Subsistence strategies and early human population history: an evolutionary ecological perspective

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Abstract

One of the keystones of the evolutionary ecological approach is the concept of energy budget, in which time and energy allocation is conceptually divided into somatic effort (growth, development and maintenance, and includes subsistence activities) and reproductive effort (which is further divided into mating effort and parental effort). Time and energy allocated to one component must be traded off against allocation to another. Using this energy budget approach in conjunction with some of the general implications of foraging theory, this article will explore the relationship between population dynamics and subsistence intensification. My discussion will revolve around two basic propositions regarding long-term human population history: 1) the near-zero growth rates that have prevailed through much of prehistory are likely due to long-term averaging across periods of relatively rapid local population growth interrupted by infrequent crashes caused by density-dependent and density-independent factors; and 2) broad changes in population growth rates across subsistence modes in prehistory are probably best explained in terms of changes in mortality due to the dampening or buffering of crashes rather than significant increases in fertility.

Keywords

Optimal foraging theory; human population ecology; carrying capacity; subsistence intensification; population bottlenecks.

Since the mid-1970s, an influential view of human forager population history has been that foragers limit fertility in a way that maintains their populations in dynamic equilibrium with available resources (Dumond 1975; Hayden 1972, 1986). Within this framework it is generally assumed that human populations grow to some limit set by the carrying capacity of the environment and stabilize around that limit, with minor fluctuations occurring due to density-independent factors affecting productivity. When productivity (i.e. the amount of energy acquired per unit area of land) increases due to intensification, this limit also increases, resulting in a new equilibrium. Thus, with the adoption of domesticates

and attendant sedentism and increases in total production, birth intervals decrease, fertility increases and average rates of intrinsic growth start to rise.

The most commonly accepted estimates for population growth rates (Hassan 1981) during the Palaeolithic are based on assumptions regarding Palaeolithic forager population density, the amount of the earth's land surface actually occupied by humans in early prehistory and the population of the earth at the end of the Pleistocene. However, anyone with a hand calculator, the formula for exponential growth and only the vaguest notion of how many people were alive 12,000 years ago can quickly determine that average growth rates through much of Pleistocene human prehistory could never have been much higher than .01 per cent, an increase of only one person per 10,000 per year. Yet, during this period, virtually the entire habitable surface of the earth was colonized by humans in what amounts to little more than the blink of a palaeontologist's eye. During the Holocene, a period which coincides with global warming, the wide-scale adoption of domesticates and increased sedentism, these near-zero rates must have begun to rise, resulting ultimately in the population of a little over 6 billion in which we find ourselves immersed today. Why were growth rates so low when essentially all humans alive were foragers? Why did growth rates increase during the Holocene?

The starting point for an alternative view of human population in prehistory in this article is Hill and Hurtado's succinct observation that 'No natural fertility population yet observed is characterized by zero growth, as would be required over much of our species' history' (1996: 471). Over the past decade or so, a number of empirical studies and theoretical treatments have appeared in the field of evolutionary ecology and related fields of evolutionary anthropology that have begun to paint a different picture about what population dynamics were like in human prehistory and how they relate to broad changes in subsistence modes. There has been a greater appreciation of the idea that individual energetic efficiency in resource acquisition and production, rather than total productivity rates or the carrying capacity of the environment, play a critical part in determining reproduction rates (Belovsky 1988; Hawkes and O'Connell 1992; Winterhalder et al. 1988). Human foragers are no longer seen as the natural resource conservationists they once were (Alvard 1998). Closer analysis of extant human foragers has shown that their modal fertility differs surprisingly little from that of horticulturalists and intensive agriculturalists (Campbell and Wood 1988; Bentley et al. 1993a, 1993b). There has been greater appreciation of the fact that effective control of fertility has been quite rare in human history, and may be limited to special circumstances surrounding the recent demographic transition. Finally, the idea that human population history has been characterized not by a series of stepped dynamic equilibria but rather a saw-tooth pattern of periods of rapid growth interrupted by infrequent but serious crashes has become increasingly recognized as an alternative explanation for near-zero growth through much of human prehistory. This in turn has interesting implications for understanding the selective environment that gave rise to human life-history characteristics, subsistence strategies and social structure (Blurton-Jones et al. 1999; Boone and Kessler 1999; Hill and Hurtado 1996: 471–2; Keckler 1997), as well as for changing rates of cumulative cultural evolution during the Upper Palaeolithic and the Holocene (Shennan 2000, 2001).

One of the keystones of the evolutionary ecological approach is the concept of energy budget, in which time and energy allocation is conceptually divided into somatic effort

(growth, development and maintenance, including subsistence activities) and reproductive effort (which is further divided into mating effort and parental effort). Time and energy allocated to one component must be traded off against allocation to another. Using this energy budget approach in conjunction with some of the general implications of foraging theory, this article will explore the relationship between population dynamics and subsistence intensification. My discussion will revolve around two basic propositions regarding long-term human population history: 1) the near-zero growth rates that have prevailed through much of prehistory are likely due to long-term averaging across a periods of relatively rapid local population growth interrupted by infrequent crashes caused by density-dependent and density-independent factors; and 2) broad changes in population growth rates across subsistence modes in prehistory are probably best explained in terms of changes in mortality due to the dampening or buffering of crashes rather than significant increases in fertility.

