et al., 1977). However, these also included the first application of standards for adult age based on the auricular surface of the pelvis, which were developed in the laboratories at Kent State University and the Cleveland Museum of Natural History (Todd-Hamann Collection) (Lovejoy et al., 1985b). Unlike other bony sites, the auricular surface exhibits developmental-like changes well into the fifth decade of life, before it finally becomes dominated by obvious degeneration (Meindl and Lovejoy, 1989; Lovejoy et al., 1995; Lovejoy et al., 1997; Meindl and Russell, 1998).

Buckberry and Chamberlain (2002) have devised a quantitative scoring system using some of our components on the presumption that such

“objective techniques” make it easier and more replicable for palaeodemographic analyses. Unfortunately, their series of Bayesian prior probabilities appears to be inconsistent (e.g. a zero probability of an individual being 55–64 years in their stage 7, yet about 25% probability for both adjacent decennial categories), and influenced largely by overly interpretive assessments of advanced degeneration. Aside from an obvious need for more appropriate graduation, some of their revisions tend to be based on overly interpreted senescent morphologies (Storey, 2005). On the other hand, there has been a consistent argument by some critics of palaeodemography that the age of adults, especially those of advanced age, are systematically underestimated, and it is now clear that much of this criticism stems from a tenacious reliance on pubic symphyseal methods. These derive nearly all of their age correlation from osseous events surrounding the closure of the “ventral rampart”, an epiphysis that is uniquely delayed in humans. Data from this skeletal site become substantially less reliable after full fusion (usually before 30 years) (Meindl and Lovejoy, 1989). Nevertheless, methods based partly or largely on this late-third-decade event continue to be used to attempt estimation of entire adult cemetery age pyramids (Baldsen et al., 2002; Herrmann and Konigsberg, 2002).

In response to this frequent criticism, and as a test to examine the effects of possible age-bias from the symphysis, we systematically re-aged the older Libben adults by using only data from the auricular surface (Table 1). The estimated ages of all the adult decedents of the original multifactorial age sequences of Libben (Lovejoy et al., 1977) have now been re-calibrated by means of the auricular surface using our original standards (Lovejoy et al., 1985b). This resulted in the ages of some burials, especially the very oldest, to be increased over previous estimates by as much as five years, and rarely even in excess of this amount. Some pubic data were in fact included, but only to align the ages of the younger

Table 1: Libben cemetery, frequencies of adult burials by age class

Age class (years)	Lovejoy et 1977 Sexes combines	This study males	This study females
20–29	.239	.245	.232
30–39	.456	.339	.222
40–49	.249	.273	.292
50–59	.056	.116	.175
60–69		.028	.073
70+			.006

adults, which occasionally resulted in revision by a few years downward. With the discarding of other skeletal age indicators, the average age of the Libben adults increased by about four years, the average age of the whole cemetery, by two.

A NOTE ON INFANTICIDE

Before turning to the effects of such a reassessment of the age distribution at Libben, there remains one additional topic of discussion in virtually any analysis of prehistoric demography—the issue of infanticide and its effect on the age distribution. Anthropologists and demographers are aware that infanticide is a widespread cultural practice *associated with high fertility*, most comprehensively studied in several Neotropical foraging and horticultural populations. It can be individual or community-based, and the levels of and the reasons for the practice vary as much as do the cultures of South America. Hill and Hurtado (1996) estimate that about five percent of all children of the forest Ache were victims of homicide, with more than a few cases occurring at a considerably older age than infancy. Perez and Salzano's study (1978) of five Ayoreo populations revealed very high levels of infanticide as well as a weak positive correlation of this with total fertility. The remarkably high level of Yanomamo infanticide was largely female (Neel, 1978). Perhaps it is difficult to care for closely spaced children. More probably, girls are seen as ineffective combatants, or (incorrectly) as less efficient food gatherers/producers.

It should therefore be noted that almost any skeletal sample has the *potential* to reflect some bias via infanticide, as such ethnographic observations establish that infants are often systematically buried away from the regular cemetery or are sometimes summarily discarded. This topic is raised so often as a potential bias in paleodemography that we will present scenarios for Libben using data from actual South African Kung, Paraguayan Ache, and Venezuelan Yanomamo mortality and fertility structures (Table 2). However, it should also be noted that the archaeological data suggest that infanticide was probably not practiced to a great extent at Libben. At any rate, if Libben had been indeed stable and reflective of a non-growing population (i.e. demographically stationary), then the conclusion must be that it had low fertility like the Kung, and poor adult survivorship like the Yanomamo. Such levels are artificially extreme, and there are other reasons why such a demographic profile is likely to be inaccurate (see below).

Table 2: Four populations: Infanticide, adult life expectancy, female total fertility. (Sources: Howell, 1979; Hill and Hurtado, 1996)

Population	Infanticide?	Longevity(\bar{e}_{15})	Fertility (TFR)
Libben (Ohio, no growth)	Unknown	24.5	5.2
Dobe !Kung (Kalahari)	Very low	54.1	4.9
Forest Ache (Paraguay)	High	43.3	8.1
Yanomamo (Venezuela)	High	27.5	8.0

THE ANNUAL INTRINSIC RATE OF INCREASE: A SINGULARLY CRITICAL VARIABLE IN PALAEODEMOGRAPHIC ANALYSIS

Despite the call for “new directions” in paleodemographic research (Hoppa and Vaupel, 2002), there remains a much greater bias in palaeodemography than errors associated with skeletal age determination. Largely unaddressed by the “Rostock Manifesto,” it is one that appears to be far more critical to an accurate assessment of past populations than the aging biases of modern osteology, real or imagined. This section examines this bias and offers a means to correct it.

A fundamental unknown quantity in any palaeodemographic analysis is the annual intrinsic rate of increase (r). How is to be estimated? Without the Malthusian parameter, paleodemography has one too many unknowns, or one too few equations. Given what we now know about the evolution of the human species, the traditional presumption of no growth (i.e. stationary demographic conditions) is not a realistic assumption in most instances. And yet, even moderate variation in the hypothetical intrinsic growth rate of any extinct population results in great ranges of predicted living age structure and mortality profile.

