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Population Growth, Carrying Capacity, and Conflict¹

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The standard model of population growth and regulation is critiqued. It is argued that any model of population growth and regulation must accommodate ten propositions, and a multitrajectory model that does so is described. This model identifies competition between groups, individual choice in reproductive behavior, the scale for spatial and temporal variation in resource abundance, and the social unit for resource access and ownership as important components of population behavior.

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1. We thank the anonymous referees for their helpful comments on the manuscript. One referee in particular made unusually detailed and thoughtful comments that led us to make a number of changes that we hope have clarified the argument and removed the ambiguities of an earlier draft. [Supplementary material appears in the electronic edition of this issue on the journal's web page (<http://www.journals.uchicago.edu/CA/home.html>).]

Human population growth and the effect of population stress on human systems have long been topics of concern for anthropologists. Growth and stress have been considered both as prime movers in culture change and as nonexistent and essentially irrelevant. Most arguments about human societal development favor slow to almost nonexistent growth and populations well below carrying capacity for most of human history since at least the Middle Paleolithic, and the archaeological record supports this view. However, potential, if not actual, rapid growth at almost all times and places appears to be a more accurate description of human reproductive capability. Resolution of these two seemingly contradictory facts—high intrinsic growth rate and low net long-term growth rate—requires a different view of human population dynamics and its relationship to societal organization.

At the risk of creating a straw man, we suggest that there is a standard model (see appendix in the electronic edition of this issue on the journal's web page) for the pattern of human population growth and its relationship to carrying capacity (K),² namely, that most of the time human populations have low to nonexistent rates of growth. Implicit in this model is a decoupling of population size from K , with changes in carrying capacity only very rarely affecting the growth rate. It is also assumed that birth rates and death rates are virtually identical, although no mechanism is posited for keeping them so. In its most extreme form the standard model simply assumes a low-to-zero net growth rate without establishing how it arises. Even when feedback mechanisms are introduced, they are often assumed to have fixed effects rather than considered as a process. Also, the standard model does not consider competition between groups a significant factor in the regulation of human population growth.

The model is often implicit and may simply assert that, until recently, population sizes have always been well below K and growth rates very low. In this formulation of the standard model it is the *intrinsic*, not

2. We do not deal with the concept of carrying capacity in detail. We realize that carrying capacity is dependent on human behavior. What one is willing to eat, how much the resource has been cropped in the past (Winterhalder et al. 1988), the technology available to gather or produce it, and capital improvements that have been made (e.g., terraces) are some of the factors that affect carrying capacity. Nevertheless, in the time spans and societies of interest to us carrying capacity, whatever it may be, is relatively constant in most cases. Most increases in carrying capacity over which humans have any control will involve increased costs, and these costs will be part of a decision matrix including the benefits of incurring them. Dewar (1984) has reviewed the concept of carrying capacity (see also Chapman 1988), especially in relationship to humans, and there is no need here to reconsider this literature in detail. We do want to stress the distinction between the equilibrium population size, K^* , as determined through population dynamics, and an intrinsic limit—carrying capacity, K —determined by measuring the total available resources. The latter represents the population level beyond which resources are inadequate for normal biological functioning, while the former represents the population level, if any, at which population size stabilizes even though there may be adequate resources for a larger population size. We will make use of both concepts.

just the net or effective, rate of growth that is low. Rates, according to this model, have been low not because of the eventual limitations of K but because humans, through a series of mechanisms that are not well understood, have kept them that way, with the result that the effects of carrying-capacity stress were only rarely felt. In other words, unlike all other animals, humans are assumed to have kept their numbers in check far below carrying capacity in a density-independent manner, thus making the value of K irrelevant.

We reject the standard model and offer in its place a multidimensional, multitrajectory model that includes factors that interact with group population dynamics. The factors include resource density, the geographic and temporal scale for resource variability, the production and decision-making units, the form of social organization, and the effect of group competition (intra- and intersocietal). We call it a *multitrajectory model* because the relationships identified in it do not lead to a single evolutionary trajectory for the form of social organization under all conditions but instead may lead to different trajectories depending on the values for the societal and environmental parameters. Our model has four major components: (1) within-group feedback mechanisms between resource availability and fertility behavior modeled as a cost-decision process based on the self-interests of family units, (2) between-group competition, (3) the geographical and temporal scale for variation in resource density, and (4) the social unit for resource access and ownership. We argue that the multitrajectory model fits empirical reality far better than simpler models with fixed effects (such as the standard model) and that it can integrate societal changes heretofore viewed as due to different factors and calling for different models.

Key to our multitrajectory model is the empirical observation that human populations, in the absence of culturally mediated behavior that reduces a female's fertility, tend to exhibit rapid growth. Periods of rapid growth may, however, be interspersed with occasional population crashes that lead to slow or no net population growth over time (Hill and Hurtado 1995:471). While periodic population crashes are demographically possible, any population facing a population crash will likely opt, if possible, for a solution other than starvation. Long-term trends, then, are misleading in that they suggest a more benign demographic pattern than may be the case in the short run and it is the short-run effects, not long-term averages, that determine behavior. This implies that we must distinguish between the average net growth rate observed over long time scales and the actual growth rate in the short term.

Equally important, we assume that populations did not exist in isolation and build group interaction (competition) directly into our model. As Anderson (1978) has pointed out, far too often demographic modeling implicitly holds groups to be in isolation without competition, even though such interaction must have been frequent if not universal in the past. We see our model as relevant to foragers, egalitarian farmers, and more complex societies, but we emphasize here those aspects of it that

are particularly relevant to hunter-gatherer societies because it is to these societies that the standard model has been most commonly applied and because this type of society typifies most of the span of human history.

Our model has number of implications: (1) The distance between the equilibrium population size, K^* , and the carrying capacity, K , for hunter-gatherer groups varies inversely with resource density. Hunter-gatherer groups living in low-resource-density areas are more likely to display long-term demographic stability, and the higher the resource density, the more likely is the occurrence either of intergroup conflict or of Malthusian growth constraints such as disease and starvation. (2) Chronic intersocietal conflict arising as populations in a region approach or exceed their equilibrium population sizes is more likely when the scale of geographical and temporal variation in resource density is commensurate with the scale of the catchment area for a group. (3) A shift to a larger-scale social organization is more likely when the scale for significant change in temporal and geographic resource-density variation is larger than that of the catchment area for a group. (4) Intrasocietal conflict is more likely when the (possibly varying) number of persons in the resource access/ownership unit is independent of the population size of the society of which it is a part. (5) A no-man's land may arise between groups when one group can substantially reduce the resource base of another. (6) A larger-scale social organization integrating groups previously isolated by no-man's lands is likely to have rapid population growth and to be unlikely to revert to smaller-scale groups. (7) The development of agriculture will involve domesticates that are highly elastic with respect to labor intensification.

Assumptions

The model we present is based on the following definition of "competition": *Neighboring groups are in competition whenever the resources used by one group are thereby made unavailable to another group that would otherwise have access to those resources.* Competition in this sense may include but does not assume warfare as its form. It need not involve direct confrontation of one group by another and may simply be the consequence of two groups' exploiting the same resources in the same area (for example, hunting animals whose migration pattern is more extensive than the catchment area of either group). In its most basic form, competition exists whenever the catchment area of one group overlaps with the catchment area of another, whether or not territorial exclusion is practiced.

The model involves the following propositions:

1. *Human populations have an intrinsic growth rate (r_0) that enables them to exceed K in a short period of time.*

It is difficult to measure r_0 directly on human populations, since it is defined as the inherent fertility rate, that is, the fertility rate (f) that would occur without behavioral modification of fertility. Even for so-called

natural-fertility populations, the current value of f need not represent r_0 accurately, as is evident from both variation in f over such populations (ranging from a low of 4.3 for the Gainj of Papua New Guinea to a high of 6.3 for the Amish [see Wood 1994:49, fig. 2.2]) and the difference between the actual value of f and its estimated potential value of ten births for breastfeeding women over a 30-year reproductive period (Jelliffe and Jelliffe 1978:126).

An intrinsic growth rate of 8 live births over a woman's reproductive span (a rate well below the estimated potential) coupled with a 50% mortality rate of offspring from birth to adulthood leads to about 4 surviving adults per reproductive female, assuming that all women of reproductive age are equally fertile. Assuming a 25-year reproductive period with half of the population preadult and half of the population male, the net growth rate would be about 0.02 adults per person per year. For exponential growth, the population doubling time is given by $\ln 2/r = 0.69/r$, or $0.69/0.02 = 34.5$ years. A population doubling every 34.5 years would have a more than eight-millionfold increase in population size in 800 years, and at this rate a single hunter-gatherer group of 1,000 reproductive persons would grow to a population size exceeding the world's current population in about 800 years. Obviously a doubling time of 34.5 years could not long be sustained. The fertility rates of 4.0–4.7 births per reproductive female reported for !Kung groups (Kelly 1995) would produce a growth rate of about 0.0023 adults per person per year, yielding a tenfold increase in adult population size over 1,000 years. This amount of increase would likely either have required a shift in resource base or led to conflict over territory or other resources.

These rough estimates highlight the fact that, even when mortality rates are high, a stabilized population size can occur only if there is substantial depression of the potential fertility rate. Of course, under extreme conditions such as those experienced by the Netsilik Eskimos, who were at periodic risk with respect to resources upon which they depended for survival (Balıkcı 1970), mortality rates increased drastically via starvation when an unexpected change in availability of resources led to the population's suddenly being above K because of a temporary reduction in the value of K . While these fluctuations in the net growth rate may average out, in the long run, to a value close to zero, the population dynamics experienced by such a group and the implications for its response to swings in its actual growth rate are obscured by focusing on the long-term average.

2. *In populations with a stabilized population density, fertility and/or mortality rates are coupled negatively (positively) with density.*

If $r < 0$ independent of population density, the population will eventually become extinct. If $r = 0$ independent of density, the population will be unable to recover from demographic accidents (famine, natural disaster, etc.), and repeated demographic accidents will eventually reduce density to zero. If $r > 0$ independent of density, then density will increase indefinitely. Only when r varies negatively with population density and ranges

from positive to negative will density become stable over time.

3. *Reduction of human female fertility occurs primarily through behavioral means or behaviorally mediated biological mechanisms rather than through uniquely biological mechanisms.*

Hypothesized biological mechanisms that might link fertility negatively to population density independent of behavioral choices or practice, such as the hypothesized reduction of fertility through interaction of physical activity with reduced body fat (Frisch 1975, 1978), seem to operate only under exceptional conditions such as extreme weight loss or unusually high levels of sustained physical activity. The more common pattern is reduction of fertility through behavioral means or behaviorally mediated mechanisms.

When correction is made for the three primary proximate factors known to limit fertility (age of marriage, deliberate fertility control, and breast-feeding-induced lactational infecundability), an estimate of about 15 births over a female's reproductive period is found whether the population is from a developed country, a developed country, or a historical European country (see Wood 1994:77–78, table 3.5, modified from Bongaarts and Potter 1983). It is evident that all populations have behavioral practices (whether intentional or not)—or, in the case of breast-feeding, interaction of behavioral practice with a biological mechanism—that keep fertility well below its potential value. As Wood (1994:31) has noted, “no natural-fertility population reproduces at its maximum biological potential. In other words, behavioral factors operate in every population to limit the fertility achieved by its members.”

4. *Lactation can be an effective mechanism for reducing fecundity.*

Survey data on world populations suggest that the most common contraceptive mechanism is lactational amenorrhea due to prolonged and intensive breast-feeding (Ellison 1994:267; see also reviews by Gage et al. 1989, Vitzthum 1994) that leads to increased spacing of births: “Differences in interbirth intervals account for most the variation in TFRs (Total Fertility Rate). . . while differences in lactational infecundability account for almost all the variation in interbirth intervals” (Wood 1994:519). Data from India suggest that lactational amenorrhea “compares quite favorably with . . . barrier methods, such as condoms and diaphragms, and is only slightly less effective than oral contraceptives and intrauterine devices in the United States” (p. 339 and references therein). There appears to be no biological limitation on the length of the period of lactational amenorrhea (p. 353). Instead, fertility returns in response to a decrease in the amount of breast-feeding as the child ages or, to put it another way, the length of the period of lactational amenorrhea is potentially under the control of a woman via the pattern of breast-feeding that she employs, since the frequency and pattern of suckling is the triggering mechanism for continual lactational amenorrhea.

The contraceptive effect of breast-feeding is common

knowledge (Jelliffe and Jelliffe 1978:117; van Ginneken 1974 and references therein) and therefore part of the cultural repertoire of individuals (see Mayer 1966 for an example from rural Tanzania). Breast-feeding may be combined with sexual abstinence as a way of extending spacing between births (see Singarimbun and Manning 1976 for an example from Java). Thus the pattern of breast-feeding may be culturally mediated (Maher 1992, Stuart-Macadam and Dettwyler 1995), but even so it does not lead to homogeneity on the part of women in terms of the pattern of breast-feeding that they employ. When attempts have been made to model birth spacing using breast-feeding as a causal factor, models that posit heterogeneity in breast-feeding patterns within a population obtain significantly better results than those that assume homogeneity (Wood 1994:361). Therefore the question of interest becomes why “so much variation in suckling behavior actually exists” (p. 370).