The diet breadth model and its implications

In any environment in which humans find themselves, there is typically a wide array of animal and plant food items that could be successfully captured, collected, processed and eaten. And yet, rarely is it the case that human populations capture, collect and consume everything that available. In some contexts, human foragers tend to ignore small mammals, reptiles and birds, while, in others, such prey are pursued and consumed. Plants foods that are relatively time-consuming to collect and process, such as acorns or other seeds, are ignored by some foragers, and routinely collected, processed and consumed by others. What kinds of factors affect how humans choose which food items to pursue, process and consume? The diet breadth model (see Winterhalder and Smith (2000) for a recent review of applications) was developed and employed to answer this kind of question. The logic of the model begins with the observation that different kinds of potential food items in the environment vary in the amount of time it takes to locate, capture or collect them, and to process or render them into a form available for consumption and digestion. Which ones should a forager expend time and energy capturing or collecting when they encounter them, and which ones should they ignore in favor of continuing the search for energetically valuable prey? To answer this essentially economic problem, the model makes several simplifying assumptions. First, foragers encounter potential food items in the environment at random. Second, foraging costs are measured in terms of time, and total foraging time is partitioned into two mutually exclusive categories: s*earch time*, or time spent locating prey items in the environment, and *handling* time – time spent pursuing, capturing, processing and consuming the prey once it is encountered. Third, foragers rank their preference in potential prey in terms of *profitability*, defined as the net energy return rate obtained per unit of time expended in handling time upon encounter. The question then boils down to this: as a forager is searching through the environment and encounters a potential food item, should she pursue it and eat it, or should she ignore it and continue to search for something more profitable? The answer is: foragers should take lower-ranked prey only as long as the return rate per encounter (profitability) is greater than the average return rate gained from searching for and handling higher-ranked prey.

One widely recognized implication of this is that high-ranked prey should be taken when encountered no matter how rare they become, and that prey ranked below the optimal diet breadth will not be taken no matter how abundant they are. This means that, given any population growth at all, depletion of foraged resources is nearly inevitable, and that depletion should begin with the highest-ranked resources. How low on a ranked list of potential prey a forager will be willing to go depends upon the encounter rates of higher-ranked prey. Thus, as higher-ranked resources are depleted, lower-ranked items are added to the diet. Lower-ranked prey are ranked lower because they entail higher handling costs per encounter. Hence, handling costs add up as diet breadth widens and broadening the diet breadth in the face of depletion of higher-ranked foods due to harvest pressure entails a decreased individual energetic efficiency. Hence, we can say that there has been a general historical trend toward lower *individual* energetic efficiency (i.e. decreased net return rate) in human subsistence strategies, with a corresponding increase in *spatial* efficiency, defined as increased average total productivity per unit area of land (see further discussion of this issue below). Very broadly speaking, the adoption and culti- vation of domesticates can be seen at least in part as the culmination of this historical trend at the end of the Pleistocene.

A second broad implication of the diet breadth model is that the traditional concept of carrying capacity as a definable limit or ceiling on growing population is far too simplis- tic. First of all, the model implies that, at any given time, there is likely to be a whole array of food items in the environment that may in fact be quite abundant, yet are not exploited because they are uneconomical to process. Second, it is clear that the relationship between population size and prey abundance is dynamic: as populations grow larger, prey abun- dance responds logistically – as prey abundance declines, efficiency also declines and population growth is slowed. Finally, we can see that the commonly accepted definition of carrying capacity as 'the upper limit of human population growth that can be achieved in a given habitat without eventual degradation of the resource base' (Hayden 1981: 412; discussed in Winterhalder et al. 1988: 322) is unrealistic: depletion is always occurring, and has an ongoing, dynamic relationship with forager population size. These implications are explored further below.

Putting the diet breadth model in a dynamic, population ecological perspective

In its original form, the diet breadth model attempts to predict the optimal diet at a single moment in time – foragers will choose only those diet items from a ranked listed of poten- tially consumable prey that will result in the highest average *net acquisition rate* (NAR). The problem, as Gary Belovsky has succinctly put it, is that 'all food in the environment cannot be consumed without decreasing its recovery rate or decreasing the ability of the consumer to harvest it in the available feeding time' (1988: 330). Hence, both the optimal diet breadth and the NAR (i.e. efficiency) of a population of foragers can be expected to change over time, with concomitant change in population growth rates and densities. Exactly how do these variables change through time and in relation to each other and what kinds of environmental conditions – i.e. resource density and distribution – will affect how they change and how rapidly? As Winterhalder et al. (1988) have pointed out, this

kind of population-resource dynamic is, as a general rule, empirically invisible to both ethnographers and archaeologists. It is invisible to ethnographers because they tend to observe human populations for relatively brief periods of time – what Winterhalder et al. refer to as the 'long ethnographic year'. Archaeologists, on the other hand, are in a position to observe such processes on a longer temporal scale, but, because of time averaging, they are typically unable to track population-resource dynamics at a scale fine enough to make real sense of it – one of the key aspects of this kind of process is that it is determined by day-to-day, individual decisions which have cumulative, recursive and, and in some cases, non-intuitive long-term consequences. Consequently, Winterhalder et al. argue that formal modeling techniques may be the most feasible way to get at population-resource dynamics over the long run. Such models are by necessity highly simplified, but, simple as they are, they have been shown to provide interesting and useful predictions about what we can expect.

There have been two major modeling efforts to put optimal foraging theory and long-term population processes into a dynamic, integrative framework with respect to human forager populations: the work of Gary Belovsky (1988) and that of Bruce Winterhalder et al. (1988). Both models attempt to integrate three dynamic processes that are key to the population-resource relationship: 1) the effects of resource acquisition and consumption on the human population growth rates, 2) the effects of changing prey densities on resource selection and 3) the effects of resource exploitation on population densities of prey. The models show how density of prey responds and changes as a function of their exploitation and how resource selection and growth rates of the forager population change as a function of resource density.

Belovsky's model combines a linear programming diet model that solves for the optimal mix of plant and animal foods with a spreadsheet-based population simulation that incorporates nutrition intake required for somatic maintenance and the production of offspring. Belovsky imagines foraging environments that vary from low to high density with respect to *primary harvestable productivity* (PHP). Primary productivity refers to primary plant growth on the landscape upon which all herbivores and predators ultimately depend. Since a considerable amount of plant-food energy is typically locked up in a form not directly available to humans – i.e. cellulose – or is out of reach of humans – as in forest canopy – *harvestable* primary productivity refers to primary plant growth that is available for human forager consumption. In habitats with low PHP, animal prey are assumed to dominate the diet since what plant growth there is must be converted into usable form by animal prey. In habitats with intermediate PHP, animal and plant foods are present in more equally distributed moderate amounts and are more nearly balanced in the forager diet. With high PHP, both plant and animal prey are available in high quantities, but, since animal prey are assumed to be higher ranked due to their lower handling costs, animal prey initially dominate the diet.