Sattenspiel and Harpending (1983) examined variations in life expectancy and crude birthrate within several of the West series of the Princeton models of mortality and age structures (Coale and Demeny, 1966) and offered an interesting observation: the cemetery age distribution of a stable population determines the crude birthrate but makes no prediction of life expectancy. Mean age at death of the cemetery predicts the reciprocal of the crude birthrate *nearly exactly* for all humanly possible values of the intrinsic growth rate (i.e. $-1\% < r < +4.0\%$). In other words, a given cemetery fixes the crude birth rate, but both mortality and growth are fully free to vary. Since the cemetery fixes only crude

fertility, how can paleodemographers choose a specific mortality level on the continuum of solutions? Bennett's (1973) analysis of Point of Pines, Asch's (1976) approach to middle woodland groups in the Lower Illinois Valley, Muller's (1997) models for late prehistoric populations in the Eastern Woodlands, and Hernandez' (2005) and Marquez' (2005) analyses of Mesoamerican cemeteries each argue for solutions based on a single hypothesized growth rate. Of course, archaeological support for a single value of Malthusian r is very difficult to find (Horowitz et al., 1988).

Life expectancy at birth is a function only of mortality. By contrast the crude birth rate depends on age-specific fertilities, the once-living age structure of the population, and even the mortality function. A different fertility measure—one stripped of any influence of maternal mortality and age structure—would address the problem. The total fertility rate (TFR) is a pure summary measure of completed fertility performance, represents the average number of live-births to women who survive to the end of the reproductive span, and has been emphasized in theoretical approaches to paleodemography (Harpending, 1997; Keckler, 1997). Also calculated as the sum of the age-specific fertility rates, the TFR is independent of the population's age structure or maternal mortality.

Whatever the average growth rate of a prehistoric population may have been, it was filling the Libben cemetery on the basis of both its death rates and its age pyramid. That is, there are many different stable population profiles, from poor longevity/medium fertility (Figure 1, lower left) to good

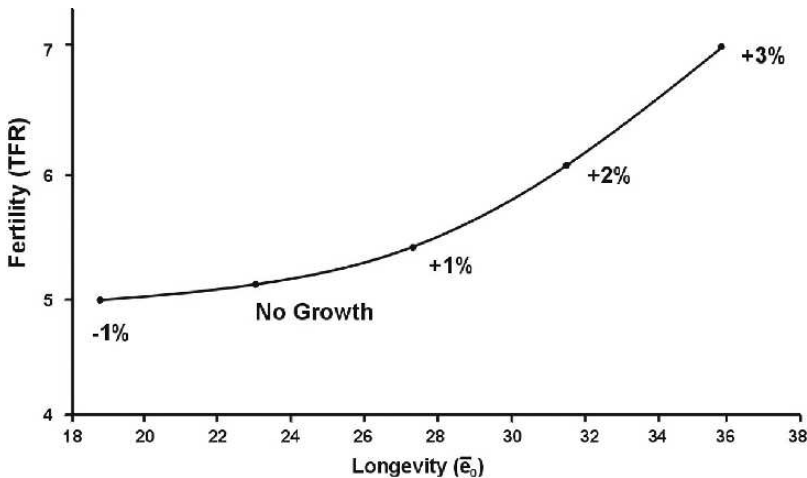


Figure 1: Demographic solution curve for the Libben Age-at-death distribution. Total fertility rate (vertical); mean life expectancy at birth (horizontal)

survivorship/high fertility (upper right), and every gradation in between, that could have produced cemeteries with identical age-class distributions. There is, in fact, a *continuum* of solutions to Libben, or to *any* single prehistoric cemetery. The determination of the numerical values for a complete demographic profile requires stable theory *and* at least one other datum. The choice of a total fertility rate from modern populations coupled with the cemetery age-sex distribution of an extinct population produces a full demographic solution, including the average stable growth rate, the once-living age structure, and the mortality profile.

VARYING THE TFR AT LIBBEN AND ITS EFFECTS ON POPULATION STRUCTURE

James Wood (1990) surveyed 70 non-contracepting populations, and calculated an average TFR of 6.1 children. However, the variance of Wood's empirical distribution is surprisingly large, and may explain his choice to substitute "anthropological" for the old term, "natural" fertility (Meindl and Russell, 1998). It is likely that the lowest values were influenced by endemic venereal diseases (see, Caldwell and Caldwell, 1983); the highest, by superior nutrition, some modern health care, and/or religious mandates for high fertility. There is also a problem of multiple sampling, especially all the low fertilities from New Guinea. The interior 35 surveyed cases of Wood's moderately skewed distribution of anthropological TFR might form a more realistic range of pre-contact, anthropological, or even "natural" fertility, in the sense of Henry (1961). We have therefore applied three modern fertility performances to the Libben cemetery—end of the first quartile (TFR for the 18th population), the mean, and beginning of the last quartile (53rd). Also, increasing amounts of especially female infanticide, "unrecovered" by the archaeologists, have been added to the paleodemographic cohorts depending on fertility level (Table 3). In the context of the Libben cemetery age distribution, each produces a net reproductive rate (in daughters per woman), and three crude rates (per person per year), i.e. birth, death, and intrinsic increase. Note that even this truncated 50% range in total fertility produces great variation in crude demographic rates (Table 4).

Not only does fertility predict annual growth rate, it also predicts the once-living age structure, and the complete mortality profile as well. For most sedentary prehistoric populations the high fertility model is favored—in fact, it might not be high enough—however, the two lower fertility

Table 3: Three hypothetical fertility models for Libben: Total fertility rates, levels of infanticide by sex

Libben Site Fertility Model	TFR	“Unrecovered” Infanticide %	
		Female	Male
High	7.0 Children	7	2
Mean	6.1 Children	5	2
Low	5.5 Children	4	2

Table 4: Three hypothetical fertility models for Libben: Net reproductive rate (daughters per woman), crude demographic rates, birth, death, increase (per person per year)

Libben Site Fertility Model	R_0	“Crude Rates”				
		b	–	d	=	r
High (7.0)	1.98	.053		.028		.025
Mean (6.1)	1.51	.049		.034		.015
Low (5.5)	1.15	.046		.041		.005

Table 5: Three hypothetical fertility models for Libben: Life expectancies at birth and at age 15, adolescent survivorship, by sex

Fertility Model	Mortality			Survivorship	
	0	$\bar{e}_{15}(\text{fem})$	$\bar{e}_{15}(\text{male})$	$l_{15}(\text{fem})$	$l_{15}(\text{male})$
High (7.0)	31	29	25	.69	.71
Mean (6.1)	27	27	24	.63	.64
Low (5.5)	23	25	23	.55	.56

models are presented to demonstrate the impact of a different TFR on all other aspects of a cemetery-based demography. For instance, very different mortality structures follow from variations in assumed fertilities (Table 5). If the prehistoric TFR was 7, then life expectancy at Libben was much better than 17th century London, even during the non-plague years (Hacking, 1975), but not as good as the time-specific figure for most Western cities during the 1918–19 influenza pandemic. Despite additions of hypothetical infanticide and extensions to adult age, both of which may be overcompensations on our part, Libben’s sex-specific mortality profiles contrast substantially to that of the Paraguayan Ache: (1) Libben life expectancies are lower, (2) the ratio of infant mortality to young

adult mortality is less for Libben (even when increased by hypothetical levels of infanticides), and (3) the survival of post-reproductive adults is contracted.

