

Fitness and Reproductive Trade-Offs in Uncertain Environments: Explaining the Evolution of Cultural Elaboration

Mark Madsen

InterNAP Network Services, 601 Union Street, Suite 1000, Seattle, Washington 98101

E-mail: mark@internap.com

and

Carl Lipo and Michael Cannon

Department of Anthropology, University of Washington, Seattle, Washington 98105

E-mail: clipo@u.washington.edu, mcannon@u.washington.edu

Received August 26, 1998; revision received December 9, 1998; accepted April 15, 1999

Dunnell (1989) proposed that cultural elaboration is likely a consequence of selection within uncertain environments. He developed the theory to the extent that it performs well in explaining the distribution of elaboration within eastern North America at regional scales. More detailed studies require development of the theory so that additional hypotheses and implications can be deduced. We draw upon theories of selection in fluctuating environments and theories about reproductive strategies to propose a simple model of selection for cultural elaboration in uncertain environments. The simple model has several general implications for the relationship between fecundity, elaboration, and other archaeological observables, including population age structure, spatial variation and mobility, and the character of environmental variability. © 1999 Academic Press

INTRODUCTION

Theory provides the maps that turn an uncoordinated set of experiments or computer simulations into a cumulative exploration.

Booker et al. (1989) *Artificial Intelligence* 40:235-282

Cultural elaboration, particularly in its most spectacular expressions in burial ceremonialism and monumental architecture, is a natural source of curiosity for archaeologists whenever and wherever it occurs. Archaeologists have given significant attention, for example, to explaining why Hopewell burials contain immense quantities of obsidian, copper, and other difficult-to-acquire materials and why Moche monumental architecture and

burials flourished for a time on the coast of Peru and then vanished. Indeed, the earliest archaeological work in many regions of the world has focused on cultural elaborations. Despite these efforts, no general explanation for elaboration has emerged. The explanations that do exist are theoretically deficient, as they characteristically contain a common thread traceable to the vitalistic foundations of nineteenth-century cultural evolution (Dunnell 1989). Until recently, however, there has been little effort aimed at explaining elaboration in light of scientific principles of human cultural evolution. Lacking a falsifiable, scientific framework for building explanations, archaeologists

are still faced with a critical question: why would people expend such enormous amounts of energy on tasks and objects seemingly unrelated to their survival or to reproduction?

If we accept the proposition that human cultural behavior evolves by the same Darwinian principles as the rest of the organic world, explanations for elaboration must be built using natural selection, cultural transmission, and drift (Dunnell 1980, 1989; O'Brien and Holland 1990). Exploring the outlines of such an explanation is the purpose of this article, not debating the wisdom or efficacy of a Darwinian approach to archaeology. Even if one assumes a Darwinian perspective for building explanations of cultural elaboration, no *single* explanation can be expected. Many possible explanations can be constructed within a Darwinian framework for any particular class of phenomena, of which all may be equally robust in terms of theory. Alternative hypotheses must be evaluated based on their ability to account for the empirical world in particular cases. Thus, our analysis in the present context is also not a *complete* explanation of cultural elaboration in all its forms and conceptions. A general explanation cannot exist because evolution is an endless interplay of general principles (e.g., natural selection, physiology, and constraints and rules for behavior) with the specific and contingent history of particular populations [Mayr 1959(1976):317]. The best one can do toward providing a "general" explanation for a phenomenon is to build increasingly comprehensive models that show how a set of invariant principles interact with variability to shape historical phenomena in consistent ways. General theories about a class of phenomena such as cultural elaboration can be *sufficient* for explaining the material world, but never *necessary*, since these theories cannot specify how the contingent history of a situation interacts with gen-

eral principles. Unlike general theory, explanations for specific instances of elaboration take the form of a narrative, showing how general principles interact with the history of a population to produce the archaeological record (O'Hara 1988).

Within the umbrella of Darwinian evolution, several investigators have begun to formulate and champion theories of cultural elaboration (Boone 1998; Dunnell 1989; Neiman 1998). Our purpose in this chapter is to explore and deepen our understanding of *one* particular theory, the "waste" explanation that was proposed by Dunnell (1989) in his discussion of elaboration in the archaeological record of eastern North America. In particular, we work to provide a quantitative model of Dunnell's "waste" explanation and to evaluate whether this model is sufficient for producing populations in which elaboration can be fixed by natural selection. Evaluating whether the theory used to construct our models is *necessary* and sufficient is outside the scope of this article. Such an evaluation requires attempts to apply and falsify hypotheses generated from the theory in the context of a particular evolutionary narrative. For a beginning to this task, we refer readers to the accompanying articles in this issue. After examining Dunnell's (1989) "waste" explanation in some detail, we examine "bet-hedging" models of reproduction in uncertain environments in order to provide a quantitative understanding of his model. We conclude our discussion by presenting details of our attempts to deduce some consequences of the model for common classes of archaeological evidence.

EVOLUTION AND CULTURAL ELABORATION

In an attempt to demonstrate the power of evolutionary theory, Dunnell (1989) examined the distribution of cultural elabo-

ration in eastern North America at the regional scale. Dunnell assumed that all organisms use, to some degree, energy in behaviors unrelated to their immediate welfare or reproduction. This assertion seems unremarkable to us, at least for vertebrates. Such expenditures of energy, termed "waste" by Dunnell, are present in all individuals at *some* level. That such expenditures are, in fact, unrelated to current survival or reproduction may seem controversial to some. Certainly, such expenditures of energy *appear* to provide a conundrum for an adaptationist argument if we had to determine the precise adaptive function that "wasteful" uses of energy performed. Rather than determine the function of waste, Dunnell attacked the problem from a different angle. He asked: Are there conditions under which expenditure of energy on elaboration or waste could be favored by selection and thus increase the level of investment within certain populations? The latter question simply seeks to assess whether selective environments exist in which waste could be a positive contributor to fitness. This is a very different kind of question than simply looking for the "function" of waste.

Dunnell's answer was that at least one set of conditions exist under which selection can favor waste within a population. If individuals (or families, corporate groups, production units, etc.) vary in the amount of energy they expend in "wasteful" activities, environments with unpredictable variance in resources could favor waste because these individuals would tend to have lower reproductive rates. In times of unpredictable resource availability, such individuals are able to better provide for themselves and their offspring through the cessation of the "wasteful" behavior (Fig. 1). Dunnell further reasoned that cultural elaboration should occur in those regions where resources would be unpredictable, rather than re-

gions where resources simply tended to be either rich or poor.

Dunnell's examination of "waste" in the archaeological record was motivated by consideration of the large-scale patterning of elaboration in eastern North America (Dunnell 1999, this issue). Within the Late Archaic and Woodland archaeological record of the eastern United States, cultural elaboration in the form of burial ceremonialism is frequent though not ubiquitous, either in space or in time. Burial ceremonialism can be traced to two separate lineages in the eastern half of North America. Elaboration in burial appears in the Maritime Archaic of southern Canada (e.g., Tuck 1984), apparently unrelated to developments further south. Extensive mortuary activity also occurs in the areas south of the Great Lakes within the phase-like entities called Glacial Kame and Red Ochre. Evidence is strong that these units eventually became the Adena and Hopewell cultural units (Caldwell 1958; Cunningham 1948; Dragoo 1963; Griffin 1948; Railey 1990; Ritzenthaler 1957; Webb and Snow 1945). Thus, in eastern North America, we have evidence of elaboration becoming prevalent within a historical lineage, eventually disappearing from the population with the rise of the so-called "Late Woodland" (see Dunnell and Greenlee 1999, this issue).

Geographically, burial ceremonialism first appears along the western and northern margins of the deciduous forest zone rather than in the biotically richer central or southern oak-hickory forest (Fig. 2). This pattern is *not* what one would expect if elaboration is the product of surpluses or leisure time. The pattern is, however, precisely what we would expect given Dunnell's explanation. Elaboration occurs earliest in those parts of the eastern forest where mast-producing species occur in low densities compared to forests further east or south and where resource levels would be the most variable (Buikstra 1981;

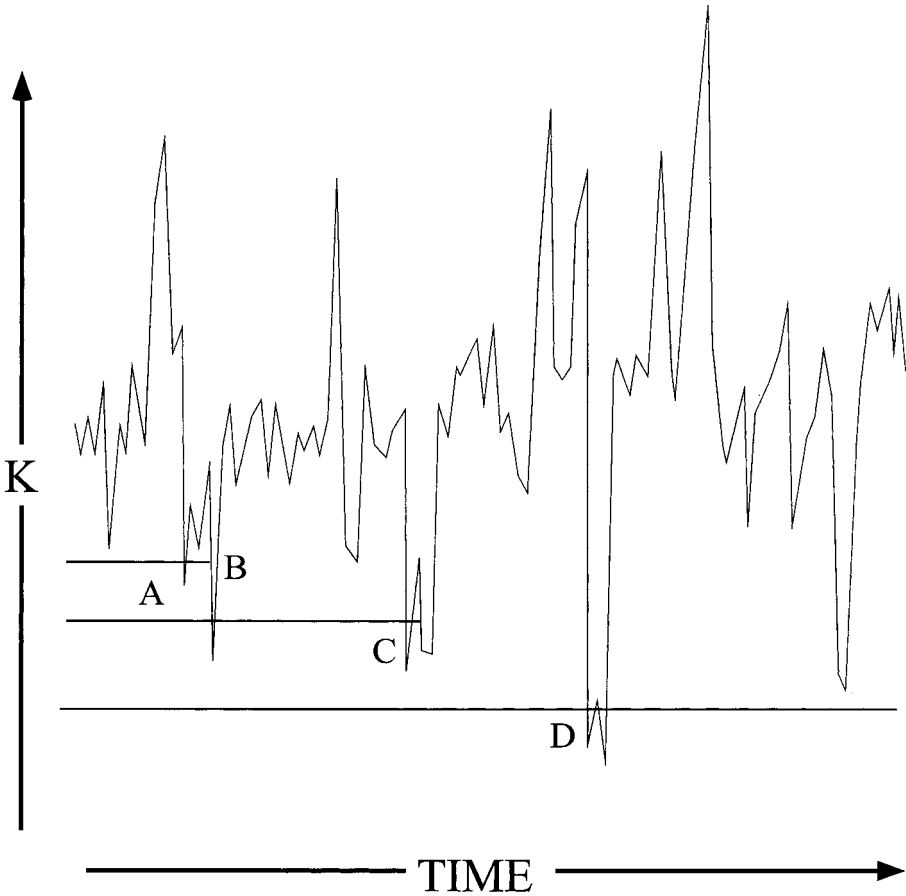


FIG. 1. Simplified model of the selection of "waste" from Dunnell (1989). Dunnell conceptualized waste as a behavior not involved in reproduction and that can act as an energy buffer in times of environmental shortfall. Here, mean "carrying capacity" (—) is held constant (i.e., no environmental trends and no change or difference in subsistence) while the carrying capacity at any point in time is highly variable. Three horizontal bars represent different populations in equilibrium at different sizes. All populations can persist through minor shortfalls in productivity (A); however, drastic shortfalls (B) and/or repetitive shortfalls (C) will cause extinction or emigration. In the short run, larger populations are more fit but, in environments which experience large unpredictable fluctuations in "carrying capacity," populations stabilized at smaller sizes by waste-type behavior will be at an advantage not only because of the smaller size but also because temporary abandonment of waste provides a reservoir of time to allow "intensification" (D).

Chapman 1975; Charles and Buikstra 1983).