5. *Decisions are both embedded in a cultural context and responsive to material conditions.*

Modeling of decision making tends to emphasize either the cultural/ideational or the external condition/material circumstances affecting how decisions are constructed. Our position is that neither the ideational nor the material framework alone adequately accounts for human decision making. Instead we argue that the cultural context provides the framework within which external/material conditions are “interpreted” and evaluated with regard to individual goals. As Bourdieu points out, “the principle of practices has to be sought . . . in the relationship between external constraints, which leave a very variable margin for choice, and dispositions” (1990:50). Goals may be either individual in origin or assimilated by individuals from their cultural milieu. The inclusion of individual goals adds to the complexity of modeling decision making in that it introduces the historical/particular into the decision-making process.³

3. The population dynamics of Tikopia (Firth 1936, 1959, 1961; Borrie, Firth, and Spillius 1957) illustrate the way in which decisions affecting population growth and control are historically contingent. Traditionally the Tikopia had a number of communal encouraged mechanisms to control population, including celibacy, coitus interruptus, a cultural norm of two children, abortion, and infanticide. The decision-making and productive unit was the family or the individual woman. Even though chiefs exerted some overall control over resources and reproduction, there is no evidence that they could enforce reproductive behavior. When, under pressure from missionaries and outsiders, infanticide and abortion were outlawed, the range of decisions available to women suddenly changed. As a consequence, the population grew from around 1,280 in 1929 to 1,750 in 1952 (37% growth with $r = 1.4\%$ per year). In the absence of abortion and infanticide as options, women were no longer able to achieve their previous spacing of births, and the consequence was population growth. When drought hit in the early 1950s, the population was saved from starvation only by food shipments from outside, and out-migration became a major means of controlling population size. A less well-documented but quite similar case is found on Ontong Java and nearby islands (Bayliss-Smith 1974). A similar situation also occurred in Europe, where, in spite of a great number of social mechanisms to control population growth, populations increased rapidly from 1750 to 1850 and famine and out-migration played increasingly important roles (Langer 1972, 1974).

The distinction we make looks to the cultural context for information on how decisions are framed and to the material/external for an evaluation of alternative decisions within that cultural context. While reduction of fertility for behavioral reasons requires a decision by a female with regard to her behavior (whether to act in a manner consistent with culturally framed behavioral schemas or in terms of an individually constructed choice), her evaluation depends first upon the way in which external conditions are given meaning—or ignored—through a culturally mediated process of evaluation.

6. *Individual choices are triggered by individual experience and made in terms of individual self-interest.*

For example, though !Kung women are embedded in a cultural context that expresses the need to breast-feed until a child is about three or four years of age, the actual age at which breast-feeding stops has declined under more sedentary conditions, when less time/energy has to be expended on obtaining resources. While altruistic acts do occur, they arise under exceptional conditions. For this reason we argue that women will not maintain a replacement level of fertility in the interest of the group—which has been called “the second tragedy of the commons” (Cohen 1995 and references therein)—as is assumed by the standard model. Rather, a replacement level of fertility must be a consequence of the dynamics, both cultural and individual, that affect individual female (and family) decision making about becoming pregnant and, if pregnant, whether the fetus will be carried to full term and, if the fetus is carried to full term, whether the newborn offspring will be allowed to survive and, if so, the quality of parenting it receives.

7. *The demographic dynamics of one group may impact the population dynamics of adjoining groups.*

Groups do not exist in total isolation but interact with one another through competition, territorial conquest, trade, and the like, all of which introduce interdependencies among adjacent groups. Even the absence of interaction due to a “buffer zone” impacts the population dynamics of a group by removing resources in the buffer zone from its catchment area.

8. *Both the geographic scale at which resource density is patchy in space and resource variability in time (yearly cycle, long-term trends) affect human population dynamics.*

The degree of resource patchiness depends upon the geographic scale being utilized. What might be a more or less random distribution of resources with small units may become patchy at a larger scale (Pielou 1969:100). The baseline scale of interest to us is the catchment area for a group; therefore we are concerned with resources that are more or less randomly distributed over the catchment area in comparison with resources that have a patchy distribution. A second source of variation is seasonal variation in the aggregate resource density during the yearly cycle over the catchment area for a group. A third source of variation is longer-term trends that affect the yearly time-dependent mean yield of resources over the catchment area.

9. *The composition of the unit of resource access/ownership is a relevant parameter for human population dynamics.*

The unit of resource access/ownership is the set of persons who have coequal rights to exploit resources within the catchment area associated with that group. When the unit is larger than an individual (extended) family, it may sometimes be referred to as a corporate group. For a hunter-gatherer group such as the !Kung San, the members of a camp make up a corporate group with respect to the *n!ore* (catchment area) of that camp. In contrast, families were the unit of access/ownership of acorn trees for the Cahuilla of southern California (Bean 1972). Although some resources may be individually owned, we are concerned here with the ownership of the bulk of resources from which nutritional and caloric needs are being met.

10. *The modeling of population dynamics across different societies requires a multitrajectory, multidimensional model.*

The Model

No single model adequately accounts for demographic processes in human societies. While a logistic growth model may adequately *describe* long-term growth patterns, since for any human population there is eventually a limitation on possible growth, what we want is not descriptive models but theory models (see Read 1990) and, moreover, models derived from theory about the processes that structure the phenomena in question. Although identifying the basic parameters for demographic processes (e.g., birth rates, mortality rates, fertility rates, average age of first conception, average reproductive period, and so on) is not problematic, their values and how those values relate to other conditions and processes are less obvious. An adequate theory model for human population dynamics must involve at least four components, each with its own submodel.

First of all, fertility rates are ultimately dependent upon decisions made by females with regard to (1) exposure to risk of pregnancy (which relates to decisions made regarding contraception, length of intensive lactation, and sexual abstinence, among other factors), (2) whether to allow the pregnancy to develop to full term, and (3) whether an offspring produced will be kept and, if kept, the quality of parenting it receives. These decisions are made not in isolation but within a cultural context that affects the range of decisions that are considered legitimate and one in which others with whom a female interacts may have an impact on her decision. In addition, her specific conditions (current demands on her time, cost of parenting, desired lifestyle for her family, and so on) affect the parameter values in whatever model is used to relate the above three components to fertility rates. Thus, while the three parts of the decision process listed above are universal, the way in which they play out in any particular situation has both an ideational and a material component. The first model takes up this

aspect of the multitrajectory model in the context of simple hunter-gatherer societies by relating the decision process regarding additional offspring to its consequences for the overall growth rate of the society.

This model lays the groundwork for the second by predicting not a single consequence for all hunter-gatherer societies but variable consequences depending on the resource density in each society's catchment area. It demonstrates that a low-resource/high-resource gradient is also a gradient in terms of the risk of exceeding carrying capacity, and the latter introduces intergroup competition into the multitrajectory model. The competition model examines the various outcomes that are likely under competition between groups, depending upon their respective demographic parameter value.

The competition model introduces a third component, namely, the scale for temporal and spatial variability in resource density in comparison with the geographic scale for catchment areas. The third model addresses this component. It illustrates that the extent to which a successful and expanding competing group (expanding through replacement of other groups or coalescence of groups) will have long-term stability depends upon the difference between the average resource density (taking into account both spatial and temporal variability) for the group prior to expansion and the density after expansion. It is only when the expanded group accrues a substantial increase in its average resource base that it can be expected to be stable. This introduces the fourth component to the multitrajectory model, namely, the composition of the resource-access/ownership unit.

The fourth model considers the effect of fission of corporate/political units under population growth, thereby shielding decision making by individuals within the corporate group from the societywide consequences of population growth. Fission may simply be triggered by the death of a living relative around whom the basic food-procuring unit was defined, or it may involve a political dimension such as might occur with lineages subdividing in accordance with political alliances. In either case, the consequences of a growing population are shifted from individual decision making to relations between units within the society, thereby leading to intrasocietal conflict. The latter, we suggest, becomes an impetus for centralization as a means to ameliorate it. Even if centralization succeeds in reducing or eliminating intragroup conflict, it does not "solve" the problem of population growth (see n. 3 above).

In brief, our multitrajectory model distinguishes a decision process and three dimensions that affect the way in which demographic processes are likely to play out (fig. 1). No single trajectory through this three-dimensional space shows how societies change from small-scale to large-scale societies.⁴ Instead, there are multiple

4. Though models of unilineal evolution of societies have long been discredited, figure 1 provides a more precise way of delineating the problem with the unilineal claim. Were the unilineal claim valid, there would be but a single trajectory through the space displayed in figure 1 rather than the potential for multiple trajectories some of which may arrive at stable configurations.

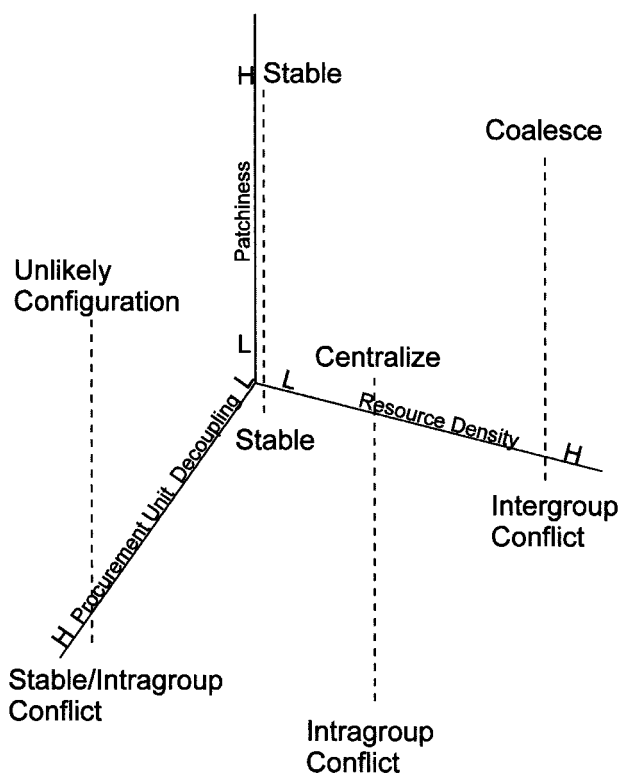


FIG. 1. The three dimensions identified as affecting the outcomes of the decision-making model and the outcomes predicted for the eight configurations defined by extreme values on each dimension. H, high; L, low.

trajectories with their own dynamics and potential for stabilization in accordance with particular sets of intra- and intergroup relationships. Stabilization can also include permanent aggression. The next several sections develop the four models that make up the multitrajectory model.

MODEL 1: FERTILITY RATES, EQUILIBRIUM POPULATION SIZE, AND RESOURCE AVAILABILITY

Our first model delineates the consequences of decision making, primarily by women as the bearers of offspring, that affect the number of children a female will produce and its impact on population size of the female's group. The "default condition" of generally high intrinsic rates of population growth even with the mortality rates that apply to traditional hunter-gatherer societies but long-term low average rates of population growth imply that we need to understand the conditions under which there can be stabilization of population size and what happens when population size is not stabilized. For this task we consider a model developed by Read (1986) that links fertility rates and equilibrium population size in comparison with K and resource availability through two

factors: (1) decision making by a woman with regard to the well-being⁵ of her family based on current demands for her time and her desire for as many children as possible—each of which is culturally mediated—and (2) the effect of resource density on these time demands.

Decision making. The model is based on two simple relationships and a decision process that links them to interbirth spacing.⁶ The first relationship is the positive effect of population size (keeping the catchment area fixed so that population size is a proxy for population density) on foraging cost per unit of resource per female, assuming that each female forages for the same number of persons (e.g., her family) regardless of population size. The relationship is positive because as more females forage over the same resource base the foraging cost per female per unit of resource must increase. The second relationship is the negative effect of interbirth spacing on total parenting costs. As the interbirth interval decreases, each female with offspring will have more dependent offspring, hence the total parenting cost will increase. The negative relationship between interbirth spacing and total parenting costs has been demonstrated for the !Kung San (e.g., Blurton Jones and Sibly 1978; see also extensive discussion and references in Surovell 2000).

We now make three assumptions about decision making that affects the spacing of offspring:

1. Women are willing to control birth spacing. Effective non-Western methods for so doing include sexual abstinence, lactational amenorrhea induced by extended breast-feeding, induced abortion, and infanticide.
2. On the average, a woman will make decisions aimed at ensuring the well-being of her family.
3. Women desire to have many offspring.

We do not claim that these three assumptions are or can be expected to be universally true. Instead, we propose to demonstrate the consequences when these assumptions hold. The degree of applicability of these assumptions relates to the kinds of behaviors that are culturally sanctioned, and therefore the model is culture-

5. Wood (1998) has also used the idea of well-being as a central component in his demographic model. He defines it slightly differently, though, considering it to refer to "any aspect of health or physical condition that is either positively associated with the probability of childbirth or negatively associated with the risk of death" (p. 104). Whereas Read (1986) used the idea of well-being with regard to decisions that women may make about spacing of offspring, Wood relates it more directly to parameter values in his demographic model: "A person's well-being can be thought of as determining (within a particular social context) a set of probabilities of surviving and reproducing at each age" (p. 105). In effect, Read deals with decision making that anticipates the deterioration in either a woman's or her children's health or physical condition should the demands on her time exceed what she can reasonably accomplish. In contrast, Wood focuses on the sequences that may arise should there be deterioration in her health or physical condition.

6. Surovell (2000) has developed a model for interbirth spacing among hunter-gatherers that is based on the two relationships we discuss but assumes an automatic effect between fertility rates and the carrying costs of young children: "If carrying costs are high, fertility will be low; if carrying costs are low, fertility can be high" (p. 495).

specific. One group for which we have evidence for their applicability is the !Kung San: "They want children, all the children they can possibly have," though this is tempered by their view that "children must have strong legs, and it is mother's milk that makes them strong. . . . a child needs milk till he is three or four years old at least," and when infanticide occurred "they spoke of the nourishment of the children as the primary reason" (Marshall 1976:166). An infanticide rate of about 1% is reported by Howell (1976:147).

The decision process arises from the fact that women (and men) will usually have multiple tasks that require time and/or energy. When the sum of the time/energy needed for all of these tasks exceeds the amount of time/energy one has or is willing to allocate to them, a decision must be made about which tasks will not be accomplished (see appendix in the electronic edition of this issue). If a woman places a high priority on the well-being of her family (where the meaning of "well-being" is specific to a cultural context), then the activities whose costs are reduced will not be directly related to the well-being of her family and will be activities for which she controls the allocation of time/energy and therefore the decisions aimed at ensuring that she has sufficient time/energy for her family's well-being. A task such as foraging has a time/energy requirement per unit of resource recovered that increases with the number/density of foraging women, keeping fixed both the number of persons for whom each woman forages and the catchment area. Therefore foraging is an activity that is directly related to the well-being of a woman's family and one for which she has little control over the average time/energy cost required per unit of resource obtained. In contrast to foraging, parenting is a time demand over which she does have control, with the number and closeness in age of offspring often serving as major determinants of the cost per unit of time of parenting.⁷ The cost of parenting is directly related to interbirth spacing of offspring. Consequently, the model posits that interbirth spacing of offspring will be modified when her total available time/energy is insufficient to accommodate both the costs of foraging and the total amount of parenting needed for the well-being of her family.