When Belovsky combined the diet model with the population growth model, a population growth trajectory characterized by *stable limit cycles* was predicted at all levels of PHP (Fig. 1). The severity (i.e. the amplitude, or ratio of peak to trough levels) of the limit cycles is determined by two factors: 1) the potential growth rate (predicted maximum level) of the forager population under a given level of PHP and 2) the predicted optimal diet breadth (i.e. in terms of relative dependence on animal vs. plant prey) at that level
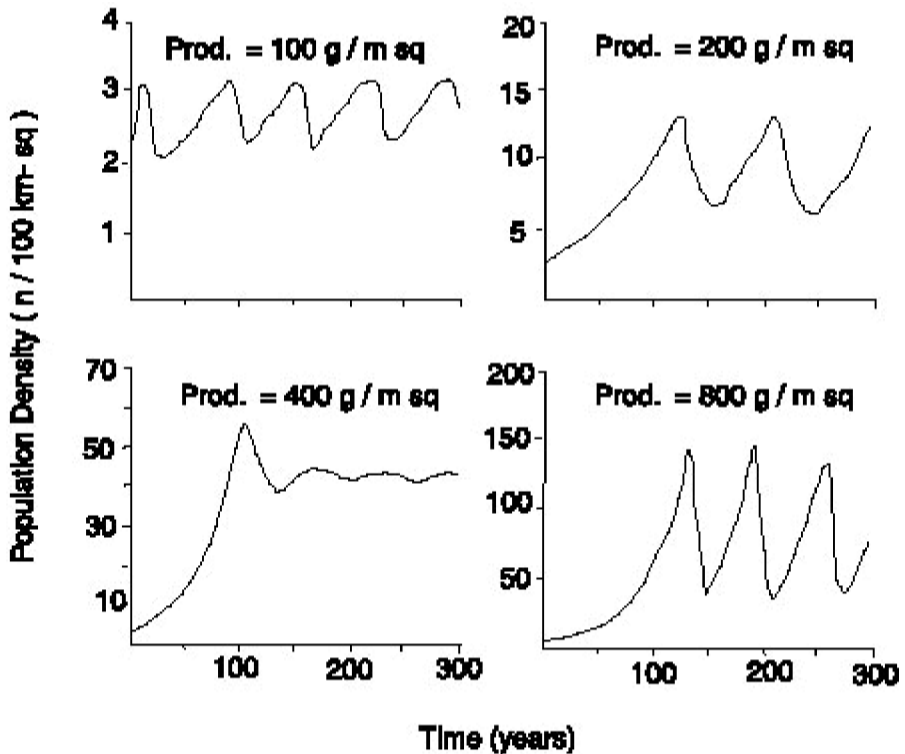
Figure 1   Chart showing stable limit cycles that develop in human forager populations at differing levels of primary harvestable productivity (PHP). Cycles are least severe at intermediate levels of PHP (400 gm/m^2). Average growth rates are about zero, even though growth phase rates can be relatively high; population density increases with PHP. Redrawn from Belovsky (1988).

of PHP. On one hand, the higher the forager population growth rate, the more quickly it will deplete prey, initiating a new limit cycle. On the other hand, the broader the array of plants and animal prey that are available, the less precipitous the population decline phase will be, because, as higher-ranked animal prey are depleted, the population can fall back on less profitable plant foods.

Hence, varying levels of PHP strongly affected the severity of the stable limit cycles. Under low PHP, the forager population growth rate is low, and the limit cycles have lower amplitude because, when animal prey were depleted first, there was little in the way of plant food to fall back on as diet breadth increased. Forager population levels are limited almost entirely by animal prey availability, and, as a result, foragers are unlikely to deplete animal prey populations entirely. Under intermediate PHP, animal prey are taken first, and, as diet breadth broadens, the availability of lower-ranked plant foods dampens the severity of population decline: intermediate PHP produced the least severe limit cycles. Under high PHP, limit cycles again increase in severity, because potential population growth is high, and, as higher-ranked animal foods are depleted, the high availability of fall-back plant foods keeps forager population levels high enough that they will continue

to deplete animal prey, perhaps to the point of extinction. One interesting potential impli-cation of this is that the adoption of domesticates would appear to be most likely in habi-tats with high PHP, as originally envisioned by Robert Braidwood.

Density-independent factors

In both the Belovsky and Winterhalder et al. models, stable limit cycles are due to density-dependent factors alone – population growth and decline and attendant prey depletion and regeneration. The addition of exogenous, density-independent factors such as climate-induced shortfalls would disrupt the pattern of stable limit cycles, depending on where in the cycle the shortfall occurs. For example, a brief (one or two season) shortfall in productivity coinciding with the beginning of a period of local population growth might have relatively little effect on a population. In contrast, even a brief shortfall coinciding with a growth peak or a population already into a decline phase, when density-dependent depletion has already started to occur, would likely have the effect of accelerating the decline and perhaps causing a serious crash or local population extinction.

For the purposes of the larger question explored in this discussion, that of changes in long-term human population growth rates, we can make the following observation at this juncture: in a perfect stable limit-cycle trajectory, the average long-term growth rate is zero, even though growth may be very high during one stage of the cycle and negative during another. Hence, any attempt to infer the 'typical' fertility behavior (or for that matter the mortality schedule) of foragers on the basis of long-term average growth rates alone is likely to be doomed to failure. Further, inferring typical fertility and mortality rates of foragers based on the few data points that are available from extant foragers is also problematic, due to potential sampling error over the whole cycle (Winterhalder et al. 1988: 320). On the other hand, if we can accept for a moment that human population trajectories are characterized in general by a saw-tooth, peak-and-trough pattern, it seems reasonable to suggest that broad, long-term increases in the average growth rate might be more realistically explained in terms of general factors that affect the average maximum that can be attained during a growth phase relative to the average minimum that occurs at the end of a decline or crash. I turn to this issue in the discussion below.