Prior to 1960 Kung fertility was actually less than Howell's famously low estimates from the 1970s. These levels were at least partly the result of infectious diseases (Harpending, 1994). Syphilis and other venereal diseases had been endemic in much of sub-Saharan Africa since their introduction by Moslem traders generations ago. The presence of venereal diseases in the Kung has been known (Howell, 1979), but the impact of infectious sterility on the reproductive histories of Kung women was only first fully appreciated by Harpending. In fact, a large area of west-central Africa north of the lands peopled by the Kung had been termed the "infertile crescent" by demographers, until the infertility epidemic was "cured" by penicillin (Caldwell and Caldwell, 1983; Harpending, 1997). Syphilis, gonorrhea, and other STDs affected women's age patterns of fertility as well, particularly the parity-progression ratios of the Kung, which mirrored those of populations with no fertility control (Howell, 1979), albeit ones with greatly reduced TFRs. Until DeBeers, the diamond miners, relocated the Kung into several refugee camps at New Xade in 2002 (Price, 2005), the Kung had exploited the desert scrub environments of Namibia and Botswana, and deservedly enjoyed a special place in anthropological studies. However, it appears that they were never a good model for stone-age demography. Fertility is the real determinant of age structure, and Kung fertility has long been artificially low. The Kung census of 1975 reveals very few dependents per producer (Table 6; Figure 2). If Libben's 10th century TFR was 7, then its living population (Table 6) was similar to the high-growth 20th-century Yanomamo, and quite unlike the Kung.

Table 6: Three hypothetical fertility models for Libben: Age structures.

Libben Site Fertility Model	Age Structure of Living Population			
	Mean Age (years)	< 15 years %	Dependency Ratio	Sibship Size
High (7.0)	18	51	1.19	5.8
Mean (6.1)	19	48	1.04	4.8
Low (5.5)	20	45	.95	4.2

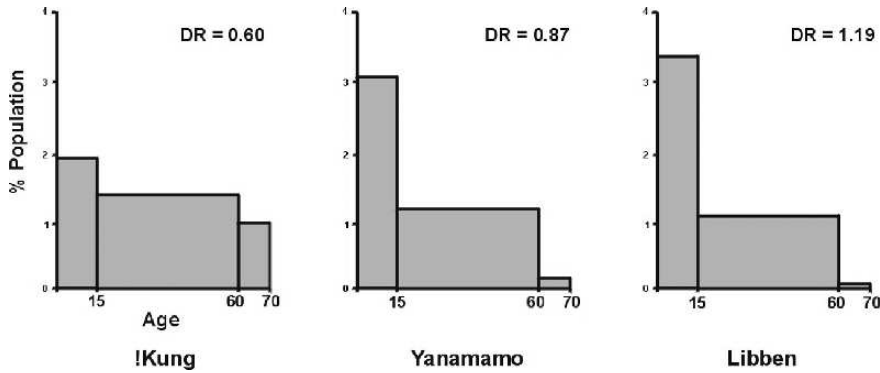


Figure 2: Age structures of populations: Sub-adults, producers, old adults. (Sources: Howell, 1979; Neel, 1978)

A NEW LIBBEN AGE DISTRIBUTION AND ITS IMPLICATIONS FOR HUMAN ORIGINS

There is no reason why women at Libben who survived to the end of reproduction would have averaged fewer than seven children. Indeed, this value is rather conservative compared to those of some of the best-studied modern foragers and horticulturalists with a history of demographic expansion. Nevertheless, even with a TFR as low as seven, Libben's average demographic profile is remarkable: Prehistoric life expectancy would have been about 30 years, the living population very young and characterized by a high dependency ratio, and the annual growth rate substantial. Such growth in turn predicts intrinsic doubling-times of less than 30 years, with occasional outmigration of related, extended families, leaving behind a core village of fewer than 100–150 people who continued to use the cemetery. Village dimensions, numbers and sizes of probable dwellings, plus the cemetery age distribution and a modern TFR combine to predict other aspects of the structure and dynamics of this Late Woodland society as well.

Some of the old approaches to paleodemography have not been very useful or particularly revealing about the human species. What conclusions can we draw from this new approach in demographic anthropology? One of the most salient issues in evolution, if not all of science, is human origins. The primary basis of the emergence of clearly identifiable human ancestors more than six million years ago was not an elaboration of material culture. Nor was it a consequence of brain evolution. Rather, it was a

demographic revolution (Lovejoy, 1981). Modern human fertility rates are biologically greater than those of even well-fed, captive chimpanzees (Table 7). In fact, free-ranging chimpanzee females have interbirth intervals which exceed four years (Sugiyama, 2004); orangutans, six (Gilders, 2000). The recovery of new fossil materials from Kenya and Ethiopia suggests that hominids of between five and six million years of age had become habitually bipedal, although not yet in a modern fashion (Haile-Selassie, 2001; Ohman et al., 2005), and must have thereby adopted novel means of environmental interaction and exploitation (White et al., 2006). It is therefore probable that such adjustments of their “adaptive profile” included alterations of their fundamental demographic characters; indeed, it is likely that compared to other hominoid primates of Africa human ancestors had become secondarily r-selected. By the same point in time, even their closest living relatives, the ancestors of chimpanzees and bonobos, were declining and had become largely relict populations in Miocene refugia, unable to successfully compete with the relatively recent radiations of cercopithecoid monkeys.