With increasing population density, foraging costs per woman will increase. If they rise sufficiently, then it will become necessary to increase interbirth spacing in order to reduce the total parenting costs if family well-being is to be kept constant (see fig. 2). With increasing population size and constant total catchment area (that is, assuming that adjoining areas are already being exploited by other groups), we would expect an increase in the spacing of offspring when assumptions 1 and 2 of the decision model are satisfied. As the spacing of offspring increases, a woman's net fertility rate decreases. If the

7. We are not excluding the possibility of shifting the cost of parenting to other persons (for example, cowives) or sharing the cost when there are scheduling conflicts. However, to the extent to which these involve reciprocity, the total cost of parenting is not reduced.

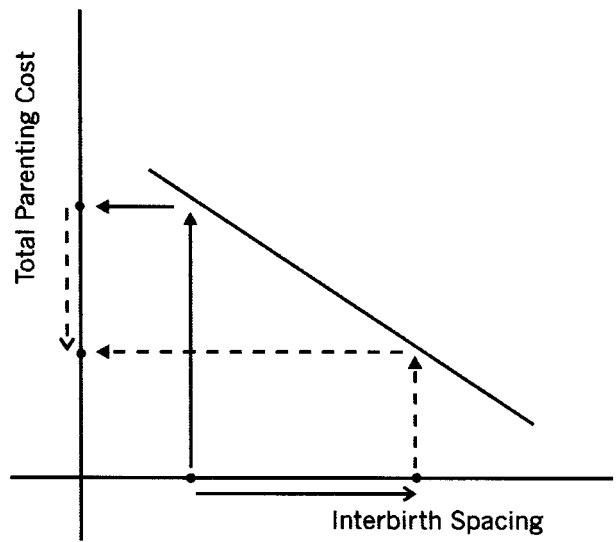


FIG. 2. *Interbirth spacing and total parenting cost (schematic).*

reduction in her fertility is great enough, the net growth rate may become negative and the population will shrink.⁸ Conversely, when the population size declines she will spend less time on foraging, and if the decrease is sufficient then she will have enough time/energy to enable her to reduce the interbirth spacing of offspring. According to assumption 3, she will now have offspring closer together while maintaining the well-being of her family in order to satisfy her desire for as many children as possible, and population size will increase.

The net effect is to couple fertility with population density (or, equivalently, with population size for a fixed catchment area). The population now meets the requirements for density-dependent population growth, namely, that the net growth rate must decrease with increase in population density (including the possibility of a negative growth rate) and increase as density decreases (see Read 1998 for a computer simulation). Or, put more simply, the decision process of each woman making choices solely in the interest of the well-being of her family will lead to stabilization of population size when the increased cost of foraging as population size/density increases sufficiently and when she places a sufficiently high value on the well-being of her family.

8. We do not exclude the possibility that mortality rates may also be increasing with increased population density, but without reduction of the expected 10–15 births over a woman's reproductive period that would occur in the absence of behavioral modification of her fertility rate, mortality rates would have to increase drastically to achieve a net negative growth rate. We think it more plausible, other than for exceptional circumstances such as populations dependent upon high-risk resources, to focus on behavioral factors leading to an increase in birth interval of sufficient magnitude that an increased birth interval, in conjunction with whatever is the current mortality rate (which may have increased as the population density has increased), yields a zero or negative net growth rate.

The last qualifier points to the fact that the model does not imply an equilibrium population size, K^* , arising from the decision model under all conditions. Rather, it implies that an equilibrium population size will be a consequence only if a forager translates the increased cost of foraging into a sufficient reduction of interbirth spacing so that, on the average, she now has a negative net fertility rate. We can view this implication in two ways. First, K^* is a function of the value a woman places on the well-being of her family, that is, on the amount of parenting she deems needed per offspring. The decision component is triggered by her total parenting cost, which is the cost, C , per offspring times the number, n , of offspring, nC . If C increases, the value of n needed to trigger a change in interbirth spacing decreases; hence, all other things being equal, the value of K^* is inversely related to the parenting cost per offspring that she deems needed for the well-being of her family. A shift in the cultural specification of what constitutes well-being in the direction of requiring an increase in time/energy per offspring will lead to a decrease in the equilibrium population size, even for the same resource base. Consequently, the difference in magnitude between K^* and K is, in part, determined by the cultural specification of what constitutes the well-being of a family. When substantial resources are required to attain what is considered necessary for the well-being of a family, the net growth rate may remain negative despite the presence of sufficient resources for more offspring, even where the mortality rate has been substantially reduced through medical resources, increased food production, and the like.⁹

Second, the decision model may not lead to an equilibrium population size if the translation of increased foraging costs into a change in interbirth spacing does not reduce the net fertility rate sufficiently to lead to a negative growth rate prior to the intervention of Malthusian parameters increasing the mortality rate. This may occur in situations in which, for cultural reasons (such as religious belief), decrease in average parenting per offspring does not translate into change in interbirth spacing. Another instance in which net fertility may remain high is the special case of migrants moving into a previously unoccupied zone (i.e., one with no competition); Surovell (2000) has argued that under these circumstances the value of r may be high for foragers even though the cost of parenting, measured as the cost of carrying children, is a limiting factor. Yet another instance in which an equilibrium population size may not be the outcome even though the assumptions of the decision model are satisfied occurs when resource density is high.

Resource density. A critical parameter for the relationship between equilibrium population size and car-

rying capacity when foraging is a primary means for resource procurement is the density of resources. Under conditions of low resource density and where resources are cropped on the basis of their natural abundance with few or no effective means to increase it, foraging results in high mobility because of the relatively quick exhaustion of resources in any one locality (Binford 1980, 2001; Surovell 2000). Classic foraging hunter-gatherers such as the !Kung San, Central Desert Australian Aborigines, and interior Eskimo groups represent this kind of foraging in regions with low density of resources.

Although hunter-gatherer groups in low-resource-density environments can be perceived as being at risk of exceeding the environment's carrying capacity because of the low density of resources, we argue the opposite. We can measure the buffering of a group against insufficient resources by the expression $K-K^*$. On an individual basis, we can measure the buffering against insufficient resources per person via the expression $(K-K^*)/K^*$.¹⁰ A more rapid increase in foraging costs than is implied by the decrease in resource density implies that both $K-K^*$ and $(K-K^*)/K^*$ will initially *increase* as resource density *decreases*, starting in a high-resource-density region; thus a hunter-gatherer society in a region with lower density of resources has more buffering against stochastic variation in resource density than one in a region with higher density of resources. As the resource density decreases, K and K^* must eventually converge, and therefore $K-K^*$ will eventually start to decrease. On a per person basis, however, the change in foraging costs with resource density decrease implies that $(K-K^*)/K^*$ should continue to increase until K^* is constrained by the decrease in K , indicating that individuals are at less risk with respect to stochastic changes in the value of K as resource density decreases.¹¹ Data on Australian hunter-gatherer groups confirm these predictions (see appendix in the electronic edition of this issue). In addition, foraging regions for these groups vary in size by more than two orders of magnitude between high- and low-resource-density regions. Environmental stochastic effects are likely to be less pronounced when averaged over a larger region in comparison with a smaller region.

We justify the claim about $K-K^*$ and $(K-K^*)/K^*$ by noting that the travel and search time required for resource procurement increases more rapidly per forager than the decline in resource density even if population density decreases in the same proportion.¹² Under relatively low-

10. These two measures need not be positively associated. The value of $K-K^*$ may decrease while $(K-K^*)/K^*$ increases, depending on the rate at which K^* changes in comparison with change in the value of K .

11. Lorna Marshall (1976:69, 107) notes that although the !Kung San have a season, *!kuma*, which can be translated as "starvation," actual starvation was unknown to her informants.

12. Suppose that under the current resource density n foragers fully utilize a catchment area of size A during the yearly round to obtain food resources for a population of size N , and therefore each forager must travel to and search over A/n units of area. If the resource density is now, say, $1/2$ as great, then $N/2$ persons, with $n/2$ foragers (keeping fixed the ratio between number of foragers and total pop-

9. One implication is that the negative net growth rate in some Western countries (or among some ethnic groups) today may be due to the perception of resources that need to be allocated to offspring in order to achieve the desired well-being of one's family (see Kaplan 1996).

resource-density conditions, then, the model implies that women will decide to increase the spacing of offspring sooner (in terms of population density) than would be predicted from the change in resource density alone. Consequently, stabilization of population size will occur at a population density smaller than would be predicted from the change in resource density alone (fig. 3), contra Wood's claim that equilibrium will always occur "at the margins of misery" (1998:110). It is groups in high-resource-density regions that will have K^* close to K or even reaching the Malthusian constraint when the population size reaches the value of K . For these groups a small change in K can lead to K^* 's being temporarily less than K^* , hence to starvation if the group has access only to the resources in its catchment area.

If neighboring groups are in a low-resource-density region, a roughly steady-state configuration can endure, since each group will stabilize well below its K and is at little risk with respect to stochastic variation in resource availability. Over the long run we might expect an overall increase in population size in response to technological and other changes that could increase the efficiency of resource procurement, but population size is still coupled with the value of K . Increases in K simply result in increases in the equilibrium value, K^* . The rate of overall population increase under these conditions will be linked to the rate of increase in resource procurement efficiency and not to the potential or net growth rate of the population.

In a region with high resource density, a population will grow until it comes close to or reaches K . When resource density becomes high enough, travel time to resources may become short enough (e.g., catchment areas will be no more than about 10 km in diameter for a local group) that it is unnecessary to carry infants while foraging, especially if not all women need to forage at the same time. For example, Goodale (1971:45) reports that among the Tiwi, a hunter-gatherer group living in a high-resource-density region, women would leave infants with cowives while foraging or hunting. Neighboring hunter-gatherer groups in high-resource-density regions are not likely to maintain a stable arrangement. A group of which K^* may be temporarily greater than K may respond by expanding its catchment area and thus entering into conflict with neighboring groups.

MODEL 2: INTERGROUP COMPETITION

Populations do not exist in isolation but interact in ways that affect the population dynamics of each group. For hunter-gatherer groups the interaction may occur mainly through partial overlap in catchment areas. For other types of societies it may take the form of defended boundaries (see Dyson-Hudson and Smith 1978). Competition, as we have defined it, is a situation in which

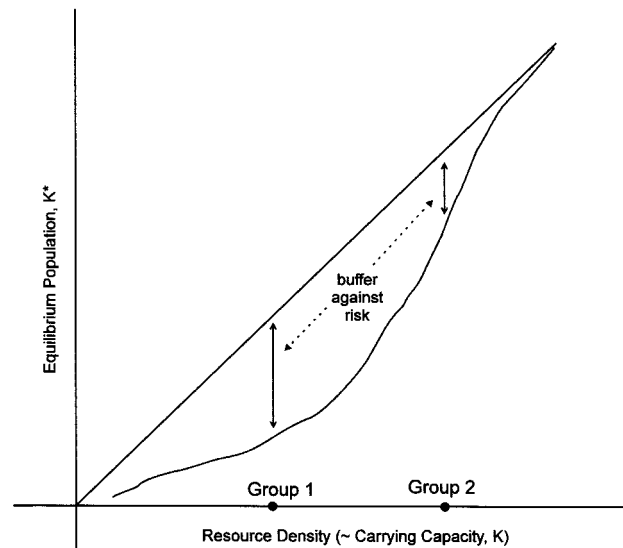


FIG. 3. Relationship between K (straight line) and K^* (curved line) illustrated by two groups with different resource densities. Group 1 has a larger buffer against resource shortage than group 2.

the use of resources by one group has the effect of removing those resources from use by the other group. It need not involve aggression or warfare, nor does it require defense of boundaries by one group in exclusion of other groups. Further, though replacement of one group by another may occur, it is not a necessary consequence of competition. Our primary interest in this section is to outline the conditions under which competition leads to coexistence versus the conditions under which it leads to replacement of one group by another.

The model we use was introduced by Lotka (1925) for competition between species and has been discussed extensively by Pielou (1969:53-75). We extend it to the case of competition between two groups each of which has a cultural identity as a distinct society (for the mathematical basis for the model, see appendix in the electronic edition of this issue).

We begin with a single population that reaches its equilibrium population size via internal mechanisms such as those discussed in the previous section and then consider how this baseline condition is affected by the addition of a second, competing population. Competition can be modeled by introducing parameters expressing the effect of one group on the other's growth rate. We will use a modified form of the standard logistic model that replaces K with an initially unspecified value, K^* . We do so because for the baseline condition we are assuming that the group has an equilibrium population size, K^* , where possibly $K^* < K$, whereas the standard logistic model assumes that the equilibrium population size is given by K . For a single population in isolation the modified logistic model of a population growing until it

ulation size), will still need a catchment area of size A to have access to the same quantity of resources per person, and now each forager must travel to and search over $A/(n/2) = 2A/n$ units of area, spending up to twice as much time procuring resources.

reaches an equilibrium population size uses two parameters: a , the intrinsic net growth rate (i.e., the growth rate that would occur if there were no restriction on the growth of the population, including reduction in fertility through behavioral practices) and K^* . For this model the net growth rate, r , at time t is given by $r = a(1 - P[t]/K^*)$. This expression indicates that the intrinsic growth rate, a , has been reduced in magnitude by the multiplicative factor, $(1 - P[t]/K^*)$, at time t . When $P(t) = K^*$, the multiplicative factor has value 0, the net growth rate is 0, and the population has reached its equilibrium population size and ceases to grow. If we let $b = a/K^*$ or, equivalently, $a/b = K^*$, then $a(1 - P[t]/K^*) = a - bP(t)$. The parameter b has the useful interpretation of measuring the impact of each additional individual on the current net growth rate of the population. For larger values of b , the impact of each additional person on the net growth rate is greater, and therefore K^* becomes smaller because $K^* = a/b$.