Population dynamics and the adoption of domesticates

The above models are designed specifically for forager populations. What kinds of changes might we expect with the adoption of domesticates? Winterhalder et al. (1988: 323) suggest that, among foragers, depletion resulting from intensification of foraging activity both decreases individual net acquisition rate *and* diminishes total yield, inevitably reducing the sustainable human population of an area. Under domestication, intensification of production may reduce individual efficiency, but, by definition, increases total yields per unit area of land, which in turn increases the sustainable human popu-lation. Further, the resource base under domestication should rarely be subject to the rates of depletion that would occur under populations ultimately dependent on primary production in a natural environment. Hence, although shortfalls and population declines

may continue under domestication, population levels among domesticators may not be subject to the same precipitous declines predicted by population dynamics models for foragers. This specific aspect of domestication may in fact be one of its most critical distinguishing characteristics as a subsistence pattern.

There are at least two additional reasons why the adoption of domesticates might be expected to dampen the amplitude of growth and crash phases, and to push long-term average growth rates to a higher level. First, there is good reason to believe that the combination of high total productivity and storability of domesticates provide a buffer against temporary density-independent shortfalls caused by inter-annual variation in precipitation, length of growing season and the like. In contrast, when foragers undertake storage, it is primarily for getting through predictable seasonal resource shortages, not unpredictable inter-annual shortfalls. Pennington (1992) studied the fertility and mortality of the !Kung in transition from a mobile to a more sedentary lifestyle that included some reliance on animal domesticates, and found that sedentism by itself did not significantly affect proximate determinants of fertility (length of reproductive span, length of birth interval – Harpending and Wandsnider (1982) had previously found similar results for !Kung living under nomadic and sedentary regimes). She did, however, find that !Kung children living under sedentary regimes with animal domesticates had a 25 per cent higher chance of reaching maturity than those still living as mobile foragers, due to the availability of supplementary foods, particularly milk, during critical periods.

A second reason why the adoption of domesticates may reduce severity of population crashes is that increased dependence on crop agriculture and pastoralism have historically tended to promote increased differentiation in access to resources – that is, social ranking and stratification. From a population ecological point of view, unequal partitioning of resources within a population has, somewhat counter-intuitively, the effect of increasing its stability over time (Lomnicki 1988: 20–34; Rogers 1992: 379–92). To see why, we can start by understanding unequal access to resources as the result of competition within a population over resources in finite supply. The character of resource competition can be thought of as varying along a continuum between two extremes that are termed *scramble* and *contest* competition (Boone 1992: 315–22). Scramble competition occurs when critical resources are economically undefendable, because they are either too unpredictably distributed in time or space or so thinly distributed on the landscape that they are not worth at any point putting up the costs of defense. Consequently, in a perfect scramble competition, all individuals in the population are said to have equal access to resources. This in turn means that with each new individual that is added to the population, the feeding rate (and, ultimately, the fitness) of all individuals in the population is reduced equally – individual resource availability is a function of group size. Now, in the most extreme case, one can imagine a growing population in scramble competition reaching a level such that the addition of just one new individual reduces the feeding rate of everyone else below what is necessary for somatic maintenance, and the entire population dies simultaneously of starvation – the proverbial straw that breaks the camel's back. This same result would occur in the instance of a sudden resource shortfall against a stationary population at the upper limit of its resource base. Of course, this extreme situation rarely occurs, because there is always some individual variation in condition, energy requirements, efficiency in acquiring resources and other factors that cause variation in

instantaneous resource access – essentially, the true carrying capacity of a population will always vary from individual to individual. The fact remains, however, that populations in scramble competition are more susceptible to crashes caused by depletion of resources.

Contest competition occurs over resources that are densely and predictably distributed on the landscape, such that they are economically defendable. In its most simplistic form, contest competition takes the form of a series pair-wise contests between individuals over resources, resulting in a ranked hierarchy based on differential access to defendable resources. When a shortfall occurs, individuals at the bottom of the hierarchy die first, leaving the surviving population with a more favorable population to resource balance. In this case, crashes, when they occur, will be less severe than in the case of scramble competition. As a result, contest competition can be said to increase population stability (Rogers 1992: 386–7).

Generally speaking, foragers tend to exploit a resource base that more closely approximates a resource structure that promotes scramble competition, because resource density is lower, and the distribution of foraged resources on the landscape is less predictable than is the case with crop agriculture (Dyson-Hudson and Smith 1978). Hence, there is a sound theoretical basis for positing that forager populations are actually more, not less, susceptible to population crashes brought about by density-dependent and density-independent factors than domesticators. Populations that are less susceptible to crashes should have higher long-term growth rates even in the absence of any major increase in fertility.

To illustrate this point, Figure 2 presents the results of a simulation of the growth trajectories over 1000 years of two populations, defined as foragers and farmers, that are subject to random density-independent shortfalls on an average of every fifty years. Each group starts with a population of 1000 and has a between-crash intrinsic growth rate of .007, a rate that has been calculated for the !Kung (Keckler 1997). When crashes occur, the foragers experience 25 per cent mortality, while among the farmers only 15 per cent of the population die. The simulation makes the simple point that two populations with the same growth rates during 'normal' periods can have very different long-term growth rates due to relatively small differences (10 per cent) in mortality during shortfalls.

Does domestication mean higher fertility?