It is the evolutionary nature of human populations to grow. For mammals a large variance in intrinsic growth rate may be manifested in a number of ways, but a high, variable fertility is the universal hallmark of a colonizing species, and certainly includes not only *H. sapiens*, but very likely its ancestors as well. This has resulted in both Pleistocene successes and, ultimately, modern population crises. For too long, paleodemographers have accepted stationary models and the mortality and age profiles that they generate without question. It is time to turn attention, instead, to the fertility performances of carefully chosen anthropological populations of the mid 20th century, and incorporate these into prehistoric models. Only when this is done will stationary demographic conditions come to be regarded as the exception, not the rule, in human history, prehistory, and evolution.

Table 7: Chimpanzee and modern human populations: Mortality, fertility, and growth

Population	\bar{e}_0	TFR	Annual Growth?
Captive Chimpanzee	29	6.2	none
Ache (Paraguay)	43	8.1	+.025
Libben (Ohio, 900 A.D.)	31	7.0	+.025
Costa Rica (1960)	65	6.4	+.025
Sweden (1960)	76	2.4	+.005

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Chapter 10

DEMOGRAPHIC AND HEALTH CHANGES DURING THE TRANSITION TO AGRICULTURE IN NORTH AMERICA

Jean-Pierre BOCQUET-APPEL, Stephan NAJI and Matthew BANDY

CNRS, UPR 2147

Paris, France

Abstract: What were the consequences of Neolithic demographic transition on population's health? The paradigmatic question asked by Mark Cohen 30 years ago is revisited: did biological stresses, which are indicators of a population's well being, increase with the transition to agriculture? Data on four North American skeletal biological markers; dental caries (31 archeological sites), porotic hyperostosis (33 sites), cribra orbitalia (22 sites) and femur length sexual dimorphism (22 sites), used as proxy for stature; are set in the same chronological framework and related to the two-stage Neolithic demographic transition? How did they co-vary? Caries frequency increase one thousand years before the transition to agriculture. This pattern probably indicates the broadening of the diet range during the time before agriculture takes place as well as the addition of sugar in the diet. As soon as the transition to agriculture takes place, and fertility increases, the prevalence of anemia markers increases and stature sexual dimorphism decreases. Overall, the picture confirms the hypothesis of biological stresses, during the transition

INTRODUCTION

The signal of a hitherto unnoticed demographic process has been detected from bioarchaeological data from about a hundred cemeteries in Europe, North Africa and North America, during the shift from forager to horticulture-farming societies. This signature is characterized by an abrupt increase in the proportion of immature skeletons over a period of 600–700 years. This indicates a notable increase in the crude birth rate and beyond that in fertility. This process has been termed the Neolithic Demographic Transition (Bocquet-Appel and Naji 2006; Bocquet-Appel, 2002). This

signature was detected thanks to a representation of the data in a relative chronological scheme, i.e. relative to the local introduction of the new economic system, and not in the usual absolute (calendrical) chronology. The change in the chronological frame of analysis, which is obtained by a simple subtraction, has the effect of ordering spatio-temporally scattered bioarchaeological data relatively to the onset of the agriculture transition only, specifically the transition whose impact we are seeking to measure. This device has enabled us to compare archaeological sites globally and not simply pairwise, as is usually the case. The approach is discussed at length elsewhere (Bocquet-Appel and Naji 2006; Bocquet-Appel and Dubouloz 2003; Bocquet-Appel 2002; Bocquet-Appel and Paz de Miguel Ibanez, 2002). The use of a relative chronological frame is not exclusive to paleodemographic data and can be applied to many other archaeological variables (e.g. Bandy, 2005). Because the different data are set within a common chronological frame, their covariations can be readily observed, as in juxtaposed time series, which are usually difficult to observe with archaeological data. Having detected the Neolithic Demographic Transition by employing this approach, we are now interested in seeking and interpreting signals produced by other relevant categories of cultural and biological data that can contribute to an understanding of the economic transition as a whole, as a systemic shift. Beyond the demographic impact of the economic transition we have already demonstrated, what were its effects, and at what tempo, on socio-political organization, cultural production and the health of populations? Among the variables representing socio-political organization, a first tempo has already become apparent, at a global geographical scale, concerning the appearance of the earliest systems of large, stable villages, over an average time duration of about 1000 years (Bandy, 2006). This is followed by a leveling-off of the birth rate during the Neolithic Demographic Transition, which is estimated at above 50%. Finally, a tempo of approximately 2000 years was necessary for the spontaneous emergence of supra-local political units, interpreted as chiefdoms (Bandy, 2005, 2006). Other archaeological markers such as increasing numbers of LBK culture enclosures in Northern and North-Eastern Europe (Bocquet-Appel and Dubouloz 2004) are linked to the population explosion of the Neolithic Demographic Transition. What of the bioarchaeological variables? In this article, we return to the paradigmatic question raised by Cohen (1977) 30 years ago: did biological stress, a negative indicator of the population's well being, increase with the transition to agriculture (Cohen 1997, 1989; Cohen and Armelagos 1984; Larsen, 1995)? And if so, how did the timing of this process relate to the two stages of the Neolithic

Demographic Transition, as postulated in its original formulation (Bocquet-Appel, 2002)? To answer this question, data on four skeletal biological indicators from about 57 North-American cemeteries were collected and superimposed over the frame of the economic shift and the pattern of the Neolithic Demographic Transition.

MATERIALS AND METHODS

The North American database has been updated by adding 23 new sites, 12 foragers and 11 farmers (Figure 1). The new profile compensates the low density of points, in the dt zone preceding the introduction of the economic change, of the figure previously published (Bocquet-Appel and Naji 2006). Criteria for selecting these sites are the same with 2 exceptions:

- i) The small number of forager sites made us discard the criteria: « *excavation of at least 50% of the evaluated cemetery size* » (Bocquet-Appel and Naji 2006:342). This was necessary in order to ensure an adequate sample size. Additionally, these sites often have a large number of analyzed skeletons. For these sites, the criterion of selection is not an issue of excavated percentage, but an issue of the absolute number of excavated skeletons. If this number is large, regardless of a small excavated surface area, the skeletal sample can be considered a representative sample of the living population.
- ii) An upper limit to ${}_{15}P_5$ high values was estimated through its correspondence in terms of TFR, by using the 45 pre-industrial life tables demographic model (Bocquet-Appel, 2002; Bocquet-Appel and Naji, 2006:356) and the relation used by Coale; Demeny, Vaughan (1983). Sites falling above this limit were eliminated from the sample.