When we introduce a second, competing population, we need to identify parameters for the second population in parallel with the parameters for the first population—that is, we need a parameter for the intrinsic growth rate of the second population and a parameter that measures the extent to which each added individual in the second population reduces its net growth rate. For convenience we use subscripts to indicate whether a parameter refers to the first population or to the second population. Thus, the population dynamics of the first population are characterized by the parameters a_1 (the intrinsic growth rate) and b_1 (the impact on the intrinsic growth rate of each individual person in the population) and the population dynamics of the second population are characterized by the parameters a_2 and b_2 . We will begin by assuming that we have two populations with $a_1 = a_2$ and $b_1 = b_2$.

To introduce competition, we need to identify parameters that measure the impact of additional persons in one population on the net growth rate of the other population, that is, for each population we need a parameter that measures the impact on the net growth rate of one population due to the addition of persons to the other population. Let b_{12} measure the impact on the net growth rate of population 1 due to increase in the number of persons in population 2 and, conversely, let b_{21} measure the impact on the net growth rate of population 2 due to increase in the number of persons in population 1. In order to keep the subscript notation consistent, we rewrite b_1 as b_{11} and b_2 as b_{22} . Thus b_{ij} measures the impact on the net growth rate of population i by the current number of persons in population j , for $i = 1, 2$ and $j = 1, 2$. If the two populations are identical in their characteristics and symmetric in their effects on each other, then $b_{12} = b_{21}$ and $b_{11} = b_{22}$. We assume that the two populations are isolated from one another with respect to reproduction. For culturally distinct groups the assumption of isolation is not exact, but marriage rules, especially prescriptive rules, ensure that rates of introduction of new individuals from culturally different groups are generally low. The effect of a low rate of move-

ment of individuals between populations for reproductive purposes can be treated as noise and will not change the qualitative relationships in the growth trajectories of the populations in competition.

Four patterns of competition arise from this characterization: (1) population 1 wins out against population 2, (2) population 2 wins out against population 1, (3) populations 1 and 2 converge to a stable equilibrium, and (4) there is an unstable equilibrium between populations 1 and 2.

For hunter-gatherer societies we can measure the parameters b_{ij} , $i \neq j$, by the degree of overlap in the catchment areas of populations 1 and 2. While a stable equilibrium between population 1 and population 2 is theoretically possible with catchment area overlap, it assumes that neither population alters its parameter values. A more likely scenario allows one of the two populations to reduce its coupling with the other through change in its competition parameter. If we allow for change in parameter value, then stable equilibrium occurs only when there is little or no overlap in catchment areas (see appendix in the electronic edition of this issue for a more detailed discussion of competition between two groups). We will assume, then, a baseline competition model consisting of two populations with the same parameters and a stable configuration in which there is little or no overlap in catchment areas.

Stable equilibrium and group extinction. When two groups in competition are at stable equilibrium and each has an adequate buffer between its equilibrium population size and the carrying capacity of the region from which the groups obtain resources (see fig. 3), we will expect long-term stability between them. This configuration allows each group to obtain sufficient resources even in the face of resource variation without increasing its competition with the other. When the buffer is not large enough to protect against resource fluctuation, a group that is short of resources must either obtain resources at the expense of a neighboring group or face reduction of its population size through higher mortality rates. The former response, say, by population 1, implies that b_{21} increases if population 1 increases the mortality rate of population 2 through aggression or, alternatively, takes over a portion of population 2's catchment area. The effect is to shift what was a stable equilibrium in the direction of a configuration in which population 1 wins out in competition with population 2, and if the parameter change is large enough population 2 will face extinction unless it withdraws from competition or counters the actions of population 1. Withdrawal from competition is likely to be only a temporary solution, because increase in population size and expansion of its catchment area by population 1 will bring it back into competition with population 2. In either case, population 2 is eventually eliminated unless it can counter the actions of (i.e., engage in aggression against) population 1 (see appendix in the electronic edition of this issue).

Cyclical pattern of expansion and fission. While population 1 expands both its size and its catchment area so as to include the catchment area of population 2 under

the above scenario, the expanded catchment area and increased population size may be only temporary. As a hypothetical example, suppose that one of several competing neighboring groups is able to expand its territory through displacement of others and thereby translate its potential for population growth into territorial expansion. If it expands into neighboring territories without increase in population density, then the local cost of resource procurement is decoupled from the overall change in population size and the local population dynamics (e.g., relationship of birth spacing to cost of resource procurement) will be largely unchanged.¹³ Consequently, after territorial expansion without increase in population density, the equilibrium population size of a subgroup for the original catchment area has not changed, and therefore we can assume that the pre-expansion person/resource dynamics are essentially unchanged. In effect, from a population dynamics viewpoint the territorial expansion is similar to what would have occurred had the original, neighboring groups simply coalesced into a single group without change in the locations of groups or in their catchment areas.

The lack of change in the parameters expressing the person/resource dynamics for catchment areas implies that fission of the larger group will give rise to new groups that can survive, potentially, on a smaller territory but with the same population density than the group prior to fission. The relationship of a subgroup to local resources will be essentially the same as the relationship it had before territorial expansion, since there is no need to postulate any change in person/resource dynamics as part of the population expansion. There is, however, a cost to maintaining a larger population as a single unit. More subgroups must be integrated into a cohesive whole, and links between subgroups must be maintained over longer distances. Further, the number of links of a subgroup to other subgroups must be greater than before if isolation of subgroups or small sets of subgroups is to be avoided.

We suggest that fission is a likely outcome under these circumstances, since the relationship of a subgroup to resources will be largely unchanged but subgroups will have higher costs if the expanded population is to maintain itself as a cohesive whole. In effect, fission costs little or nothing in terms of resource availability per person and reduces the cost of maintaining the linkages with distant subgroups required to keep the larger group intact. Fission will simply return the territorially expanded group to smaller subgroups spatially configured similarly to the situation prior to expansion.

Stability through shift to a higher population density. In contrast, increase in population size through increase

in population density as well as territorial expansion introduces a cost in terms of mortality rates if a subgroup breaks off from the expanded group. If the larger group were to split into subgroups, each with a territory comparable to its catchment area prior to territorial expansion but now with an increased population density, a new subgroup would have a population density that could not be sustained by the catchment area available to it. Prior to the population increase it had a population density determined by its equilibrium population size, K^* , in accordance with its catchment area; after the increase it had an equilibrium population size K' , with $K' > K^*$. The extra population was maintained only because each local subgroup was able to get resources not only from its immediate catchment area but also from the entire territory of the expanded group of which it was a part. In contrast, a new subgroup would have access only to the resources of its own catchment area, and therefore its population would be bounded by its previous equilibrium population size, K^* . But if the population size for that catchment area grew to K' when territorial expansion took place and $K' > K^*$, then the mortality rate for the subgroup would have to increase until the population size was once again given by K^* .¹⁴ The increase in mortality rate that must be experienced by a subgroup if it breaks off from the expanded group with its higher population density becomes a substantial deterrent to fission.

Long-term outcomes. Though both patterns of population expansion involve territorial expansion and, presumably, some kind of new social organization, the long-term outcomes for the two scenarios differ substantially. Territorial expansion without increase in population density can result in a cycle of territorial expansion by one of the competing groups followed by a return to smaller territorial units. From the viewpoint of a local group, the system will appear unstable, since each local group is at risk of losing out in competition with a neighboring group.¹⁵ But the pattern of expansion followed by fission is a cycle that could repeat itself without any long-term change in the structural configuration of a large territory partitioned among local groups. There

14. Alternatively, it might be able to get access either to new resources (e.g., introduction of horticulture or agriculture) or to an increased quantity of resources (e.g., introduction of irrigation) from its catchment area due to modes of resource procurement made possible by the larger population. Introduction of a new resource may allow for a higher density in the same catchment area and subdivision into smaller groups. The extent to which this can occur will depend on whether variability of the new resource is of the same or an expanded scale.

15. An important component of our formulation is that intergroup conflict had a significant impact on group extinction. Massacres, although infrequent, did occur, and entire communities would be wiped out. Those who did survive would flee to other groups, and the social unit would disappear. Such group extinctions were surprisingly common where data are available, with perhaps more than 10% of all basic social groups becoming extinct per century (Soltis, Boyd, and Richerson 1995). Where archaeological information is good, the intensity of warfare can be seen to change over time. For some time periods group extinction rates can be very high (exceeding 50% per century) (LeBlanc 1999).

13. We are assuming that the population growth occurs primarily on the boundaries, with interior subgroups being more or less isolated from the changes. While migration from the interior to the boundary would allow for temporary increase in the fertility rate for an interior subgroup through reduction of population density, the population of interior groups would still be limited by the local of K and would simply grow until the net growth rate was again zero.

would be a kind of stability through the cyclical repetition of territorial expansion by one subgroup followed by the splitting of that group into smaller groups.

The pattern of endemic warfare found in parts of New Guinea appears to be an example of this cyclical pattern. For example, Strathern (1971) reports that local groups around Mount Hagen may expand their territorial base through warfare, but in time fission takes place and new local groups are formed. A similar pattern prevailed for the Kuma (Reay 1959).

MODEL 3: SPATIAL AND TEMPORAL VARIABILITY OF RESOURCES

We have suggested that a group in competition with neighboring groups may increase in size through territorial expansion with or without increase in population density. As noted above, these two types of expansion will have different long-term consequences. We need now to characterize the conditions under which we expect each of these types of expansion to occur. The key factor is the scale at which there is spatial and temporal variation in resource distribution in comparison with the scale for catchment areas and the temporal scale for resource variability.

By the *scale of spatial variation* in the abundance of a resource we mean the average size of a patch for that resource, where a patch is a region within which the resource has an approximately uniform and relatively high-density distribution in comparison with areas outside it. By the *scale of the catchment area* we mean the average area of the catchment area for a group in the context of competing groups. We assume that prior to any territorial expansion all catchment areas are comparable in size. By the *scale of temporal variation* in resource abundance we mean the time period for cyclical reduction and increase in the abundance of a resource. Generally the time scale is likely to be on a yearly basis, but it could be longer, as, for example, with cyclical changes in rainfall patterns.

We assume that the cultural rules (such as corporate or individual ownership of resources and rules for sharing of resources) by which minimal social units (such as a nuclear or extended family) have access to resources ensure that the average abundance of resources is available to groups throughout the catchment area at any point in time. We do not assume any particular means by which this occurs, and access might be gained in a number of ways, such as movement of social units and redistribution of resources. Nor do we require that any single social unit potentially have access to all the resources in the catchment area. Rather, we are assuming only that no social unit faces a shortage of necessary resources for which other social units have a local surplus.

One group with seasonal variation in resource abundance. We first consider a single group and its response to temporal variation in resource abundance. Under the above assumptions we may assume that a relevant parameter for population dynamics for a group is the average resource abundance over the catchment area at a

point in time. The average resource abundance may also vary over time, and in general we expect more such variation in more seasonal environments (fig. 4). According to Liebig's Law of the Minimum, the equilibrium population size, in the absence of storage, responds to resource minimums in the cycle of varying resource abundance.¹⁶ Therefore, even though the total resource abundance may be about the same, the group facing greater temporal variability in resource abundance will have a lower equilibrium population size.

Competing groups with seasonal variation in resource abundance. We now consider three competing groups. Suppose that the scale of spatial variation in resource abundance is substantially smaller than the scale of catchment areas (see fig. 5). Regardless of the location of a catchment area, the average resource availability is

16. It might be argued that a group with temporal variation in resource abundance should use storage to even out the highs and lows of resource abundance, but this argument is based on the premise that the group has the goal of larger population size. For a population stabilized well below carrying capacity as discussed in model 1, there is no resource shortage for any family, and so there is no gain at the level of a family unit to be achieved by storage. Storage, however, may have a social cost. For example, the Cahuilla required that storage of acorns be done publicly so that everyone would be aware of the amount of food being stored by a family (Bean 1972). It seems likely, then, that storage would only be introduced under circumstances in which it could be demonstrated that it produced gain that outweighed its costs.

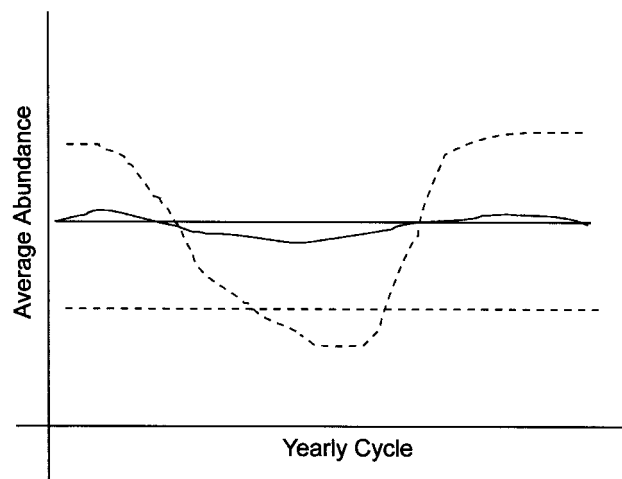


FIG. 4. Hypothetical yearly cycles with little and substantial seasonal variation in resources. Resource abundance at a point in time is averaged over the relevant catchment area. Carrying capacity is determined by the minimal resource abundance during the year. Dashed line, K for pronounced seasonal variation in resource abundance; solid line, K for minimal seasonal variation in resource abundance. Both graphs have approximately the same total quantity of resources summed over the year (areas under the curves are approximately equal).

