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Optimization Theory in Anthropology: Applications and Critiques

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1 Introduction

Optimization theory has found increasing use within anthropology, where it is employed to generate explanatory hypotheses concerning cross-cultural and intracultural variation in ecological, economic, and reproductive aspects of human behavior. As is true in other disciplines (e.g., evolutionary biology, economics, psychology), the optimization approach has generated both enthusiasm and criticism. This paper reviews, at an introductory level, some representative applications of optimization models in anthropology, the sources from which these models have been drawn, and the criticisms and possible limitations associated with this mode of explanation.

The Logic of Optimization Theory

In order to grasp what the various anthropological applications of optimization models have in common, as well as to establish some basis for evaluating criticisms of these analyses, it is useful to specify the analytical properties characteristic of explanatory models in general, and optimization models in particular. Since optimization research is in a nascent stage of development within anthropology, the rather elementary discussion that follows is perhaps more representative of the way anthropologists use these models than a more sophisticated exposition would be.

I begin with the assumption that all models are necessarily caricatures of the real world. Although the degree of complexity in a model may vary as a function of several factors (including the goals of the research, the state of empirical knowledge, and the historically given level of theory development), the instrumental purpose of model building is simplification of the real world to some manageable or desirable level. This simplification allows

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research to proceed with a reductionist or "piecemeal" (Krebs, Stephens, and Sutherland, 1983) approach to greater understanding of complex realities. Obviously, then, models are not complete explanations for any complex phenomena, or phrased another way, they do not satisfy our frequent longing for holistic or synthetic accounts of the real world. To carry out this larger task, models must be linked to each other and to additional theoretical constructs (as well as to empirical data) in some way. That is, models must be embedded in some larger *theory*. ¹

Optimization models share in this dual characteristic of explanatory models: individually they offer handy ways of breaking complex explanatory problems into manageable chunks, and usually they are linked to some more general theory or research program. That is, particular optimization models can be useful tools for piecemeal analysis, and they are often easily linked to larger frameworks—both methodological ones (such as the mathematical techniques common to optimization analyses) and explanatory ones (such as theories of economic rationality or natural selection).

All optimization models exhibit certain defining features: (1) an *actor* that chooses or exhibits alternative states; (2) a *strategy set* (the range of options an actor chooses from or exhibits); (3) a *currency* (the cost-benefit measure that is maximized or minimized); and (4) a set of *constraints* (all those factors that determine the feasible strategy set and the payoff to each option).²

In considering this set of features, we must keep in mind that their identities in any particular case are not necessarily obvious. That is, in order to decide who the actor is, what the feasible set of strategies consists of, and what the currency and payoff to each strategic option might be, one must consult both theory and data relevant to the case at hand. Furthermore, the relative importance of theory versus data varies from one element to another. The identification of the actor and of the currency can often be derived deductively from theoretical principles, whereas the content of the strategy set and the relevant constraints must be arrived at more inductively or intuitively. As Maynard Smith (1978) has emphasized, when any optimization model is subjected to empirical test, one necessarily tests the validity of one's assumptions about the identity of these component factors.

Sources of Optimization Theory

Anthropologists have drawn primarily on two existing research traditions as sources for optimization models: neoclassical economics and evolutionary biology. In terms of formal logical structure, analytical methods, and even in many cases terminology, it is becoming increasingly clear that there is little difference between models drawn from these two sources. This conclusion is supported by evidence indicating independent con-

vergence, direct borrowing, and a growing amount of cross-disciplinary research.³

However, there is a difference between economic and evolutionary optimization models in terms of their substantive referents and theoretical scope. Substantively, while both frameworks generally focus on individual actors/phenotypes as the locus of alternative strategies, the justifications provided are quite different. Neoclassical economics assigns causal primacy to rational choice (the efficient allocation of available means to arbitrary ends), but it does not attempt to offer an explanation for the primacy of individual actors as the locus of optimal decision-making. Nor, except in the special case of profit-maximizing firms, do economists account for the content (i.e., optimization currency) of actors' ends; instead, these goals are taken as "givens" to be explained by other theories, and the only truly general currency—utility—is a subjective construct derived inductively from an actor's "revealed preferences" (Wong, 1978)—that is, behaviorally realized choices.

In contrast, neo-Darwinian theory assigns causal primacy to a historical process of evolution, and especially (as concerns the design features of organisms) to the process of natural selection of genotypes via the differential survival and reproduction of the phenotypes they (help) produce. The role of the individual phenotype as the locus of strategic design is justified by the contingent relation between gene replication and individual action (Dawkins, 1978). As a consequence the optimization currency can be defined in terms of this contingent relation. That is, theory provides fairly good grounds for assuming that selection has designed actors to choose, or exhibit, the alternative strategy with the greatest positive effect on the replication rate of the genes coding for this strategy, or for the capacities or values producing this strategy. This deduction from general theory then requires that one decide on the appropriate measure of gene replication; this may be inclusive fitness, individual (classical) fitness, or often some proxy for fitness that the researcher—and the actor—can actually hope to monitor as an outcome of alternative strategies.4

One consequence of these substantive contrasts between economic and evolutionary optimization theory is in their differing explanatory scope. Because evolutionary theory seeks to account for the *content* as well as the form of actors' strategies, it is considerably more ambitious than economics, even within the confines of particular optimization models or hypotheses. Indeed, it can be argued that the capacity for rational choice, and the form of actor's utility functions, are necessarily products of evolution—cultural and genetic—and thus that evolutionary theory is necessary to provide closure to economic theory (e.g., Hirshleifer, 1977; Richerson, 1977).⁵

Table 11.1
Comparison of economic and evolutionary/ecological optimization model

	forme and evolutionary/ecological	optimization models		
Theoretical and methodological variables	Economics	Evolutionary biology		
Model components		, -0,		
(1) Actor	Individual or firm	Individual phenotype Range of feasible phenotypes		
(2) Strategy set	Range of feasible choices			
(3) Currency	Utility, monetary profit	Individual or inclusive fitness, proximal correlates (e.g., energy efficiency)		
(4) Constraints	Payoff structure, information, cognitive abilities	Same, plus constraints on design and genetic variation		
Analytical methods	Graphical and mathematical maximization (extremum), game theory	Same (but less advanced?)		
Ultimate design force	Human nature and culture (exogenous)	Natural selection (locally variable)		
Proximate causal forces	Rational choice, survival in a competitive marketplace	Genetic programming, learning, decision-making, social transmission		
Primary decision sets	Commodity production, exchange rates, consumption choices (in monetized economies)	Foraging strategies, reproductive strategies, spatial organization, social interactions		

A second consequence of the differences between these two sources of optimization models is found in the differing uses anthropologists have made of them. For the most part, optimization models drawn from economics have been used to study production and exchange in peasant economies, whereas models from evolutionary biology and ecology have been employed in analyzing human strategies of foraging, reproduction, and land use. (See table 11.1 for a summary of the contrasts between these two sources of optimization models.)

In this review, I focus primarily on evolutionary/ecological models, for three reasons: (I) as argued above, neo-Darwinian theory offers the more general explanatory framework; (2) the focus of this volume is on the evolutionary basis of optimization arguments; (3) I am more familiar with evolutionary/ecological models and applications than with economic ones. But if the boundary between economic and evolutionary theory continues to blur, we can expect that future anthropological uses of optimization models will reflect this, and become increasingly synthetic in character.

2 Anthropological Applications

Anthropological applications of optimization models have a rather short history. This is perhaps due to several factors, including the qualitative mode of argument frequently favored in a discipline with one foot in the humanities and the other in the social sciences, and the bias in most of the social sciences against reducing social institutions and processes to the action of self-interested individuals [which dates at least to Durkheim's (1938/1895) dictum that social facts can only be explained by social facts, and that individual psychology is subservient to "collective representations"]. Nevertheless, the cross-cultural and evolutionary perspectives of anthropology have led to repeated attempts to establish lawful regularities governing human behavioral variation (Harris 1968), and in recent years growing interest in economic, ecological, and evolutionary theory has seen increased numbers of anthropologists making some use of formal models from these fields.⁶

Several factors have contributed to this recent growth of anthropological interest in optimization models. One is simply that only recently were such models available treating ecological and evolutionary topics, as opposed to narrowly economic ones. But equally important is the frustrating state of conventional research programs in ecological anthropology, which are characterized by a paucity of formal theory, testable hypotheses, and rigorous tests (Johnson 1978). This has led to a failure to articulate theory and data in a productive fashion, and as a result the field has been dominated by narrowly particularist or inductive studies on the one hand, and unresolvable polemical debate on the other (e.g., Sahlins 1978 vs. Harris 1979, Harris and Sahlins 1979; Friedman 1974, 1979 vs. Rappaport 1968, 1984). In the absence of much progress in theory building, the advantages of optimization models, especially when based in general evolutionary ecological theory, are considerably magnified.

In the current context, then, optimization models offer specific advantages over conventional anthropological approaches to understanding human behavioral variation. First, they provide a relatively rigorous basis for generating hypotheses from general theory. Second, most such models provide explicit, quantitative predictions, which facilitate empirical tests. While critics might not feel that optimization models actually deliver on all these promises, I believe I have fairly characterized their advantages as perceived by anthropologists who utilize them. The examples discussed below can serve to evaluate these assertions, as well as to illustrate the kinds of uses to which these models have been put by anthropologists.

Rather than a cursory review of a large number of anthropological

optimization studies, this paper will illustrate the approach as it has developed thus far in the area of hunter-gatherer socioecology, via examination of four topics: (1) optimal systems of land tenure and spatial organization (Dyson-Hudson and Smith, 1978; Cashdan, 1983a); (2) foraging-group size (Smith 1981, 1985; Hill and Hawkes, 1983); (3) reciprocal food-sharing (Kaplan and Hill, 1985b); and (4) optimal birth-spacing (Blurton Jones and Sibly, 1978; Blurton Jones, nd, a, b).

Hunter-Gatherer Land Tenure and Spatial Organization

Anthropologists have long recognized the diversity of human systems of land tenure, but usually analyzed this data with an inductive, atheoretical approach. That is, little attempt was made until recently to formulate general models, or test them systematically against the ethnographic and archaeological record. The need for such an effort became quite apparent in the 1960s, as a protracted controversy over the origin and significance of territorial/private property systems arose. On the one hand were a number of popular works making aggressive claims concerning the instinctual basis of territoriality and private property (e.g., Ardrey, 1966; Lorenz, 1966). While anthropologists gave these little credence (Montagu, 1968; Alland, 1972), there remained a division of opinion concerning the universality of human territoriality. One position held that territorial exclusion was characteristic of even the simplest hunter-gatherer societies, and linked this practice to male solidarity in hunting and defense, and thus the practice of patrilocal residence (Radcliffe-Brown, 1930-1931; Service, 1962; Williams, 1974), or to the resource-conservation effects of private property as compared to common property (Speck, 1915; Speck and Eisley, 1939). An opposing perspective argued that patterns of land tenure were responsive to changes in economic and ecological circumstances, and that huntergatherers in particular were subject to localized resource fluctuations, and thus needed to exhibit fluid residence and communal access to resources to buffer this fluctuation (e.g., many authors in Lee and DeVore, 1968).

The balance of anthropological opinion has historically shifted from one side to the other, with the fluid group/communal access view holding the upper hand in recent years. But the striking thing about this debate is the tendency of each side to dismiss the arguments of the other, and deny the validity of empirical evidence supporting the opposing view. Thus, universal-territoriality proponents portray cases of fluid group composition and spatial arrangement as products of (often undocumented) colonial disruption or depopulation, while the nonterritorial dogma holds that all of the territorial cases are the product of trade or unusual conditions, or that the systems of exclusive land tenure described by some ethnographers are depictions of native ideology (or even that of the observer) rather than native practice.⁷

Research on territorial behavior in other species (especially birds) was also hampered for many years by an "either/or" opposition over the causes, significance, and range of variation of these phenomena. The elementary but compelling argument by Brown (1964) that territorial aggression is costly and should therefore only be expected to evolve when the fitness benefits to the territory defender exceed these costs reoriented research toward a more productive path. The accumulation of both theory and experimental and natural observations on territorial behavior over the succeeding twenty years has been impressive (Brown and Orians, 1970; Schoener, 1983; Davies and Houston, 1984).