The new profile (Figure 1) is slightly different than a previous published one (2006): in the $dt = -2000$ to -1000 zone, the profile clearly has a bump, rising from 23% to 25% before rapidly decreasing to reach its minimum value of 19%, around 200 years before the introduction of the economic change. The profile then increases abruptly to reach the value of 29% at $dt = 1200$ years. One has to mention however, that few sites are present after $dt = 1000$ since we include only sites predating western contact. The continuation and possible termination of the profile is therefore not evident in the chart. The tempo is thus, for the moment, underestimated if we consider $dt = 1000$ to be the end of the profile. Presently, the bump in the pre-transition zone does not have a clear explanation. It could be an artefact

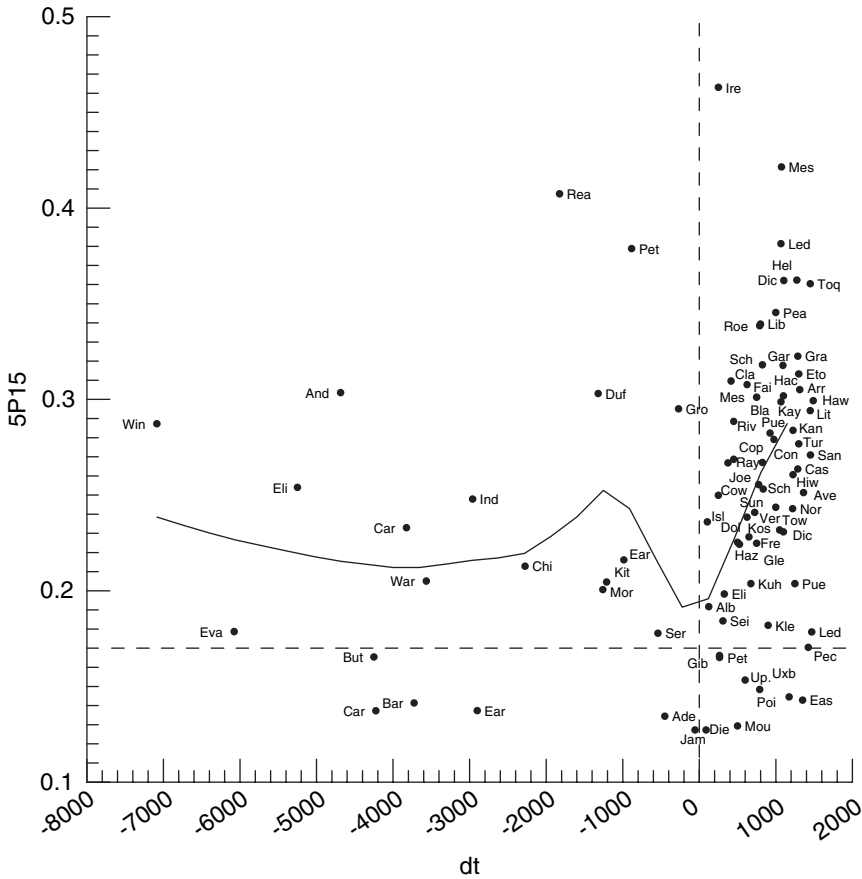


Figure 1: Changes in the proportion of immature skeletons aged 5 to 19 years (abbreviated as 5p5) during the transition from foraging to horticulture-farming, represented by dt

of site sampling, or it could also be due to a real effect of increased fertility for the sedentary or semi-sedentary shell-midden foragers (Bocquet-Appel and Naji 2006; Bocquet-Appel 2006), related to their putative low mobility.

The data on common biological indicators were gathered from the literature (see references in Figures 2–5). The indicators are frequencies for: i) dental caries (31 sites, see Figure 2), ii) porotic hyperostosis (33 sites, see Figure 3), iii) cribra orbitalia (22 sites, see Figure 4) and iv) sexual dimorphism in maximum femur length, used as a proxy for stature (22 sites, see Figure 5). The main reason for selecting these indicators was the frequent publication of the relevant data in bioarchaeological analyses, as well as the fact that these indicators are regularly used in population comparisons. It

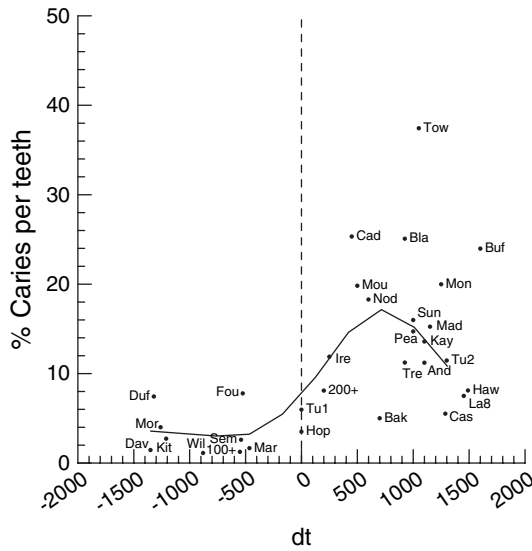


Figure 2: Frequencies of caries during the transition from foraging to horticulture-farming, represented by *dt*. (References: Anderson, 1968; Black, 1979; Butler, 1971; Driscoll, 2001; Martin et al., 1991; Powell, 1988; Ryan, 1977; Sciuilli, 2002; Steckel and Rose 2002; Vradenburg, 1999)

should be noted however, that there are relatively few published cemeteries with a statistically significant sample of more than 30 observations and that the criteria used to establish frequencies are not entirely uniform, despite apparent agreement among authors. In this study, each indicator is based on a sample of at least 20 individuals (or, more accurately, 20 observations), or, in the case of dental caries, 640 teeth (20 individuals *32 teeth). To make up for the small number of sites matching our criteria, we sometimes combined data from several sites defined by archaeologists as culturally and geographically homogenous.