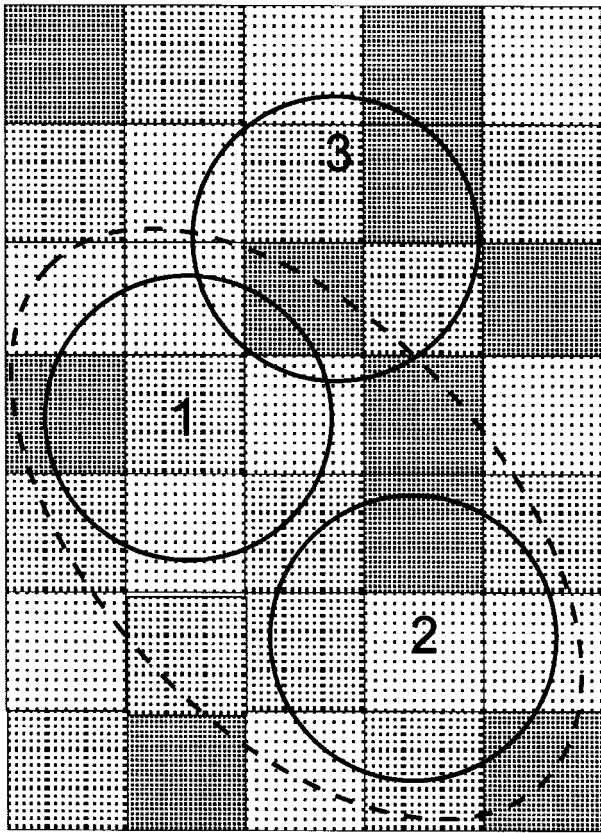


FIG. 5. Scales for resource variation (small squares) and catchment areas (circles). Darker shading, higher average resource abundance. The groups with catchment areas 1 and 2 have consolidated into a single group with a large catchment area. This area has the same average resource density as the smaller catchment areas, and therefore there will be no increase in population density. The consolidated group (1 + 2) will have no competitive advantage over group 3.

about the same and therefore so is the temporal graph for resource variation. If groups 1 and 2 were to coalesce, the resource availability per individual for the newly formed, larger group would be essentially the same as it was initially for the two groups of which it was composed. We expect no change in population density for the combined group in comparison with the density for each of the two groups prior to coalescence.

In terms of competitive advantage, the increase in the catchment area for the coalesced group, group 1 + 2, implies that the parameter b_{13} is now reduced to a new value, $b_{1+23} < b_{13}$. This is because the portion of the catchment area represented by overlap in the two catchment areas measures the competitive impact of one group on the other due to the use of resources otherwise available to that group. For group 3 the portion of the catchment area represented by overlap has not changed,

but for group 1 + 2 the approximate doubling of the catchment area reduces the impact of the overlap portion by approximately half. The effect on equilibrium population size, assuming that parameter values do not change further, is mainly a slight increase in the size of group 1 (fig. 6, bottom). There has been minimal impact on the competitive relationship between group 3 and the coalesced groups 1 and 2 in comparison with the situation before they coalesced (fig. 6, top).

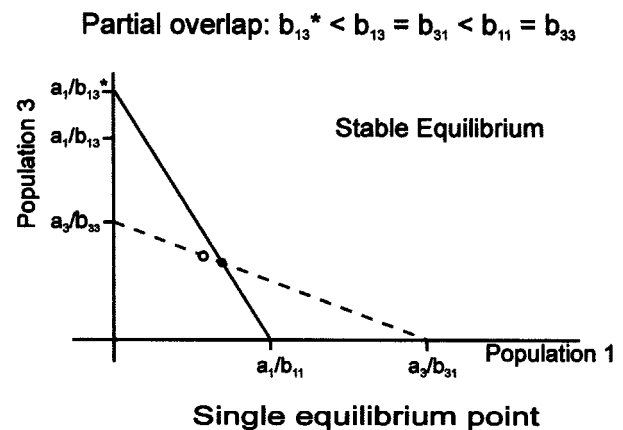
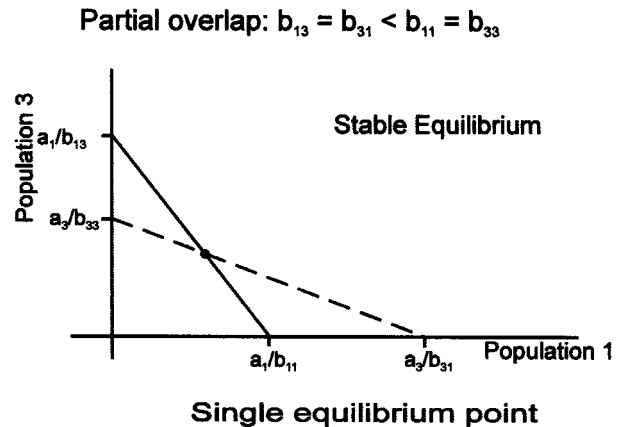


FIG. 6. Competitive relationships between group 1 and group 3 before group 1 and group 2 coalesce (top) and between subgroup 1 of group 1 + 2 and group 3 after group 1 and group 2 coalesce (bottom). The impact of group 3 on subgroup 1 has been reduced, but the carrying capacity of subgroup 1 has not changed. The stable equilibrium point shifts slightly to the right in favor of subgroup 1. No qualitative change in the relationship between (sub)group 1 and group 3 has taken place.

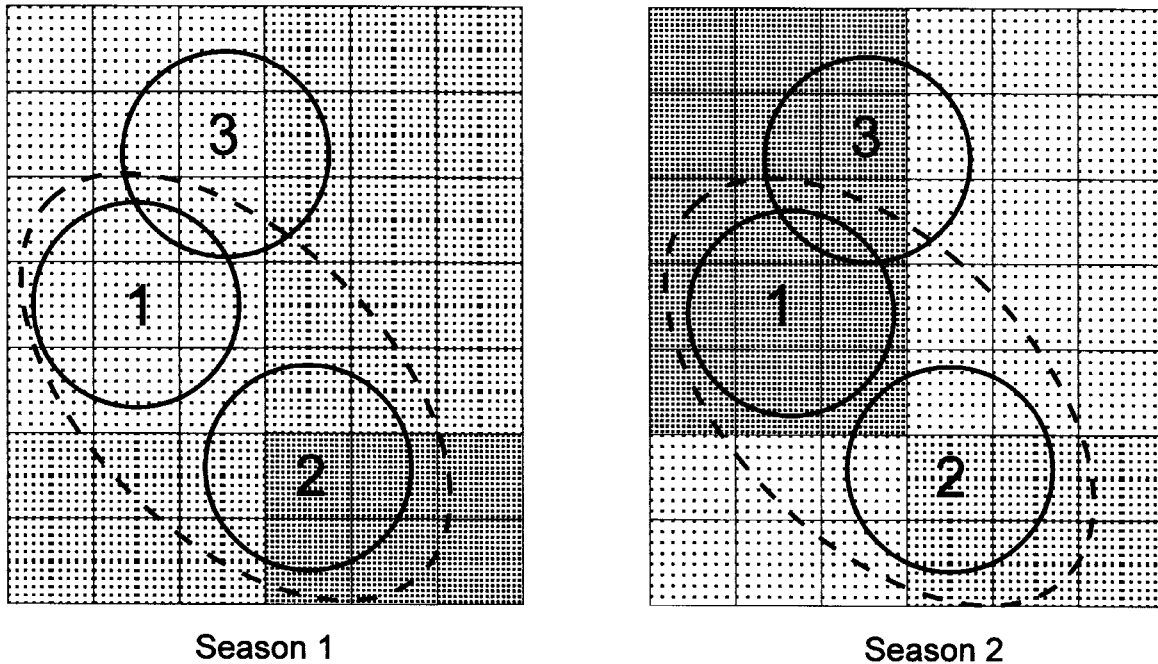


FIG. 7. Scales for resource variation (squares) and catchment areas (circles) in two seasons. The groups with catchment areas 1 and 2 have consolidated into a single group with a large catchment area. This area has greater average resource abundance than the smaller areas for both seasons, and therefore there will be an increase in population size and population density. The consolidated group (1 + 2) will have a competitive advantage over group 3.

Thus the larger group formed by coalescence of groups 1 and 2 has achieved neither a gain in resource availability in comparison with the two groups of which it is composed nor a competitive advantage. It now has the cost, however, of maintaining itself as a larger group. Returning to two constituent subgroups has no cost in terms of mortality rates, and therefore we assume that the larger group will split into subgroups comparable in size with the groups from which it was formed.

A different scenario occurs when (1) the scale of resource variability is large in comparison with the scale of catchment areas, (2) there is seasonal variation in resource abundance, and (3) seasonal resource abundance in one resource patch is out of sync with variation in other resource patches (fig. 7). Groups 1 and 2 have the lowest equilibrium population sizes because of the low abundance of resources for group 1 in the first season and for group 2 in the second season (fig. 8). If they coalesce into a larger group with a new, larger catchment area, this new group will have greater resource abundance because the seasonality in resource abundance for catchment areas 1 and 2 is out of sync and one area has a higher abundance of resources when the other area has a lower abundance of resources. The net effect is greater equilibrium population density for group 1 + 2 than for group 3.

The population of the consolidated group will increase

in size and therefore in density until it reaches its new equilibrium population density, K_{1+2}^* . Since $K_{1+2}^* > K_3^*$, the new group will have a competitive advantage over group 3, for $b_{33} = b_{22} = b_{11} > b_{11}^*$, where $a/b_{11}^* = K_{1+2}^*$ (fig. 9). Resource variability on a scale larger than the scale for catchment areas introduces a qualitative change in the competitive relationship among groups that initially had similar parameters. Coalescence of groups that are out of sync in terms of seasonal resource variability can shift a competitive relationship to one in which the newly formed group may win out in competition with other groups. Since the population density has also increased, fission is not as likely.

While the new group may win out in competition with smaller groups, territorial expansion is ultimately limited by two factors. First, smaller groups have the option of coalescing in the face of competition from a larger group that then restructures the competition as competition between groups with comparable parameters. Second, as the size of the territory expands, the scale of the total catchment area of the expanding group will increase and eventually exceed the scale of spatial variation in resource abundance. At this point the relationship of the group to resources matches the configuration in the model discussed above, in which increase in the territory of a group does not lead to increase in popu-

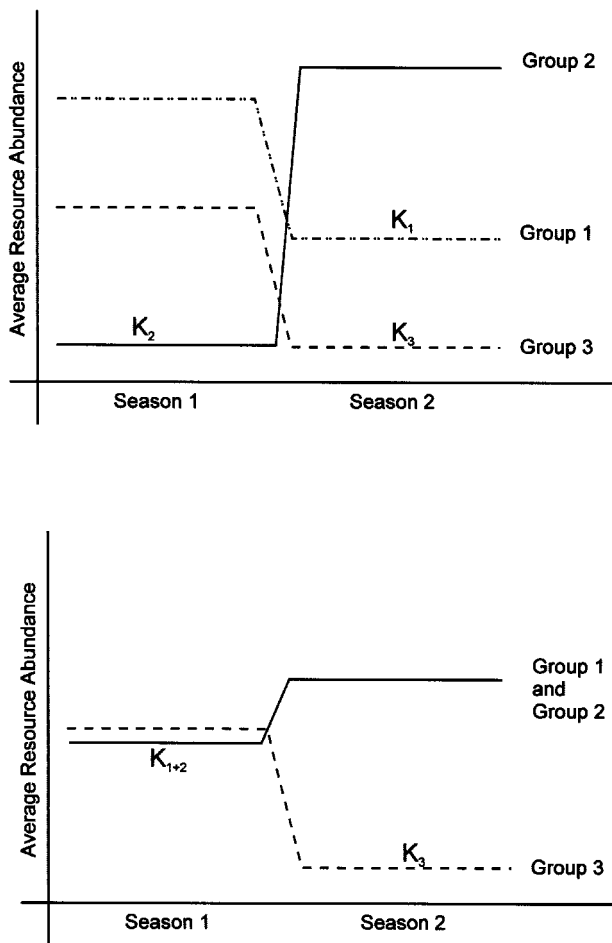


FIG. 8. Average resource abundance for each of the three catchment areas in figure 7 (top) and for catchment areas after groups 1 and 2 have coalesced (bottom). Solid or dashed line, abundance by season. Carrying capacity for a catchment area is constant and based on the minimal resource abundance during the year. The combined group now has a larger carrying capacity, K_{1+2} , than either group 1 or group 2 before coalescence.

lation density. Fission now becomes a more likely outcome of further territorial expansion.

MODEL 4: THE RESOURCE ACCESS/OWNERSHIP UNIT

The logistic model for population growth assumes that the addition of a person to a group has equal effects on resource availability for all persons in the group. Similarly, the competition model assumes that the addition of a person in one group has equal effects on resource availability for all persons in the other group. These models fail to take into account that culture frames the way in which individuals have access to resources. Ownership of resources ranges from corporate to individual, and the

kind of ownership may depend upon the particular resource. When food resources are obtained through agriculture or horticulture, rights to land and access to land become major determinants of the ability of individuals or social units to produce food resources. Coupled with rights of ownership or access are rules of inheritance that affect the distribution of land rights and access to land in the next generation. These rights are highly variable from one society to another.

The assumption that impacts on food resources arising through change in the population structure are distributed across all individuals in a group is valid only to the extent that cultural rules for ownership and sharing of resources

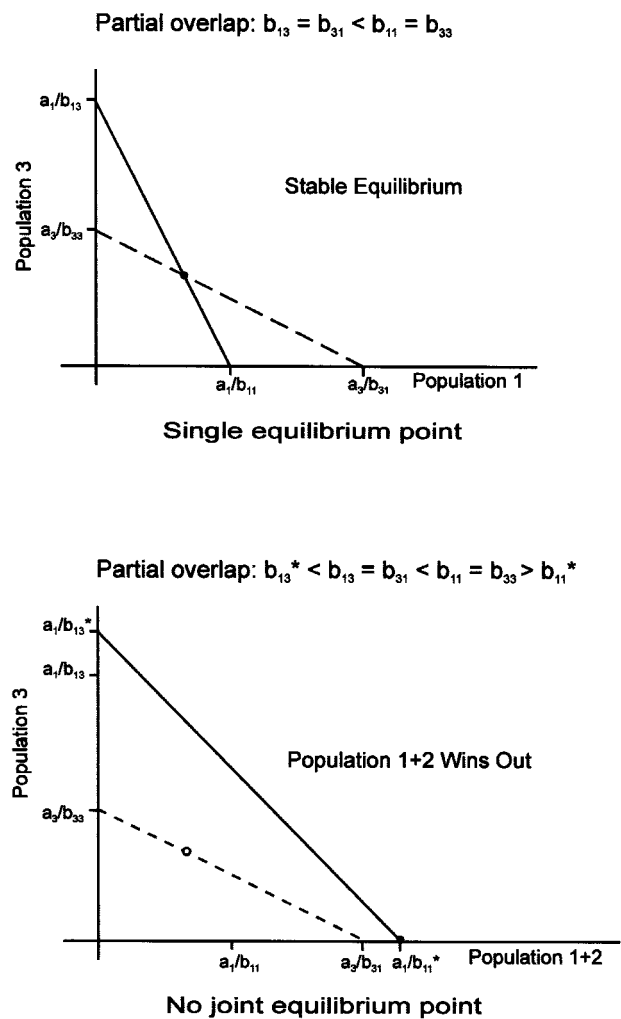


FIG. 9. Competitive relationship between group 1 and group 3 before (top) and after (bottom) group 1 and group 2 coalesce (see figs. 7 and 8). After coalescence, the impact of group 3 on group 1 has been reduced and the carrying capacity of group 1 has increased; the stable equilibrium point changes qualitatively to a configuration in which group 1 + 2 wins out in competition with group 3.

ensure the availability of resources to all with little inequity. So long as local surpluses and shortages are eventually redistributed over time scales relevant for decision making, the assumptions of the models are satisfied, and we can ignore (for modeling purposes) the details of how individuals or social units have access to resources. When a large animal is killed, a local surplus is created, and in most if not all hunter-gatherer societies there are cultural rules requiring sharing or redistribution of the meat. Here the time scale for procurement and redistribution is measured in days and is comparable to or shorter than the time scale for making decisions about spacing of offspring. Contrariwise, when there is storage of foods, local food surpluses may be stored and owned by the food-producing unit with only limited redistribution. Any redistribution may be linked to rituals or other events that occur only annually or even less often.