Dunnell's "waste" explanation performs well when evaluated against the tasks it set out to accomplish. First, the model accounts for the temporal and spa-

tial pattern of cultural elaboration in pre-historic eastern North America, at least at the regional scales for which data are most readily available. Second, the explanation is a demonstration of how Darwinian analysis can be applied to an important

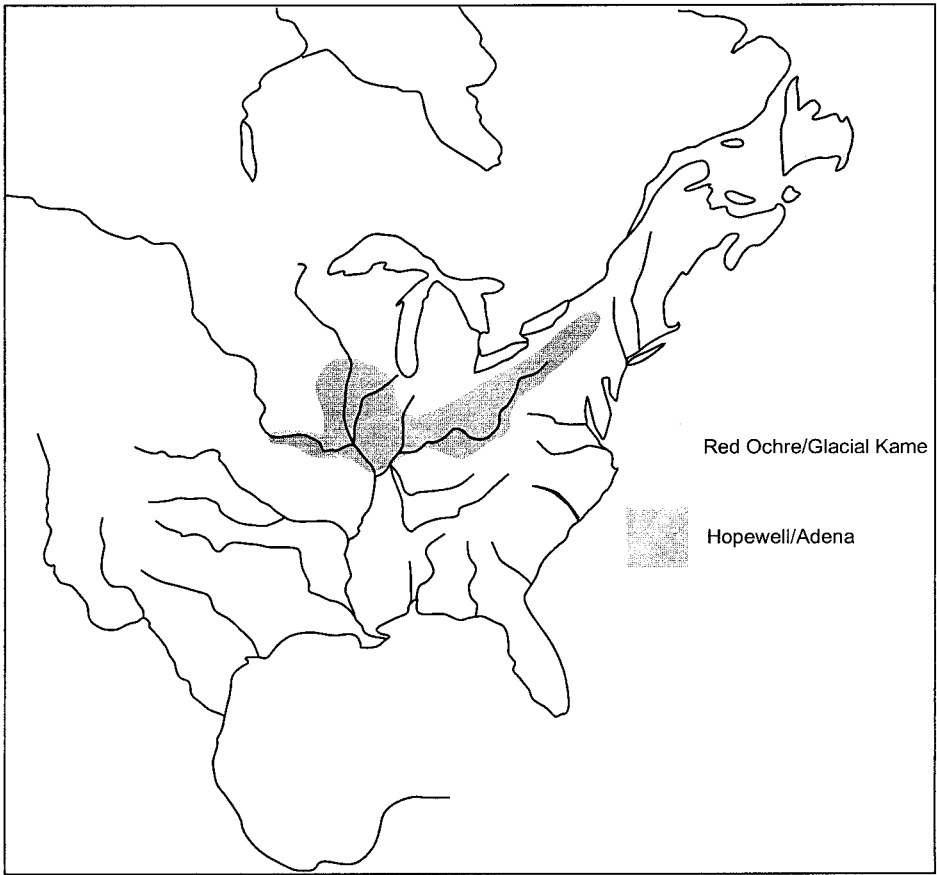


FIG. 2. Distribution of early cultural elaboration in eastern North America. The distribution of Hopewell/Adena and the Red Ochre/Glacial Kame mortuary complexes corresponds closely to the northern, marginal, and energetically unpredictable edge of the oak-hickory forests with the earliest evidence occurring in the most northerly and marginal environments.

archaeological problem that, at first glance, appears to provide a conundrum for explanation via natural selection. Although Dunnell's model is potentially applicable to parts of the archaeological record in other parts of the world, Dunnell did *not* set out to create a quantitative model of "waste" or to examine the evolution of waste within any specific population in his 1989 paper (Dunnell 1999, this issue).

The need for further theoretical development stems from the desire to use the explanation at finer scales of analysis, as

evidenced by the other articles in this volume. The original theory, however, is cast in terms too general to specify the quantitative relationship between reproduction, energy use, and environmental uncertainty for individuals, since Dunnell's focus was on the distribution of phenomena at regional scales. Our purpose here is to work within the high level structure of Dunnell's explanation and formulate a theory of the evolution of elaboration suitable for use in drawing hypotheses about individuals and populations.

FITNESS AND SELECTION IN TEMPORALLY VARIABLE ENVIRONMENTS

The key to expanding and developing Dunnell's explanation for cultural elaboration lies in understanding the effects that variation in resources has on fitness and the historical trajectories that selection can create for these traits. Environmental uncertainty plays an important role in evolution because traits take on adaptive value only in the context of particular environments. When environments vary over time, the fitnesses of traits necessarily fluctuate, even if the set of traits that any individual possesses have not changed. When environments vary slowly with respect to the speed with which replication of the traits occur, selection may "track" the changes effectively by slowly changing the frequencies of the traits within the population. When environments vary quickly with respect to the rate of replication, however, individuals may encounter many environmental circumstances that are more or less optimal for the traits they possess. Selection, in such circumstances, may yield a more complex trait history, including the possibility of apparently "suboptimal" traits increasing in frequency (Seger and Brockmann 1987). It is the scenario in which "suboptimal" traits succeed over more apparently "optimal" traits that we potentially find the conditions in which "waste" may persist in populations.

In this context, Dunnell's explanation for cultural elaboration can be seen as a specific case of a more general phenomenon—of selection acting on heritable variation in temporally uncertain environments. The argument is supported by regional patterns of cultural elaboration in eastern North America. Other investigators, following independent lines of reasoning, have produced models that are formally equivalent even if based on dif-

ferent proximate causes (e.g., Boone 1998). The theory, however, predicts something that may be seen by some as counter to strict Darwinian principles: individuals with the highest reproductive output do not necessarily have the highest fitness. At first glance this statement would seem to be false, since traditionally fitness is *defined* as reproductive success. To understand how lower reproductive rates can actually result in higher fitness values requires examining the nature of fitness.

What Is "Fitness?"

At a common sense level, fitness is meant to convey a quantitative sense of how well individuals are designed for survival or reproduction in their current environment. Beyond this vague notion, however, there are many uses of the term "fitness" in the literature of evolutionary biology (e.g., Dawkins 1982; Endler 1986; Michod 1999). For our purposes, the most important distinction between modern fitness concepts is the difference between assessing fitness at the level of individuals and measuring it as a property of classes of traits (Madsen and Lipo 1999). The goal of our discussion of fitness is to examine each fitness concept with respect to its utility in explaining the evolution of heritable traits. Thus, what drives our exploration is the pursuit of dynamic sufficiency in our understanding of fitness (Lewontin 1974).

Perhaps the most influential fitness concept is the notion that fitness is equivalent to the reproductive success of individuals. Often referred to as "individual fitness," this concept is the most common technical definition. Within evolutionary ecology especially, fitness is typically treated as design for individual survival and reproductive success, measured through proxies or "currencies." Despite its ubiquity, this notion of individual fitness is problematic. Hamilton (1964a, 1964b), for ex-

ample, noted the fact that natural selection will favor traits that cause an individual's genes to be passed on, regardless of whether the individual is, itself, successful at producing offspring. The classic example is, of course, sterile castes within social insects. If we hold that fitness is defined strictly as reproductive success then we must conclude that sterile workers have zero fitness because they produce no offspring. Hamilton's answer to this fallacy was to argue that individual fitness was too narrow a concept, since it ignored the effects on the transmission of traits that accrued by virtue of kinship. The broader concept of "inclusive fitness" is the way Hamilton and others solved problems with individual fitness, though the general problem remains. It is now generally appreciated among evolutionary biologists that individual and inclusive fitness simply may not capture all kinds of phenomena that can create evolution by selection within a population (Michod 1999).

Implicit in population biology models is another concept of fitness, equally important and in many ways more useful. In population genetics, fitness is a technical term that denotes the rate of increase of a *type* within a population (also known as the Malthusian parameter or Fisherian fitness of a type). This conception of fitness is due to the writings of Fisher and Haldane, who were worked along with Wright for formalizing the linkage between Mendelian genetics and Darwinian natural selection. Fitness, in this sense, is a statistical property of a class of individuals within a population, not a "capacity" of any particular individual. Fitness, in this sense, is not determined entirely by the heritable capacities of individuals. Because fitness is being measured as the rate of increase of a type, many factors beyond heritability can affect the value we measure, including frequency dependence and variability in the environment. The

fitness of traits is a *summary* measure of how heritable capacities interact with the environment and with other traits in the population (Michod 1999). As such, fitness measured solely at the level of traits is another way to solve the problems of the concept of fitness as reproductive success.

How do we relate the preceding definitions of fitness? Ideally, we would find that they are equivalent but distinct ways of looking at the heritable capacities of individuals. Sadly, this does not appear to be the case. At the level of traits, or "Fisherian" fitness, the most commonly used measure of fitness is the intrinsic (or "geometric") rate of increase of a trait (hereafter symbolized as " λ "). The intrinsic rate of increase of a trait is equivalent to the average lifetime of reproductive success by individuals carrying the trait. This equivalence is only valid, however, at a constant population density, without age structuring in the population and without frequency dependent effects. These and other conditions, however, are unlikely to be common. Consequently, under normal circumstances, lifetime reproductive success may not be a good general predictor for how heritable traits spread within a population (Charlesworth 1990; Murray 1997).

If the fitness of traits and the reproductive success of organisms are not typically interchangeable, we must determine the proper relationship of these concepts. Which conception of fitness is fundamental to evolutionary explanation? Although both uses of fitnesses have places in evolutionary studies, we believe that fitness should be considered a statistical property of traits, not as individual reproductive success, for several reasons. First, from a strategic standpoint most research questions focus on the history of traits or groups of traits, not on individuals. We must be able to express our models, therefore, in terms of the frequencies of traits. We do not claim, of course, that the indi-

vidual is irrelevant and that evolutionary theory can be reduced to a sterile "artifact physics." On the contrary, individuality is still critical in evolutionary models since individuals are the locus of behavior and thus form the interaction between traits and the environment in which they make a difference. Rather than reject the notion of individual reproductive success, we are merely saying that the statistical summary of these real-world interactions—fitness—should occur at the level of the traits we are trying to explain.

Additionally, while individual reproductive success is certainly a major reason why traits can outreplicate one another (especially for genetically transmitted traits), reproduction at the level of the individual is only a contributing factor. Frequency dependence and the environment within which traits are expressed may have equal or greater effects on the actual rates at which traits propagate within a population (Charlesworth 1990; Michod 1999; Seger and Brockmann 1987). Finally, reproductive effort itself is a complex outcome both of heritable capacities (both cultural and genetic) and selection operating within a context of trade-offs occurring throughout an individual's lifespan (Roff 1992; Stearns 1992). Fundamentally, reproductive effort and reproductive success are traits that *contribute to but do not constitute* the replication of all of an individual's genetically heritable capacities. Reproductive effort and reproductive success are traits that must be explained in terms of the spread of heritable information.

Moreover, reproductive success is only a measure of biological reproduction and thus genetic replication. Fitness, in the sense of reproductive success, has diminished explanatory value when individual capabilities are inherited through a combination of genetics and culture. Only a fitness concept that operates at the level of traits offers us the ability to disentangle

the effects of environment and interaction on trait frequencies as these effects are manifested through dual systems of inheritance. In the case of traits such as reproductive effort and reproductive success that are inherited through both cultural and genetic replication, it is clear that a concept of fitness that considers frequencies of traits rather than individuals is necessary to achieve our goal of dynamic sufficiency.

It is with the concept of fitness operating at the level of traits that we now are able to tackle the explanation of cultural elaboration. In our study of "waste," we can now build a model for cultural elaboration that links the fitness of a culturally transmitted trait with optimal reproductive effort in a temporally variable environment. Building this model requires several elements. These elements include an understanding of the dynamics of selection in variable environments, a theory of reproductive effort in variable environments, and a general argument linking the effects of a cultural trait (e.g., burial ceremonialism) to potential reproductive effort.