Inspired by these successes (as of 1976), and frustrated by the polemical nature of much of the anthropological literature, Dyson-Hudson and I formulated the basic principles of what had by then become known as the "economic defendability model" of spatial organization in terms that we felt could be readily applied to the existing anthropological data set. Retaining the basic optimization logic and diversity-explaining orientation of the ecological theory, we formulated a simple, qualitative version of the argument (Dyson-Hudson and Smith, 1978). Briefly, we considered two dimensions of resource value (density and predictability), and argued on various grounds that the benefits of territorial exclusion were most likely to exceed the costs when resources were both dense (but still scarce relative to demand—i.e., not "superabundant") and relatively predictable in space and time. Since this was only one of the four possible combinations of resource quality in our 2 × 2 formulation, we went on to predict other optimal patterns of land tenure and spatial organization associated with the three other idealized resource distributions (figure 11.1).

While primitive in execution, the economic defendability model does exhibit the characteristic features of an optimization model: (1) the actors consist of groups of varying size and spatial exclusivity; (2) the currency, though never formally specified in Dyson-Hudson and Smith (1978), is some measure of the net return of resources per unit time spent in harvest and defense; (3) the strategy options consists of the alternative forms of land tenure and resource division considered in figure 11.1; (4) the constraints are defined by the local resource qualities (density and predictability) and by the actor's abilities to harvest resources, monitor the movements of others, and defend a locale against trespass.

Although this model only offers qualitative predictions, and is obviously a grossly simplified version of any actual situation, it has the virtue of allowing one to move from rather sterile "either/or" arguments about human territoriality to an attempt to explain cross-cultural, historical, and even synchronic intracultural (resource-specific) variation in land tenure. Provisional applications to a number of foraging and pastoral/agricultural societies indicate substantial qualitative support for the model. For

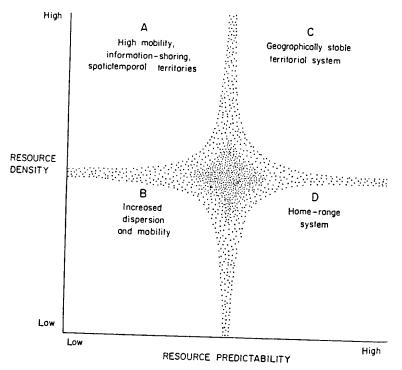


Figure 11.1

The economic defendability model of spatial organization. Resource density and predictability combine to determine costs and benefits of alternative forms of land tenure and sociospatial interaction (from Dyson-Hudson and Smith, 1978).

example, Richardson (1982) found that the degree of territorial exclusiveness (as codified in rules of ownership, privileged access, and hereditary rights) varied between Indian groups within the Northwest Coast region of North America, in such a way that locales with denser and more reliable resource concentrations were more territorial. This parallels the findings of Steward's (1938) research on variation in land tenure within the Great Basin and that of Bishop on historical shifts in land tenure accompanying changes in resource availability and utilization in the Canadian Subarctic (both cases discussed in terms of the economic defendability model by Dyson-Hudson and Smith, 1978).

In contrast, Cashdan (1983a) has examined four San or Bushman societies, and argues that a pattern opposite to that predicted by the model holds—groups with the scarcest and most unpredictable resources have the tightest controls over access (although none of the four actually exhibit territorial exclusion to any degree). She interprets this as a special pattern

of territoriality due to human cognitive and information-sharing abilities. However, her arguments have been challenged on the grounds that control of access to the social group has different adaptive significance and ecological causes than does territorial exclusion (Smith, 1983a; Hill, 1983; cf. Cashdan, 1983b). Specifically, I suggest (1983a, nd) that the systems of controlled access described by Cashdan involve reciprocal access to resources on the lands of neighboring bands, and that the social controls on this access are designed to prevent cheating ("free rider" phenomena) as well as to reduce inefficient foraging-area overlap. Further research is clearly needed to explore these issues, as well as to test the economic defendability explanation of territoriality in a more rigorous fashion, following the example of behavorial ecology (reviewed in Davies and Houston, 1984).

Foraging Strategies and Optimal Group Size

The most extensive application of evolutionary/ecological optimization models within anthropology has been in the study of hunter-gatherer production strategies. Here, models developed by evolutionary ecologists under the rubric of optimal foraging theory (OFT) have been borrowed and adapted to the human context.

In both ecology and anthropology, OFT has been used to predict foraging behavior as the outcome of relatively simple "decision rules for predators" (Krebs, 1978). As is characteristic of optimality theory in general, OFT is best viewed as a "shortcut" approach to understanding foraging decisions. First, the details of perceptual and cognitive mechanisms are generally ignored (see Staddon, this volume). Second, it is assumed that foraging outcomes as expressed in operational currencies (e.g., net rate of energy capture) are correlated with fitness, but this assumption is usually not directly tested. Nevertheless, and despite the complexity of actual foraging processes, OFT has been relatively successful both in generating research and in accounting for a substantial portion of relevant empirical data (Krebs, Stephens, and Sutherland, 1983; Pyke, 1984). Anthropological applications, although more limited in number and often less rigorous in method, generally share in these accomplishments (Smith, 1983b; Winterhalder, 1987; Hill et al., 1987).

Standard OFT models are explicit in their optimization logic. The actors are individual foragers (who may sometimes cooperate in groups). The currency in most OFT models is the expected net rate of energy capture while foraging, although more complex currencies involving multiple nutrients (linear programming) or risk-sensitive measures (where both mean and variance are assayed) are sometimes employed. The strategy set varies according to the type of decision being considered; most models fall under one of the following categories: diet choice; patch (foraging area) choice; movement rules (time allocation, searching paths); and foraging group size.

The constraints incorporated vary considerably from one model to the next, even within decision categories; indeed, much of the recent OFT literature is devoted to analyzing the effects of incorporating alternative constraints into a family of models (e.g., perfect information versus information gathering, deterministic versus stochastic outcomes, various perceptual mechanisms, and "rules of thumb"). These "second-generation models" have had little impact on anthropological applications of OFT, but the example discussed here—foraging group size—involves just this element of examining alternative assumptions about the constraints governing individual decisions.

Group foraging activities are conspicuous features among human hunter-gatherers, and are implicated in many widely accepted scenarios of hominid evolution (review in Hill, 1982). By the logic of optimal foraging theory, foraging groups should arise when each member gains an advantage (not necessarily equal) relative to solitary foraging. This advantage may be due to increased mean harvest rates (in detecting or capturing prey), decreased variance in individual food intake, simple aggregation at resource concentrations, or some other benefit of grouping (such as improved predator detection, resource defense, etc.) (reviews in Schoener, 1971; Bertram, 1978; Smith, 1981; Pulliam and Caraco, 1984).

Although many anthropologists have speculated on the selective factors favoring cooperative foraging among hunter-gatherers, relatively few formal models on this topic have been presented, and even less often have empirical tests been attempted (Smith, 1980, 1981; Heffley, 1981; Beckerman, 1983; Hill and Hawkes, 1983). Of the available applications, I shall discuss my own study of Inuit foraging groups (Smith, 1980, 1981, 1985). I choose this example not only because I am most familiar with it, but because it shows how problems with the initial optimization model revealed by empirical tests can lead to further model building in an attempt to uncover factors not considered initially.

The Inuit (Canadian Eskimo) foragers I studied harvest a variety of prey species under varying conditions (Smith, 1980). Because it is the conditions and foraging techniques, not just the prey species, that determine the payoff structure, I refer to the foraging options as "hunt types." If cooperative foraging is undertaken whenever it increases per capita foraging returns, then different hunt types might be characterized by different payoff structures as a function of group size. My initial hypothesis, which I termed the per capita maximization hypothesis, was that foragers should seek to form groups that maximize the per capita net rate of energy capture, defined as

$$\overline{R} = \frac{\sum_{i=1}^{n} (E_{a} - E_{e})}{f \cdot n},\tag{1}$$

where n is the foraging group size, t is the duration of the foraging period (e.g., a single hunt), and E_a and E_e refer to food energy acquired and metabolic energy expended, respectively, by each member of the foraging group during t. Lacking perfect information, foragers might still develop (or culturally inherit) the ability to predict the expected value of R for different group sizes that pertain to each hunt type, and then choose the optimal group size for each type.

Data from 10 hunt types (361 hunts) revealed that when the optimum is n = 1, the prediction is generally met (5 out of 6 hunt types), but that when cooperative foraging is favored, the model group size frequently exceeds the optimum (Smith, 1981). In an attempt to explain this finding, and improve upon the predictive power of the simple per capita maximization model, three additional factors have been considered (Smith, 1985): (1) conflicts of interest between individual foragers, given different opportunity costs; (2) kinship structure of foraging groups; and (3) the effect of different sharing rules (governing division of the harvest). Let us now consider some of these factors.

In the best of all possible worlds, an individual would not only know what the optimal group size was under each foraging condition, but would have no trouble finding a place in such a group. But what happens if a forager cannot find a group of $n^* - 1$ other foragers to join (where n^* is the optimal size, i.e, the size associated with R_{max} , the maximum per capita return rate)? An efficiency-maximizing forager should still attempt to maximize his or her own return rate, by choosing from the available options that which yields the highest R. As several analyses have recently shown, this "selfish" choice shifts the solution away from a single "optimal group size" to a range of possible equilibrium group sizes, which will often be larger than that which maximizes per capita return rates (Sibly, 1983; Pulliam and Caraco, 1984; Clark and Mangel, 1984; Smith, 1985).

The exact equilibrium depends on the dynamics of group formation. For simplicity, consider the case where there are only two options: to join a group of n-1 foragers (and become the nth member) or to forage alone. Assuming equal division of the harvest at the end of the foraging period, the optimal forager should seek to join the group as long as

$$\overline{R}_{n} > \overline{R}_{1},$$
 (2)

where R_n is the per capita return rate (as well as the actual rate of each group member if equal sharing occurs) for a foraging group of size n. At the point where this inequality reverses, it will be preferable to forage alone. I have termed this the "joiner's rule" (Smith, 1985). In contrast, once a member of a foraging group, a selfish efficiency maximizer should favor the addition of the nth forager only as long as

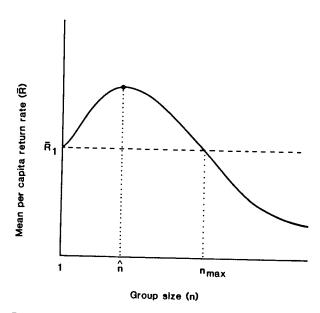


Figure 11.2 Graphical representation of the conflict between the "joiner's rule" and the "members' rule." Per capita returns peak at \hat{n} , the size at which members will obtain the maximum share, but foragers faced with the option of solitary foraging will improve their return rate by joining groups as large as n_{\max} (the size where the per capita return rate \overline{R}_n is equal to the solitary return rate \overline{R}_1). This model can be generalized by substituting \overline{R}_a , the expected return rate from *all* available alternatives open to the prospective joiner, for \overline{R}_1 (from Smith, 1985).

$$\overline{R}_{n} > \overline{R}_{n-1}. \tag{3}$$

A conflict between the joiner's rule [equation (2)] and the members' rule [equation (3)] will arise whenever

$$\bar{R}_{n-1} > \bar{R}_n > \bar{R}_1. \tag{4}$$

A graphical version of this conflict of interest (figure 11.2) indicates that whenever the expected returns from solitary foraging are low relative to the per capita returns from group foraging, individuals will attempt to join groups even though this pushes group size above the optimum. If members are never capable of excluding joiners (or if the costs of doing so are too high), the resulting group size will approach the Nash equilibrium (Pulliam and Caraco, 1984, p. 146), whereas complete ability to exclude [Vehrencamp's (1983) "despotism"] will keep the average group size (including those excluded and forced to forage alone) below the per capita optimum.