Another complexity not taken into account by these models relates to the potential growth in population size of the resource access/ownership unit.¹⁷ In some cases the corporate group for resource access/ownership may be an extended family, and the size of extended families, for a given fertility rate, is independent of overall population size. Extended families are typically based on common affinity to a living ancestor, and they are likely to split along sibling lines when the focal ancestor dies.

In other cases, such as lineage systems, the corporate group may grow if there is a net positive growth rate, but it may also split for internal, structural reasons as the number of members increases. The lineage may subdivide when the members of a subgroup within it no longer see it as in their interest to remain part of it. Internal conflict that may arise as population size increases can be resolved through splitting into smaller, daughter-lineage groups.

In both of these examples the size of the corporate group for access to and ownership of resources is largely independent of population growth. Even if the current spacing of offspring leads to a net positive growth rate, fission of the corporate unit may decouple the long-term population size of the corporate group from a net positive growth rate for the population as a whole. In this situation population growth will translate into an increase in the number of corporate groups and not in the size of each corporate group.

According to the decision model on birth spacing, it is when a woman's costs (parenting costs plus food procurement/preparation costs) are high that she makes a decision to defer the next pregnancy. Where the size of corporate units is decoupled from the long-term popula-

tion growth of the group as a whole and the corporate group is also the unit for resource access/ownership, then her food procurement/preparation costs will be unaffected (in the short run) by any increase in the population size of the group as a whole. Therefore she will space offspring on the basis of her assessment of her costs, and her decision will not be affected by its consequences for net population growth. If her assessment leads to birth spacing that translates into a net positive growth rate, then the population size of the group as a whole will increase through increase in the number of corporate groups (cf. Cowgill 1975). If her assessment leads to birth spacing that translates into a net negative growth rate, then the population size of the group as a whole will decrease. In both cases the model implies that her decisions about birth spacing will not be affected by the changes in the overall population size of the group.¹⁸ What will be changing is the number of corporate units attempting to utilize the same catchment area.

With an increase in the number of corporate units and a catchment area bounded by the presence of other groups, the outcome of an increase in the number of corporate units must be conflict between corporate units for access to resources (Carneiro 1970). In contrast to competition that may lead to aggression between groups in different societies, the conflict under the conditions discussed here is conflict within a society. While individual corporate units may be wiped out, within-group conflict does not lead to an increase in the overall catchment area, and therefore we will expect endemic conflict under the conditions posited here. Population size is stabilized only through elimination of excess corporate units (e.g., directly through aggression or possibly through migration if that is feasible), but the positive net growth rate of corporate units not engaged in conflict is unaffected and consequently an excess number of new corporate groups is continually produced (cf. Evans-Pritchard 1940, Irons 1975, Sahlin 1961, Strathern 1971, Brown 1964).¹⁹

18. This need not be strictly true for a net negative growth rate. If the woman's assessment of costs is related to the current population size of the group and the net growth rate is negative, the size of the group may decrease (e.g., the constant value for the overall size of an extended family depends on birth spacing) and her decision may now be to decrease spacing between births. The decreased spacing between births may lead to growth of the group (within the overall limits on its size), which would again trigger an increase in the spacing of births. The overall result would be cyclical increase and decrease in birth spacing. It is interesting to note that if the resource access/ownership unit is the nuclear family, then her cost assessment includes only a fixed cost of procurement of resources and the variable cost is the parenting cost. If the fixed cost of procuring resources is high enough, she may space offspring sufficiently far apart that the net growth rate is negative. But when the nuclear family is the group the negative growth rate will have no effect on her total costs, and so the model predicts that females will continue to have a birth spacing that leads to a negative net growth rate. Kaplan (1996) has made essentially the same argument to account for the below-replacement birth rates in a number of Western countries.

19. Aggression may increase the mortality rate in groups engaged in it, but not all groups will be engaged in aggression at any one point in time. Groups not engaged in aggression will continue with the same birth spacing, thereby leading to the production of new groups through fission as a group grows.

17. There need not be a single resource ownership unit for all food sources. Some resources may be corporately owned and others individually owned. For the !Kung San most resources are corporately owned, though some resources such as honey may be individually owned. Again, the unit may vary depending on the season and the kind of resource. Among the Netsilik the resource access/ownership unit in the winter may have consisted of 10–20 families when they were hunting seals on the pack ice but a single extended family when they were salmon-fishing (Balikci 1970:115). We will be concerned here with the largest resource ownership unit for a resource that contributes the majority of the food upon which the group depends over at least a time period of a few weeks or months.

SUMMARY

We have distinguished three independent dimensions each of which has an effect on how the basic decision-making model will play out (see fig. 1).

The first dimension is resource density. The effect of higher resource density is to decrease the spacing of births more rapidly than the increase in density. As a consequence, the model predicts an equilibrium population size for hunter-gatherer groups in regions with low resource density and a nonequilibrium population size in regions with higher resource density.

The second dimension is the patchiness (taking into account simultaneously both geography and seasonality) of resources. With low patchiness relative to the size of a catchment area, we expect endemic intergroup competition, as all groups have comparable time and geographic scales for access to and quantity of resources. High patchiness at a scale below the size of a catchment area leads to stable coalescence of groups (or takeover of territory), as the population density will increase after coalescence because the larger group has access to a larger average resource base throughout the year.

The third dimension is the degree of decoupling from population growth of the corporate group through which individual families have access to resources. When the corporate group is decoupled from overall population growth by virtue of fission, then we predict intragroup conflict, since growth in the number of corporate groups will lead to a total population size that exceeds the carrying capacity of the group's total territory.

Returning to figure 1, we see the eight possible configurations of high (H) and low (L) rankings for each of the three dimensions—resource density, patchiness of resources, and decoupling from population growth of the corporate group. With the exception of (L, L, L) and (L, H, L), each configuration has a different pattern for its outcome, ranging from stability for the (L, L, L) combination to centralization for the (H, H, H) configuration.

Conclusions

The multitrajectory model that we have developed underscores the complexity of the relationship between population growth and societal change. Rather than population growth's being a universal "prime mover" for societal change, as some have argued, or the exceptional condition, as others have argued or assumed, the matter is more complex, especially since both parameter values and structural relationships that affect the long-term demographic outcome are culturally dependent. The cultural dimension makes it difficult to consider the demographic consequences of the potential for rapid population growth for a group as being explicable within an ecological context alone. Moreover, groups do not exist in isolation; only by including the existence of other groups and their potential for competition can we hope to have realistic models of these factors. We have also argued that specifiable types of social organizations and subsistence strategies

will have the capacity for changing the organizational and structural relationships of their societies. There is nothing inherent in hunter-gatherer or other social structures that results in zero population growth. It is not growth itself that is automatic or a given but the potential for rapid growth that always exists among humans. Potential growth is always under some degree of control, with the control ultimately linked to carrying capacity, but control does not necessarily mean absence of growth. It is probably fair to say that in most times and places in the recent past, population growth and consequent competition were the norm. It is this reality that we must take into account in our models.

The outcome of the self-centered decision model for reproductive decisions may be a population in equilibrium or one that fails to achieve equilibrium, depending on the valuation placed on the well-being of one's family and how that translates into birth spacing. The latter depends not only on one's evaluation of having another child under one's current circumstances but on the way in which that evaluation is made within the context of cultural meanings that may transcend individual calculations. Culturally imposed limitations (including religious ideology) on contraceptive methods and/or abortion may lead to direct conflict between individual calculations about the desirability of having another child under one's current circumstances and actions that are socially acceptable.

Throughout our discussion we have kept the self-centered decision model constant while varying parameter values to make it more evident that seemingly radically different consequences "on the ground" may simply reflect the differential effects of the same decision model in different contexts. At the same time, restructuring of the interplay among individual decision making, societywide demographic implications, and intergroup relations does occur, making any single structural model of this interplay inadequate. Rather than a single model we have posited a multitrajectory model that can assume different structural states depending on both the cultural and the ecological context. The multitrajectory model shifts the emphasis to understanding the conditions under which transitions from one state to another may occur and determining when those transitions are likely to represent a long-term restructuring of relationships rather than a "temporary" readjustment to a perturbation.

Since larger-scale systems have additional costs associated with them (for example, the costs involved in maintaining an organizational structure that links social, economic, and other units), there is a tendency for larger-scale organizations to dissipate. Ultimately individuals and groups must bear those costs and therefore must make either individual or collective decisions about the benefits obtained versus the possibility of "opting out" as more or less self-sufficient units. We have argued that a key factor for evaluating the consequences of this kind of calculation is the demographic consequences of restructuring. When restructuring produces an increase in population density, there is a cost for opting out, namely, the introduction of Malthusian constraints because the increased population density cannot be maintained under

the prior, lower level of organization. As individuals or groups opt out, it becomes increasingly difficult to meet daily metabolic requirements in comparison with one's earlier condition, and this makes it more likely that some kind of evaluation will be made of the organizational cost of opting out versus its increasingly apparent Malthusian consequences.

We suggest that it is this kind of dynamic that helps us to understand the different trajectories that different societies and cultures have followed, ranging from hunter-gatherers that have maintained small-scale societies virtually to the present to Western societies for which change in both organizational form and population size/density has been more or less constant throughout their history. For some trajectories the long-term population consequence is stability in the classic sense of a stable equilibrium point, such as our model for a hunter-gatherer society in a low-resource-density region. For other trajectories the stability takes the form of an attractor—the locality within the phase space for population trajectories in which the populations are most likely to occur—but has no single equilibrium point. Our model for populations in high-resource-density areas in which the scale of spatial variation in resource abundance is small in comparison with the scale of catchment areas is a case in which an attractor characterizes the long-term outcome. Yet other trajectories may lead to quasi-stability arising from the decoupling of groups otherwise linked through resource competition via a no-man's land in which neither group can maintain a long-term presence because of competition from the other. The latter introduces yet another possible trajectory, namely, a more highly centralized system that can control between-group competition and thereby gain access to the no-man's land, thus gaining an immediate increase in the carrying capacity of the region containing the no-man's land and creating the conditions for its own maintenance as population density increases in response to the acquisition of the no-man's land's resources—but that is another story.

Comments

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19 IX 02

It is true that there is a great deal of literature that deals with human population change in terms of quite unsatisfactory concepts and assumptions. Read and LeBlanc do well to point this out, and their ten explicit propositions and clear definition of between-group competition are useful to consider and mostly persuasive. Many of the results derived from their models are at least suggestive and interesting. Nevertheless, there are serious limitations in their assumptions, and I believe that their models could be greatly improved by better grounding

in additional considerations relevant for fertility rates. Rather than lumping nearly all previous thought as a traditional "standard model"—a rhetorical ploy that overstates the originality of their own work and that few are likely to find convincing—they might have read the literature more widely and more thoughtfully. Publications by demographers, in particular, are very scarce among their references. Appendix A (in the electronic edition of this issue) acknowledges diversity in previous approaches, but this has, quite literally, the character of a tacked-on appendage and does not effectively counter the charge that they have created something of a straw man.

The central omission I see in their propositions is the anticipated material benefits of children once the children have grown past infancy. They appropriately consider costs of parenting to the mother, but, as far as I can tell, their models do not take into account any benefits expected from children other than maternal pleasure in seeing infants in a perceived state of "well-being." Where are the usual suspects so extensively discussed in the demographic literature, such as labor contributions of even relatively young children and the expectation that grown children will be a source of security in one's old age? To be sure, the nature and extent of present or anticipated material benefits from children vary greatly with the environmental, technological, and cultural circumstances. That is just the point. Precisely because of their variability, adequate models of fertility change cannot neglect them, and the attempt to understand their variation is a central part of our task.

A related problem is that Read and LeBlanc's models give too little attention to the fact that individuals other than the prospective mother often have strong interests in her fertility performance. This is not to say that a mother's individual self-interest is not a critical concept. Rather, it is to say that her calculations as to what is most in her interest will be strongly affected by the actual or expected behavior of relevant others as they pursue *their* self-interests. This means that models must take into account the interests of others, especially husbands and other close relatives, who also stand to bear costs and anticipate benefits from children. Modes of production, size and composition of producing units, and size and composition of units with sharing rights should figure far more prominently in our models. This is especially so for inegalitarian societies, in which tribute, taxes, and rents are important, but it is also true for the relatively egalitarian societies with which Read and LeBlanc are mainly concerned in this paper.

The literature bearing on these matters is huge, and I will only mention two cases with which I am especially familiar. In my own publications (Cowgill 1975b: 519–20; 1996), dismissed by Read and LeBlanc as "standard model," I touched on these topics, but too briefly and elliptically to have made much of an impression, I fear. Bledsoe and Banja (1997) provide a much clearer and particularly thought-provoking example, in which women's child spacing is closely related to their perceptions of their own health and their interest in preventing

damage to their child-bearing capacity (fecundity) through inopportune pregnancies. In this case, a concern with what might be called maternal well-being utilizes child spacing to meet a goal that may often translate into greater total fertility over a woman's reproductive life span. This is just one illustration of the sorts of things modelers should be more aware of.