Selection in Temporally Variable Environments

Although few real environments are constant in productivity and structure, basic population genetics (and more recently, cultural transmission) models are constructed using an implicit assumption that selection pressures don't change. In other words, it is commonly assumed that the fitness of a trait is constant. Early exceptions included analysis of frequency-dependent effects by Wright, Haldane, and others, but systematic treatment of the dynamics of selection with stochastic fitness coefficients is a relatively recent endeavor. Dempster (1955) noted that in temporally variable environments, the fitness of a trait was best measured by the

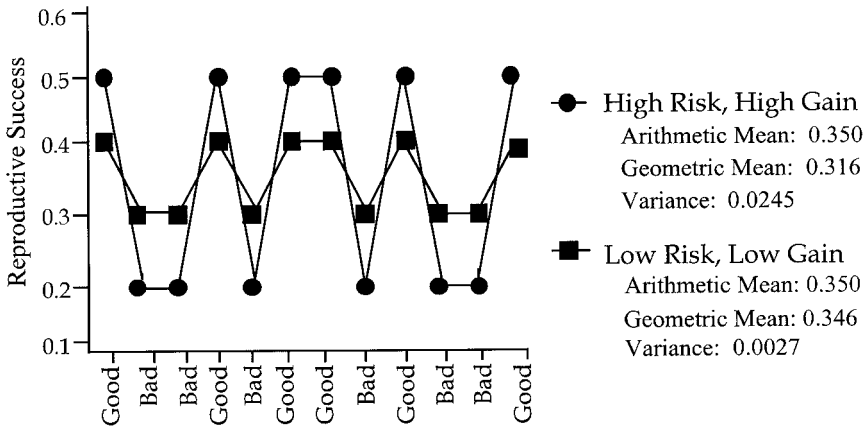


FIG. 3. Bet-hedging: a demonstration of the geometric and arithmetic means. Two reproductive strategies are shown: one with high birth rate or “fecundity” (circles) and the other with lower fecundity (squares). These strategies are placed into a series of “good” and “bad” years. During “good” years, both kinds of strategies succeed, but during the “bad” years resource shortages cause child mortality proportional to the number of children a parent needs to feed. Good years select for the high risk, high-fecundity strategy since the low-fecundity “type” increases at a lower rate than the high-fecundity type. During bad years, the payoff for the high-fecundity strategy is particularly low, since child mortality will preferentially affect those with larger family sizes. In a random mix of good and bad years the high-fecundity strategy experiences a greater variance in the rate at which it spreads in the population. The geometric mean of payoffs in each kind of period shows that the low-fecundity strategy has the higher rate of increase.

geometric mean of its fitnesses in each environmental state. Like the well-known arithmetic mean, the geometric mean is a measure of central tendency. The geometric mean of a series of numbers (of length n) is merely the n th root of the product of the numbers and thus is multiplicative rather than additive. Dempster recognized that since reproduction is inherently multiplicative, the best measure of fitness would therefore be a statistic that paralleled the behavior of reproduction. Gillespie (1977, 1991) and others have taken this fundamental observation and developed a theory of selection in stochastic environments (e.g., Tuljapurkar 1990).

Several predictions of the theory are quite general. First, stochastic variation in the fitness of a trait is often a sufficient condition for the maintenance of several different expressions of traits within a population. Second, the effects of spatial variation in the environment are quite dif-

ferent than temporal variability. Spatial variation, coupled with mobility, leads to fitness values that are the arithmetic mean of fitnesses in each environment, so long as the time required to move between different areas is small, relatively speaking. In such situations, few of the effects noted below are important (Seeger and Brockmann 1987). Finally, due to the multiplicative nature of replication, selection in a stochastic environment will tend to favor those traits that display the lowest variance in fitness across environmental states (Gillespie 1977; Slatkin 1974). The latter result is quite general and gives rise to a “bet-hedging” quality to evolution in temporally variable environments as well as to trade-offs in life-history traits such as reproductive effort.

A simple example illustrates the bet-hedging effect (Fig. 3). Take two reproductive strategies, one with high birth rate, or “fecundity” (shown in Fig. 3 as circles),

and the other with lower fecundity (shown in Fig. 3 as squares). In a constant environment and if the transmission of the "strategy" is reliably transmitted to descendants (whether genetic or cultural), we would naturally expect that the strategy with higher innate fecundity would come to dominate the population. The outcome in variable environments, however, is very different. Assume an environment partitioned into "good" and "bad" years. During "good" years, resources are assumed to be plentiful enough to allow parents of both kinds of birth rates to supply and care for their offspring. "Bad" years, on the other hand, are characterized by resource shortages in which parents may have difficulty feeding their offspring, with child mortality proportional to the number of children a parent needs to feed.

Good years, obviously, will select for the high-risk, high-fecundity strategy. During good years, the low-fecundity "type" continues to increase, but at a lower rate than the high fecundity type. During bad years, the situation is reversed. The payoff for the high-fecundity strategy is particularly low, since child mortality will preferentially affect those with larger family sizes. When one examines a random mix of good and bad years, it is easy to see that the high-fecundity strategy experiences a greater variance in the rate at which it spreads in the population. If we calculate the geometric mean of payoffs in each kind of period, we can see that the low-fecundity strategy has the higher rate of increase.

Variability in the Allocation of Reproductive Effort

The simple "bet-hedging" effect just described is quite general. One can use the mathematics of variance minimization to explain features of life insurance, strategies for purchasing and selling stocks,

and risk minimization in behavioral ecology as well as trade-offs concerning reproductive effort. In our analyses, we are concerned with how the simple mechanics of bet hedging and the geometric mean fitness effect may create evolutionary trade-offs in the allocation of energy to reproduction as opposed to survival or even cultural elaboration.

An important problem in the evolution of reproductive strategies is the optimal allocation of energy to reproductive effort over the whole lifespan, taking into account the "costs" of reproduction (Stearns 1992). In particular, models derived from reproductive effort theory that focus on clutch size are relevant to our concerns. All of these models have their roots in the work of David Lack who, in 1947, pointed out that birds should produce the number of eggs ("clutch size") which fledges the most offspring, even if the clutch size is below the maximum possible for a species.

In an environment where there is variation in the juvenile mortality rate that is correlated to the family size a parent must provision (due, for example, to variation in resources), individuals with larger numbers of dependent offspring should experience greater variation in bringing offspring to adulthood. At the level of traits, many individual traits can affect "clutch size," including rules for birth spacing and age at first reproduction. In a temporally variable environment, selection should manifest itself as an increase in the frequency of those traits that yield lower variance in reproductive success, due to the effects of the geometric mean principle discussed above. In a nicely designed experiment, Boyce and Perrins (1987) found exactly this effect in birds studied over a period of 22 years. We now turn to the expansion of this model in ways that potentially will allow us to link reduction of variance in reproductive suc-

cess with traits related to cultural elaboration.

A simple model of reproductive effort in a temporally variable environment. For a simple model of reproductive effort in variable environments, we begin with Schaffer's (1974) analysis of the effects of survival variation on optimal reproductive effort. Although the results are known to be much more complex in age-structured populations, Goodman (1984) has shown that Schaffer's model has the same qualitative behavior as more complicated models that incorporate increased demographic sophistication (e.g., Charlesworth 1990). Importantly, the Schaffer model, because of the importance of the linkage with population growth, is written in terms of "absolute" fitness (i.e., growth rates) rather than the relative selection coefficients of population genetics (Michod 1999). This feature of the model makes it particularly applicable in our study of traits related to reproductive rates that are transmitted both genetically and culturally.

In our simple model, the rate at which a set of traits contributes to population growth (i.e., the geometric rate of increase) is determined by three factors: fecundity, numbers of offspring, and adult survival. Equation 1 describes the relationship between these factors contributing to the rate of increase

$$\lambda_i = m_i s_i + S_i, \quad (1)$$

where m is fecundity for the trait group, measured in offspring per unit time, s is the proportion of those offspring surviving infancy; and S is the "adult" survival probability thereafter. The subscripts indicate that the rate is on a per-trait or per-trait group basis, not for the population as a whole. For simplicity, Schaffer (1974) combined fecundity and juvenile survival into a single value called "effec-

tive fecundity," a measure of the ability to produce offspring and raise them to independence. In what follows, therefore, $E = ms$.

For a particular phenotype, there are likely to be changing values of each of these parameters (effective fecundity and adult survival) in an environment that is varying unpredictably. Therefore, with the simplification that the environment may be represented by "good" or "bad" periods and that over the long run both occur in equal proportions, the mean rate of increase of a single phenotype is given by

$$\bar{\lambda}^2 = \lambda_g \lambda_b, \quad (2)$$

where the subscripts g and b stand for "good" and "bad" periods, respectively. The second set of subscripts for the trait group involved has been left off for clarity.

Environmental variability can be represented in Eq. 1 by introducing a parameter that equals the departure (d) from an overall "average" fecundity

$$\begin{aligned} \lambda_g &= E(1 + d) + S \\ \lambda_b &= E(1 - d) + S \\ \bar{\lambda}^2 &= [E(1 + d) + S][E(1 - d) + S] \\ \bar{\lambda}^2 &= (E + S)^2 - d^2 E^2. \end{aligned} \quad (3)$$

Across a mix of good and bad periods, there is a value for reproductive effort that maximizes the rate of increase of the phenotype within the population. To determine this value, we first calculate each phenotype's maximal rate of increase and then explore the relationship that exists between phenotypes with differing values of effective fecundity as measured by d .

The reproductive effort (F) that maximizes each phenotype's rate of increase is found by differentiating Eq. 3 with respect

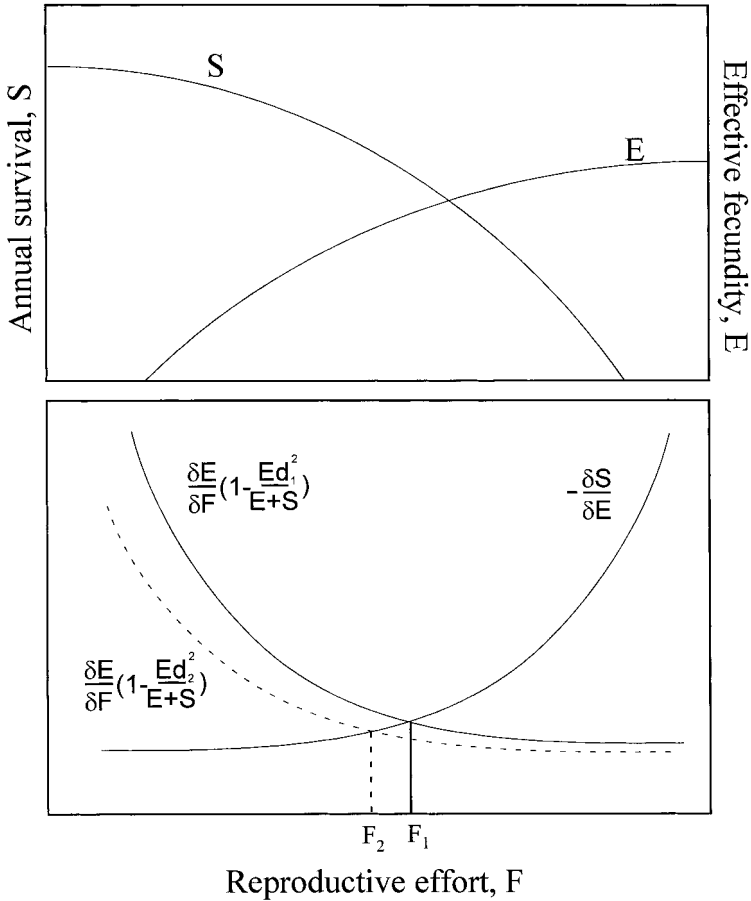


FIG. 4. The effect of adult survival and effective fecundity on optimal reproductive effort. In the top panel, we show that probabilities of adult survival (S) decreases with increasing reproductive effort and effective fecundity (E) increases with increasing reproductive effort because increasing reproductive effort likely means decreased parental investment per offspring. Taking the first derivatives of the functions (bottom panel), the intersection of the two functions is the optimal reproductive effort for a given trait group. Note that the *decreased* reproductive effort (dashed line, bottom panel) actually results in a greater probability of adult survival (F_2) than greater effort (F_1) although this strategy will yield smaller than maximum numbers of offspring at any one time.

to F and finding the value of F at which the differential is equal to 0.

$$\frac{\partial \lambda^2}{\partial F} = 2(E + S) \frac{\partial E}{\partial F} - 2Ed^2 \frac{\partial E}{\partial F} + 2(E + S) \frac{\partial S}{\partial F}. \quad (4)$$

After some algebraic rearranging, Eq. 4 is set equal to 0 when

$$\frac{\partial E}{\partial F} \left(1 - \frac{Ed^2}{E + S} \right) = - \frac{\partial S}{\partial F}. \quad (5)$$

If both adult survival and effective fecundity are concave functions of energy devoted to reproduction, the highest rate of increase will be achieved at an intermediate level of reproductive effort (Fig. 4). As shown in the top of Fig. 4, it is reasonable to assume that probabilities of adult survival will decrease with increasing repro-

ductive effort, simply because of the risks and costs associated with reproduction. Similarly, it is reasonable to assume that effective fecundity will increase with increasing reproductive effort, but will be concave instead of convex. The reason for this is that fecundity itself is only one aspect of the composite parameter "effective fecundity." The other component is juvenile survival, and it is reasonable to suppose that there is an inverse relationship between juvenile survival and reproductive effort, since increasing reproductive effort likely means decreased parental investment per offspring.