In the above discussion, I suggested that higher average growth rates among agriculturalists may result from the fact that they are in general less susceptible to population crashes due to altered resource depletion rates and changes in resource structure. Still, it is possible that general increases in average fertility may also be a contributing factor in increased growth rates under domestication, as has been commonly argued. I want to begin an evaluation of this issue with the observation that, over the past decade, closer analysis of foragers, horticulturalists and intensive agriculturalists from historical and ethnographic sources has revealed a surprising uniformity in fertility rates across all subsistence modes. In 1988, Campbell and Wood published a cross-cultural compilation of total fertility rates (TFR) of seventy forager, horticulturalist, and intensive agricultural societies from the contemporary ethnographic record that showed there were no significant differences in TFRs across subsistence practices. Hewlett (1991) published a similar
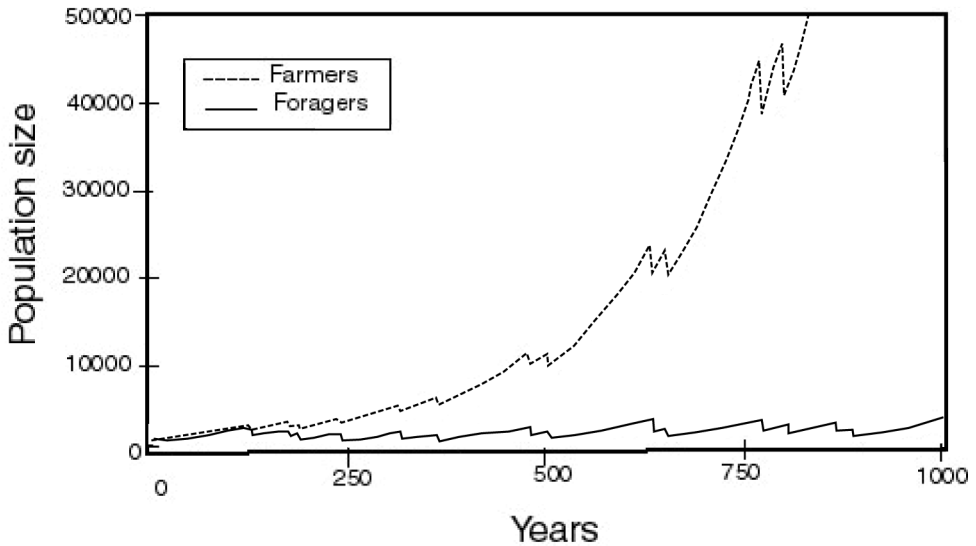
Figure 2   A simulation of two population trajectories, labeled farmers and foragers, that experience population crashes randomly at an average rate of once every fifty years, iterated over 1000 years. Intrinsic rate of growth between crashes for both populations is equal at *r* = .007. Farmers experience 15 per cent mortality during crashes, foragers 25 per cent mortality. A difference of only 10 per cent mortality during infrequent crashes can make the difference between near-zero growth and near-exponential growth.

analysis of forty mobile and sedentary foragers and pastoralists that indicated slightly higher fertility rates among pastoralists, although the difference was not significant. In 1993, Bentley et al. published an extensive critique and re-analysis of the Campbell and Wood study, presenting a new cross-cultural comparison of fifty-seven forager, horticultural and intensive agricultural groups. Bentley et al. (1993a, 1993b) used a subset of the Campbell and Wood sample, excluding populations with high levels of sterility and also attempting to correct for the inflated sample size due to the inclusion of non-independent cases (ethnic groups that were closely related). These results showed no significant difference in TFRs between foragers and horticulturalists, and that intensive agriculturalists had significantly higher fertility rates than either of the other two groups (Fig. 3). All three subsistence categories had the same modal TFR of 6.0 live births per woman.

Bentley et al.'s finding that intensive agriculturalists have higher fertility than foragers, but that horticulturalists do not, strongly suggests that the specific circumstances associated with the initial development of sedentism and higher total productivity associated with food production *alone* cannot account for the increase in growth rates thought to be associated with the adoption of domesticates. Further, all three subsistence groups show considerable variation in fertility, and subsistence mode by itself remains a poor predictor of fertility. As Pennington (1996) points out, knowing that a particular group has a mean TFR of 5.0 would not help very much in predicting that group's subsistence pattern.

More recently, Sellen and Mace (1997: 886) carried out a phylogenetic analysis of the relationship between fertility and subsistence modes in sixty-nine cultures. Instead of
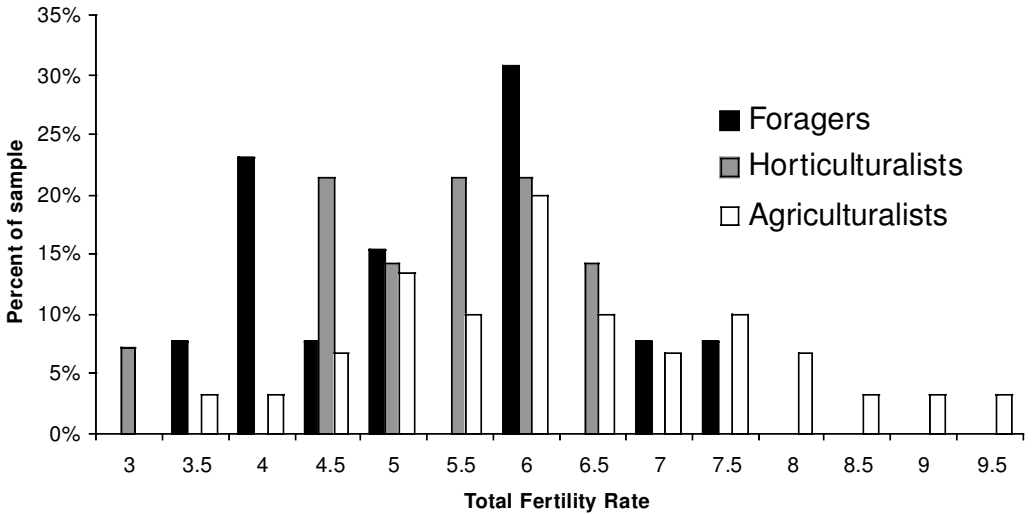
Figure 3   Comparison of total fertility rates (TFR) across subsistence modes, based on a sample of fifty-nine forager, horticulturalist and intensive agriculturalist populations. Only intensive agricul-turalists have significantly higher TFRs than the other groups ($p = .004$, Mann-Whitney). Redrawn from Bentley et al. (1993a: Fig. 2, using data from Appendix I).