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In 1971 Murdock presented his enigmatic Huxley Memorial Lecture, "Anthropology's Mythology," with a pair of then dramatic claims: neither culture nor social structure could be reified to serve as an explanation. Social structure and culture were our characterization of patterns of interactions between individuals, not the source of these interactions. Anthropologists had to abandon subjects of a superorganic nature and deal with individuals and their productions to explain what we call "social" and "cultural." After a half-century in anthropology, Murdock was introducing a programme that would echo for the next half-century—focusing ethnography, cross-cultural research, and theory on diversity of individual experience and choice, not commonality and conformance.

Read and LeBlanc are to be congratulated for a fine beginning in the task of unravelling the representation of population processes into a potentially more individuated form. With these tools we may better represent the ultimate constituents of population processes—individual men and women—not only with respect to individuated biological processes but with respect to choices, behaviour, and ideational and contextual influences on individual outcomes. Indeed, we may be able to explore the emergence of culture and social organization. In short, they have proposed a framework that supports knowledge-based input (including culture) into the modelling of the emergent properties of human population processes.

In one sense they are telling us nothing new—they have simply taken a number of existing monocausal theories and demonstrated that none of these are capable of properly describing population processes as these unfold across people and time, much less explaining these processes. They are claiming that the phenomena are too complex for simple material explanations because they are driven by individual histories and individual decisions based on personal information, desires, and objectives. That is, populations are composed of female and male bodies and their experiences.

What is new is that, in contrast to many of our colleagues, they do not stop at deconstruction but instead begin to come to grips with the problem of reassembling bodies and experiences into what we perceive as population processes. The particular manner in which they have chosen to do this is appropriate to the kinds of data

we can reasonably expect to bring to problems situated in history and prehistory or even in contemporary contexts. Certainly, from the perspective of newer forms of individual-oriented modelling ("agent-oriented" modelling) this framework suggests a number of solutions to the difficult problems encountered in attempting to develop models and simulations based on the "standard model."

Having said this, there is still a lot of work to be done. Most of the detail of Read and LeBlanc's framework is directed towards reassembling the three dimensions of their final model to represent a context in which individual decisions will be expressed. Although they have outlined many of the kinds of decisions that might be made that would affect fertility and life, the connection between these decisions and knowledge about how these decisions might express themselves is as yet not defined. It is likely that a generalization of their framework to more "complex" population contexts will require considerable modification. There is much more to consider than the immediate context of population processes and their impact on people's ideation and the converse. This framework is, however, an important contribution to the programme of accounting for the emergence of group processes from individual action.

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Read and LeBlanc's multitrajectory model is a welcome contribution to the field. Along with critics of the density-independent "standard model," the authors invite us to assess common practices in human demographic modeling. I would like to comment on the implications of some of their propositions for demographic modeling at larger spatial and temporal scales. If the processes underlying their model are really significant in determining long-term demographic outcomes for hunter-gatherer societies, then they should be accounted for in any model attempting to resolve human evolution (although this should also be determined by the scale of the study).

When modeling demographic expansion coupled with spatial expansion, most researchers have used carrying-capacity estimates that are derived from the literature on contemporary hunter-gatherer groups (e.g., Steele, Adams, and Sluckin 1998). These estimates are taken as either the theoretical carrying capacity (K) or the equilibrium population size (K^*), but in both cases they are typically used in a "standard model" of logistic growth function with constant growth rate. Because spatial/demographic expansion models need estimates of K (or K^*) that cover the whole range of potential environments covering the surface of interest (typically at a regional or continental scale), one usually lacks sufficient em-

pirical data to serve as a reference. K values must therefore typically be built up by using data from other regions with similar environmental conditions for which data on population densities are available. However, choosing "similar" conditions is usually a subjective task, mostly based on the comparison of vegetation density or net carbon production. The geographical distribution and seasonal variability of resources are rarely taken into account. Conversely, Read and LeBlanc suggest that the uneven distribution and seasonality of resources, here called "resource patchiness," are key components of the modeling of intergroup competition outcomes and thus of the understanding of long-term demographic patterns. Taking into account the patchiness of resources therefore seems necessary for sound estimates of carrying capacity. However, it is not a straightforward undertaking, particularly in demographic models in which competition or changes in resource procurement behavior are potentially important such as the acculturation-versus-replacement models with regard to hunter-gatherers and farmers in Europe (e.g., Barbujani, Sokal, and Oden 1995, Rendine, Piazza, and Cavalli-Sforza 1986). Moreover, with increased computer power, one is now able to take into account variations in environmental conditions such as climate and vegetation changes over time. It therefore seems important to account for this environmental dynamism not only in resource densities but also in growth rates over time. Yet it remains necessary to test the contribution of this added complexity when modeling at large spatial and temporal scales.

Another interesting demonstration by Read and LeBlanc is the counterintuitive fact that populations in low-resource-density areas (low K^*) will have long-term demographic stability and therefore will less be likely to suffer population crashes than populations in areas of higher K^* . This behavior is seldom reflected in conventional stochastic simulations of population demography because the values of the parameters that dictate the behavior of the stochasticity do not vary with density. This invariably leads to a situation in which groups living in low-resource-density environments such as desert areas demonstrate the highest propensity to crash. As Read and LeBlanc emphasize, there are many reasons to distinguish between the actual growth rate (on short time scales) and the net growth rate (an average over long time scales). The latter is misleading because it masks short-run demographic fluctuations, which are more important than long-term demographic averages in shaping population behavior. Whereas the stability in low-resource-density areas and the actual growth rate have direct implications for the outcome of the multitrajectory model, they also have consequences for models that link demographic growth to human population genetics.

Many parameter estimations in human population genetics, such as the time since the divergence time of a given group or population, crucially rely on assumptions about human demography. Taking into account population extinctions and recolonizations is important in estimating population census size (Eller 2002). Similarly, Read and LeBlanc's model strongly suggests the impor-

tance of realistically modeling population crashes and recoveries.

Read and LeBlanc succeed in justifying a more complex approach to population growth modeling. However, we still do not know if this extra level of complexity is justified for all spatial and temporal scales. Adding realistic components to a "standard model" is necessary only if it has been shown to have a significant impact on the model output. Beyond a certain scale (spatial or temporal), it may be that satisfactory population demography reconstruction could be achieved even if not all of Read and LeBlanc's assumptions were included.¹

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Read and LeBlanc's article contains quite a wide range of modelings put together in what might be considered the outline of a "theory of everything" in population dynamics. The argument is fairly coherent, with clearly understandable steps, inviting thorough investigation and perhaps further development. Notwithstanding their clarity, however, I think some of the steps in the argument are taken too quickly. For instance, the assertion " K^* is a function of the value a woman places on the well-being of her family, that is, on the amount of parenting she deems needed per offspring," is to be taken against the background of arguments considering the decrease or increase of fertility rates, but one cannot, generally speaking, directly predict stabilization levels from dynamic situations if the information at hand is no more specific than that a population parameter is changing. Consider, for instance, a group consisting of 1,000 people in a certain year and a growth rate of 1/1,000 per person per year. If the next year the growth rate is 1/1,001, the third year 1/1,002 etc., the growth rate is more closely approaching zero but the population is growing infinitely. If the growth rate is approaching zero *fast enough*, a finite value for the population may in fact be obtained (cf. Van der Blij and Van Tiel 1975: 213, 216), but such fine-tuning is probably not to be expected in capricious historical circumstances.

If a decrease in fertility results in a negative growth rate, there is a risk of extinction and the process of population decline must somehow be curbed, resulting in still other uncertain outcomes. Furthermore, when a birth rate initially equal to a certain constant death rate is temporarily less than that death rate, a group may indeed decrease in numbers, but the number may stabilize again at a lower level (than initially) when the birth rate reaches the very same old value.

Stabilization requires that birth and death rates (b and d) be equal, not that they be high or low. Thus situations 1 and 2, in which $b_1 = d_1$ and $b_2 = d_2$, both indicate

1. I thank Laurent Excoffier for his comments and suggestions. I am supported by Swiss NFS Grant No. 31-054059-98.

stabilization even when $b_1 > b_2$ (where presumably situation 2 is somehow associated with greater physical well-being—less instantaneous risk of death combined perhaps with lower parenting costs). The possibility that $K^*_1 < K^*_2$ cannot be excluded.

A result of this is that the Australian data in figure D of appendix C in the electronic edition (resembling figure 3) may be interpreted not only as confirming a regression line but also as less easily predictable when occurring in the righthand group (high- K) than when occurring in the lefthand group (low- K). Explained variance seems less with the righthand group, and a high K seems to allow for more erratic demographic histories. It is true that the data of the righthand group have an ascending tendency, but since the axis scales are only relatively known the question remains whether the converging effect at the righthand side of the graph is as large as Read and LeBlanc suggest. By focusing on regression rather than variance they limit somewhat the “multi” in the multitrajectory of their general argument.

Other uncertainties may crop up in the explanation of violent conflicts over resources. In appendix F Meggitt’s book (1977) on the Mae Enga is mentioned, and in it we find things also mentioned in the present article such as fission processes (p. 5) and competition over land as a scarce resource (pp. 13, 178–79, 183). A dense population might be seen as an easy explanation of most Mae Enga wars, but Meggitt (pp. 98–99) also mentions Mae Enga women’s disapproval of the initiation of these wars (“The land . . . does not command people to fight for it” [p. 99]). Another complicating factor here is that, because of clan exogamy, the political units are not identical to the demographic reproductive units. Mae Enga women apparently do not see the point of warfare between Mae Enga clans. In fact, one would expect here a desire for birth spacing due to women’s labor burden. Perhaps Read and LeBlanc can elaborate a bit on why at least some Mae Enga *men* deem(ed) warfare necessary, in contrast to women. Of course, an answer could be (appendix F) that a lowering of the birth rate is not easily accomplished, but this argument can be turned against the reasoning in factor 1 of model 1, where lowering of the birth rate, not increase in violence, is associated with increasing population density.

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Human population growth, along with problems of pollution, environmental degradation, and warfare, is the one of the long-term challenges facing humankind. With this paper, Read and LeBlanc advance the theoretical debate on human population socio-ecology by presenting an integrated set of hypotheses. The graphic models are useful tools for illustrating theoretical relationships between hypothetical variables. The theory takes account of interplay between micro-level phenomena such as re-

productive decisions and macro-level phenomena such as collective aggression and property arrangements. Multilevel connections between individual decisions and higher-level processes such as overpopulation provide a methodological challenge to anthropologists engaged in historico-explanatory, as well as applied, research. Read and LeBlanc’s models have implications for debates about the evolution of social complexity, human relations with regard to the environment/resources, and the anthropology of war. The theory Read and LeBlanc present deserves close attention. I have several critical suggestions:

1. The assumption that decisions are contingent upon individuals’ perceived self-interest certainly stimulates debate. On this assumption, Read and LeBlanc propose that altruism occurs only under “exceptional conditions.” Many will take exception to this characterization of human sociality. Read and LeBlanc leave aside inclusive fitness (Hamilton 1964), other theories of nepotism (Jones 2000), and the psychology and evolution of prosocial behavior (Batson 1991, Sober and Wilson 1998), while rightly critiquing the “standard model” supposition that fertility patterns naturally lead to replacement levels of growth. As much as decisions to stop or continue breast-feeding, definitions of the self are likely to vary according to sociocultural context. Altruism and extended nepotism are undeniably more than the exception in human history.

2. An issue that could use discussion, as one of the paper’s central concepts, is the definition of “carrying capacity” and the degree to which historic and prehistoric human population levels approach its estimated theoretical levels (see, e.g., Chagnon 1997, the protein debate). While recognizing that humans affect carrying capacity or “total available resources” through social behavior and technology, Read and LeBlanc also define K (n. 2) as the population level beyond which resources are inadequate for normal biological functioning. It is unclear whether carrying capacity is the resource base or the population level. If carrying capacity is extended through crosscutting ties across categories, such as *hxaro* exchange (Wiessner 1977) or seal-sharing partnerships (Wenzel 2000), the assumption of competition implying a territorial group’s exclusive access to resources needs further scrutiny.

3. Dealing with individual-level explanations for reproductive decisions in relation to resource density, Read and LeBlanc recognize the advantages of focusing on individuals, where detailed understandings of motivation and behavior can be documented (e.g., Mines and Gourishankar 1990, Shostak 1983). These understandings can be aggregated into higher levels, such as that of the network, but those of higher levels cannot be disaggregated to that of the individual (Bernard 1988: 47). Group identities are really categories, since they do not imply regular cooperation among individuals (a group), and should not be confused with collective strategies of defense and aggression. The applicability of group-level explanations, particularly group selection (Spencer 1967), to social phenomena such as collective defense and aggression should

be viewed skeptically (Williams 1966, Daly and Wilson 1983), and individual-level explanations for social phenomena should be explored. Furthermore, the theory could benefit from an explicit distinction between phylogenetic (evolutionary) histories of population growth and the proximate (decision-making) and ontogenetic (developmental) processes and conditions implied in the fertility, competition, resource accommodation, and ownership models.

4. Individual decision making in the model of fertility is integrated into the models of competition between groups, group reactions to resource variability, and multiple-level ownership, but the explanations of the last three models focus on group costs and benefits. For example, in the discussion of “decoupled corporate units,” if decisions lead to net positive or negative population growth, then what changes is the “number of corporate groups,” thereby creating conditions for conflict between resource-access/ownership units. In this argument, population size is stabilized only through “elimination of excess corporate units.” Beyond the group-selection problems identified above, the property model does little to account for the issues of hierarchical systems of ownership (Gluckman 1965) or systems of crosscutting (Schlee 1997) and collective (Humphrey 1998) property rights so common in non-Western societies. Access to resources is unlikely to be as homogeneous as Read and LeBlanc assume. There are individual winners and losers within categories of owners, as well as conflicting collectivities, and thus fertility varies with ecological parameters and inheritance strategies (Mace 2000). The complex issue of ownership and property has regained a central position in economic anthropology, and the consensus is that property has at least as much to do with relations between people as with control over resources (Hann 1998, Hunt and Gilman 1998).