In the Inuit case, the relative ability of "members" versus "joiners" to

determine the size of foraging groups varies according to the circumstances of group formation. For example, beluga whale hunts are localized and small groups of hunters arrive independently at the site, form loosely cooperative groups that attempt to encircle the prey, and then divide the catch at the end of the hunt. Here, early arrivals ("members") would find it difficult or impossible to exclude later arrivals ("joiners"), and the data indicate that the result predicted by the joiner's rule [equation (2)] is approximately met (Smith, 1985). Breathing-hole seal hunting, involves different and less clearly understood group-formation dynamics, but the data suggest that the resulting group sizes represent a compromise between the interests of joiners and members (Smith, 1985).

The joiner/member model predicts conflicting optima based on different opportunity costs (forgone opportunities) facing those who already "belong" to a foraging party versus those who are seeking to do so. There are at least two factors that can modify or even eliminate these conflicts of interest, at least in theory. One of these is the increased overlap of interests produced by inclusive fitness considerations where group members are closely related (Rodman, 1981; Smith, 1985). Another is communal sharing at a central place (i.e., camp) by a set of foragers (Hill and Hawkes, 1983; Smith, 1985). Only this second type of situation will be summarized here.

The situation envisaged by the communal-sharing model is one in which foragers, singly or in groups, set out from a central base to forage, and upon returning at the end of a foraging period pool the entire catch and divide this catch equally. This sharing rule differs from that assumed in the joiner/member model, and this altered constraint results in a different optimization rule for foraging group size. Specifically, the optimization rule that can be derived under central-place sharing is to increase the size of any foraging group to n members as long as

$$n\overline{R}_{n} - (n-1)\overline{R}_{n-1} > \overline{R}_{1} \tag{5}$$

(Smith, 1983, 1985; Hill and Hawkes, 1983).

Several interesting contrasts with the predictions of the joiner/member model result from communal sharing. First, equation (5) expresses the optimal decision rule for *all* foragers in the sharing network, regardless of their status as "member" or "joiner" of a foraging group. Second, because foragers will benefit by maximizing the per capita share of the entire camp rather than their own personal harvest rates, there is no conflict of interest over size of foraging groups. Third, the optimal (equilibrium) group size under the communal-sharing rule will always be greater than or equal to that which maximizes per capita returns for a foraging group [specified in equation (3)], but less than or equal to the maximum size determined by the joiner's rule [equation (2)]. Finally, as long as the communal sharing rule is

strictly adhered to, and foragers attempt to maximize their own share (and hence total harvest for the sharing network), the equilibrium group size will approach Pareto-optimality (maximizing total benefits for the community) rather than the pessimistic Nash equilibrium (selfish maximizing) that might otherwise prevail. This is because the communal-sharing rule results in a payoff structure where the marginal contribution of a foraging group member is equal to the marginal cost of not joining the group (i.e., the expected solitary return rate) (Smith, 1985, p. 52). Obviously, this convenient intervention of the Invisible Hand begs several questions, one of which—the conditions under which a communal sharing rule might evolve—is the next topic examined here.

Reciprocal Food Sharing

The reciprocal exchange of resources is a striking characteristic of human social groups. Furthermore, the extent of such sharing, in terms of its frequency and intensity (proportion of total resources shared), is highly variable from one context to another, within and between societies. Here, I shall focus on reciprocal sharing involving one type of resource—food—and one social context—sharing between (rather than within) family units among human foragers (although the optimization model discussed is sufficiently general that it could be applied to other contexts and resource types with little modification).

Hunter-gatherers are an interesting test case for explanations of food sharing because there is a substantial anthropological literature discussing the extensive sharing practices typical of this mode of subsistence (e.g., Isaac, 1978; Gould, 1981, 1982; Hayden, 1981; Wiessner, 1982). Over the years, anthropologists have advanced various alternative explanations for this. Some of these, such as the argument that foragers possess an ethic of "generalized reciprocity," strike me as tautological, or at least highly limited in explanatory power. Dut one widely accepted view holds that food-sharing is a device to buffer the fluctuations in the daily food supply of individual foragers that seem to be the typical lot of foragers. This view is plausible and logically coherent, but needs to be stated in a form that can generate precise and varied predictions, to facilitate testing and allow one to account for diversity in the extent of sharing practices from one resource, situation, or society to another.

One useful way to satisfy these requirements is to use an optimization model coupled to the concept of risk aversion developed in economics and recently applied in evolutionary ecology (see note 3). The basic elements of risk-sensitive optimization (where "risk" refers to the effects of stochastic variation in resource income) can be incorporated in a very simple model of individual benefit as a function of resource income—that is, what an

economist would term a "utility function," and a biologist might label a "fitness function."

The model as considered here involves the following assumptions (see Schaffer, 1978, for a more general and rigorous treatment, and Kaplan and Hill, 1985b, for an extended discussion and application): (1) Each actor is subject to random variation in harvest rates, as measured over some relevant unit of time (e.g., per day). (2) All actors in some local set experience approximately the same *expected* harvest over the long run. (3) The stochastic variation in harvest rates is unsynchronized between actors (e.g., everyone has good days and bad days, but not on the *same* days, except by chance). (4) The marginal value of resources consumed by any actor over the relevant time unit exhibits diminishing returns; that is, beyond some frequently realized point, additional units of food consumed are worth less in the currency of utility or fitness. This diminishing marginal value assumption (convex-upward value function) is graphed in figure 11.3. (5) The

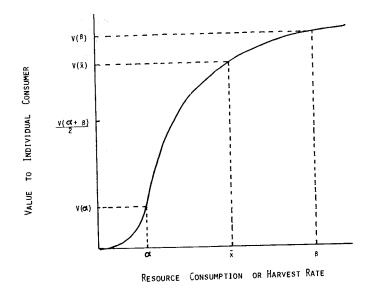


Figure 11.3 A risk-reduction model of resource sharing. For any actor, the rate of resource harvest is a random variable with a symmetric distribution whose mean is \overline{x} and whose range (or standard deviation) is from α to β . With a diminishing marginal value curve (i.e., reduced utility or fitness to consumption of additional units), those actors who pool their resources and consume equal shares will realize a higher and more certain value $V(\overline{x})$ than those who consume their own resources at a stochastic rate with the same distribution as the harvest rate, since the expected value of the latter strategy is equal to $V(\alpha + \beta)/2$ [i.e., the midpoint between $V(\alpha)$ and $V(\beta)$ on the value axis]. For an accelerating function (i.e., below the inflection point on a sigmoid function such as hypothesized here), the converse results hold.

currency actors seek to maximize is the total expected value obtained from resource consumption over the long run. (Note that the currency thus is not measured directly in resources consumed, but by a measure of value that transforms resource consumption via the utility or fitness function.) (6) Finally, it is assumed that actors do not have any significant alternative sources of the resource(s) is question, nor alternatives to local consumption (i.e., local self-sufficiency prevails).

Given these assumptions, one can generate a number of predictions; further predictions can be obtained by altering or relaxing the assumptions, as shown below. First, actors will reap higher value (greater utility or fitness) if they can somehow avoid or reduce variation in their resource consumption rate. This is because, given a diminishing-returns value function, the mean value of a stochastic consumption rate $[V(\alpha + \beta)/2]$ in figure 11.3] is always less than the value of the corresponding mean $[V(\bar{x})]$ in same]. In other words, given a diminishing-returns function, an actor should always be risk-averse, preferring a lower-variance option (or a sure bet) to a higher-variance option with the same mean. Of course, the means of different options may not be the same, but an actor should be willing to forgo a certain amount of returns [up to $V(\overline{x}) - V(\alpha + \beta)/2$] in order to eliminate risk. One way to do this might be to harvest resources with a lower associated variation in harvest success, even if the overall return rate is also lower; but let us assume here that this option is not available, or has been utilized as much as is optimal, with unwanted variation in the harvest rate remaining. We can then predict that actors who pool their (e.g., daily) catch with a sufficient number of other foragers, then taking an equal share of the total pool (which share, by the law of large numbers, should approximate \overline{x} , or at least show a narrower frequency distribution around \overline{x}), will reap a higher total value [equal to $V(\bar{x})$ if there is no cost to this sharing].

The most obvious implication of this model for the analysis of food sharing is that food sharing will increase in frequency, extent, and/or intensity as the degree of unsynchronized variation in (e.g., daily) food harvest increases. The comparison implied here could be intracultural, referring to different resource types within a single economic system, or it could be cross-cultural (e.g., hunter-gatherers in environments that differ in the predictability of resource harvest). Despite the various simplifying assumptions (discussed further below), the model strikes me as plausible, and corresponds with my impressionistic assessment of the ethnographic record. For example, most hunter-gatherers are reported to share meat resources far more frequently than they do plant foods, and the former seem to be characterized by greater variability in harvest rates.¹²

But impressions and plausibility can mislead, so careful tests are obviously preferable. The only such test I am aware of is that by Kaplan and Hill (1985b), who collected a wealth of data on foraging activities and

sharing practices of Ache Indians in Paraguay (see also Kaplan et al., 1984). These data show that different resource categories differ in the amount of daily variation in harvest rates by individual families, and that the degree of unsynchronized variation is directly correlated with the amount of sharing that occurs between these family units (table 11.2). These results are precisely those predicted by the risk-reduction model.

What is *not* predicted by this model is the finding that individual Ache differ in their long-term foraging success rates. As Kaplan and Hill point out, this violates assumption (2) listed above; and indeed we might expect this assumption to be regularly violated, given the ubiquity of individual differences in foraging abilities. Relaxing this assumption could lead to two different (not necessarily mutually exclusive) outcomes: decreased sharing or "hidden trade" (nonfood compensation for the more productive producers). Decreased sharing, while certainly a possibility, is likely to be less rewarding under most constraints than is compensation, since even the best foragers will find it difficult to avoid substantial stochastic variation. "Hidden trade" could take many forms, but ethnographic data indicate that exceptional producers are usually rewarded with increased political authority, prestige, assistance, access to mates, and ultimately fitness (Kaplan and Hill, 1985a). Further empirical and theoretical work is needed to explore these issues.

Another assumption of the risk-pooling model that may frequently be violated is the last one noted above—that alternative sources of goods, and outlets other than local consumption, are absent. The most likely such alternatives include *storage* (which allows households to buffer daily variation in food income) and *trade* (which serves both as a source of goods and as an outlet for marketing surplus production). Again speaking impressionistically, both of these phenomena do seem to be correlated with decreased

Table 11.2
Relationship between package size, interfamily harvest synchrony, and sharing frequency for different resources among Ache foragers^a

Resource class	Mean daily standar deviation across families in calories acquired		Percentage of calories consumed outside of acquirer's family		Mean package size (kcal)
	9,019		91		2,516
Meat resources	7,318		83		6,517
Honey	•		52		1,118
Collected resources	2,283		34		_,
Regression coefficient		$r^2 = .61,$		$r^2 = .45$,	
(log-log)		p < .000001		<i>p</i> < .0001	

a. Source: Kaplan and Hill (1985b, tables 2 and 3 and text).

food sharing among hunter-gatherer societies. For example, it is often noted that articulation of foragers with mercantile institutions such as the fur trade (e.g., Leacock, 1954; Balikci, 1964), or adoption of some horticulture allowing increased storage (e.g., Cashdan, 1980), is associated with reduced reciprocity and increased socioeconomic independence of individual households. Again, additional research is needed to examine the extent to which risk reduction versus other factors is responsible for these strategic shifts in social and economic relations. But the model discussed above, simplified as it is, provides a useful starting point for further inquiry.