The frequency of dental caries is defined as the percentage calculated over all the *permanent* teeth in individuals in a given sample, i.e. those 6 years of age or more on average. The frequency of porotic hyperostosis (related to external table of the parietal bones) and cribra orbitalia (orbital region of the frontal bones) is defined as the percentage calculated over all the relevant bones observed in subadults. The heterogeneity of the age classes used by various authors to define “subadults” must be pointed out here, since the upper limit of the age group is variously given as “< 18 years”, “< 16 years”, “< 1 years”, “subadults”, “children”. As for the lower age limit of the group, the lack of any definition in most cases

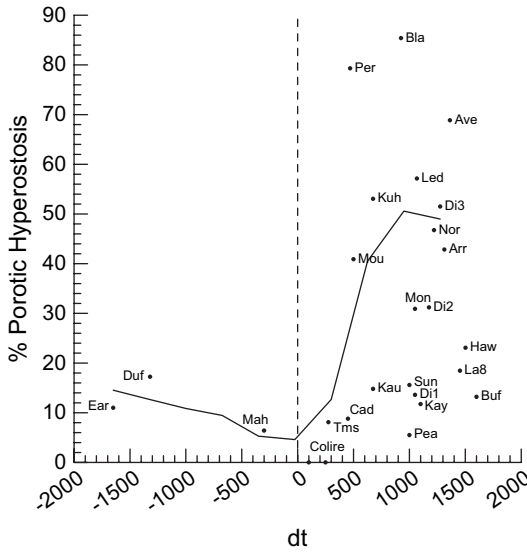


Figure 3: Frequencies of porotic hyperostosis during the transition from foraging to horticulture-farming, represented by *dt*. (References: Atwell, 1991; Burnett, 1999; Goodman et al., 1984; Martin et al., 1991; Milner and Smith 1990; Palkovich, 1980; Reinhard et al., 1999; Rose et al., 1984; Ryan, 1977; Steckel and Rose 2002; Williams, 2005)

does not allow the well-known under-representation of the 0–4 year age class to be addressed satisfactorily. This lack of accuracy prevents ready comparisons between sites and weakens the information drawn from these indicators. This study uses only individuals of 16 years of age and under, and assumes that the frequently used “subadult” category is equivalent to the “< 16 years” age group. Maximum femur length ($N \geq 20$, for each sex, i.e. 40 individuals at least) was recorded directly except in 2 cases (Madisonville and “Middle woodland”) where the inverse regression of femur length to stature was used (Sciulli and Giesen 1993).

These indicators were then placed within the relative chronology (*dt*) through their C14-calibrated BP dates or, if these were missing, through their cultural chronologies as defined by the authors. Interpreting the variations in these biometric characteristics invokes the so-called “osteological paradox” which has been discussed at length elsewhere (see for example Wright and C.J. Yoder Cassady 2003; Cohen, 1997; Wood et al., 1992) and which we shall only briefly address here in the light of the observed pattern of the Neolithic Demographic Transition (see Figure 1). The paradox is based in part on variations in the shape of an age distribution, caused by variations

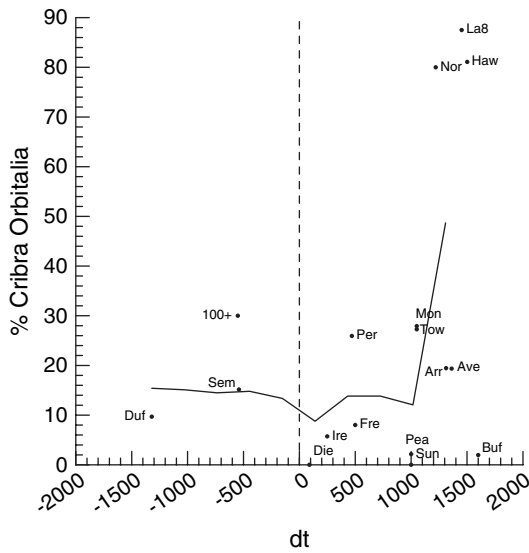


Figure 4: Frequencies of cribra orbitalia during the transition from foraging to horticulture-farming, represented by dt . (References: Anderson, 1968; Driscoll, 2001; Larsen, 2002; Milner and Smith 1990; Owsely and Bruweldheide 1997; Palkovich, 1980; Steckel and Rose 2002; Williams, 2005)

in the population's growth rate. It should be noted that if the frequency of an indicator is calculated relatively to individuals in the same age class, then its frequency will be independent from the age distribution and will be called, in the remainder of this article, its *incidence*.

The profile of variation in the frequency of caries in dt is shown in Figure 2. As is well known (Larsen, 1995; Turner, 1979), the occurrence and increased frequency of caries predates the shift to agriculture, as Figure 2 also shows. Where $dt = -1500$ years, the frequency is low, at around 3–4%. It then rises with a change of slope at around $dt = -500$ years. However, this early increase in caries frequency is somewhat suspect since there are no data points in the crucial period between -500 and 0 dt . Caries frequency levels off at around 17% at $dt = 700$ – 800 years, and eventually drops to around 11% at $dt = 1300$ years. While the increase of caries frequency with the transition to agriculture is a robust pattern, the subsequent decline is produced by very low values for three sites from the south-western United States (Hawikku and San Cristobal) and northern Mexico (Casas Grandes). Residents of these sites employed stone grinding implements, which are known to reduce caries frequency (Larsen, 1995:188; Powell, 1985).

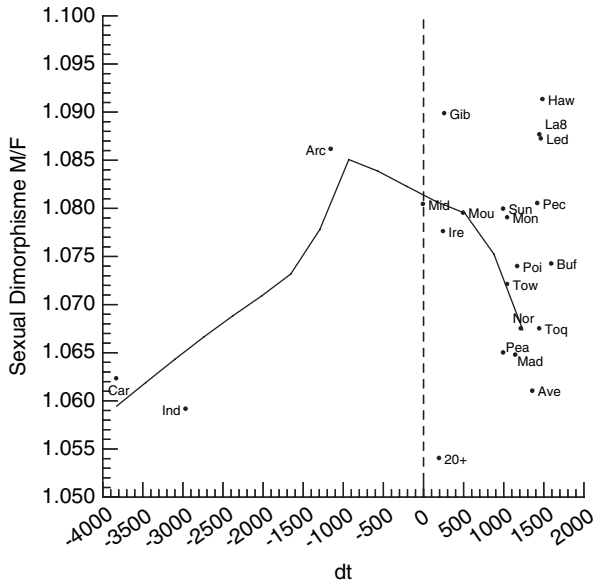


Figure 5: Sexual dimorphism for the femur during the transition from foraging to horticulture-farming, represented by dt . (References: Bennett, 1973; Boyd, 1986; Buikstra, 1976; Driscoll, 2001; Herrmann, 2002; Hooton, 1930; Milner and Smith 1990; Powell, 1988; Sciuili, 2002; Steckel and Rose 2002)

If the data had represented *incidences* as defined above instead of total frequencies, for juvenile age classes for example, then the impact of a potential increase in life expectancy could have been ruled out, but this cannot be done with the data from the literature. Theoretically, there are three alternative interpretations of the profile observed: i) increased dietary carbohydrate intake (Turner, 1979; Larsen, 1997) during the transition, reflecting a notable change in the hunters' diet; ii) higher life expectancy and therefore a larger number of surviving individuals who could have developed caries (Wood et al., 1992); iii) both possibilities together. The interpretation of the profile is therefore conditional, where the impact of diet is concerned, upon the assumption that longevity (probability of death) remained approximately constant, and, symmetrically, regarding the impact of longevity, upon a carbohydrate intake that also remained approximately constant. The situation is more complex for the impact of both variables. With this hypothesis, caries frequency and life expectancy increase, perhaps simultaneously but not necessarily so. Although the reorganization of the hunters' meat-based diet is a certainty, mortality data is lacking. We have nevertheless assumed that mortality remained much the same during the

transition. This leads us to the naive explanation that the increase in caries frequency resulted from an increase in dietary carbohydrate intake.