Reply

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We are pleased with the broad range of perspectives and interesting directions for future consideration expressed in the comments. We do feel somewhat caught in the middle, though, as these are avenues to be explored were we writing a book rather than a paper. As it is, we had to delete sections of our original text because of page limitations and relegate other parts to the online version—not, as Cowgill’s implies, because of their secondary importance but on the basis of what we thought would be of greater interest to most readers. We will restrict our comments to a few areas of disagreement and to areas where elaboration is needed.

The concerns raised by van Dokkum about carrying capacity highlight the reason that K (which can be expressed in terms of density, or in terms of the maximal

number of persons sustainable in a fixed region) may be a less useful parameter (except as a way to identify an upper bound) than K^* (equilibrium population size in a fixed region). His comment that a population can continue to grow even with a declining growth rate points out the dependency of the logistic growth model on an assumed rate of decline in the growth rate. Similarly, his observation that stasis only means that the death rate equals the birth rate (ignoring migration) underscores the problem with using K as a predicted equilibrium value for a population.

Ziker and Ray identify another problem with K —that it does not take into account the effect of sharing resources over appropriate geographical and temporal scales. The importance of the pattern of sharing can be seen in the transition from a primate form of social organization (in which a troop tends to practice territorial exclusion) to a hunter-gatherer form of social organization (in which individuals have access to resources throughout the region used by the set of individuals who recognize one another as kin). As one of us has argued (Read 1987), two factors are critical for this transition. One is whether sharing of resources over a larger catchment area will lead to a qualitative change in the carrying capacity of that area in comparison with the carrying capacity associated with small groups practicing territorial exclusion as in model 3. The second is the centrality of culturally constructed kin relations expressed through a kinship terminology (Read 2001) that provide the basis for cooperation among individuals even without the face-to-face interaction that appears to be important for maintaining troop cohesiveness in primate species.

The importance of a culturally constructed basis for sharing is underscored by examples such as *hxaro* exchange among the !Kung San and the sealing partnerships of the Netsilik Eskimo (Van de Velde 1956, Balikci 1970). In both cases exchange partners are deliberately selected from individuals without a close (cultural) kin connection (Wiessner 1977; Balikci 1970: 137). Biological brothers may share for reasons relating to altruism and kin selection, but biological strangers share parts of a seal for nonaltruistic reasons that arise through culturally formulated sealing partnerships in conjunction with other dyadic relations that serve to minimize serious outbreaks of conflict in winter sealing camps. The degree to which this kind of sharing would continue to take place under conditions of significant intragroup competition or when resources were critically short (i.e., they were starving) is, however, less evident. The !Kung San have been below carrying capacity as hunter-gatherers for the reasons discussed in the text, and the ethnographic present for the Netsilik is a time period when the population is not undergoing the periodic starvation that occurred when caribou herds could not be found in the fall.

While we find the issues raised by Ziker with regard to group selection of considerable interest and our work may be relevant to them, we did not use the terms “selection” or “group selection.” In fact, the evidence avail-

able about conflict arising at any level of social complexity would seem to provide stronger support for cultural group selection (see below) than for biological group selection. To extend our thoughts beyond what we wrote, we note that, although some proponents of group selection have made unwarranted claims, as Ziker indicates, group selection can occur if three conditions are met: (1) variation in traits expressed at the group level occurs between groups, (2) intergenerational inheritance of traits occurs at the group level, and (3) there is differential survivability of groups according to group traits (Wilson 2002). That there can be turnover of groups under competition is not problematic, and so the competition argument establishes the equivalent of individual fitness at the group level. More problematic for group selection, though, is the mechanism by which group-level traits are expressed and inherited. This problem is reduced when we note that neither the group traits nor the inheritance need have a biological basis. In human societies social institutions and cultural constructs provide a means for traits both to be expressed at a group level (such as through an ideology of sharing) and to be maintained through time (via cultural reproduction); thus the first two conditions for group selection are met with cultural traits. Even more, the ability of a human group to assess and evaluate its conditions and then to act upon and change the characteristics of the group (Read 1990: 54–55; 1996) provides a fitness mechanism for cultural traits that transcends group extinction as the basis of a fitness measure. This ability also circumvents the unrealistic multigenerational time scale for change in cultural traits that would obtain if differential fitness arose only out of group extinction and replacement. We can call this process *cultural group selection* in contrast to biological group selection arising from biologically based traits and differential survivability of groups.

We implicitly use cultural group selection with our model 3 when we argue that if a coalition of groups leads to a marked increase in population density then there is a built-in “pressure” at the individual level for maintaining the larger group despite its costs. Under these conditions fission will eventually translate into individuals’ discovering that they have insufficient resources for survival, since most groups resulting from fission will have a population density that cannot be maintained without access to resources throughout the larger catchment area of the coalesced group. Thus individuals or groups will see it as in their interest to maintain a society organized at a larger scale despite its costs. That kind of assessment and restructuring can occur on a time scale that precludes either individual fitness or group fitness (in the sense of group turnover) as necessary properties for the change to occur.

We are not sure what Cowgill means when he says that our “central omission” is “the anticipated material benefits of children once the children have grown past infancy,” since our propositions are stated in terms of general processes rather than specific instances of those processes. “Material benefits of children” would be subsumed under proposition 6: “Individual choices are trig-

gered by individual experience and made in terms of individual self-interest,” where the experience and choices in this instance would relate to the material benefits obtained from offspring. We do not object to including material benefits obtained from children as part of fertility decisions so long as their inclusion is justified by the ethnographic context. In the case of foragers, however, young and even adolescent children contribute negatively to the caloric needs of families (Kaplan et al. 2000). There is more evidence for a positive contribution by children among farmers by ca. 10 years of age, but the literature is rather thin and vague on the subject (see Caldwell 1983, Mueller 1976, and Nag, White, and Peet 1978).

Inclusion of material benefits obtained from children would require modification of the form of our decision model, in keeping with our comment: “We do not claim that these three assumptions [of the model] are or can be expected to be universally true.” Our intent in focusing on a single relatively simple decision model was, as Fischer observes, to determine the model’s consequences when we take into account the following: (1) the relationship between the ideational and the material in decisions made by individuals or groups, (2) the implications of interaction among groups for the dynamics of any group or society, (3) the implications of social organization for the relationship between decision making (which may be through individuals, an individual consulting others, consensus in minimal social units, and so on) and the material conditions that have an impact on decisions, and (4) the implications of the scale of temporal and spatial variability in resources for short- and long-term stability and instability of different modes of social organization.

If we simply focused on the material benefits obtained from children we would capture only the local decision making by a family, not the implications of the decoupling of fertility decisions from their societywide population consequences. How can the high fertility rates implied by the material-benefits model in a labor-intensive agricultural context be maintained over long periods of time without leading to a disastrously large population? Egypt provides an illustrative example (see *Population and development* 1978), since local decision making plays itself out in a rural environment in which child labor and “old age insurance” have had significant impact on family-level fertility decisions but there is also an urban environment of population centers linked to the rural hinterlands that are integrally tied to population growth.

Prior to the 1800s the population size of Egypt varied from around 2 to 6 million persons with no particular long-term trend (Jankowski 2000). In the 1800s sewer systems and other sanitation measures were introduced that decreased the mortality rate substantially. This, in conjunction with economic expansion, initiated the high growth rate that continues to the present (Jankowski 2000:103). Rural family sizes have averaged about 4–5 living offspring per family, a growth rate that doubles the population each generation. While census data on family

sizes in rural families before the 20th century are lacking, it is likely that the pattern of women's having a total number of living offspring well above replacement rates is applicable for the past several hundred years. Peasant farming has changed very little during this period and has always been labor-intensive.

The basis for long-term stability in population size despite a high rural fertility rate is suggested by a graph of the rural population size versus crop area (see fig. 10) (crop area takes into account the multiplicative effect of double and triple cropping on the cultivated area). From 1887 (the first date for which census data are available) to the 1940s, growth in rural population size matched growth in the crop area, and thus the population size in rural areas stayed in balance with agricultural production. The rural areas achieved this balance by shedding excess population into the urban areas. From the 1940s onward (and augmented by the introduction of DDT spraying that further reduced the mortality rate) rural population growth appears to have exceeded the ability of the urban areas to absorb migration from the rural hinterlands and so rural population growth began to exceed growth in crop area. It appears that urban areas have acted as population sinks, allowing the rural areas to have high fertility rates without directly experiencing the consequences of a growing population.

Prior to modern systems of sanitation and medical care, urban centers also had high rates of mortality through periodic plagues that wiped out large portions

of the urban population (Sayyid-Marsot 1985, Petry 1998). This suggests that the long-term stability of Egypt's population, even with high fertility rates in rural families, was due to urban centers' having population boom-and-bust cycles as they grew in response to migration from the hinterlands. At the same time, the rural areas tended to be shielded from the effects of a growing population through migration to urban areas and so could continue with high fertility rates driven (as many have suggested) by the need for agricultural labor and for care in one's old age.

In pharaonic Egypt the situation may have been different, as there was proportionally a much smaller urban population. Pharaonic Egypt had 300–400-year intervals (the so-called Old, Intermediate, and New Kingdoms) of social stability punctuated by societal crises often accompanied by widespread famine and starvation (see Bell 1971). Malthusian checks may have affected the entire population, whereas under conditions of peasant agriculture in combination with urban centers such checks seem to be affecting urban more than rural populations.

The material-benefits argument, it should be noted, is subsumed within Becker's (1975, 1976) economic model of the family as a firm. We did not deal explicitly with Becker's model or with yet another prominent demographic model—Caldwell's model of intergenerational wealth flows (Caldwell 1976, 1982; but see critique by Kaplan 1994)—because our interest lies in the interplay between population dynamics, on the one hand, and

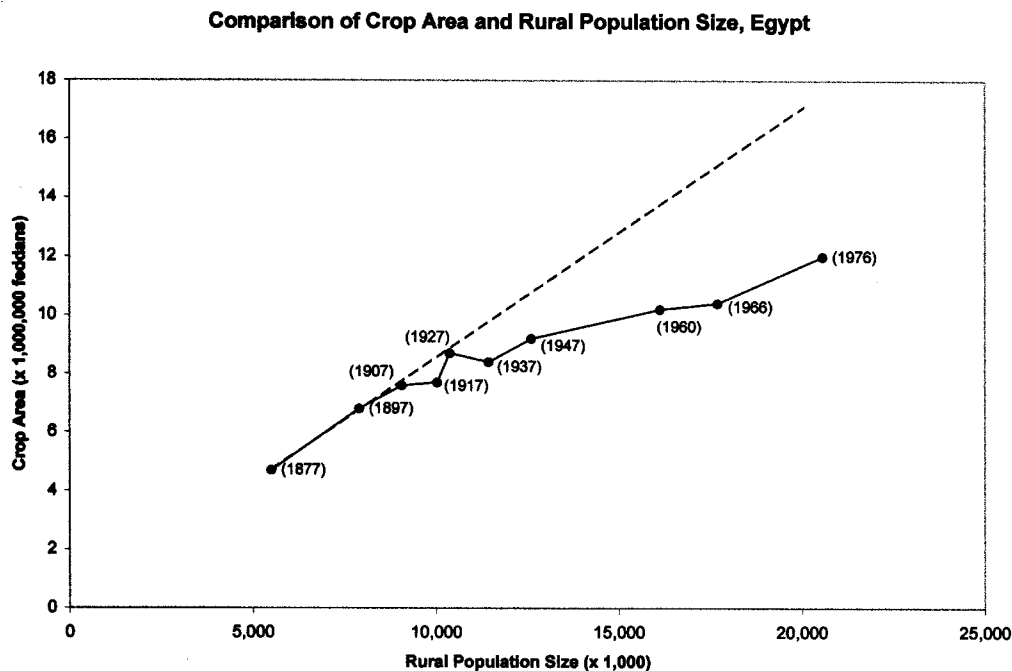


FIG. 10. Comparison of rural population growth with increase in crop area in Egypt, 1877–1976. Dashed line, constant ratio between population size and crop area. Numbers in parentheses are census years. Data come from Population and Development (1978:tables 2.5.1 and 3.1.4).

their broader cultural, social, and ecological context, on the other. This goal is increasingly shared by many demographers (see discussion by Pollak and Watkins 1993, Fricke 1997, Kertzer 1997, among others), though it is hardly a new perspective for anthropological demographers such as Bledsoe (1990), Greenhalgh (1988), Hammel (1990), Handwerker (1986), Kertzer (1995), Kreager (1985), and Townsend (1997). Demographers have made this shift because it has become increasingly evident that standard demographic theorizing (for example, demographic transition theory) has failed in not taking into account the impact of cultural setting: "The new era . . . is marked by a self-conscious search for methodologies that will allow demographers to incorporate cultural meanings into their explanation of demographic processes" (Fricke 1997:825). As noted by Caldwell and Caldwell in a study of high fertility in sub-Saharan Africa, that region "may well offer greater resistance to fertility decline than any other world region. The reasons are cultural" (1987:409).

The implications of cultural setting for fertility behavior and its effects on population size become more complex when the consequences of fertility decisions affect a woman's position with respect to both her natal group and the group of her husband (and possibly other social units). Cowgill's comment about the interest of others in her fertility is only one aspect of the multidimensional social aspect of fertility decisions. Another aspect is highlighted by Ziker's comment that "property has at least as much to do with relations between people as with control over resources"—though we find it difficult to imagine that it might be any other way, since one person's having control over a resource means that another does not and a relationship between them is inevitably involved. Nor need there be consistency among the individuals or groups involved in the various dimensions that bear on fertility decisions, as van Dokkum notes with regard to Mae Enga women's disagreeing with Mae Enga men about the need for warfare. It should be noted that the men did not like warfare, but their survival was at stake and they had no choice but to fight.

At a detailed level we need to incorporate all of this complexity into our modeling of human processes, and for this we agree with Fischer that "there is still a lot of work to be done." One of the promising methodologies for this work is multiagent simulation; "agent-based models support a *model-centred social science* that rests on strongly legitimated connectionist, autonomous, heterogeneous agent-based ontology and epistemology" and "agent-based modeling should emerge as the preferred modeling approach . . . [because] social behavior results from the interactions of *heterogeneous agents*" (Henrickson and McKelvey 2002: 7295).

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