Optimal Birth Spacing

The examples discussed thus far, since they all utilize material currencies, can with equal validity be viewed as standard economic logic applied to nonmonetized economies or as human evolutionary ecology. But evolutionary theory argues that phenotypic costs and benefits are important only to the extent that they are correlated with reproductive measures. Our final example concerns an application of the optimization approach to human reproduction, where the contrast between economic and evolutionary optima should be clearest. Here, unlike in economic demography, the evolutionary optimization assumption is that children are valued as ends (increased fitness) rather than strictly as means (to such ends as family income, parental security, or the like). 13

As in previous examples, the optimization approach has been brought to bear on an area of existing anthropological interest, in order to increase the rigor and productivity of both method and theory. On the basis of extensive research by himself and others, Richard Lee (1972, 1980) has described the birth-spacing and foraging practices of !Kung San foragers in the Kalahari region of southern Africa. Lee found that nomadic, bush-dwelling !Kung women had an average interbirth interval (IBI) of nearly four years, while those who settled at cattle posts had much shorter IBIs. He argued that this pattern made sense, given that nomadic !Kung women nurse young children on demand, carry children much of the time through the fourth year of life, and make frequent day-long trips away from camp to collect wild foods, while cattlepost women are much more sedentary and have early-weaning foods available. In fact, Lee's data indicated that for nomadic women, IBIs less than four years long would increase the mother's carrying load dramatically, because of the need to carry two children at a time.

Lee's explanation of !Kung birth spacing is an important contribution to our understanding of hunter-gatherer demography; but like most orthodox ecological anthropology, it remains unclear concerning the definition of satisfactory adjustment and the mechanisms that produce it. On the first point, we can ask, "If wide birth-spacing means less work, why not just

have one child, or none at all?" On the second, if we believe that IBIs are adjusted to fit local ecological conditions, what are the selective forces that shape this fit? And if these be a form of natural selection (or its effects as realized through rational choice, physiology, etc.), why is it the !Kung women do not have as many children as they can?

These questions have been systematically tackled within an optimization framework by Nicholas Blurton Jones (Blurton Jones and Sibly, 1978; Blurton Jones nd, a, b). Using a simulation model, Blurton Jones and Sibly tested the basic hypothesis that !Kung women adjust birth spacing to maximize the number of children successfully raised to adulthood. Here, the actors are the mothers (not the fathers, the children, etc), and the currency maximized is reproductive success. The strategy set, at least in a simple formulation, consists of the various possible IBIs. The simulation incorporated a large number of constraints (including women's foraging rates, family food requirements, travel distances, children's age-specific weights and survivorship) derived from Lee's research plus information on human physiology, to define the payoff to various IBIs. It assumed that the main selective forces affecting reproductive success (e.g., heat stress, exhaustion, dehydration, food supply for children) are determined by the average weight women carry, not extreme weight (e.g., back injury).

The Blurton Jones and Sibly simulation confirmed that a four-year IBI produces the most even trajectory of average backload throughout a !Kung woman's reproductive career; shorter spacing produces a very sharp upturn in backload, exceeding levels likely to cause heat stress in the dry season (or else insufficient loads of food returned to camp), while longer IBIs lead to lower but fluctuating backloads that can be viewed as "labor underutilization" (lost opportunities for maximizing reproductive success). However, the simulation could not directly test the central prediction of the optimal birth-spacing model: that !Kung women who had IBIs shorter or longer than four years would raise less children. For this, Blurton Jones (nd,a,b) turned to empirical data on individual demographic outcomes collected by Howell (1979 and unpublished field data).

These data confirm the trade-off between IBI and reproductive success postulated in the original simulation. First, calculated backloads (as determined by IBIs) are strongly correlated with offspring mortality; the best fit to the mortality data is provided by a decelerating asymptotic curve (figure 11.4). Second, the optimal IBI predicted by this curve centers on 48 months, which matches the observed IBI frequency distribution. Third, child mortality is not affected by IBI length for first intervals of women's reproductive careers, nor for any intervals of women settled at cattleposts; both of these results are as predicted, given the altered constraints on carrying and food requirements pertaining to these cases. Finally, death of unweaned infants is followed by shortened IBI, indicating "replacement" of

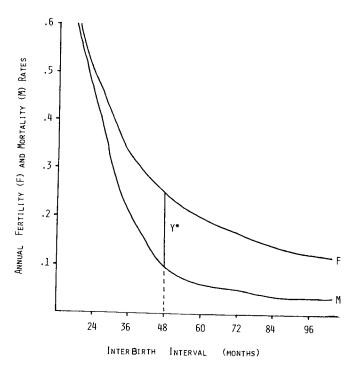


Figure 11.4 Birth-spacing optimization for !Kung women. For lengthening interbirth intervals, annual fertility (curve F) declines by an exponential function of -1 (by definition), while empirical data on mortality as a function of backloads associated with various intervals fits a logistic regression curve with a steeper, but eventually asymptotic shape (curve M, the annual mortality of offspring under ten years of age). The net yield of offspring successfully raised (to age ten) is given by Y = F - M, whose highest value occurs at $Y^* = 48$ months (after Blurton Jones nd, a, table 3).

these offspring, whereas death of older children has no effect on IBI—again, as expected given the assumption that carrying children under four is the primary constraint on maximizing reproductive success.¹⁵

In summary, the optimization model developed by Blurton Jones and Sibly performs remarkably well in predicting details of the reproductive ecology of !Kung foragers. Given the prominent didactic role the well-studied !Kung play in textbooks, generalizations concerning huntergatherers, and theoretical treatises on human ecology, the importance of these findings is considerable. Furthermore, it is reassuring that Lee's original insights into the causes of long IBIs are upheld and refined by the optimization approach, which in turn is able to provide precise predictions, suggest numerous empirical tests, and anchor the explanatory argument to a general theory of adaptation.

3 Critiques and Limitations

In terms of several widely accepted criteria for scientific utility—generating new explanations, providing testable hypotheses, linking observations to general theory—optimization theory in biology and the social sciences has been successful. Nevertheless, this approach has been subject to some rather strong criticisms regarding its limitations and potential for abuse. To avoid undue redundancy with other contributions to this volume, I restrict my review primarily to criticisms of the application of optimization models to human social behavior.

Even within this bailiwick, my review is necessarily selective. Issues that are strictly methodological or empirical (e.g., the validity of an energy efficiency currency in studies of human foraging strategies—see Smith, 1983b) are passed over in favor of more general issues. The emphasis is on ecological/evolutionary (rather than strictly economic) topics. The questions reviewed here are arranged in order of increasing specificity to anthropological inquiry, and involve the relation of selection to optimization/maximization, the realism and explanatory sufficiency of optimization models, the constraints placed on individual choice by culture, and the differing currencies in cultural versus genetic evolution.

Does Natural Selection Produce Optimization?

This is obviously a broad issue, and one of much current interest in evolutionary biology and philosophy, as testified by a substantial literature (see references in note 19). The reason for bringing it up here is that critics of anthropological optimization research have challenged the theoretical bases for the optimization postulate. As noted above, there are two such bases: the utility-maximizing assumption of neoclassical economics and the

fitness-maximizing assumption of neo-Darwinism. The former is discussed further in a later section.

The most sustained anthropological critique of attempts to anchor optimization in neo-Darwinism is due to Sahlins (1976a), who argues that selection does not maximize anything, including fitness: "Selection is not in principle the maximization of individual fitness but any relative advantage whatsoever Nothing is thus asserted about maximization. In the science of economics, it is true that there is only one appropriate answer to any problem of resource allocation: 'the one best answer,' gain optimus maximus, the particular distribution of resources which maximizes utilities from the means in hand. But natural selection is not the one best; it need be only one better" (pp. 74-75; original italics; sequence rearranged). Besides emphasizing the contrast between economic maximization and natural selection, Sahlins (1976a, pp. 71-107) is at pains to derive the neo-Darwinian propensity to postulate fitness maximization from the ideological influence of bourgeois economic theory: "The Darwinian concept of natural selection has suffered a serious ideological derailment in recent years. Elements of the economic theory of action appropriate to the competitive market have been progressively substituted for the 'opportunistic' strategy of evolution Darwinism, at first appropriated to society as 'social Darwinism,' has returned to biology as genetic capitalism" (pp. 71-72). In this view, the confusion between selection and maximization is no accident, but a historically specific example of the dialectic between socioeconomic structure and ideological superstructure postulated by various "externalist" theories in the sociology of knowledge, especially Marxist varieties.

There is much to be said in favor of Sahlins's arguments. With respect to the linkage between selection and maximization, his critique at least has the virtue of comprehending that the logic of selection involves the reproductive advantage of one unit (be it allele, organism, or lineage) relative to another. A surprising number of the critics of evolutionary optimization arguments have confused neo-Darwinian logic with a Panglossian notion that these models assume some form of global optimization at the level of populations or species (as noted by Maynard Smith, 1978, p. 42; for other examples, see Slobodkin and Rapoport, 1974; Slobodkin, 1977; Martin, 1983). Sahlins to his credit avoids this misunderstanding.

Yet he suffers from another: he conflates the *process* of selection with its *results*. The process *is* one of relative advantage only, not of maximization or optimization. But at least since the days of Haldane and Fisher, neo-Darwinists have realized that small relative advantages can have a large cumulative effect, and it is plausible that one of those effects (given sufficient genetic variation and consistence of selection pressures) will often be not just a trajectory of improvement in designs, but a resulting design that

can fairly be characterized as "optimal" with respect to the fitness currency, the design problem, and the relevant constraints. Sahlins (1976a, pp. 76ff.) comes close to admitting this possibility, but demurs on the basis that environmental change is ubiquitous, hence selective consistency is untenable. This, of course, is a matter for empirical resolution (Jochim, 1983). But it might also be pointed out that selection could—and in some cases demonstrably has—favor the evolution of capacities for phenotypic adjustment to rapidly shifting environmental conditions. Such abilities are clearly central to behavioral aspects of phenotype.

When behavioral ecologists (including the anthropological variety) invoke optimization arguments, then, they are not granting Panglossian directionality to natural selection; rather, they are postulating that phenotypic capabilities whose outcome is "optimal" in some clearly specified sense will evolve, given sufficient conditions (noted above). Viewed this way, optimization models are merely shortcuts to understanding the outcome of evolutionary history—in Etter's (1978, p. 167) apt phrasing, "These methods investigate the teleologies of evolution, on the assumption that conditions presumed by a model actually hold in the real world." ¹⁶ To recognize optimization theory as a shortcut, a simplified and ahistorical approximation to a mechanistic and opportunistic process, does not deny its usefulness to science, although it may serve to alert us to the potential for abuse, and for mistaking the shortcut for the real thing.

As far as the derivation of optimality thinking from neoclassical economic theory, or from the ideology of advanced capitalist society in general, I do not think Sahlins's view is unreasonable. Neither do I think it is very original, sophisticated, nor entirely consistent with his general critique. 17 The glib correlation between the economic interests of capitalist society and the ideological bases of science does not explain why the ideologues of evolutionary optimization are so assailed by critics from all sides-from the left, from the right (e.g., creationists), and from the center (e.g., inductivists). Nor does it account for the uses of evolutionary game theory in subverting the official ideology of utilitarianism ("the greatest good for the greatest number ...") through the irresolvable conflicts of interest and the social dysfunctions of Nash equilibria, as discussed below (and see especially Hirshleifer, 1982); dialectical materialism has no monopoly on contradiction. None of this is meant to support an argument that scientists develop their ideas in a social vacuum, nor to deny that biologists have borrowed many optimization concepts from neoclassical economics. But I see little evidence that this has necessarily been accompanied by a conservative political outlook, or that evolutionary optimization models have regularly been used (wittingly or not) to support the status quo. 18

Taken to its logical conclusion, the critique of all science as socially conditioned ideology must raise doubts that "we can ever hope to do

anything but create a reflection of the current dominant political and economic structure in our reconstructions of the past" (Keene, 1983, p. 148). Accepting this pessimistic, and highly deterministic, view leaves one unable to resolve scientific disputes, except by political sympathies. A less extreme position is that scientific theory and practice is socially conditioned, but not absolutely determined thereby. If so, then the heuristic and explanatory power of optimization theory must be amenable to empirical examination by standard criteria of science. By such criteria, the ideological origins or uses of theory are irrelevant, no matter how interesting (or disturbing) we find them from a sociological or political perspective.