We follow Blom et al. (2005) in interpreting porotic hyperostosis as a skeletal manifestation of marrow hyperplasia produced by iron deficiency anemia in childhood. It is now widely recognized that early interpretations of the condition as reflecting an iron-deficient diet were premature (Blom et al., 2005; Holland and O'Brien 1997; Kent, 1986; Larsen, 1995; Stuart-Macadam, 1992). The condition is instead more appropriately understood as a product of marrow hyperplasia, which itself has a complex and multifactorial etiology. Contributing factors can include diet, but also congenital conditions, and, importantly for our purposes, parasites and infectious disease. Following an extensive study of skeletal material from Peru, Blom et al. conclude that "environmental stressors, such as parasites or disease, rather than specific dietary practices were more likely to be associated with childhood anemia in these coastal Andean samples" (2006:166; see also Kent, 1986; Walker, 1986).

Understood in this fashion, porotic hyperostosis therefore may be read as an admittedly imperfect index of pathogen load in the human environment, and therefore a generalized indicator of health. The incidence of porotic hyperostosis in our sample increases with the transition to agriculture (see Figure 3). Porotic hyperostosis incidence was roughly 8–10% during the forager period. An increase in incidence is apparent with the transition to agriculture at $dt = 0$. However, a truly dramatic increase in porotic hyperostosis incidence takes place some centuries after the agricultural transition, beginning at $dt = 300$ and increasing rapidly to a peak and stabilising at 40% at $dt = 1000$. The effect of the agricultural transition on porotic hyperostosis incidence was therefore not immediate but was rather delayed for some centuries. This pattern may reflect the fact that dense human settlements and high regional population densities, both expected to be associated with increases in the pathogen load of populations, did not appear immediately at $dt = 0$, but were a somewhat delayed product of the rapid population growth of the NDT.

Cribra orbitalia is a condition similar to porotic hyperostosis, affecting the orbits rather than the cranial vault. It is understood to be an early manifestation of porotic hyperostosis, with a similar etiology (Blom et al., 2005:153; Stuart-Macadam, 1989). The profile of variation in the frequency of cribra orbitalia (see Figure 4), which hovers between 10% and 20%, does not correlate directly with the economic shift. The frequency increases abruptly some time after the onset of the economic shift, at around $dt = 1000$. This delayed increase in incidence is therefore in some ways similar to that of

porotic hyperostosis, discussed above. However, the time frame involved is much longer.

Additionally, the pattern is suspect because the abrupt increase at $dt = 1000$ is produced entirely by the high values for three sites: San Cristobal, Hawikku and Norris Farm. In order to eliminate the hypothesis of these sites being outliers, we tried to understand why their frequencies were so high by looking for a common explanatory factor other than pathological frequency, such as geographical location (two sites are from the NM and one from IL) or analytical bias (two sites were studied by Stodder (Stodder et al., 2002) and one by Milner and Smith, 1990), but with no result. Furthermore, some studies (see Larsen, 1997 for a summary) provide evidence of a variable relationship between the regions of the skull where cribra orbitalia occurred. For these reasons, we will refrain from imputing significance to the observed pattern of cribra orbitalia incidence at present.

The profile of variation in sexual dimorphism in maximum femur length is used as a proxy variable for stature (see Figure 5). We know that stature estimators from the literature, based on reference samples, are biased by the same errors as techniques for age estimation (Bocquet-Appel, 1981: 214). The best estimator, up to a constant, is therefore the bone segment which contributes the most to stature: the femur. The large number of studies showing a correlation between stature and the variation of overall living conditions, since the nineteenth century and during world conflicts (see: Arora, 2005; Steckel, 1992; Eveleth and Tanner 1976), are sufficiently convincing to make it unnecessary to call on other major factors. Furthermore, it is well known that sexual dimorphism increases in times of abundance and decreases in times of scarcity (Baten and Murray 2000; Komlos, 1994; Nicholas and Oxley 1993; Tanner, 1962). Even though the data-points indicating forager populations (Figure 5) are sparse and relatively scattered, we can see that the profile does not indicate an increase in dimorphism during the transition, but a decrease. This pattern is indicative of a qualitative degradation of nutrition, which is associated with health. Furthermore, as was the case with porotic hyperostosis incidence, the decline in stature sexual dimorphism displays a delay relative to the agricultural transition, with a dramatic decline evident at $dt = 500$. Though the theoretical linkage between pathogen load and sexual dimorphism is not obvious, this pattern could possibly be explained in the same manner as the delayed increase in porotic hyperostosis incidence.

HEALTH AND DEMOGRAPHY

The Neolithic Demographic Transition has been postulated as a two-stage process (Bocquet-Appel, 2002). The first stage was characterized by a dramatic increase in human fertility, and a resultant surge in the rate of population growth, coincident with the transition to agriculture. This stage has been documented by previous publications (Bocquet-Appel, 2002; Bocquet-Appel and Naji 2006). The second stage was characterized by an increase in mortality, produced by an increase in infectious disease and parasite infestation. This second stage is theorized to have been related to increases in regional population density and in the size of human settlements, in turn produced by the rapid growth of the first stage. The increase in mortality in the second stage resulted in a decrease in the rate of population growth. This decrease was documented in a preliminary fashion using archaeologically measured rates of population growth in three regions of Latin America (Bandy, 2005). Bandy's data show that the decrease in population growth in the second stage, at least for the areas in his sample, took place between $dt = 600$ and $dt = 800$ (Bandy, 2005:S113).