Thus, if we graph the first derivatives of the functions (following Eq. 5), the intersection of the two functions is the optimal reproductive effort for a given trait group (Fig. 4, bottom panel). The graph illustrates what Boyce and Perrins (1987) showed empirically: in temporally variable environments the geometric mean fitness effect will lead to smaller-than-maximum numbers of offspring at any one time.

Since it is clear that the environment has an important impact on determining optimal reproductive effort, in order to link the reproductive effort model to evolutionary dynamics our next step is to examine the effects of changing environmental structure. First, we can ask about the effects of increased variability in the environment. Within our model, the magnitude of the difference between good and bad years is measured by d , the departure from the overall average effective fecundity. As depicted in the bottom panel of Fig. 4, the effects of increasing d lead to shifting the fecundity curve to the left. Thus, increasing environmental variability will lead to selection for decreased reproductive effort in our simple model. This is an important conclusion of the simple model presented here, though the result is hardly novel. Boone's (1998) model of cultural elaboration, for exam-

ple, although based on models of r - and K -selection, describes the same selection pressure for intermediate levels of reproductive effort in uncertain environments. What differentiates the bet-hedging model from Boone's explanation is that we postulate no other causes for elaboration other than an energetic link between reproductive effort and elaboration. No proximate mechanisms such as costly signaling or conspicuous consumption are required.

The model presented here does require, however, an understanding of how cultural transmission interacts with the bet-hedging effect described earlier. With multiple-trait groups present in the population that vary in allocation of energy to reproductive effort, we can work backward from Eq. 3 to determine the rate of increase of each trait group. Obviously, the trait group whose reproductive effort is closest to the optimum for a given value of d will have the highest rate of increase. Thus, the square root of Eq. 2 represents the rate of increase for each set of traits. By scaling the λ -value of one trait group to that of another, we can examine the likely effects of linking reproductive effort to a culturally transmitted trait, since most cultural transmission models, like those in population genetics, are written in terms of relative fitness coefficients, not the absolute fitness described by λ .

Cultural transmission and the simple model of reproductive effort. The hallmark of cultural transmission is the fact that replication of cultural traits is not linked to biological generations, but is continuous throughout one's lifetime (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). Although a full analysis of dual-transmission systems would necessitate beginning with models that explicitly represent both genetics and culture, we believe that a simpler model is a good starting point for making deductions about the dynamics of reproductive effort in cultural

populations. To approximate the effects of continuous transmission through life history, we begin with Seger and Brockmann's (1987:194) analysis of a haploid model with overlapping generations and iteroparity. Although this model provides an excellent starting point to explore transmission and reproduction, it is *not* meant to represent our view of how bet-hedging and reproductive effort will be incorporated into theories of cultural transmission. Because the details of fitness measures depend critically on the nature of "mating" systems, future work will be aimed at incorporating stochastic variation in fitness within more detailed transmission models of the kind proposed by Boyd and Richerson (1985). The Seger and Brockmann model, however, provides a reasonable place to begin our discussion.

In our simplified model, the continuous nature of cultural transmission is approximated by overlapping "generations" and allowing all individuals "alive" at each time period in the model to continue transmitting. Overlapping generations are represented by allowing a proportion (s) of the current time slice's individuals to survive and replicate during the next interval. Since the fraction of individuals is assumed to be a simple random sample, some individuals will replicate many times during their lifetime, others only a few or once. Thus, each period of time is represented by a population with a proportion of existing individuals and a number of "new" individuals, interpretable as biological children and "naïve" in a cultural sense. The latter exist in the proportion $1 - s$. If we consider a population with two phenotypes, one representing low allocation in reproductive effort (A), and the other high allocation (B), the frequency of phenotype A in the population (p) is

$$p_{t+1} = p_t[s + (1 - s)W_t/V_t], \quad (6)$$

where W_t is the relative fitness of phenotype A in generation t (since fitness is variable over time) and V_t measures the population mean fitness in generation t as

$$V_t = 1 + p_t(W_t - 1). \quad (7)$$

In addition to measuring the degree of overlap between transmitting generations, the parameter s is proportional to the "amount" of environmental variability individuals tend to experience over their lifetimes in a changing environment. When s is near 0, individuals tend to experience only a few swings between environmental states. When s is near 1 and the overlap of generations nearly complete, however, nearly all individuals survive indefinitely relative to the model and live to experience many environmental states. We recognize that the method representing cultural transmission as overlapping generations in a lottery contest is hardly faithful to the kinds of complex environments we envision providing the selective environment for cultural elaboration. This simple model, however, allows us to examine the effects of temporal variability that occurs quickly or slowly with respect to an individual's lifetime.

To introduce environmental variability into our simple model, we again assume, as with Schaffer's analysis earlier, that variation is partitioned into "good" and "bad" periods, which occur in a stationary random distribution in approximately equal proportions. In such an environment, the equilibrium proportion of phenotype A is the frequency (p) that maximizes

$$f(p) = s\sqrt{V_g(p)V_b(p)} + (1 - s) \times [p\sqrt{W_g W_b} + (1 - p)], \quad (8)$$

where $V_i(p)$ are the population mean fitnesses in good and bad periods (Eq. 7)

and W_i are the individual fitnesses in good and bad periods (in fact, the W_i are merely the λ values in Eq. 3, scaled to frequencies).

Equation 8 is composed of a weighted average of two geometric means, with the population geometric mean fitness in the first term and the individual geometric mean in the second. When the parameter s is near 0, individuals experience few episodes of environmental variation and the right hand term of Eq. 8 contributes the most weight to the frequency of phenotype A in the population. In this scenario, the factor that matters is the geometric mean fitness of each phenotype across good and bad periods. Thus, when there is little overlap in transmission because traits are not transmitted culturally, only the fitnesses of each trait averaged across environments play a role in the dynamics of selection.

When s is large, however, more weight is given to the first term in the equation. The first term emphasizes the effects of the population's geometric mean fitness. Population mean fitness averages the fitness of all phenotypes across environmental states. In this scenario, both individual and population geometric means favor reduced reproductive effort in variable environments (and thus linked "wasteful" traits). The population's geometric mean fitness may be maximized, however, when there is a polymorphism of the two phenotypes rather than a pure population of high-fecundity or low-fecundity individuals (with associated linked cultural traits). The parameter s is large whenever there is strong overlap between generations, the condition used here to indicate a high degree of continuous cultural transmission. Thus, we predict that whenever the relevant traits are being transmitted culturally, selection in a variable environment could easily support the maintenance of a polymorphism of "wasteful" traits in linkage with lower re-

productive effort alongside high-fecundity traits with no associations to elaboration. Of course, outside the context of our simple model, all of these variables are continuous, and we would expect to see a continuous distribution of traits maintained in the population, if our argument holds despite the simplifications made here.

Limitations of the simple model. Apart from the obvious simplifications made in the formal model described above, there are deeper limitations to the model. The model is inadequate whenever there is age structure in the population or, in other words, whenever age-specific fecundities, adult survival probabilities, or probabilities of cultural transmission differ. Charlesworth (1990) and others (e.g., McNamara 1997) have outlined a theory of selection in variable environments for age-structured populations. Although the mathematics are complex compared to those used here, there is little evidence that the major qualitative conclusions are contradicted by these developments (Goodman 1984).

A more serious problem with the model described above lies in the simplification of the environment into "good" and "bad" classes in equal proportions. The simplification is made to make calculation of the geometric means simple for purposes of the formal model. Although seemingly harmless, we need to be sure that the simplification does not obscure details that might mitigate the utility of the theory for archaeological purposes. Gillespie's (1991) discussion of selection in variable environments is quite a bit more general than the model described above, but the mathematics are often analytically intractable. Gillespie uses diffusion approximations to explore the theory, and his conclusions support the general qualitative picture described here. Since we are particularly interested in exploring the dynamic properties of the model not easily expressed

through equations, we use a simulation approach here to validate the dynamic sufficiency of our model and to deduce from it implications that might be archaeologically relevant.

ARCHAEOLOGICAL EXPECTATIONS OF THE BET-HEDGING MODEL

The Linkage between Reproductive Effort and Cultural Elaboration

Dunnell's (1989) explanation of cultural elaboration can now be cast as a form of selection for variance reduction. Individuals that practice behaviors related to elaboration, in his model, tend to succeed in variable and marginal environments since on average they have lower fecundity due to energy that is channeled from reproduction into other uses. Those individuals with lower fecundity necessarily tend to have lower variance between good and bad periods than individuals with higher fecundity (and lower investment in elaboration). Therefore, selection favors the suite of traits that link lower fecundity with investment in cultural elaboration, as long as lower fecundity and elaboration tend to occur together. In terms of our model of reproductive effort in a temporally variable environments, this generalization can be explained as a consequence of variable environments in which selection favors those traits that have the lowest variance in their rate of increase across environmental states. When examining traits that determine reproductive effort, the geometric mean principle applies—a trait may increase within a population because it has the lowest variance in success even if it does not result in the highest reproductive effort and success. This conclusion runs counter to the common view that fitness is *defined* as individual reproductive success. This view is widely supported, however, both in mathematical models of fitness (Charlesworth 1990;

Gillespie 1977, 1991; Tuljapurkar 1990) and through consideration of the nature of fitness itself (Dawkins 1982; Michod 1999). That bet-hedging is a feature of real populations in variable environments has also been observed in animal populations (Boyce and Perrins 1987; Bulmer 1984, 1985; Cohen 1966; Nilsson et al. 1996).

A final step in developing a formal theory that underlies Dunnell's (1989) explanation of cultural elaboration, then, is to specify the connection between elaboration and the evolution of reproductive effort in variable environments. Since these traits potentially have independent transmission histories, it is clear that there is no *necessary* connection between reproductive effort and elaboration. Under particular circumstances, however, there can be an evolved *linkage* between them. This linkage is becomes clear by examining the possibilities afforded by separate cultural transmission of traits related to elaboration and traits related to reproductive effort. If we suppose that each trait has two states (high and low elaboration investment and high and low reproductive effort), four trait groups are formed by the combination of traits. Given the relationship between environmental variability, reproductive effort, and survival described above, we can see immediately that the phenotype investing large amounts of energy into elaboration *and* high reproductive effort should be selected against quickly in all conceivable environments. The other "pure" combination, low investment in elaboration and low reproductive effort, can be expected to exist in most populations and in most environments, though it is unclear at what levels.