If my arguments are correct, Sahlins's reasons for opposing selection-asrelative-advantage and selection-as-optimization theory are less cogent than they first appear to be. I would submit that this is so even if several other technical objections to evolutionary optimization theory are taken into account.19 But in the special case of social interactions ("special" to biology, but obviously central to anthropology and the other social sciences), I think there is a powerful objection to the optimization viewpoint. This is the realization that strategic interactions characterized by conflicts of interest can lead to evolutionary outcomes quite different from those specified by models of simple individual optimization—a realization first formalized by mathematical economists as "the theory of games" (von Neumann and Morgenstern, 1944; Luce and Raiffa, 1957; etc.) and subsequently given a neo-Darwinian basis in the theory of "evolutionarily stable stategies" or "ESS theory" (e.g., Maynard Smith 1974, 1982; Parker 1984; Parker and Hammerstein, 1985). Put in more ordinary language, when the relative payoffs of different alternative strategies or phenotypic attributes depend on what other individuals in the population are doing, the course of natural selection (or rational choice) cannot be predicted from simple optimization criteria. This is because a strategy that has high payoff when it is rare (and rarely encountered) in the population may have low payoff when common.

The theoretical elaboration of this principle, the counterarguments to it, and the hosts of different types and subtypes of games that can be observed or hypothesized involve complexities that are beyond the scope of this paper. A few simple points can be made here. First, the challenge to optimization theory posed by strategic interaction is fundamental in a way that questions about the details of genetic mechanisms, imperfect information, or cognition and the like (see the previous note) are not—at least to my mind. That is, the results of selection (or rational choice) when there are conflicts of interest cannot usefully be interpreted as "fitness maximization plus some deviation due to constraint x," but rather need to be analyzed in a completely different way (Dawkins, 1980, provides a clear discussion of this). Rather than asking what the optimal solution might be (given a set of

options, constraints, and objective function), evolutionary game theory asks what stategy or set of stategies will be *unbeatable* (assuming each actor takes into account what other actors are doing, and "chooses" the feasible payoff that is highest given that the other actors are equally self-interested). Of course, it is possible to redefine "optimal" in game-theoretic or frequency-dependent terms—the optimal stategy is then the one that yields the highest payoff in the face of what others are doing—but this is a rather specialized and attenuated meaning of optimal, and it is probably less confusing to call this particular spade by a different name.

Second, ESS/game theory shows that conflicts of interest between "actors" (genes, traits, individuals) structure the payoffs (in fitness or utility) in such a way that the best that actors can achieve is quite often worse than could be achieved if they were (coerced into) cooperating. A simple example of this is the "joiner's rule" for foraging group size discussed above. A population of foragers following such a rule (e.g., join a group as long as the payoff is higher than foraging alone) will not usually end up on an adaptive peak in terms of the mean fitness of its individual members, but if the rule is an ESS it will be the best strategy to follow, in the sense that any forager who deviates from it will be worse off. Thus, viewed through the glasses of ESS theory, the simple optimization approach is not a "shortcut"—it is a blind alley (and one I myself wandered up in my initial attempts to explain foraging group size, as noted earlier).

The implications of this disjunction between individual fitness (or utility) maximizing and the evolutionary (or economic) equilibrium are perhaps just as profound as those following from the critique of naive group selectionism raised in the 1960s and 1970s (e.g., Williams, 1966; Dawkins, 1976; Bates and Lees, 1979).20 The first critique made the common equation between natural selection and "the good of the species" problematic, replacing it with "individual fitness maximization." In turn, the ESS/game theory critique makes fitness or utility maximization problematic, and suggests that many social phenomena are ridden with pervasive or even insoluble contradictions between the best interests of each individual and the interests they can realize in collective interaction.²¹ I suspect that ESS theory will eventually force us to rethink not just the pervasive emphasis on functional explanation in the social sciences (including Marxism-see Elster, 1982, on Cohen, 1980), but the rationalist, individual strategizing wing as well. With ESS/game theory, we should no longer be surprised to find that people do not behave in "their own best interest," if the best is defined without benefit of the ESS logic.

Is Optimization Evidence of Adaptation?

The question posed in this subsection, while not quite the inverse of that in the previous, does stand it on its head. Rather than looking at selection and

asking whether it produces optimal adaptations, here we find ourselves looking at apparently optimal phenotypes and asking whether their optimality gives us any reason for concluding they have been designed in some way by selection.

There are really two aspects to this epistemological challenge to optimization theory. The first argues that since optimality explanations are normally synchronic demonstrations of a correlation between predicted and observed phenotypic variation, they cannot be direct evidence of an evolutionary (diachronic) process of adaptation. The second critique argues that the link between behavioral trait and adaptation must always pass through some proximate mechanism or set of mechanisms, and that standard optimality analyses that ignore or avoid this necessary linkage are in error.

On the first issue, I find myself in direct agreement with the charge: a synchronic correlation is not a diachronic causality. It should be possible to use optimality theory diachronically, and thus to explore the evolutionary dynamics as a population of traits evolves toward the optimal (or evolutionarily stable) outcome, but because of the extreme time span required this is rarely done. Certainly none of the examples discussed earlier in the paper provide this kind of evolutionary/diachronic analysis (although one empirical case of the evolution of territoriality cited by Dyson-Hudson and Smith begins to do so). Viewed as current end points of some (poorly understood) evolutionary process, these examples indicate that patterns of human behavior do match those predicted by optimality models in particular cases; but to view them as accounts of the evolutionary process that produced these outcomes is to confuse product with process, a state of the world with a "just-so story" about how the world came to be the way it is.

Since a given product could be produced by various alternative processes, the distinction has some significance. But I doubt that it has as much significance as some critics of adaptation have attributed to it (e.g., Gould, 1980; Gould and Lewontin, 1979). For while some adaptationists may make "consistency with natural selection" (i.e., design for fitness maximization) their only criterion for judging the success of adaptive explanations, most recognize that this is a very weak stance. In the case of human behavioral phenotypes in particular, we face a multiplicity of possible causal factors that could account for such consistency, as discussed in the final section of this paper. I certainly agree with the critics of adaptationism that a mere correlation between the optimality predictions and the observed phenotypes is not sufficient evidence that we are looking at an adaptation shaped by natural selection; but I do not agree that until we have all the relevant information on genetics, development, and evolutionary history (a tall order!) we had best stay quiet (cf. Gould and Lewontin, 1979, Gould, 1980, and Kitcher, this volume). The research findings generated by optimal foraging theory, for example, have greatly advanced our understanding of foraging behavior in a wide variety of species (including our own) despite the almost total lack of genetic, developmental, and evolutionary data.

What then are the implications of empirical evidence demonstrating consistency between optimization models inspired by neo-Darwinian theory and human behavior? First, that we should undertake further research to try and determine the evolutionary forces that led to this consistency. The particular selective forces, accidents of history, cultural or genetic instructions, and cognitive mechanisms that led to this correlation cannot be established through optimization models per se—though these can be helpful in suggesting likely possibilities. Obviously, however, if we continue to find that neo-Darwinian optimization models do an excellent job in predicting real-world phenotypes, and no alternative theory does a better job, we have some reason for supposing that there is a causal connection between the variables identified as important in that theory (expanded to include possible cultural evolution, as noted below) and the historical processes that may have occurred in the real world. If we can gather the data to test this supposition, we should do so; but if the task is too difficult (e.g., how can we study the past demographic history of small nomadic hunter-gatherer populations?), I see no reason to dismiss the inquiry guided by optimization theory as a fanciful parlor game.

In sum, in seeking and finding consistency between behavioral choices and theoretically optimal phenotypes, I am making no *specific* claim about the historical or evolutionary causes that might have produced this consistency. These must be investigated using additional theoretical and empirical means. The fact that evolutionary hypotheses are particularly difficult to test means that we shall often find ourselves with good evidence for optimizing but little or no evidence for the historical/evolutionary causes of same. This may be an uncomfortable position, but I do not think it is an untenable one.

The second critique examined in this subsection is aimed precisely at the agnostic position about specific causal mechanisms I have invoked in dealing with the first. A number of discussions of human behavior from a neo-Darwinian perspective (particularly several in Chagnon and Irons, 1979) have attempted to blunt charges of genetic determinism by arguing that no assumption about particular proximate mechanisms is being invoked when they search for and find instances of "inclusive fitness maximization" in humans. Several critics have found fault with this strategy; the most detailed argument is that of Kitcher (1985, chapter 9).

Kitcher argues that since patterns of human behavior (we would say, more generally, patterns of phenotypic variation in any species) are expressions of underlying dispositions, learning mechanisms, and the like, and since it is these "proximate mechanisms" (as they are called) that have

evolved and that therefore require evolutionary explanation, research strategies that focus directly on the behavioral patterns and sidestep the difficult questions about proximate mechanisms and evolutionary histories are incorrect and "profoundly misguided." In Kitcher's view, this approach "... introduces evolutionary considerations in the wrong place. There is much striving to show that the end products of a complicated process really maximize human inclusive fitness. Usually the striving is in vain. The products should not be expected to maximize inclusive fitness. Yet, even if they were to do so, the proper focus of evolutionary attention is on the mechanisms that drive the process. In the haste to see fitness maximization everywhere, those mechanisms—and the historical process in which they figure—are ignored" (p. 329).

Kitcher's points here are two. First, because proximate mechanisms must serve to map genetic instructions onto a wide variety of environments, we must expect "mistakes" (nonoptimal behavior) to be quite frequent; the mechanisms will maximize fitness (if truly designed by selection) only on average. This is actually a conservative reading of Kitcher's position, for at several points he uses stronger language, stating that whether or not the behavioral products of proximate mechanisms maximize fitness is "irrelevant" (pp. 288, 298) and that studies that demonstrate how often they do teach us "little" (p. 307) or (even stronger) "shed no light on what really needs evolutionary explanations—to wit, the proximate mechanisms" (p. 307).

The more cautious reading of Kitcher's argument is one that I have some sympathy with, and will return to in the final subsection of the paper when discussing cultural evolution. The stronger version strikes me as dubious, or even logically incoherent. If we give the hypothesis that proximate mechanisms have evolved by natural selection serious consideration, how can we treat the fitness consequences of much mechanisms (as mediated through their behavioral products) as irrelevant? And if, as is often the case, we are relatively ignorant about the possible proximate mechanisms at work and their evolutionary history, what sense does it make to eliminate evidence on these fitness consequences, taken as an average over a set of proximate mechanisms? Surely the evaluation of specified patterns of behavior in terms of their fitness consequences sheds some light on the adaptiveness of the proximate mechanisms that underlie these patterns. More specifically, if the mechanisms evolved and are maintained because of their net fitness-enhancing effects (the primary adaptationist hypothesis), and if the only or main way these effects can be realized is through behavior, then the auxiliary hypothesis that the behavior produced by these mechanisms will have a net fitness-enhancing effect is at least a reasonable, and certainly not an "irrelevant," one. 22 For if a mechanism is fitness-enhancing on average, then the behavioral effects of this mechanism must also be so. To determine the average fitness effects, we must collect data on particular instances; hence these cannot be "irrelevant," but must be of the essence to any but Platonists. The problem is, we often do not know which proximate mechanisms are connected to which behavioral outcomes, and here Kitcher's critique (in its weaker form) is valid. But the stronger version does not cohere.