Figure 6 displays archaeologically reconstructed population growth rates for five prehistoric cases, relative to the NDT. Three of these cases are described by Bandy (2005): Oaxaca, the Basin of Mexico, and the Titicaca Basin. Two other cases have been added from published archaeological sequences. The first is for Southwestern Colorado, and the second for the Ontario Iroquoians. The Colorado data is based on a series of momentary population estimates by Richard Wilshusen, (1999a,b; Lipe and Varien 1999), while the Iroquoian growth rates are taken from Gary Warrick's dissertation (1990, Table 47). Each point represents a momentary estimate of population growth. A regression line was fitted using the Loess technique, in the same manner as employed for the paleopathological data. The fitted line clearly shows the same pattern reported by Bandy: rapidly increasing population growth prior to $dt = 500$, with decreasing population growth (but not population decline) between $dt = 500$ and $dt = 800$. The rate of population growth stabilizes after $dt = 800$ between 0.1% and 0.2% annually.

Several of the classes of paleopathological data collated and presented here have direct relevance to this second stage of the Neolithic Demographic Transition. The two-stage model predicts that human disease and parasite

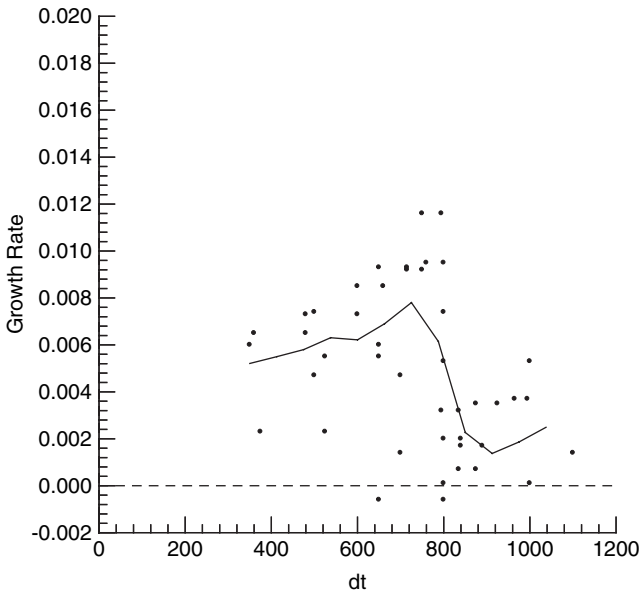


Figure 6: Rates of population growth in five archaeological sequences, relative to dt . The two-stage pattern is evident; (References: Bandy, 2005; Lipe and Varien 1999; Wilshusen, 1999a,b; Warrick, 1990)

levels will increase during the second stage of the transition, at the same time that the rate of population growth declines. The model therefore predicts that incidence of porotic hyperostosis and cribra orbitalia, interpreted as measures of disease and parasite infestation, will remain low for several centuries after the beginning of the Transition and will subsequently increase between $dt = 500$ and $dt = 800$.

Figure 7 displays the signals of porotic hyperostosis, cribra orbitalia, and dental caries. While caries frequency increases at $dt = 0$ or before, dramatic increases in the incidence of porotic hyperostosis and cribra orbitalia are evident during the second stage of the NDT (figure 6), between $dt = 500$ and $dt = 800$. These results are consistent with the predictions of the two-stage model of the NDT, suggesting that the emergence of high pathogen loads did not occur immediately with the transition to agriculture but was rather a threshold phenomenon related to the high population densities achieved only some 500–1000 years after the transition had already taken place. The first epidemiological transition (Barrett et al., 1998) was therefore associated with the second stage of the NDT.

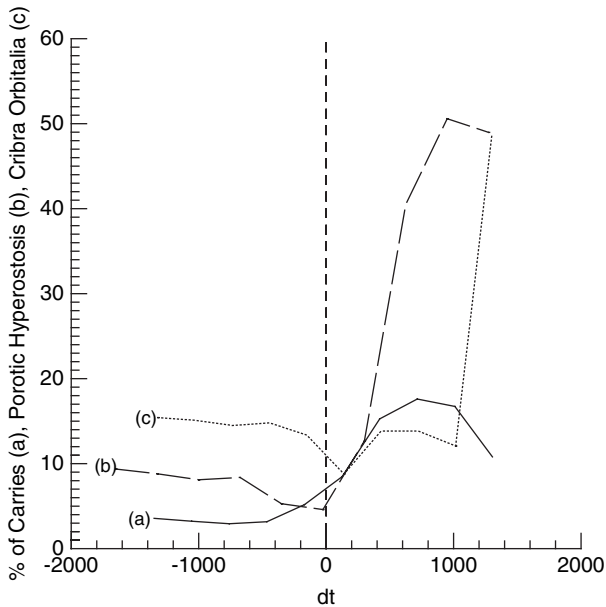


Figure 7: Frequencies of caries (a) porotic hyperostosis (b) and cribrra orbitalia (c) relative to dt

CONCLUDING REMARKS

Relatively to the timing of the transition to agriculture and assuming that life expectancy at 6 years of age (roughly the average age for the first permanent molars) remained approximately unchanged during the transition, the frequency of caries increases at $dt = -1000$ years. This pattern probably indicates a broadening dietary range before the advent of agriculture, and the addition of sugars in dietary intake (Flannery, 1969). Furthermore, after the farming economy appeared, there is evidence of: i) an immediate explosion in the birth rate and, underlying this, in fertility (see Figure 1), probably as a by-product of a sedentary economic system; ii) a delayed increase in the incidence of anaemia indicators. iii) a delayed decrease of stature sexual dimorphism, which may be the continuation of a trend that had already appeared during the forager period. The overall pattern clearly confirms the hypothesis of biological stress during the transition (Cohen, 1989; Cohen and Armelagos 1984; Larsen, 1995). Significantly, however, it also confirms the two-stage model of the NDT and of a delayed mortality increase between $dt = 500$ and $dt = 800$. The forager system sustained a population with

a very low demographic density (Bocquet-Appel et al., 2005), and apparently qualitatively better nourished, but the system was fragile to stochastic environmental fluctuations. This pattern is strikingly different from the farming system, which, at the peak of its emergence might have sustained a population with a local demographical density that may have been 1000 times higher or more than in the earlier period. The population, though qualitatively less well nourished and less healthy, was sustained nonetheless by a system that had foreseeable potential for economic production and was therefore probably more robust than the previous one to stochastic fluctuations.

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