Remaining are the two intermediate phenotypes. It is important to notice that there is no "mechanical" linkage between the two traits, only an evolutionary association in phenotypes. That is, these traits are free to vary in frequency within a pop-

ulation as a function of transmission and selection. What requires explanation is why the association might be preferentially successful, and thus evolve into a stable set of traits whereby the two traits are transmitted to others almost as a package.^{1,*} In some individuals, the balance between traits in the tradeoff may not be successful. For example, individuals who attempt *both* high investment into elaboration and high reproductive effort are likely to fall victim to severe environmental perturbations when they occur. Over time, we expect that selection will yield a series of associations between traits involved in energetic tradeoffs and the emergence of stable phenotypes with well-defined trait values for both investment in elaboration and reproductive effort. It is in this evolutionary sense that we link traits for cultural elaboration with traits affecting reproductive effort. In the proximate sense, however, the traits have little to do with one another during their transmission and expression as behavior.

Finally, evolutionary models are silent with respect to the forms that traits governing elaboration or reproductive effort take. Within the class of traits related to elaboration, for example, all we can say is that from the perspective of evolutionary theory, the traits must be costly and not contribute to reproductive effort and success. The form that the traits take is a historical matter, defined by innovation and novelty at some point in the past, passed down by cultural transmission within and between lineages, and modified enroute by the cultural analogs of mutation and "recombination." Similarly, traits governing reproductive effort may affect any number of biological variables. For example, birth spacing above the minimum, age at first reproduction following maturity, and reproductive lifespan each are likely to have a culturally transmitted

component. The evolution of these traits is likely to be complex, since selection *for* the cultural trait will likely result in selection *of* underlying biological parameters. Thus, when we consider the role of cultural transmission it is particularly clear that the linkage between elaboration and reproductive effort is an evolved, not mechanical, association.

The Relationship between Theory and Simulation Modeling in Evolutionary Archaeology

The next step in transforming this general discussion about variability in environments, reproductive behavior, and cultural transmission into a set of potential test implications is to expand and explore the sufficiency of the model in detail. It is one thing to argue that selection might produce change in the frequency of a particular trait; it is quite another to understand how those frequencies dynamically vary in particular environmental and phenotypic conditions. In this regard, simulation is a useful tool for developing specific expectations that investigators can use to develop hypotheses for empirical situations.

Simulation modeling, however, has a bad reputation in archaeology, primarily because many using it have not recognized that simulation plays a limited role in science. Simulation modeling should not be used to build "digital replicas" of a prehistoric system or society. Given enough lines of program code, the programmer can replicate virtually any behavior desired in their simulation model—but have we learned anything new by "programming in" all of the behaviors and effects we already knew existed?

While replicating the past is a poor use of simulation, it is entirely appropriate for exploring the sufficiency of a theoretical model or set of equations when solving the equations directly is difficult or impos-

* See Note section at end of article for footnote.

sible. One can also use simulation for deriving test implications from a mathematically complex model for testing against empirical data. Simulation is also an excellent means for studying the complex interactions of the components of a theory prior to performing expensive and possible destructive analysis. Finally, as Dunnell (this issue) notes, Darwinian evolution is fundamentally a stochastic theory; and in such theories no single test case is adequate to falsify a particular hypothesis. Instead, the test implications deduced from our models need to be balanced against a *distribution* of cases to determine the utility of particular model or hypothesis. Simulation has a part to play in such hypothesis tests and will help investigators develop expectations for how frequently, given chance and necessity, particular evolutionary trajectories might be expected.

In our minds, the best use of simulation in science is to explore the complex interactions of a set of *simple* assumptions in a statistically significant manner. For example, if one postulates that natural selection is responsible for the success of a given trait, a simulation that includes an explicit "selection" step will not tell the researcher anything new. Selection, in this case, has been "programmed in" from the very start. In contrast, if we begin with a model where agents inhabit a simple environment and obey simple rules for reproduction, foraging, and other behaviors, it is entirely appropriate to use the simulation to study the dynamics of selection among the agents and their environment. Such a model can be used to determine what environmental and demographic circumstances might create the observed trend in genotypes or cultural replicators, and thus the observed trend in phenotypes. The latter approach, termed "agent-based" or "individual-based" modeling, has been followed by Epstein and Axtell (1996) in

their "Sugarscape" model and is the approach we follow here.

Individual-based modeling is a relatively new paradigm in the simulation of systems with many interacting parts (Judson 1994; Kohler and Carr 1996; Langton and Hiebeler n.d.). Traditional approaches to simulation tended to represent the behavior of systems of individuals through differential equations representing the modal behavior of individuals taken as a group. Modeling selection in such simulations is unsatisfactory for our purposes, since one is completely specifying the nature and intensity of selection through the equations. Individual-based modeling offers a different approach. It allows the dynamics of selection to *emerge* through the natural interactions between individuals and objects representing their environment. In many ways individual-based simulation models, a philosophical outgrowth of object-oriented programming methods, represent a powerful technique for building and exploring the implications of selection models.

The change in perspective is significant. Researchers have come to appreciate that many of the complex phenomena we see around us are simply the global consequences of local behavior. Such studies have begun to revolutionize many aspects of economics and political sciences. In general, individual-based approaches have led to the development of theory that can better account for the stochastic nature of historical change. Agent-based models allow us to develop theories and explanations however necessary, but force us to state these explanations in quantitative terms. Because evolutionary theory is fundamentally quantitative, this feature of simulation modeling is enormously beneficial. In addition, agent-based simulations permit anthropologists to examine their assumptions, such as those posed by evolutionary ecologists, about behavior in complex scenarios and test whether (and under what conditions) these assumptions

can generate the classes of phenomena that they predict.

Simulations cannot, and will never be able to, generate *explanations* for a particular empirical case or class of phenomena. In contrast to what we call the “digital replica” approach to simulation, we believe that simulations are not producers of theory. The simulations we discuss below merely allow us to explore the theory developed in the simple model described above in situations that are more realistic. The purposes of such explorations are to deduce additional test implications or to judge the sufficiency of the explanation for the phenomena in question.

We based our simulations on a programming architecture known as SWARM. SWARM is an emerging standard for agent based modeling that has been under development at the Santa Fe Institute for the past several years (see <http://www.santafe.edu/projects/swarm/>). SWARM is unique in that it permits scientists to create very complicated models and to explore aspects of multidimensional interaction (requiring sophisticated programming) with minimal effort on the programmatic “mechanics” of the actual application (e.g., memory management, display management, etc.) For this reason, SWARM is serving as a central focus to a wide range of researchers in fields such as anthropology, economics, biology, physics, and archaeology. A number of archaeologists have begun using SWARM to examine issues such as the formation of villages and the effects of environment on agriculture (e.g., Kohler and Carr 1996).

Elements of a Simulation Model for Waste as Reproductive Trade-Off

To model life-history trade-off predictions in a variety of environmental conditions and to examine whether (and under what conditions) life history models can actually generate the classes of “wasteful” phenomena that they predict, we built an

agent-based simulation of these processes. The basic components of our waste simulation consist of a population of agents with variable phenotypes and a variable environment that consists of a single food resource, arbitrarily called “sugar,” following Epstein and Axtell’s “SugarScape” model. Agent phenotypes are created with the ability to move, to forage for food to meet metabolic needs, and a set of rules for interacting with others and reproducing new agents throughout their lifetimes. The features of the simulation include biological reproduction, realistically uncertain environments, and phenotypes composed of “genetically” and “culturally” transmitted traits.

To examine the effects of unpredictable environments on reproductive success, the rules of reproduction are an important component of our model. When agents reach a tunable minimum age for reproduction, they can reproduce provided they meet several biological and cultural conditions or thresholds. In order to reproduce, both females and males must possess a biologically determined minimum amount of energy as well as a surplus that is determined by a culturally inherited preference. Each of these traits maps to biological and cultural forms of energy storage. Females also have a biologically and culturally determined amount of time they must wait between births (i.e., birth spacing). If an agent that is ready to reproduce meets an agent of the opposite sex who is also ready to reproduce, a new agent is born. This new agent inherits biological parameters from its parents in a simple Mendelian manner (without crossover) and inherits an initial random sample of its parent’s cultural repertoire. Juvenile agents are born without fully developed movement or foraging capabilities; normal development yields adult capabilities according a linear function throughout “adolescence.” During development, parents actively invest en-

ergy into child rearing by providing children sugar resources to make up for any foraging shortfalls children may encounter due to partially developed subsistence skills.

A second key feature to our simulation is cultural transmission. The phenotypes of agents were modeled to be composed of traits that were transmitted both culturally and genetically. Cultural traits are transmitted as follows. As agents move around the landscape, they encounter one another opportunistically. When encounters occur, there is a probability that the agents will “talk” to each other and exchange cultural traits. In the simulation, cultural traits are modeled as “tokens” that can be one of three types. The first type can be taken without cost to an agent; such tokens represent “memes” that are selectively neutral. The second type invokes a cost in energy to the receiving agent. “Costly” tokens model the codes for phenotypic traits that use energy that can be put into reproduction but are instead “wasted” on activities or phenotypic elaboration that has no short-term fitness benefit (i.e., does not increase the intrinsic rate of growth, λ). Agents are not required to take these tokens but are given a cultural rule that determines the maximum token cost that an agent is willing to pay. The third kind of tokens are ones which code for cultural preferences for time between births, the amount of energy surplus required before having a child, and the maximum token cost the agent is willing to pay. These tokens have no cost and result in the replacement of the receiver’s preference by the preference of the transmitter.

Because tokens flow culturally and genetically through the population independent of one another, persistent phenotypes are emergent properties of token combinations that individuals possess at any given moment in time or, in other words, phenotypes are statistical counting

units and have no “reality” as types (Dunnell 1971). To account for the effect of agents with constantly changing phenotypes, the simulation tracks the reproductive success of phenotypic classes rather than individual agents. The analogous procedure in population genetics is to track the success of genotypes rather than individuals (Dawkins 1982; Roff 1992). Within our simulation, we do not model the norm of reaction or complex development; possession of the codes for a phenotype means that the phenotype is expressed, regardless of environment. We realize that lack of phenotypic plasticity and “meme”/environment interactions will be seen by some as a fundamental flaw but we believe that models should begin simply and expand in complexity only when warranted.

We have defined “wasteful” traits as behavior or structures that have a cost in the short run but are a benefit in reproductive success over the long run by lowering the variance of fitness. The “traits” that are passed via inheritance in our model, however, refer to propensities, not behavior. Thus, we need to track both the “codes” that agents possess and their actual expressed behavior, since the latter involves an element of chance. In our simulation, we examined the distribution of values across three variables of interest: the agent’s interbirth interval, the amount of sugar stored, and the energy spent on cultural tokens. Phenotypes for tracking the amount of “wasteful” behavior were created by treating each variable as a dimension and dividing each dimension into a series of modes and by creating a paradigmatic classification. Though selection is not explicitly programmed into the simulation, we expect that the frequencies of phenotypes in the population will change as a consequence of differential reproduction and cultural transmission.

In order to examine the effect of selection on the frequency of these pheno-

types, agents were subjected to a suite of environmental conditions in which the rate of sugar growth was varied. The kinds of environments we studied included constant, cyclical, and chaotic growth and environments with periodic failures. The effect of spatial variability and mobility was examined by allowing agents to move greater or lesser distances to search for resources. Tracking the number of children each individual produced and their lifetime expression of “wasteful” behaviors permitted us to calculate the geometric and arithmetic mean fitnesses for phenotypes. In addition, we tracked changing patterns of age structure of the population, population size, and variances over time as well as the distribution of wasteful behaviors in the population.