The second point of Kitcher's critique is that evolutionary explanations properly apply only to proximate mechanisms. The stated implication is that adaptive considerations are irrelevant to more distal products of these mechanisms, such as behavior. In what sense is this true? Both behavior and cognitive/neurophysiological mechanisms are aspects of phenotype, so neither can be identified as the units of selection or inheritance; rather it is information (genetic and cultural) that is transmitted and exhibits differential fitness (Cloak, 1975; Dawkins, 1982). Interpreted radically, Kitcher's argument would impel us to hold all evolutionary arguments in abeyance until we understand the specific genetic and cultural instructions underlying the aspects of phenotype we are interested in. (Note that this would logically apply as much to proximate mechanisms as to behavior; that is, we would have to trace phenotypic traits all the way back to DNA and the neurophysiology of long-term memory before we could profer any adaptive argument whatsoever.) If we moderate the argument somewhat, it becomes a claim that analyses that do not identify the proximate mechanisms and evolutionary histories connected to the behavioral patterns of interest are incomplete. This is closely analogous to the claim discussed in the first part of this section, and one I agree with; but, as before, it is not sufficient grounds for abandoning optimization hypotheses about behavior, only for abandoning conclusions that these offer direct evidence of evolutionary history. And this last caveat is one that applies to proximate mechanisms with equal strength.

Are Optimization Models Realistic?

A third set of criticisms of the optimization approach revolves around the issue of realism. The issue in this case is the simplification or caricature of particular phenomena, rather than of evolution in general. In anthropology, this critique has often been linked to claims that such models might apply to other species (that lack culture) or to certain societies (those with market economies), but not generally. An example of the former is Lee's (1979, p. 434) statement that "mechanical models drawn from animal behavior and animal ecology, however sophisticated, cannot do justice to any but the simplest of cultural ecological phenomena" (see Jochim, 1983, and Keene, 1983 for similar views). The issues of cross-cultural rationality and human uniqueness are taken up below; here I consider the broader issue of simplification versus realism.

decline along both of the other axes.²³

With respect to realism in particular, the trade-off is that an increase in this attribute usually reduces the range of different situations or systems the model applies to, the precision of the predictions it will generate (as more and more factors whose exact effect is unknown are considered), or both. Thus, any criticism of an optimization model as unrealistic is incomplete unless one goes on to ask what will be sacrificed if it is modified or abandoned in order to increase realism. If one is very fortunate, the alternative may yield a large increase in realism at a small cost of reduced generality or precision. But most critics have no alternative model in mind, except some Platonic ideal of pure Realism, unimpaired by declines in generality or precision.

There is probably nothing inherent in optimization theory that make its models less realistic than others; indeed, by fitting utility functions to observed behavior, one could build decision models that mimic human cognition and behavior in very circumscribed areas quite nicely (though the resulting model would be unique to the situation, or even the individual for which it was constructed). In practice, however, simpler models are easier to understand and work with, and are invariably preferred in the early stages of incorporating the optimization approach into a field of research for this reason. This is certainly the case in anthropology, and to a lesser extent evolutionary biology, in comparison to economics and engineering, where a longer history of optimization research has created a greater demand for complex, realistic, situation-specific models.

In a field like anthropology, then, what one sees is a "research frontier" of expanding but still-novel optimization models (of the simple, relatively unrealistic sort) encountering conventional, informal and particularistic research that can often sincerely claim to be more realistic than the upstart optimization models. The short-term result is predictable: the old guard, and all those who favor detailed, realistic analysis (description?) of particular cases as an end in itself, charge optimizationists with being unrealistic and ill-equipped to deal with the complexities of the real world. The upstarts, and all those who favor a strategy of explaining particular cases in

terms of general theory, argue for quantitative tests but against abandoning a model unless a more-or-less equally general alternative is available. But if the short term appears at a stalemate, the long term (judging from the experience of other disciplines, and the hints already apparent at this stage in anthropology) promises vigorous hybridization at the frontier, and the proliferation of models exhibiting varying degress of realism, generality, and precision. But judging from the examples of other sciences, natural and social, there will continue to be room for simple, highly stylized and "stripped-down" models of the sort discussed here, though I expect they will be more complex than at present, and better accepted as components of an integrated research strategy.

Before leaving this topic, something should be said about the specific issue of cognition and imperfect information, as this is a key area where anthropological applications of optimization theory lack realism. The simplest and most tractable optimization models are deterministic: the currency is a mean or expected value (with no attention paid to risk or variance) and the actor is assumed to operate with perfect information (complete lack of uncertainty). This is obviously unrealistic. Dealing only with the matter of uncertainty, ²⁴ it is hard to deny that, as one critic of perfect-information models in anthropology has put it, "Ecological optimization models differ drastically from actual decision-making procedures and hence are not likely to predict actual behavior on that basis" (Jochim, 1983, p. 164), or that, as another puts it, "In reality, decisions are based on a mix of information, ignorance, error, and lies" (Moore, 1983, p. 183).

Two responses to these criticisms will be noted here. One is that, while often more realistic, imperfect information models are not necessarily of greater scientific utility. If one is directly concerned with the structure of information and its effects on behavior, then of course the perfect-information assumption is foolish; but in other contexts, especially the initial forays into a field by an optimization approach, simpler models may be preferable. At the least, such models may reveal the degree to which imperfect information affects strategic outcomes. This baseline allows a "piecemeal" adjustment in predictive power and realism to occur at a suitable point, as data and theory accumulate suggesting how uncertainty (as well as other factors) should be incorporated into one's models (cf. Johnson, 1982; Krebs, Stephens, and Sutherland, 1983; Krebs and McCleery, 1984).

A second point is that even if actors are not the "know-it-alls" caricatured in the models, if the strategies they play are heritable (culturally or genetically) and have been shaped by a history of natural selection, actors might come to perform "as if" they had more-or-less perfect information about the long-term probabilities of various outcomes and conditions. This justification is one reason economists have turned to selection to explain

phenomena such as profit-maximization in uncertain environments (note 5), and is behind the current interest in "rules of thumb" in areas of evolutionary ecology, such as optimal foraging theory (reviewed in Krebs, Stephens, and Sutherland, 1983). In invoking selection, one must consider the extent to which the currency favored by selection is congruent with that postulated by a simple optimization model. And as Sahlins (1976) reminds us (see above), one must also keep in mind the fact that selective pressures can change, and that selection is opportunistic rather than omniscient (see also Jochim, 1983). But the central point remains: the cognitive or information endowments of foragers should not be uncritically read as defining the compass of optimization models, even "realistic" ones.

Individual Choice, Adaptation, and Cultural Logic

Optimization methods, by themselves, are devoid of explanatory content. Such content is provided by substantive theories, of which two have been discussed in this paper: neoclassical economics and (more fully) neo-Darwinism. I have noted that the former is virtually mute when it comes to answering what actors maximize, and why. All of the models summarized herein, while employing formalisms first developed in economics, have been anchored to the theory of natural selection by the assumption that the currency maximized and the causes of optimal design are the result of selection for increased fitness (probability of genetic replication) in past generations. Our final set of critiques concerns the validity of this assumption, in the face of the presumed role of culture in determining the form and content of human behavior.

This is obviously an extremely broad and complex topic. I shall break it down into three questions: (1) How much genetic determinism is necessarily implied in applying models from evolutionary biology to human behavior? (2) Do optimization models project an egoistic individualism at odds with what we know of cultural tradition? (3) Does culture have a logic and determining force independent from organic evolution? My answers will necessarily be brief and provisional.

The specter of genetic determinism has been especially pronounced with respect to sociobiological assertions regarding human behavior, but some critics have also tarred what they have labeled the "fallback" position of ecological or evolutionary determinism (Gould, 1980; Boucher et al., 1978, contra Alexander, 1978; Emlen, 1980) with the same brush. For these critics, either the hypothesized optimization tendencies are due to genetic evolution of specific propensities to maximize fitness in response to specific stimuli—in which case they partake of genetic determinism and fly in the face of what we know about cultural determination of human behavior—or else they have nothing to do with natural selection (a theory, after all, of genetic evolution) and hence have no basis in evolutionary theory.

Between this rock and hard place, there may be a middle way. Granting that we know surprisingly little about the ontogeny of the sort of behavioral processes that figure in most ecological optimization models, let us accept the conventional anthropological view that very little in the way of specific behavioral instructions is encoded in genetic programs. How might genetically adaptive behavior arise? Three main proposals are frequent in the literature: through prepared learning, through fitness-correlated evaluation of consequences, and through a parallel process of cultural evolution. Prepared learning (Seligman, 1981) refers to genetically encoded propensities to learn certain behavioral patterns easily; a paradigmatic, relatively well-studied case is that of language acquisition (e.g., Lenneberg, 1967; Geschwind, 1972). Note that the degree of "preprogramming" need not specify any of the particular content of the behavioral pattern (e.g., English versus Chinese), only the basic form (acquisition patterns, Chomsky's "deep structure").

Though it is debatable, I doubt that prepared learning is important for most areas of ecological adaptation in humans. The remaining two factors are, I would argue. Cultural evolution will be discussed at the end of this section. Fitness-correlated evaluation of consequences (Durham, 1976, 1979, 1987) may arise through natural selection acting on either cultural or genetic variation (Boyd and Richerson, 1985) and refers to a process whereby actors evaluate the outcome of their choices by some measure of success correlated with fitness—what we might term "ethnofitness." The evolutionary programming here does not specify the motor patterns or behavioral propensities of actors, but only the criteria they use to evaluate consequences of their own actions, however originally motivated.

To use a trite but heuristic example, there is nothing "in the genes" to make some people prefer hunting of big game, and others small-game hunting or gathering. Yet the archaeological and ethnographic record clearly reveals a tendency for these preferences to follow regular patterns, and research using optimal foraging models indicates that the pattern may be largely the result of foragers evaluating different options by a simple rule involving opportunity costs and energy return rates (reviews in Smith, 1983b; Winterhalder, 1987; Hill et al., 1987). If so, the selection of alternatives is by their consequence, as measured by foraging efficiency. The measure of consequence here presumably has evolved (by genetic and/or cultural evolution); it is the following of this rule, rather than any innate tendencies to engage in one specific foraging tactic or another, that is responsible for the tendency to vary foraging behavior toward the local optimum.

Foraging behavior, or subsistence in general, is of course but a single (some would say marginal) aspect of human social behavior. The further caution might be raised that whereas foraging is a category of behavior

humans share in some detail with other species, hence suggesting certain homologous cognitive mechanisms might be at work, kinship and ritual (for example) are unique, or uniquely developed, aspects of our behavior. Is there any reason to suppose that "evaluation by consequence" is as important in these and other areas as it appears to be for foraging, or that the evaluative criteria are as closely correlated with fitness? Empirically, the answer is far from clear (on this point, compare Alexander, 1979, Chagnon and Irons, 1979, and Durham 1987, to Boyd and Richerson, 1985, Kitcher, 1985, and Richerson and Boyd, this volume). This suggests we would do well to take an agnostic position, awaiting further research. But I think there is considerable agreement that some kind of decision-making process is a widespread—though not exclusive—mechanism of behavioral variation. Indeed, that most ubiquitous form of learning, operant conditioning, is best considered a form of selection by consequence, where the selection is by the actor, and the consequence (determined by environmental contingencies) is given a valence by natural selection (Skinner, 1981).

