1

New Perspectives on Hunter-Gatherer Socioecology

Eric Alden Smith and Bruce Winterhalder

Introduction

Hunter-gatherer lifestyles have characterized most of hominid history. The fact that humans evolved in the context of foraging economies is widely recognized, but its implications are only slowly being uncovered. The broad qualities shared by foraging populations have had a profound influence on the evolution of hominid morphologies, behavioral capacities, and social formations. As a result, analysis of hunter-gatherer behavior should play a prominent role in the understanding humans assemble about themselves, and particularly in the development of anthropological knowledge.

The goal of this volume is to provide explicit discussions of an innovative perspective on human foraging behavior. The various chapters express differing viewpoints and cover diverse topics, but exhibit substantial theoretical unity. In particular, the separate analyses have in common an attention to modeling, an emphasis on hypothesis testing, and a socioecological approach to the subject of hunter-gatherer behavior.

Socioecology is concerned with the application of ecological theory to the analysis of social behavior (Crook 1970b). To this end, it focuses on the contribution of ecological adaptation processes to the variability observed in foraging or social behavior. Socioecology relies on sets of theoretically related models which produce fairly explicit hypotheses. The models are built on optimization assumptions drawn from contemporary evolutionary ecology (Pianka 1978). The intent is to develop middle-level generalizations about human foraging societies, generalizations that are nonobvious, robust, and capable of being empirically validated.

Throughout the volume, the stress is on adapting, rather than simply adopting, models and approaches developed in evolutionary ecology. We believe that the studies included here constitute a vigorous demonstration of the possibilities for socioecological analysis of human foraging strategies. Later sections of this chapter (and chapter 2) provide further discussion of socioecological theory and method, and an introduction to the specific applications described in subsequent chapters. We will now briefly outline the anthropological context of this work, and discuss how this approach may help to advance ecological anthropology in general, and hunter-gatherer studies in particular.

Cultural Ecology: Problems with Functionalism and Empiricism

Attempts by anthropologists to analyze human behavior as ecologically adaptive have had an erratic history (Anderson 1973; Baker 1962; Hatch 1973; Helm 1962; Rappaport 1971a).

Early twentieth-century anthropologists in the United States adopted particularist and historical research approaches (Damas 1969a; Harris 1968; Netting 1971:1-4). Led by Franz Boas and his students, these anthropologists cultivated an atmosphere of "theoretical austerity" (Hatch 1973:224). They rejected broad materialist or ecological explanations, at least partly because these approaches were associated with determinism and ethnocentrism. There were attempts in anthropology to correlate large-scale distribution of cultural patterns with regional features of geography (see Damas 1969a; Helm 1962), work led by Mason (1905), Wissler (1926), and Kroeber (1939). But while documenting correlation, these anthropologists avoided ecological generalization (Damas 1969a:1; Helm 1962:630; Netting 1971:3). Instead, they adopted the position of "environmental possibilism"--the view that environment places broad constraining boundaries on sociocultural phenomena, but has little influence on the features that develop within those boundaries.

Dissatisfaction with the particularist orientation produced more general theoretical approaches to many anthropological subjects during the 1930s and 1940s (Netting 1971:3-4). One major orientation was functionalism. Functionalism focuses on the role that recurrent social activities play in maintaining the social structures and viability of the community (Radcliffe-Brown 1935 1956:180-81). The theory cautiously cites an analogy with the function of structural aspects of living organisms. A second approach, the materialist or ecological orientation, developed principally in the work of Steward (1955; Steward and Murphy 1977; Helms 1978; Murphy 1977). Steward sought systematic ways of studying the relationship between sociocultural life and the environment. He emphasized the intervening variables--technology, material culture, and economic relationships--linking particular aspects of sociocultural life to the local ecology. Thus his analyses avoided the superficial results of deterministic theories, which linked culture directly to habitat on broad geographic scales, as well as the general poverty of the possibilist approach. Steward paid careful attention to unique aspects of local habitats, to the distributions of plants and animals, and to comparative studies of the adaptive histories of local groups, technologies, and economies. Many of his ideas grew from detailed ethnographic studies of hunter-gatherers (Steward 1938).

This brief history contributes two points to an understanding of contemporary cultural ecology (or ecological anthropology). First, Steward's work established that the materialist or cultural ecology perspective could help to explain sociocultural features of human groups. Although the specifics of his method have been questioned (Vayda and Rappaport 1968), Steward's work chartered ecological anthropology and established its empirical tradition (Helm 1962:638-39). The second point is the pervasive influence of functionalism on cultural ecology. Practitioners of this subject are consistent in recognizing the functionalist underpinnings of their approach (Netting 1971:4; Damas 1969a:9; Helm 1962:631-32). Environmental features are used as independent variables in the construction of adaptive or functional rationales for behavior. Biological adaption concepts or analogies provide the criteria for the analysis of behavior in an environmental context. Although Vayda and Rappaport (1968; see also Vayda and McCay 1975) reject the "materialism" of Harris (1968) and the "cultural ecology" of Steward (1955), their own formulation--"ecological anthropology"--retains a functionalist core (see Rappaport 1971a:243).