Discussion of Archaeological Expectations

Though the SWARM simulation we constructed contains relatively few dimensions along which individuals can vary, the parameter space of “possible” simulation runs is still enormous. In addition to the large parameter space, the need to examine evolution in stochastic environments across a large number of simulation runs means that the results discussed below are necessarily preliminary, even though they are the results of observing many runs over a wide set of parameters sampled from the available space. Nevertheless, the simulation runs shed light on the relationship between “wasteful” behavior and environmental effects, mobility of agents, age structure, and the distribution of wasteful phenotypes across populations.

The effect of environmental uncertainty. The most general result of the model is that marked unpredictability in the environment is indeed capable of creating selection for “wasteful” behavior within the simulation populations. Figure 5 depicts the results from four different simulation

runs in two different environments—predictable (left) and unpredictable (right) with two different populations. One population was composed of only wasteful phenotypes while the other population was made up of only nonwasteful phenotypes. In a constant environment, both the arithmetic and geometric mean fitnesses of nonwasteful phenotypes were uniformly higher than those of the wasteful phenotypes. In other words, in constant environments, selection did favor those trait complexes that maximized the reproductive effort of individuals. In unpredictable environments, however, “wasteful” phenotypes tended to have higher geometric mean fitnesses than nonwasteful variants, all other things being equal, and consequently increased in frequency within the population. Thus, as the bet-hedging hypothesis predicts, the general premise of the “waste” model appears to hold true. Additionally, we believe that the model is correctly constituted, since rarely were populations driven to fix either “wasteful” or nonwasteful phenotypes; under all reasonable circumstances the population was composed of a mixture of different levels of investment in “waste,” as one would expect when individuals experience many environmental fluctuations during their lives.

Mobility. Unlike our simple formal model of bet-hedging, agent-based simulation allowed us to examine more complicated implications of the model such as the effects of spatial variation and migration. Understanding the effects of mobility are critical to real-world applications of evolutionary models, since settlement patterns are directly linked to subsistence and thus to fitness. Additionally, settlement patterns are relatively easy to study from regional archaeological data, thus forming a natural way to begin applying evolutionary models to the record. From a purely theoretical perspective, mobility and migration act as a form of income

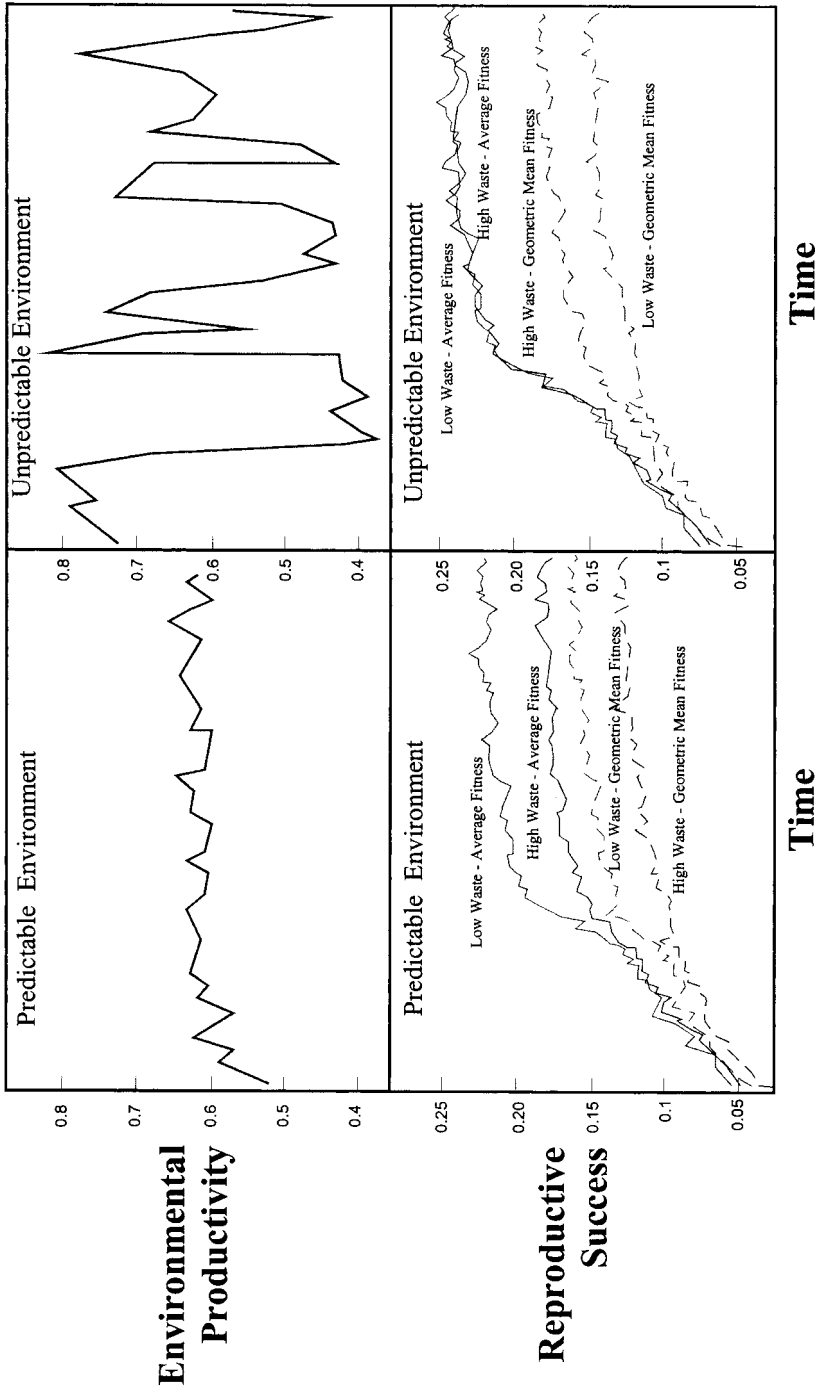


FIG. 5. Demonstration of how "wasteful" phenotypes are more successful in variable environments than less "wasteful" phenotypes. This figure presents the results from four different simulation runs in two different environments—predictable (left) and unpredictable (right) with two different populations. In each environment, two kinds of populations were introduced: one population was composed of only wasteful phenotypes and one population made up of only nonwasteful phenotypes. In a constant environment, both the arithmetic and geometric mean fitnesses of nonwasteful phenotypes are uniformly higher than those of the wasteful phenotypes. In unpredictable environments "wasteful" phenotypes have higher geometric mean fitnesses than non-"wasteful" variants. These phenotypes consequently increased in frequency within the population.

averaging, so long as the fitnesses of a single phenotype are not spatially autocorrelated (Levene 1953; Seger and Brockmann 1987). Migration tends to have an ameliorating effect on the tradeoff between the total number of children and the number of surviving children. That is, individuals can lessen the effects of uncertainty by moving from an area of low productivity to one of high productivity. Figure 6 summarizes a set of runs designed to examine the effects of mobility. In two sets of simulation runs, we systematically varied the "search radius" within which individual agents were able to search for and move toward energy resources, indicated pictorially in Fig. 6 by the length of arrows linked to agents.

The simulation runs on average demonstrated that populations of agents that are given the ability to see and move over larger distances evolve lower levels of "waste" than populations that are more restricted in their movement. This finding is consistent with what evolutionary biologists have observed with respect to the bet-hedging effect in other species (see Seger and Brockmann 1987; Charlesworth 1990; Roff 1992). It also potentially informs on the relationship between cultural elaboration and sedentariness. It has often been argued that cultural elaboration results from resource intensification and permanent settlement (see discussion in Sterling, this issue). In our simulation of bet-hedging effects, however, levels of wasteful behavior became fixed within the population despite the fact that none of the agents were immobile and dependent upon a single location in the environment for subsistence. This effect demonstrates that sedentariness, as it is usually thought of, is not required for selection to favor "waste." Sedentariness merely increases the strength of selection for waste in unpredictable environments.

Demographic structure. Selection for waste was also linked to the average age

distribution of the simulated populations (Fig. 7). During each simulation, we recorded the age at death of each individual, allowing us to study the probable effects of bet-hedging on skeletal populations. We also took periodic "censuses" of the living population in order to examine the demography of our simulated populations. Across our simulation runs, populations with higher frequencies of "wasteful" behavior tended to have a equal ratio of adults to juveniles within the population and in death assemblages. Runs in which waste was selected against tended to yield populations with higher juvenile mortality as well as a large proportion of juveniles to adults in the living population derived from higher birth rates. Thus, the tradeoff effect acts not only to increase the geometric mean fitness of the population, but also to alter the age distribution of the population through increased survival as well as the mechanical effects of lower birth rates on the age structure of a population.

Phenotypic polymorphism. Finally, we found that we could measure the degree to which a "wasteful" phenotype can coexist with other phenotypes in a stable polymorphism (Fig. 8). To do this, we scaled phenotypic dimensions such as culturally transmitted birth spacing intervals, accumulation of sugar, and average expenditure of energy on "expensive" culturally transmitted traits along an index of "wastefulness." Placing the populations into predictable and unpredictable environments, we examined the population distribution across this index. As Fig. 8 shows, while the *mean* value of this "wastefulness" index is not affected by selection, markedly unpredictable environments yield phenotypic distributions that are strongly *right-skewed*, or skewed in the direction of having more "wasteful" phenotypes. This finding has significant potential for archaeologists seeking to measure degrees of "wastefulness" in the

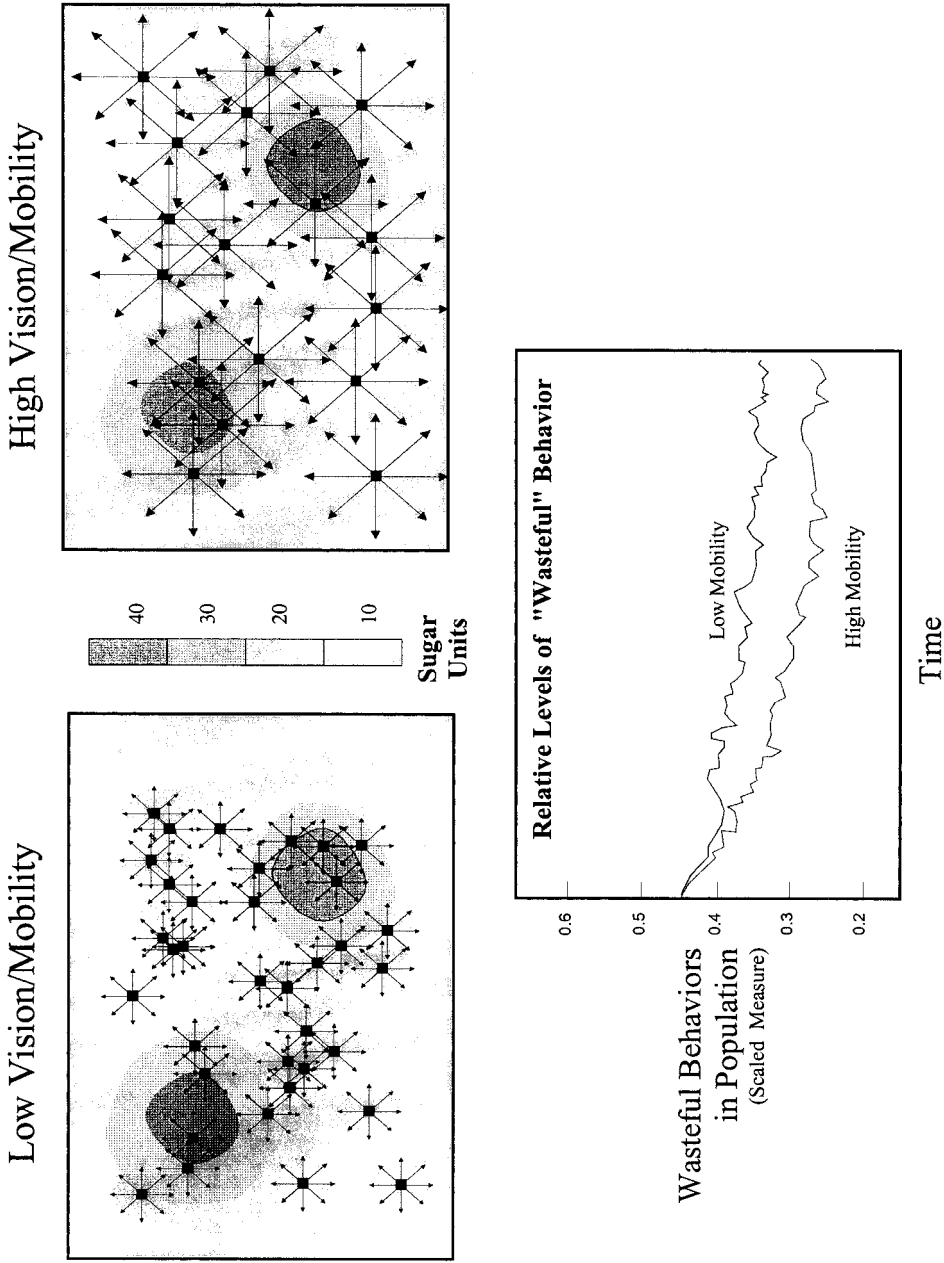


FIG. 6. The effect of mobility on selection for "wasteful" behavior. This figure presents the results of two sets of simulation runs in which we systematically varied the "search radius" within which individual agents were able to search for and move toward energy resources. The search radius is indicated pictorially by the length of arrows linked to agents. Populations of agents with higher mobility (upper right panel) evolve lower levels of "waste" than populations that are more restricted in their movement (upper left panel).