But phrasing the mechanisms of optimization this way, while it may steer us clear of the most prominent shoals of genetic determinism (sensu strictu), still yields a very egoistic, individually focused view of human social behavior. In this regard, optimization theory remains true to its source in neoclassical economics, that shrine to social satisfaction of individual needs. The tradition in much of anthropology is different, and could fairly be phrased as an inversion of economics: the individual satisfaction of social needs. Again, our most persistent Jeremiah here is Sahlins: "For the central intellectual problem does come down to the autonomy of culture and of the study of culture. Sociobiology challenges the integrity of culture as a thing-in-itself, as a distinctive and symbolic human creation. In place of a social constitution of meanings, it offers a biological determination of human interactions with a source primarily in the general evolutionary propensity of individual genotypes to maximize their reproductive success" (1976a, p.x). In the extreme form of cultural determinism espoused by Sahlins (see especially 1976b), cultural systems each have their own internal logic, which dominate any individual motives (fitness-maximizing or not) and replace the trajectory of natural selection with that of cultural teleology: "The wisdom of the cultural process consists in putting to the service of its own intentions natural systems which have their own reasons" (Sahlins, 1976a, p. 67).

Metaphor or not, many readers may be impelled to ask what the "intentions" and "reasons" of culture might be, and how they come to exist. Though the tradition of sociological functionalism is venerable, it does not seem to have produced a convincing and widely accepted rationale or generating mechanism. Beyond some vague arguments concerning the social construction of meaning and the logic of semiotics, Sahlins offers no

further answer.²⁵ Yet most anthropologists cling to the conviction that culture determines human behavior, and that individual optimization—whether motivated by rational self-interest or the imperative of fitness-maximization, it does not matter—cannot explain social and cultural patterns, only conform to them. (A recent expression of this view by an ecological anthropologist is presented in Rappaport, 1984, pp. 397–402.)

To a large extent, this disagreement is much older than optimization research, perhaps as old as social philosophy. The methodological individualists have been battling—or talking past—the sociofunctionalists for a long time. ²⁶ It would be immodest to suggest a direct resolution. There is one avenue currently being explored within anthropology and biology that may hold some promise, however: a theory of cultural evolution.

When an actor exhibits strategic behavior conforming to optimization predictions, various proximate causal mechanisms could be responsible: trial-and-error learning, prepared learning, fixed action patterns, and—for humans—rational choice or adherence to cultural tradition. In all of these cases, the ultimate values guiding the "choice" of goals or alternatives must arise by some evolutionary process. For the last two, characteristically human, mechanisms, it is unlikely that the evolutionary process is limited to changes in gene frequencies. That is, some process of cultural evolution is at least partially responsible for the observed patterns. Even Economic Man acts to maximize status (culturally defined), and exchanges culturally defined goods in socially defined manners; and the accepted means of pursuing individually adaptive ends, even the fitness payoff structure, are socially and culturally conditioned for our species in a way that might make the standard neo-Darwinian optimization approach incomplete.²⁷

If constraints, strategies, and even goals sometimes evolve by selection acting on culturally transmitted variation, we may have a partial answer to the paradox posed by cultural determinism. For to stop at the position Sahlins does, postulating a "cultural reason" only loosely constrained by biological (and technoeconomic) possibility, is to indulge in a form of "cultural creationism." 28 We need to explain how cultural elements come to exist and exert such a determining role over human action. Cultural evolution can explain how values and institutions not inscribed in our genes arise. But it can perhaps do much more than this, for the following reason: cultural evolution may not necessarily tend to maximize genetic fitness. This result is preliminary, based on recent quantitative models of the interaction of genetic and cultural evolution (Cavalli-Sforza and Feldman, 1981; Pulliam and Dunford, 1980; Werren and Pulliam, 1981; and especially Boyd and Richerson, 1985). But it seems almost certain that, whatever its quantitative effect, the qualitative effect of any system of cultural transmission not "symmetric" with genetic transmission (i.e., equal inheritance from each biological parent) will cause the evolutionary trajectory of human behavior to deviate from that predicted by fitness optimization.²⁹

If this is so, we may have the second answer to Sahlins's paradox of cultural determinism: the source of "cultural reason." Selection acting on cultural variation, whenever it deviates significantly from the genetic fitness optimum, will lead to social traits difficults to interpret in utilitarian, let alone Darwinian, terms. This does *not* mean that culture is maladaptive overall, only that it *sometimes* will be so (see note 29). Of course, this presents an entirely new set of arguments for explaining the evolution of human behavior, and, to quote Boyd and Richerson (1985), "greatly complicates the analysis" of this evolution. The cases reported in this paper would seem to be satisfactorily analyzed using standard Darwinian assumptions (while of course allowing for phenotypic flexibility and selection by consequence, not narrow genetic determinism). But other, less utilitarian aspects of human social behavior may require a new kind of optimization theory, incorporating aspects of the developing theory of cultural evolution.³⁰

Notes

- 1. I use the term "theory" in two senses, a generic sense and a specific one. The generic referent is any nonempirical claim or argument; it is in this sense that I speak of "optimization theory." No sense of unity or consistency is necessarily implied in this use of the term. The more specific referent is any collection of explanatory arguments that does exhibit substantial internal consistency and unity; this second sense is the one referred to in the use of the term noted here. That is, particular theories consist of various models linked to each other and to other elements via deductive operations, bridging arguments, and the like. In this second sense, then, there is no "theory of optimization," but rather a large number of optimization models that (while sharing certain formal characteristics) are embedded in a relatively smaller but still diverse set of theories (e.g., the theory of consumer choice and optimal foraging theory).
- 2. Maynard Smith (1978) provides a somewhat different typology, which includes the strategy set ("phenotype set") as a subset of the "constraints" category (see also Oster and Wilson, 1984). I view this difference between us as semantic rather than substantive. As I have just indicated, the set of feasible strategies is subject to constraints (i.e., not all strategies we can conceive of are necessarily available in ontogenetic or evolutionary time).
- 3. Some key references in support of my generalizations include the literature on optimal foraging theory (reviewed by Pyke, Pulliam, and Charnov, 1977; Krebs, Stephens, and Sutherland, 1983; Pyke, 1984), life history strategies (reviewed by Horn and Rubenstein, 1984)—especially that utilizing dynamic optimization methods (e.g., Schaeffer, 1983), evolutionary game theory, or ESS models (reviewed by Maynard Smith, 1982; Riechert and Hammerstein, 1983; Parker, 1984; Parker and Hammerstein, 1985), theory concerning risk and uncertainty (e.g., Caraco, 1980, 1981a,b; Real, 1980; Rubenstein, 1982; Stephens and Charnov, 1982), and theory on parental investment—in this case authored by both biologists and economists (e.g., Trivers, 1972, 1974; Maynard Smith, 1977; Hirshleifer, 1978; Rubin, 1979; Samuelson, 1983; Rubin, Kau, and Meeker, 1979).

- The convergence of economic and evolutionary optimization models has been reviewed both favorably (Rapport and Turner, 1977; Hirshleifer, 1978) and critically (Sahlins, 1976a), although in neither case do we have a recent or sustained analysis.
- 4. There is considerable literature on the problematics of "fitness" as a measure of adaptive consequence, as well as on the level at which natural selection is most effective, or effective at all, in producing design (and therefore any approximation of optimal design). Sober (1984) contains many of the key papers from this literature, and Williams (1966), Maynard Smith (1976), Wade (1978), Wilson (1980, 1983), Uyenoyama and Feldman (1980), and Dawkins (1982) should be consulted as well. The point I am making here is that the theory of natural selection provides a framework for examining these questions fairly rigorously, and allows continued attempts to extend and improve matters in this regard; this is in some contrast to the situation in neoclassical economic theory.
- 5. One of the more striking illustrations of this dependence of economics on evolution is provided by the use Alchian (1950) made of "natural selection" (loosely defined) to rescue the assumption of profit-maximizing as the strategic goal of firms in a competitive capitalist economy. While central to microeconomics, the profit-maximizing assumption encounters two difficulties: (1) A firm is not an individual actor, but rather a collection of individuals, many of whom may have competing goals (i.e., maximizing individual utility may often conflict with maximizing the profits of the firm to which the individual belongs, and detecting such "cheating" or "slacking-off" may often be difficult, or more costly to the firm's profit picture than letting it slide). (2) Imperfect information and rapidly changing market constraints make profit maximization difficult even for dedicated seekers of profit. Empirical evidence indicates that firms do not always make choices that maximize expected profits, although apparently they tend to do so more often than might be expected given the problems of conflicting interests and imperfect information noted above. Alchian's solution to this dilemma was to argue that while these objections are valid, in a competitive marketplace those firms whose members tend to possess utility functions that (for whatever reason) are congruent with maximizing firm profits will tend to outcompete less successful firms, resulting in an evolutionary trend toward the condition previously assumed without sufficient support (i.e., firms are actors that attempt to maximize expected profits) (for further discussion, see Winter, 1975; Hirshleifer, 1977; Nelson and Winter, 1982). Alchian's solution is thus a form of group selection, but raises some of the same issues found in the literature on group selection in organic evolution (e.g., how do firms initially attain the critical frequency of profit-maximizing necessary for group selection to be effective?). Boyd and Richerson (1980) have attempted to fill this lacuna by building theory that specifies plausible individual-level mechanisms of cultural evolution (such as imitation of peers when information on the expected utility of options is costly to obtain).
- 6. I am not certain which study might lay claim to being the first anthropological application of an optimization model, but perhaps it is Davenport's (1960) application (or misapplication—see Read and Read, 1970) of a game-theory model to analyze the fishing-location strategies of small-scale Jamaican commercial fishermen. In any case, very little work in this tradition occurred within anthropology for another decade or so.
- 7. In recent years, discussions have begun to appear that recognize the variety and ecological context of hunter-gatherer land tenure (e.g., Wilmsen, 1973; Knight, 1965; Binford, 1980; various authors in Williams and Hunn, 1982). And anthropologists studying systems of land tenure among nonforagers have also developed a more sophisticated set of analyses (e.g., Goody, 1976). However, I would still claim that anthropologists have made far too little use of general theory and formal models of land use, such as those developed in geography, economics, and evolutionary biology, and that as recently as five years ago the simple dichotomization discussed in the text still prevailed.

- 8. Note that the per capita harvest rate is not necessarily equal to the actual or mean rate that each group member gets, unless there is an equal or random distribution of the harvest. Among the Inuit foragers I studied, such an equal division of the harvest does in fact typically occur, but this is not always the case among human foragers, nor is it typical of nonhuman social carnivores.
- 9. Hill and Hawkes (1983) have done the earliest and most extensive theoretical and empirical work on the effects of central-place sharing on foraging group size. Data on Ache foragers, who approximate the condition of central-place sharing, tentatively support some of these predictions (Hill and Hawkes, 1983).
- 10. Many (but not all—cf. Gould, 1982) foragers do possess an ethic of widespread, if not quite "generalized," reciprocity. But to point to such an ethic is not to explain its existence, nor the sharing behavior it may help motivate. In other words, the ethic—like any value or belief—is a proximate mechanism or element in a longer causal chain. Even less satisfactory is the frequent argument that sharing rules are a "leveling device" impelled by an "egalitarian ideology." As has been pointed out by others (notably Cashdan, 1980), this view fails to explain variation in sharing rules or the rise and eventual dominance of nonegalitarian, nonreciprocal systems. In addition to these logical and empirical difficulties, the views I criticize here are inconsistent with evolutionary theory, being examples of naive group selectionism or social teleology.
- 11. The assumption that there is no cost is an important one. Logistical costs are likely to arise for most systems of sharing, but these are relatively easy to measure. More difficult to consider are costs due to cheating on the part of some members of the sharing network, or other costs associated with social relations (such as disputes). Kaplan and Hill (1985b) provide a more extended discussion of these considerations. Even if there are costs, sharing can still be adaptive as long as these costs are less than the net advantage of consuming $V(\bar{x})$ rather than $V(\alpha + \beta)/2$. Whether selection will favor sharing simply because it is adaptive is a more thorny issue, as discussed in the subsection on optimization versus evolutionary equilibrium.
- 12. A more commonsense explanation of the differential sharing of meat versus plant foods is that the former are more subject to spoilage, and come in larger packages than individuals or households can easily consume. This is empirically correct, but is not an alternative explanation. If the shared resource (e.g., meat) was not characterized by variation in individual harvest rates, or did not produce diminishing returns if consumed in very large amounts, then there would be no need to share it. These are precisely the conditions assumed to favor sharing in the risk-reduction model, and implicitly assumed in the commonsense view.
- 13. I am not claiming here that one of these positions is empirically more correct than the other—there has been no direct test of these two assumptions on the same data set—but simply that they are theoretically distinct and that the evolutionary view is presently more theoretically complete than the economic one. It may be possible to use cultural evolutionary theory to provide a more complete theoretical grounding for economic demography, so as to explain why actors might make reproductive decisions that maximize economic or status variables rather than fitness [see, for example, Boyd and Richerson's (1985, pp. 199ff.) scenario for the cultural evolution of the demographic transition]. It should also be pointed out that, properly conceived, there is less conflict between children-as-means (economic demography) and children-as-ends (evolutionary biology) than suggested in the text. For one, some economic demographers and economists of the "new household economics" persuasion (e.g., Becker, 1981) are willing to view households as producers—not just passive consumers—that produce such "goods" as children and clothe, feed, and educate them in order to satisfy certain demands [though as Etter (1978) points out, an inherent ambiguity in specifying the