dividing the sample into modal subsistence categories, as Bentley et al. and Campbell and Wood had, Sellen and Mace supplemented their fertility estimates for each population in the sample with estimates of percentage of dependence on agriculture derived from a computerized version of the world ethnographic sample, an expansion of George Murdock's *Ethnographic Atlas*. This essentially turned dependence on agriculture into a more or less continuous variable. Additionally, in an attempt to control for Galton's problem (the influence of non-independence of populations in the samples due to historical relatedness), they constructed a global genetic phylogeny based on data on the distribution of human genetic polymorphisms collected by the Cavalli-Sforza team. First, within groups of phylogenetically related cultures, the best predictor of variation in fertil-ity was variation in dependence on agriculture. Second, they used multiple regression analysis to test the association between dependence on agriculture and fertility by examin-ing the variance in phylogenetically unbiased sets of contrasts rather than variance in the raw values (i.e. fertility rates and percentage dependence on agriculture) themselves. Using a subset of the sample in which fertility estimates and estimates of dependence on agriculture were taken within twenty years of each other, the regression analysis showed that for each 10 per cent increase in dependence on agriculture, there was an increase of 0.4 births per woman. If we accept that intensive agriculturalists are in general more dependent on agriculture than horticulturalists and foragers, these findings are generally consistent with Bentley et al.'s analysis.

Most explanations that attempt to account for a systematic relationship between fertility and levels of subsistence technology point to a specific circumstance or characteristic associated with the technology itself and then posit how this circumstance affects specifically the *proximate* determinants of fertility. For example, one widely held idea about why the fertility of mobile foragers should be lower is that mobility is incompatible with mothers caring for more than one non-ambulatory child at a time, and hence birth intervals among foragers are lengthened through various cultural practices, resulting in lower completed fertility (Sussman 1972). Elsewhere, the availability of weaning foods derived from crop plants has been cited as a mechanism leading to earlier weaning and shorter birth intervals following domestication (Buikstra et al. 1986).

Determinants of fertility fall into two general categories (Handwerker 1983: 6). The first are proximate determinants (Wood 1990), which include such variables as the mean age at menarche, exposure to conception, lactational infecundity and the like. The second category – which Handwerker calls intermediate factors – consists of factors associated with political, economic and ecological conditions that ultimately determine the total time and energy budget that parents have available to produce and rear offspring. I want to suggest that, when we are talking about long-term patterns in fertility associated with subsistence, it may be more useful to begin by looking at broad patterns inherent in these intermediate variables – that is, those conditions associated with the overall energy budget of a household – and ask how subsistence technology relates to energy budgets and the trade-off between the time and energy devoted to child rearing relative to subsistence and other household maintenance activities.

Human families have a finite time and energy budget out of which various activities associated with survival, maintenance and reproduction must be funded. As noted above, time and energy expenditures are commonly subsumed under two categories: *somatic effort*, comprised of the time and energy spent in survival and maintenance; and *reproductive effort*, comprised of the time and energy expended in the production of offspring. Reproductive effort can further be divided into *mating effort* (finding mates) and *parental effort* (effort expended in producing and rearing offspring). At this point I am concerned mainly with fertility in already formed households, and will concentrate mainly on the trade-off between somatic effort (maintenance of the existing household) and parental effort. Hence, we will be interested in two general classes of economic activity: 1) the time and energy expended in acquiring or producing food, shelter and other resources to maintain the existing household and 2) the time and energy expended in provisioning children. The more time and energy that must be put into resource acquisition and processing to support the existing household, the less time and energy is left over for reproduction and rearing additional children. Hence, we might expect that the total number of children that a family can successfully raise should be directly affected by the *net efficiency* of the family's food- and shelter-producing regime and how it relates to the total household budget.

In general terms, horticulture and agriculture both constitute forms of subsistence intensification. Subsistence intensification is a process by which the amount of time or energy required to produce and/or process food increases relative to the amount produced (Brookfield 1972). In other words, the labor cost per unit of food increases with subsistence intensification. Typically this occurs when items are added to the diet that require

more time to harvest or process to render them edible and digestible, or because cultivation techniques are adopted that require more ground preparation and maintenance. In either case, the predicted consequence of subsistence intensification is decreased *individual labor efficiency*; that is, an individual expends more energy for each calorie acquired or produced. The pay-off to intensification is that more calories per unit area of land become available, making it possible for more individuals to survive and reproduce on less land. In other words, subsistence intensification results in higher *spatial efficiency*. This in turn results in higher local population densities.

There is, of course, no reason to think that all horticulturalists operate at a lower production efficiency than all foragers, or that all intensive agriculturalists are less efficient than all horticulturalists. In fact, it is clear that these subsistence categories overlap and represent only general tendencies. Variation in local ecology – particularly that which is related to the amount of biomass available for human consumption and the relative ease with which food production and processing can be accomplished – will cause variation in the level of production within a general subsistence regime. Horticulturalists living in a rich temperate or tropical environment might well maintain production at a higher level of efficiency than, say, mobile foragers living in an environment like the Great Basin of North America where animal biomass is relatively low and the labor cost to collect and process seeds and other plant foods is high. In fact, much of the variability and overlap in fertility rates between subsistence regimes indicated in Bentley et al.'s data may well be the result of variation in food acquisition efficiency caused by differences in local ecology.

However, we should expect that, in any particular region where intensification is taking place, there should be a general trend towards decreased efficiency of food acquisition or production, and that any increase in fertility that might occur after the adoption of a more intensive technique must come from gains in handling or processing efficiency, improvements in the productivity of cultigens and the like.