Population Age Distributions

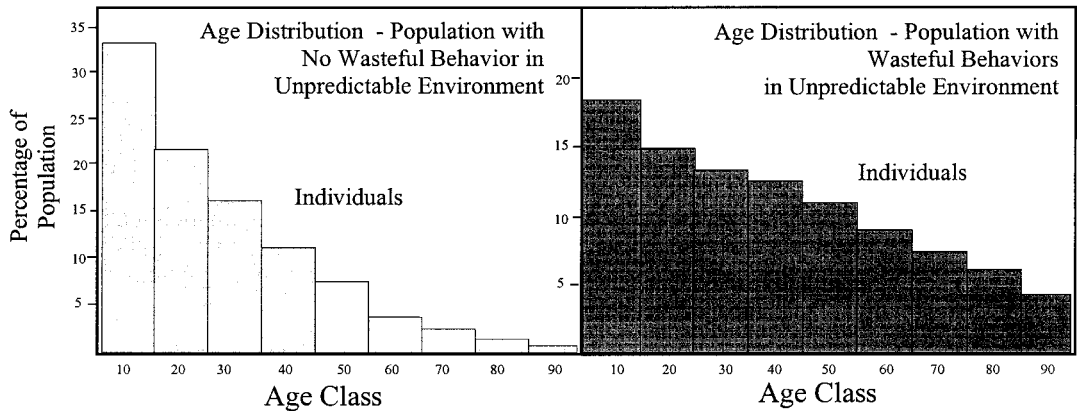


FIG. 7. The effect of “wasteful” behaviors on age distributions. In simulation runs in which waste was selected against (left panel), populations tended to have higher juvenile mortality as well as a large proportion of juveniles to adults in the living population. In populations with higher frequencies of “wasteful” behavior (right panel), age distributions tended to have an equal ratio of adults to juveniles within the population.

archaeological record. Given the difficulty of measuring the “wasteful” behavior of *individuals* in archaeological circumstances, these results show that the overall distribution of elaboration within a population, even scaled at ordinal levels, might be sufficient to examine bet-hedging effects in real archaeological data.

Consequences for empirical research. Although selection can favor costly artifact classes in variable environments due to the bet-hedging effect, the model does not specify the form that such artifacts can take. Waste will follow historically contingent trajectories within each cultural tradition. Determining the form that any particular instance of “waste” takes is a matter of historical analysis that requires examining a particular dataset in a particular ecological setting. Additionally, the form that “wasteful” artifacts take potentially provides the variability for other kinds of selective processes. For example, artifacts involved in trade-offs in reproductive effort and success may also be related to costly signaling, functional specialization, and redistribution. It is impor-

tant to recognize that because of diminishing returns for any one kind of energy expenditure, there are often multiple evolutionary solutions for reducing variance and creating the life history trade-off effect. The fixation of any particular trait may require additional fitness consequences resulting from food redistribution and other kinds of functional organizations.

In such cases, these proximate mechanisms can act to intensify selection for costly artifact classes. Increased investment in mound building, for example, may be driven by the bet-hedging effect. However, the fixation of mound building within the population may be due to its role in creating a large-scale food sharing system. An important lesson that archaeologists can learn from these results is that they should pay close attention to the frequency of wasteful traits *within* populations, which may be the result of a suite of varied and complex evolutionary forces.

In addition to examining the historical trajectories for artifact classes, archaeologists must also be aware of the role that

Unpredictable Environment

Distribution of Waste Behavior

mean = 32.234
s.d.= 25.289

Individuals

Scaled Waste Behavior

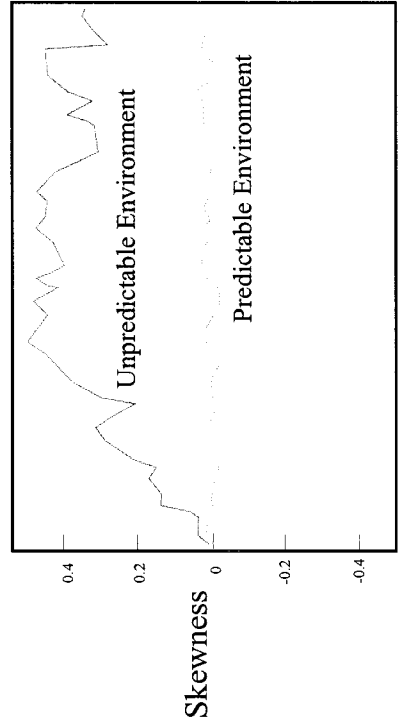
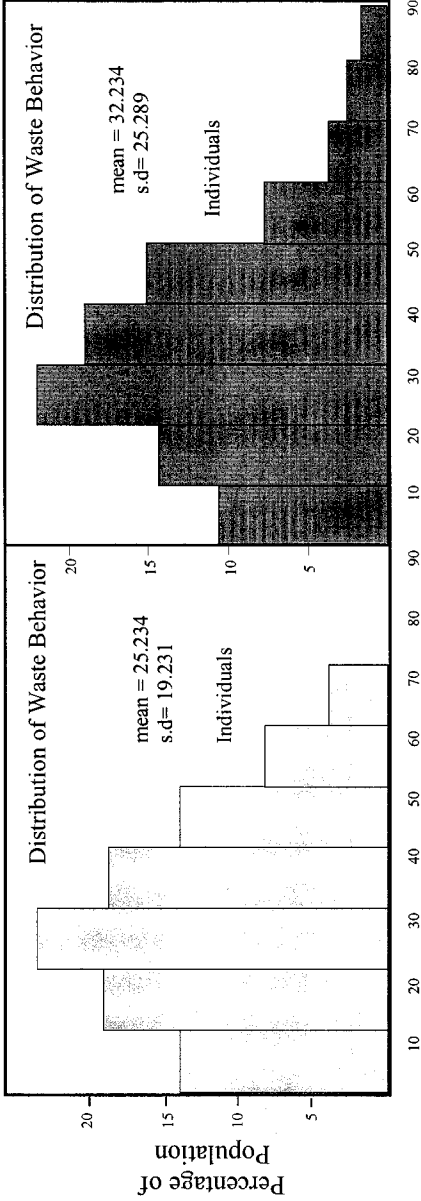
Predictable Environment

Distribution of Waste Behavior

mean = 25.234
s.d.= 19.231

Individuals

Scaled Waste Behavior



subsistence systems play in creating the selective environment for “wasteful” traits. The ability to store resources and buffer shortfalls with multiple sources of food, for example, potentially decreases the bet-hedging effect and thus selection for “wasteful” traits. On the other hand, populations that depend upon a single food staple or live in sedentary, dispersed settlements may provide particularly strong selective environments for “wasteful” traits since small changes in productivity have large impacts on these kinds of settlement systems. Also, as we mentioned earlier, one clear result of the model is that “wasteful” traits will increase as mobility decreases within an uncertain environment due to geographic restrictions, population in-filling, or changes in settlement patterns. Thus, there should be a clear relationship between the level of “wastefulness” seen in populations and the details of settlement strategies.

Like the study of subsistence systems, skeletal data may also play a role in examining how the bet-hedging effect is expressed within a particular population. As has been discussed, life history trade-offs manifest themselves in biological variables, such as population age distribution and birth spacing intervals (e.g., Katzenberg 1996; Skinner 1997). Some of these variables should be measurable in carefully controlled skeletal samples through estimates of age at first birth and age at death, though considerable additional simulation work needs to be done to focus

on how the effects discussed above would be manifested, if at all, through the taphonomic and analytic filters imposed by most skeletal death assemblages.

Finally, fine-grained studies of environmental conditions will provide one of the strongest avenues of information for studying the bet-hedging effect in the archaeological record. New high-resolution studies of past climatic conditions provided by ice cores, deep sea drilling, tree rings, and coral growth records will undoubtedly serve as a rich source of data for archaeologists examining the selective conditions for “wasteful” phenotypes (e.g., Meeker et al. 1997; Melice and Roucou 1998). These new, yearly and decadal level records of past rainfall and temperature can easily generate information about the amplitude, frequency, and magnitude of environmental failures. It is important to recognize that single or isolated environmental downturns are not sufficient to create the bet-hedging effect. In order for there to be selective pressure for wasteful behavior, individuals must experience at least several environmental perturbations. It is the *transition* between good and bad periods of environmental productivity, and thus fitness, that creates variance in success for wasteful vs non-wasteful phenotypes. Studies of environmental variability should focus on the examination of the variability using such statistics as the coefficient of variance, which consider the effect of differences in means on the absolute amount of vari-

FIG. 8. Polymorphic population compositions in predictable and unpredictable environments. Using a scaled measure of “wastefulness” composed of phenotypic dimensions such as culturally transmitted birth-spacing intervals, accumulation of sugar, and average expenditure of energy on “expensive” culturally transmitted traits and placing the populations into predictable and unpredictable environments, we examined the population distribution across this index. While the mean value of the “wastefulness” index between the two kinds of environments was not markedly different, the skewness values for the two populations are markedly different (bottom graph). That is, unpredictable environments yield phenotypic distributions that are skewed in the direction of having more “wasteful” phenotypes (upper right). Populations in more predictable environments, on the other hand, are relatively evenly distributed (upper left graph).

ance. In addition, there cannot be an absolute requirement for the minimum amount of variability that populations must experience for there to be selection for wasteful "phenotypes." The amount of variability necessary to generate the bet-hedging effect is always a product of population densities, subsistence systems, settlement strategies, and the overall productivity of the environment.

CONCLUSIONS

In this article we have attempted to use a simple mathematical model and agent-based simulation to understand the conditions under which selection would favor the life history trade-off that may be expressed in "wasteful" phenotypes. It is important to recognize that the explanation provided here is *sufficient* but not *necessary* for any particular case of cultural elaboration. First, given any particular case, only some of the many evolutionary solutions to coping with unpredictable environments result in the expression of wasteful behaviors. No individual must engage in wasteful behaviors in order to cope evolutionarily with variability in the environment. Second, cultural elaboration may be favored by selection for reasons other than unpredictable environments. These selective environments potentially include selection for costly signaling, functional specialization, and functional integration. Understanding if the bet-hedging effect is responsible for increasing investment in wasteful behavior is an empirical matter that can be solved by looking at empirical effects deduced from the model, such as skeletal age distributions.