- sources of these demands remains). From the evolutionary side, we must remember that kinship and reciprocity structure family interactions in such a way that the net economic contribution of children to family income, insofar as it may affect parental and sibling survivorship and reproduction, is just as valid a component of fitness calculations of alternative reproductive strategies as is the direct contribution of each child to parental fitness.
- 14. The optimal IBI is that which maximizes net yield of children surviving. Using the backload/mortality regression and the !Kung demographic parameters, this peaks at 50 months, but shows a fairly broad plateau from 42 through 54 months—hence, the mean IBI for this "optimality plateau" is 48 months. Because of the way in which Howell's data were collected, IBIs cluster at 12-month intervals, making the sample size for the actual optimal IBI (50 months, n = 2) too small to compare to that for the mean optimal IBI (48 months, n = 17). In any case, the fit is remarkably close (see Blurton Jones, nda, for further details).
- 15. The exact selective pressures shaping !Kung IBIs cannot be directly ascertained from Blurton Jones's retrospective analysis of demographic rates, as he is quick to admit. From ethnographic accounts by Lee and others, as well as the simulation results of Blurton Jones and Sibly (1978), it seems likely that backload is determined by a complex set of variables, of which the most important are birth spacing and subsistence mobility. Settled women need not forage as widely for food, and they have available weaning foods (in the form of milk and cereals) from the cattle posts that their bush-dwelling sisters lack (Lee, 1980). Bush women who lose an infant are released from backload of both child and food (for lactation requirements), whereas death of an older child reduces only food demand, which is not quantitatively sufficient to allow additional "replacement" reproduction without taking backload above the critical limit (or, alternatively, reducing food carried below the critical limit needed to support herself and her dependents).
- 16. Similar conclusions are drawn by most proponents of optimization models in evolutionary biology. As examples: "Rather than a grand scheme for predicting the course of natural selection, optimization theory constitutes no more than a tactical tool for making educated guesses about evolutionary trends" (Oster and Wilson, 1984, p. 284). "The role of optimization theories in biology is not to demonstrate that organisms optimize. Rather, they are an attempt to understand the diversity of life" (Maynard Smith, 1978, p. 52).
- 17. The cultural tradition Sahlins's remarks belong to was established by Marx himself, who even applied it to the topic under discussion here, as in the following passage: "It is remarkable how Darwin recognizes among beasts and plants his English society with its division of labour, competition, opening up of new markets, 'inventions,' and the Malthusian 'struggle for existence'" (Marx to Engels, letter dated 18 June 1862, in McLellan 1977, p. 526; quoted in Sahlins, 1976a, pp. 101ff.). The tradition continues to play a role in the optimization controversy (e.g., Morales and Levins, 1974; Keene, 1983; Lewontin, 1984). As for consistency, Sahlins's antiutilitarian relativism seems at odds with his glib use of historical materialism to account for shifts in intellectual fashion.
- 18. Certainly economics and evolutionary biology have often been vulgarized to support politically conservative views. But my point here is that these phenomena are not basic to or inherent in optimization approaches, and that liberal or even radical views can just as readily be served by strategic evolutionary and economic thinking (for example, Dyson-Hudson, 1979, and Hrdy, 1981, in evolutionary biology; Elster 1982, and Roemer, 1982, for Marxian political economy).
- 19. These objections include (1) the possible lack of requisite genetic variability; (2) the

existence of selectively neutral variations; (3) the possibility that various genetic complications (epistasis, pleiotropy, heterozygote superiority, meiotic drive) generate maladaptive genotypes; (4) the multiple selective factors affecting phenotypes, which make atomization into separate adaptive values problematic; (5) developmental constraints that prevent optimal phenotypes from being generated in ontogeny; (6) neurological or cognitive constraints that prevent animals from gathering enough information to behave optimally; and (7) the epistemological difficulties associated with formulating and testing optimality hypotheses. Reviews of these issues from a number of different stances are found in Maynard Smith (1978), Lewontin (1979), Dawkins (1982), Oster and Wilson (1984), Krebs and McCleery (1984), Kitcher (1985, chapter 7), and several chapters in this volume, especially Emlen's contribution. I have not had room (nor expertise) to deal with most of these issues in this paper. While recognizing the validity of these critiques in principle, I must record my observation that much of the antiadaptionist literature is far more speculative—pointing to possible complications and "just-so stories" about hypothetical voles and poorly understood phenotypic traits—than the bulk of the adaptationist literature (with the possible exception of adaptationist analyses of human behavior, which are often atrociously lacking in evidence and logical rigorthough no more so on average than the rest of social science, I would contend).

- 20. The "group-selection controversy" is far from dead—or better stated, it continues to mutate and evolve into new forms. The reference in the text is to the original, naive formulation that held "good-of-the-species" arguments to be isomorphic with Darwinism, or that attempted to derive group advantage from natural selection theory without use of rigorous mathematical argument (e.g., Dunbar, 1960; Wynne-Edwards, 1962). The more recent mathematically based debates about the form and frequency of selection at various levels of biological organization are a different matter. With reference to human behavior, Boyd and Richerson's (1985, chapter 7) models suggesting that the conditions favoring group selection may be more commonly encountered in the case of cultural evolution than in the case of genetic evolution also offer a more sophisticated and precise basis for explaining the existence of traits with reference to their groupsupporting functions. Although as yet relatively untested, this line of inquiry is given tentative support in James Peoples's (1982) provocative reanalysis of Rappaport's (1968, and cf. 1984) functionalist view of intergroup conflict among the Tsembaga Maring of highland New Guinea. Peoples's analysis is also relevant to a question addressed by Hirshleifer (this volume)—to wit, can evolution provide a way out of dysfunctional Nash equilibria that result from individual self-interest? (See also note 21.)
- 21. Extended discussions of this in terms of human socioeconomic processes can be found in the literature on "collective decision" (e.g., Olson, 1965; Schelling, 1978; Hardin, 1982; Elster, 1978, 1982). An explicit link to evolutionary theory and a direct attack on the wisdom of the Invisible Hand is provided in an extremely stimulating essay by Hirshleifer (1982—see also Hirshleifer, this volume).
- 22. The argument sketched here depends on at least one additional assumption, that the aspects of the environment relevant to the proximate mechanism(s) in question have not recently changed sufficiently to make products of the mechanism(s) maladaptive. The validity of this assumption, while an empirical issue for any particular mechanism, depends in general on the specificity of the mechanisms involved (as well as on the stability of the environment). I think much evidence and theory favors the view that human cognitive mechanisms are relatively (though not absolutely, whatever that would mean) "general-purpose" or "open" (for futher discussion, see Mayr, 1974; Dyson-Hudson, 1983). If so, then these mechanisms should continue to produce adaptive responses (on average) even in markedly altered or novel environments.
- 23. If Levins's model of models is approximately correct, then "any use of models involves

some implicit or explicit ranking of these three attributes by the modeler. The optimum toward which we aim our models will be determined—as in any optimization problem—by a combination of goals (what are the strategic objectives of our research? how do we plan to test the model?) and constraints (what relevant theories are available? what kinds of data can we hope to collect?)" (Smith, 1983b, p. 637).

24. Risk is incorporated into optimization models more easily; indeed, it plays a central role in two of the models reviewed in this paper (land tenure and resource sharing). For further discussion of the role of risk in anthropological optimization theory, see Smith (1983b, pp. 638–640) and Winterhalder (1987).

25. Neither do other nonevolutionary cultural determinists, nor biologists influenced by them. As example of the latter, consider the following "explanation" in support of Sahlins's (1978) critique of a (rather dubious, I would admit) cultural-materialist explanation of Aztec sacrificial cannibalism proposed by Harner (1977): "Human cultural practices can be orthogenetic and drive toward extinction in ways that Darwinian processes, based on genetic selection, cannot. Since each new monarch had to outdo his predecessor in even more elaborate and copious sacrifice, the practice was beginning to stretch resources to the breaking point" (Gould and Lewontin, 1979, p. 583). Just how this argument really explains Aztec sacrifices, I fail to see; at best it could account for an escalation of same, given some initial reason why sacrifice was practiced, and given the motivation of individual monarchs to compete with (the reputation of) their predecessors. But the givens here carry the bulk of the explanatory load, and remain undemonstrated and unaccounted for.

26. This conflict, involving economic optimization models, is well exemplified by the "formalist" (read, neoclassical) versus "substantivist" (read, cultural relativist) debate that occupied economic anthropology for well over a decade, and still flares up in border skirmishes now and then. Many of the key position papers in this dispute are included in the reader edited by LeClair and Schneider (1968; see also Sahlins, 1969, 1972; Godelier, 1972; White, 1973; Donham, 1981).

27. The claim just made does not entail, nor do I subscribe to, the further claim that social institutions or structures are autonomous causes of individual behavior. Instead, I hold a view more akin to game theory and other sophisticated versions of methodological individualism that recognize the emergent properties of social interaction and social evolution, while still seeking the causes of these at lower levels of organization (e.g., Dawkins, 1976, p. 89; Elster, 1982).

28. I am indebted to William Durham (1987) for this clever phrase.

- 29. How much of a deviation is subject to various estimations, given the formal assumptions and informal prejudices of the various judges. It is important to note that cultural evolution (as opposed to plain cultural determinism) offers no basis for asserting that the system of cultural transmission as a whole leads to maladaptive (by neo-Darwinian measures) outcomes. Durham (1976) argues that only low-cost low-benefit traits will evolve culturally away from fitness optima, while Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1980, 1985) obtain much stronger deviations than this under their particular model assumptions. It is also important to note that the only evolutionary force capable of creating sustained deviations away from fitness optima is natural selection acting on cultural variation (with asymmetric inheritance, as in horizontal transmission or unequal contribution from parents) (see Boyd and Richerson, 1985). Whether selection acting on cultural variation is actually strong enough to override the effects of biased transmission and guided variation (evaluation by fitness-correlated consequences) programmed into the human brain by genetic evolution remains an empirical question (Flinn and Alexander, 1982; Boyd and Richerson, 1985).
- 30. Richerson and Boyd (nd) have constructed a model of "runaway selection" involving

cultural transmission that is analogous to runaway models of sexual selection, which (under proper values of model parameters) produces results they interpret as similar to those implied by Sahlins's (1976a,b) views of "cultural reason." They have gone on to suggest the application of this model to an empirical case involving the association of giant yams with prestige in a Micronesian society. It is not clear that one would want to call this an optimization model (they do not), but to the extent that some measure of fitness (combining cultural and genetic components) is maximized, the suggestion may not be completely absurd.

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