Two important implications flow from this perspective on the energetics of subsistence intensification and the trade-off between resource acquisition and reproduction presented above. First, if individual efficiency (labor per unit of food) declines under intensification, holding other conditions equal, it seems reasonable to expect that fertility should actually *decrease*, not increase, with subsistence intensification, since parents have to work harder and longer to support themselves and their offspring. Second, in an area where subsistence intensification is taking place, we should expect local population density to increase as a result of the increased spatial efficiency of food acquisition or production, regardless of whether the population growth *rate* increases or stays the same. Hence, one expectation is that, with the increase in subsistence intensification and processing costs associated with domestication, fertility initially may actually decrease, even while local population densities increase because of increased spatial efficiency of production (Hawkes and O'Connell 1992: 63). Bentley et al.'s (1993a, 1993b) data on the relative TFRs of foragers, horticulturalists and intensive agriculturalists, discussed above, would seem to support at least part of this proposition in the sense that horticulturalists on average have about the same or even a slightly lower TFR than foragers.

To summarize thus far, the only prediction that we can really make about the relationship between level of subsistence intensification and fertility is that, *ceteris paribus*, fertility ought to decline with increased subsistence intensification. The fact that it does

not – at least with respect to intensive agriculture – then becomes an interesting question. How can parents, if they are working at a lower efficiency, afford to support yet more children than before? I discuss two possibilities below.

One possibility is that the additional effort comes from males. There is abundant evidence that under intensive agriculture the relative contribution of males to food production increases as the total household workload increases (Ember 1983, although Ember views this in terms of a relative decrease in the participation of females). A fairly robust defining feature of horticultural societies is that the bulk of the food energy consumed is produced by women. Under these circumstances, the effect of male contribution to subsistence on the survival of offspring is low. Hence, in the trade-off between parental effort and mating effort, males in horticultural societies should invest more in mating effort and in male-male competition over access to females (Lancaster and Kaplan 1992; Lancaster 1997). These appear to be the main determinants of the matrifocal, matrilineal character of the majority of horticultural societies. Under agricultural intensification, the workload necessary to provide sufficient food to raise offspring increases to the point where women cannot do all the work. At this point, the trade-off for males between parental effort and mating effort shifts back in favor of parental investment – male PI becomes critical to survival of offspring. The result is a shift to patrifocal, patrilineal family systems, where males contribute a significant proportion of labor to the household budget.

Another possibility is that the net contribution of children to the household budget increases under intensive agriculture. In the few quantitative studies of production and consumption over the life cycle that have been carried out on forager and horticulturalist groups, the available data have shown that children do not produce more food than they consume until about the age of 20 (for Piro and Machinguenga horticulturalists, Kaplan 1996: fig. 4; for Ache foragers, Kaplan 1996: fig. 4; Kaplan et al. 2000: fig. 3), a time when they begin to marry and produce children of their own. Kaplan (1996) argues that the reason net production in children occurs so late in foragers is that the skills required to carry out efficient hunting and collecting activities take this long to acquire, a factor which, he argues, explains the evolution of the long period of juvenile dependence in humans (see also Kaplan et al. 2000).

In contrast, Kramer (in press) carried out a similar study of production and consumption over the life cycle among traditional Maya agriculturalists, where she found that girls achieved net surplus production by age 12 and boys by age 17. Since they do not marry and start new households until the age of about 19 or 20, there is a period of up to about six years when children are net contributors to the household fund. In an analysis of the total amount of labor required to maintain a typical Maya household (measured in hours of labor per week), Kramer also found that parents were not able to produce all the required work alone. Hence, she argues that the labor contribution of older children actually underwrites the production of additional younger children in the Maya household by reducing the workload on their mothers (mean fertility in her sample was 7.0).

In summary, the picture that is beginning to develop is that the specific circumstances surrounding the adoption of domesticates and attendant sedentism are not themselves sufficient to explain observed increases in fertility, since available evidence suggests that significant increases in fertility do not occur until dependence on agriculture is already

well established. Rather, changes in the household energy budget resulting from reorganization of the relative contribution of men, women and children may turn out to be a more promising explanation for increases in fertility that occur with the adoption of agriculture.

Can catastrophic mortality explain near zero growth?

Our present knowledge of the relation between subsistence mode and fertility indicates that increases in fertility under agriculture may at least partly explain the apparent increase in growth rates under domestication, although such increases may not have become a factor until agriculture was relatively well established. Since the data on subsistence mode and fertility reported in the above discussion are essentially synchronic in nature, they cannot be used, strictly speaking, to test directly the diachronic proposition that increased dependence on domesticates *causes* increased fertility (Sellen and Mace 1997: 287). However, the data do indicate that foragers are capable of fertility levels as high as agriculturalists, and no forager group has a fertility level low enough to explain the near-zero growth that must have been in place through most of the Pleistocene. We are left with the possibility that infrequent catastrophic mortality interspersed with periods of relatively rapid growth explains this pattern. Unfortunately, the empirical data needed to test such a proposition are even less forthcoming than those relating to subsistence and fertility. The following observations, however, can be made.

Classical models of logistic population growth assume that animal populations grow until they reach a stable state at or near *K*. Recent empirical work in population ecology, however, has shown that many animal species, including large mammals, are characterized by periods of growth interrupted by relatively infrequent crashes brought about by starvation, disease and other environmental factors that may be, to varying extents, density independent (Dunbar 1987: 77; Mangel and Tier 1993; Young 1993). Young (1993) surveyed a series of eighty documented natural die-offs in large mammals, including herbivores, carnivores and primates, which were characterized by peak-to-trough reductions in population of at least 25 per cent. Within the sample, Young found that the modal degree of population reduction during crashes fell in the range of 70 per cent to 90 per cent, although he suggested that this might be partly due to under-reporting of die-offs of lesser severity. There was also a pronounced paucity of die-offs involving reductions of greater than 90 per cent, which Young suggested may be due to the fact that natural selection tends to eliminate populations susceptible to total extinction (ibid.: . 414). Interestingly, all three classes of mammals (herbivores, carnivores and primates) were equally represented in the 70–90 per cent range, although carnivore die-offs were more likely to be caused by disease, while herbivore and primate die-offs were more likely to be caused by habitat decline and starvation.