That explanations of cultural phenomena are sufficient but not necessary also means that it will never be possible to examine the characteristics of a given environment and predict the equilibrium frequency of "wasteful" phenotypes.

Moreover, the form of "wasteful" behavior or artifacts is historically contingent. Rather than being predictive, the life-history trade-off hypothesis is a relatively simple *null* model for the expected distribution of traits related to the bet-hedging effect in the archaeological record.

Increasing the sophistication of the simulation may well enhance the model's ability to account for variability in cultural elaboration in space and time, however. For example, although there may be complicated rules for translating inherited information into behavior (in other words, decision making algorithms), this initial model was purposely built to be very simple. That is, we were simply seeking to determine if the actions of transmission and selection are adequate for generating the conditions necessary to favor "wasteful" kinds of phenotypes. More sophisticated models for translating phenotypic variables into behavior along the lines of those built by Boyd and Richerson (1985) and Cavalli-Sforza and Feldman (1981) or even the newer work on "meme" theory by Gabora (1997) and others (e.g., Lynch 1996; Lynch and Baker 1986, 1993, 1994; Payne 1996; Pocklington and Best 1997) may increase the sufficiency of the theory.

ACKNOWLEDGMENTS

First and foremost, we gratefully acknowledge the inspiration, comments, and corrections given to us by R. C. Dunnell. Obviously, this work is an outgrowth of his earlier research, so in a very real sense this article would not exist without his help. We are also thankful for comments on the original manuscript by Deborah Schechter as well as discussion by Eric A. Smith and his students. Kim Kornbacher assisted the authors by editing the final manuscript. Portions of the original research for this article were performed by Madsen with support from the National Science Foundation Graduate Fellowship program and with assistance from Sigma Xi.

NOTE

¹ From the point of view of an organism, the relationship between the traits for investment in elabo-

ration and reproductive effort is the "somatic budget," which is the notion that there is a finite amount of energy that an organism can expend. From this somatic budget individuals must allocate energy to metabolism, extraction of further energy from the environment, and reproduction as well as social interaction and cultural replication. Trade-offs in the allocation of this energy are inevitable; energy used for one purpose may not be used for another. From our discussion of reproductive effort, we can expect trade-offs between the number and survival of offspring in variable environments. Similarly, we can expect other trade-offs to exist, even between forms of social interaction (e.g., burial ceremonialism) and reproductive effort.

REFERENCES CITED

- Boone, J.
1998 The evolution of magnanimity—When is it better to give than to receive? *Human Nature* 9:1–21.
- Boyce, M. S., and C. M. Perrins
1987 Optimizing great tit clutch size in a fluctuating environment. *Ecology* 68:142–153.
- Boyd, R., and P. J. Richerson
1985 *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.
- Buikstra, J. E.
1981 Mortuary practices, paleodemography, and paleopathology: A case study from the Koster Site (Illinois). In *The archaeology of death*, edited by R. Chapman, I. Kinnes, and K. Randsborg, pp. 123–132. Cambridge University Press, Cambridge, England.
- Bulmer, M. G.
1984 Delayed germination of seeds: Cohen's model revisited. *Theoretical Population Biology* 26:367–377.
1985 Selection for iteroparity in a variable environment. *American Naturalist* 126:63–71.
- Caldwell, J. R.
1958 *Trend and tradition in the prehistory of the eastern United States*. American Anthropological Association Memoir, Menasha.
- Cavalli-Sforza, L. L., and M. W. Feldman
1981 *Cultural transmission and evolution: A quantitative approach*. Monographs in Population Biology, No. 16, Princeton University Press, Princeton.
- Chapman, C. H.
1975 *The archaeology of Missouri I*. University of Missouri Press, Columbia.
- Charles, D. K., and J. E. Buikstra
1983 Archaic mortuary sites in the central Mississippi drainage: Distribution, structure, and behavioral implications. In *Archaic hunters and gatherers in the American midwest*, edited by J. L. Phillips and J. A. Brown, pp. 117–145. Academic Press, New York.
- Charlesworth, B.
1980 *Evolution in age structured populations*. (second ed.). Cambridge University Press, Cambridge.
- Cohen, D.
1966 Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12:110–129.
- Cunningham, W. M.
1948 *A study of the Glacial Kame culture in Michigan, Ohio, and Indiana*. Occasional Contributions from the Museum of Anthropology of the University of Michigan, No. 12, Ann Arbor.
- Dawkins, R.
1982 *The extended phenotype: The gene as the unit of selection*. Oxford University Press, Oxford.
- Dempster, E. R.
1955 Maintenance of genetic heterogeneity. *Cold Spring Harbor Symposium on Quantitative Biology* 20:25–32.
- Dobzhansky, T.
1970 *Genetics of the evolutionary process*. Columbia University Press, New York.
- Dragoo, D. W.
1963 *Mounds For The Dead*. Carnegie Museum, Pittsburgh.
- Dunnell, R. C.
1971 *Systematics in prehistory*. Free Press, New Haven.
1980 Evolutionary theory and archaeology. *Advances in Archaeological Method and Theory* 3:35–99.
1989 Aspects of the Application of Evolutionary Theory in Archaeology. In *Archaeological thought in America*, edited by C. C. Lamberg-Karlovsky, pp. 35–99. Cambridge University Press, Cambridge.
- Endler, J. A.
1986 *Natural selection in the wild*. Monographs in Population Biology, No. 21, Princeton University Press, Princeton.
- Epstein, J. M., and R. Axtell
1996 *Growing artificial societies: Social science from the bottom up*. MIT Press, Cambridge MA.
- Gabora, L.
1997 A day in the life of a meme. In *The nature, representation, and evolution of concepts*, ed-

- ited by Philip van Looche. Routledge Press, New York.
- Gillespie, John
 1977 Natural selection for variances in offspring numbers: A new evolutionary principle. *American Naturalist* 111:1010–1014.
 1991 *The causes of molecular evolution*. Oxford University Press, New York.
- Goodman, D.
 1984 Risk spreading as an adaptive strategy in iteroparous life histories. *Theoretical Population Biology* 25:1–20.
- Hamilton, W. D.
 1964a The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1–16.
 1964b The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17–52.
- Judson, O. P.
 1994 The rise of individual-based models in ecology. *TREE* 9:14.
- Katzenberg, M. A., D. A. Herring, and S. R. Saunders
 1996 Weaning and infant mortality: Evaluating the skeletal evidence. *Yearbook of Physical Anthropology, Yearbook Series* 39:177–199.
- Kohler, T. A., and E. Carr
 1996 *Swarm-based modelling of prehistoric settlement systems in southwestern North America*. Paper presented at Paper presented at the Archaeological Applications of GIS Colloquium II, September 1996, Forli Italy.
- Lack, D.
 1947 *Darwin's finches*. Cambridge University Press, Cambridge.
- Langton, C., and D. Hiebeler
 n.d. *SWARM simulation platform for the simulation of complex systems*. Santa Fe Institute, Santa Fe.
- Levene, H.
 1953 Genetic equilibrium when more than one ecological niche is available. *American Naturalist* 87:331–333.
- Lewontin, R. C.
 1974 *The genetic basis of evolutionary change*. Columbia University Press, New York.
- Lynch, A.
 1996 The population memetics of birdsong. In *Ecology and evolution of acoustic communication in birds*, edited by Donald E. Kroodsma and Edward H. Miller, pp. 181–197. Cornell University Press, Ithaca, New York.
- Lynch, A., and A. J. Baker
 1986 Congruence of morphometric and cultural evolution in Atlantic island chaffinch populations. *Canadian Journal of Zoology* 64:1576–1580.
- 1993 A population memetics approach to cultural evolution in chaffinch song: Meme diversity within populations. *American Naturalist* 141:597–620.
- 1994 A population memetics approach to cultural evolution in chaffinch song: Differentiation among populations. *Evolution* 48:351–359.
- McNamara, J. M.
 1997 Optimal life histories for structured populations in fluctuating environments. *Theoretical Population Biology* 51:94–108.
- Madsen, M. E., and C. P. Lipó
 1999 **Keywords in evolutionary archaeology: Fitness**. Paper presented at the 63rd Annual Meeting of the Society for American Archaeology, Chicago, IL.
- Mayr, E.
 1959 Where are we? *Cold Spring Harbor Symposium on Quantitative Biology* 24:409–440.
- Meeker, L. D., P. A. Mayewski, M. S. Twickler, S. I. Whitlow, and D. Meese
 1997 A 110,000-year history of change in continental biogenic emissions and related atmospheric circulation inferred from the Greenland Ice Sheet Project Ice Core. *Journal of Geophysical Research-Oceans* 102:26489–26504.
- Melice, J. L., and P. Roucou
 1998 Decadal time scale variability recorded in the Quelccaya summit ice core delta O-18 isotopic ratio series and its relation with the sea surface temperature. *Climate Dynamics* 14:117–132.
- Michod, R.
 1999 *Darwinian dynamics: Evolutionary transitions in fitness and individuality*. Princeton University Press, Princeton.
- Murray, B. G., Jr.
 1997 Population dynamics of evolutionary change: Demographic parameters as indicators of fitness. *Theoretical Population Biology* 51:180–184.
- Neiman, F.
 1997 Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in classic Maya terminal monument dates. In *Rediscovering Darwin: Evolutionary theory in archaeological explanation*, edited by C. Michael Barton and G.A. Clark, pp. 267–290. American Anthropological Association, Arlington.
- Nilsson, P., J. Tuomi, and M. Astrom
 1996 Bud dormancy as a bet hedging strategy. *American Naturalist* 147:269–281.

- O'Brien, Michael J., and Thomas D. Holland
 1990 Variation, selection and the archaeological record. *Archaeological Method and Theory* 2:31–80.
- O'Hara, R. J.
 1988 Homage to Clio, or, toward a historical philosophy for evolutionary biology. *Systematic Zoology* 37:142–155.
- Payne, Robert B.
 1996 Song traditions in Indigo Buntings: Origin, Improvisation, Dispersal, and Extinction in Cultural Evolution. In *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma and E. H. Miller, pp. 198–220. Cornell University Press, Ithaca.
- Pocklington, R., and M. L. Best
 1997 Cultural evolution and units of selection in replicating text. *Journal of Theoretical Biology* 188:79–87.
- Railey, J. A.
 1990 Woodland Period. In *The archaeology of Kentucky: Past accomplishments and future directions*, edited by D. Pollack, pp. 247–374. Kentucky Heritage Council State Historic Preservation Comprehensive Plan Report No. 1, Lexington.
- Ritzenthaler, R. E.
 1957 The old copper culture of Wisconsin. *Wisconsin Archaeologist* 38:183–332.
- Roff, D.
 1992 *The evolution of life histories*. Chapman and Hall, London.
- Roughgarden, J.
 1979 *Theory of population genetics and evolutionary ecology: An introduction*. Macmillan, New York.
- Schaffer, W. M.
 1974 Optimal reproductive effort in fluctuating environments. *The American Naturalist* 108:783–790.
- Seeger, J., and H. J. Brockmann
 1987 What is bet-hedging? In *Oxford surveys in evolutionary biology*, edited by P. H. Harvey and L. Partridge, pp. 182–211. Oxford University Press, Oxford.
- Skinner, M.
 1997 Dental wear in immature Late Pleistocene European hominines. *Journal of Archaeological Science* 24:677–700.
- Slatkin, M.
 1974 Hedging one's evolutionary bets. *Nature* 250:704–705.
- Stearns, S. C.
 1992 *The evolution of life histories*. Oxford University Press, Oxford.
- Tuck, J. A.
 1984 *Maritime provinces prehistory*. National Museum of Canada, Ottawa.
- Tuljapurkar, Shripad
 1990 *Population dynamics in variable environments*. Springer-Verlag, New York.
- Webb, W. S., and C. E. Snow
 1945 *The Adena people*. University of Kentucky, Lexington.