The question then arises as to what extent human populations have been subject to periodic die-offs in their evolutionary history. Several lines of indirect evidence lead to the conclusion that infrequent, but severe population crashes may have been a chronic condition of human population history. First of all, as pointed out at the beginning of this article, it is difficult to reconcile the high rates of growth (and the potentially high

reproductive capacity) observed in modern human populations, including modern foragers, with the extremely low overall rates of growth estimated throughout most of human history unless one argues that periods of relatively high growth were counterbalanced by periodic population crashes. Hassan (1981: 254), using the geometric growth equation in connection with plausible estimates of population sizes at different points in the European and Middle Eastern prehistoric sequence, has estimated that at most overall growth rates up until the Neolithic transition ranged between .00007 and .011 per cent per year. Yet even the modern !Kung, who live in a relatively marginal foraging environment, have a calculated growth rate of .7 per cent ($r = .007$) (Keckler 1997), while a tropical foraging group, the Ache of Paraguay, sustained a pre-contact growth rate of 2.5 per cent ($r = .025$) (Hill and Hurtado 1996: 258). To see the problem more clearly, we can take the !Kung growth figure of $r = .007$ and apply it to a starting population of 10,000: such a population would grow to the present population of the earth in about 1900 years.

Based on the fertility data collected by Campbell and Wood (1988) and Bentley et al. (1993a, 1993b), Hill and Hurtado observe that, on average, 'the maximum interbirth interval that can be attained in poorly nourished, non-contracepting populations with late weaning is about 48 months . . . [this] implies six live births if reproduction begins at age twenty and ends at forty years of age' (1996: 471). Since most studies of such populations indicate a mortality rate of about 50 per cent, this implies growth rates far above what could have been possible during much of human history. Hill and Hurtado argue that, with a an average TFR of 6.0, juvenile mortality would have to have been close to 67 per cent to produce near zero growth, yet no traditional population with such high rates has ever been observed.

Another line of empirical evidence for catastrophic mortality in more recent prehistory comes from mortality profiles of prehistoric skeletal populations (Keckler 1997). Such populations often exhibit a high proportion of prime-aged adult deaths, resulting in a flattened mortality profile, compared to the usual U- or J-shaped profile (with higher mortality among the young and old) that typically characterizes mammal populations. These flattened mortality profiles do not easily fit any known model life table. Keckler examined four prehistoric skeletal populations: a combined sample of Neandertals, and three forager-horticultural series from North America – Libben, Dickson Mounds 1 and Oneota. In a series of simulations using life-table characteristics of two hunter-gatherer populations, the !Kung and the Ache, as well as the Coale and Demeny West Model 1 life tables, Keckler showed that, by adding random population crashes involving reductions ranging from 10 per cent to 54 per cent at a mean rate of one every thirty years, he could generally produce both the near-zero overall population growth rates estimated by Hassan as well as the flattened mortality profiles observed in four skeletal populations. Keckler concluded that human population growth in the past is likely to have been characterized by what he refers to as a biphasic pattern: relatively long periods of growth counterbalanced by short intervals of catastrophic decline.

The main problem with this study is one of equifinality. Lower archaeological recovery rates for juveniles and older individuals could also produce higher proportions of prime-aged adults in cemetery populations. However, Keckler's alternative interpretation of skeletal mortality patterns with high rates of adult deaths is tantalizing, and analysis of

more large skeletal series with an eye toward filtering out the effects of differential recovery rates may resolve this issue.

One promising avenue of empirical investigation of this problem comes from analysis of genetic variability in modern human populations. Recent analyses of variation in modern human mtDNA have shown that episodes of population growth and decline leave characteristic signatures in the nucleotide site differences between pairs of individuals (Harpending and Rogers 1993). Harpending et al. (1993) presented an analysis that indicates that the modern human population arose from a population expansion that occurred between 30,000 and 80,000 years ago from a prior effective population size of only 1000 to 10,000 females. Ambrose (1998) has argued that one or more bottlenecks occurred in the late Pleistocene due to climatic downturns. One event in particular appears to have been caused by the eruption of Mt Toba, Sumatra, approximately 70,000 years ago, which may have decimated human populations outside tropical refugia. While these proposed bottlenecks are clearly on a much larger scale than the kind of local or regional crashes proposed in this article, they may indicate that population crashes have played a significant role in shaping the structure of modern human populations.

Conclusions

In the above discussion, I have made a number of claims regarding the nature of early human population history, nearly all of which have been made previously by a wide array of investigators in the field of evolutionary anthropology, very few of which have been widely recognized or accepted in the field of anthropological archaeology. The revised picture I have attempted to put together is by necessity very broad and tentative in nature. However, several preliminary conclusions can be drawn.

First, the idea that carrying capacity represents a static ceiling around which human populations maintain an equilibrium has been outmoded for some time. It has begun to be replaced with more dynamic view of the relationship between population density, prey density, individual energetic efficiency and reproduction rates. Second, the fertility rates of traditional populations across all subsistence modes vary considerably around the same mode and nearly the same mean; the continued search for ways in which the specific circumstances of subsistence strategies tweak the proximate determinants of fertility does not seem a very profitable avenue of investigation for explaining broad changes in growth rates in human history. Rather, a closer look at the ways in which individual energetic efficiency, resource depletion rates and resource structure vary generally across subsistence modes and affect population growth rates and densities appears to be in order. Finally, the idea that infrequent, but serious population crashes have played a substantial role in shaping past human population trajectories deserves a closer look. Population crashes are rare events viewed from the perspective of the human lifespan – if they were not, there would be no one alive today to muse on the human condition. The fact that they are so infrequent appears to have led to the perception that they are abnormal or atypical events. There is a growing theoretical and empirical basis for believing that population crashes are not atypical, and that they may provide the most parsimonious explanation of near-zero growth rates through much of

human prehistory, and why growth rates increased markedly with the introduction of domesticates.

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