Many of the methodological shortcomings of human ecology can be traced to its heritage of empiricism and functionalism. Internal anthropological critiques have focused on the latter, stating that cultural ecology is no more than old functionalism revitalized by association with biological concepts (Friedman 1974; Hallpike 1973; Jorgensen 1972; Orans

1975; cf. Rappaport 1977). Some of the problems of functionalism thus continue to dismay the proponents and arm the foes of this approach. These include descriptive research and a strong bias toward inductive argument; normative, case-unique analyses; after-the-fact construction of explanations; a bias toward equilibrium or homeostatic models; and the use of nonrefutable hypotheses. The cultural ecology approach can verge on circularity: extant behaviors are adaptive because they exist in adapted populations. Few criteria have been developed for assessing the degree to which behaviors are adaptive, or perhaps nonadaptive or maladaptive, and almost no attempt is made to examine alternative hypotheses as a basis for judging the adaptiveness of observed behaviors (Alland and McCay 1973:150-51; Alland 1975:65-66). The insights generated by this approach are numerous, but the method leaves some doubts about the behavior-environment articulations identified, and about the reasons given for them. Are the adaptive causes hypothesized only correlations? If causes link the variables, are they the ones identified?

There is no simple way to get around the problems associated with functionalism. Recent fieldwork in cultural ecology has avoided some of them by focusing on a measurable and common attribute of human and nonhuman biotic communities: energy flow. The field studies of Rappaport (1968 1971b), Thomas (1973), Kemp (1971), and Nietschmann (1973) all consider the energy-provisioning aspects of adaptation. In these studies generalizations about adaptations are given definite operational content through the measurement of energy production, consumption, and expenditure (Jamison and Friedman 1974; Montgomery 1978). The results can be compared over a wide range of human communities and evolutionary situations.

Hunter-Gatherer Studies

Ethnographic Research

Hunter-gatherer studies reflect the disciplinary history of cultural ecology, some of its problems, and the recent attention to questions of energy flow. Empirical studies of contemporary hunter-gatherers have flourished in the last two decades, strongly influenced by ecological adaptation concepts. The intensive research on San (Bushmen) peoples is well known (Lee 1972a 1979; Lee and DeVore 1976; Marshall 1965; Silberbauer 1972; Wiessner 1977), but foragers in the Arctic and subarctic of North America have also been studied in depth (e.g., Anders 1967; Berkes 1977; Binford 1978; Foote 1968; Foote and Williamson 1966; Freeman 1971 1976; Feit 1973; Kemp 1971, Jarvenpa 1977; Nelson 1969 1973; NHRC 1976; Rogers 1963; Usher 1971). Foraging populations with mixed subsistence systems living in parts of Amazonia (e.g., Siskind 1973; Hames 1979; Vickers 1976), Africa (e.g., Marks 1976 1977b), and Asia (e.g., Gardner 1972; Peterson 1978; Williams 1974) have received attention as well. For the most part these studies adopt ecosystem or energy flow concepts to show how the behavior functions in the particular habitat within which it occurs.

There have been several attempts to construct a general model of band society, timeless and placeless (Service 1962; Williams 1974; Jochim 1976; King 1975). However, these formulations have often been achieved at the expense of ignoring or explaining away diversity. Variability is ascribed to abnormal conditions, extreme or marginal environments, acculturation, or some other factor (Martin 1974). Divergent positions have been taken on issues such as the degree of patrilocality, territoriality, group cohesion, or adherence to formal marriage rules to be expected of "normal," "average," "pristine," or "ideal" hunter-gatherers. For example, the patrilocal-territorial band model of Radcliffe-Brown (1930) and Service (1962) has recently given way to the bilateral, fluid membership model of Lee (1972a). Although these two positions differ, they share the assumption that the hunter-gatherer adaptation is a uniform one. The possibility that diverse behavioral forms characterize hunter-gatherer societies and that *the range of variation* is the correct subject for explanation is generally unrecognized in these typological approaches.

The variability among different hunter-gatherer societies should not be surprising. Populations lumped together by this designation have been drawn from a large number of geographical areas, cultural traditions, and temporal periods, and they have inhabited every environment yet colonized by human beings. Variation within individual societies, or even within local populations of foragers, is equally prevalent, although masked by the common anthropological habit of reporting field research in normative terms (Pelto and Pelto 1975).

General models of hunter-gatherer social organization and behavior are increasingly at odds with evidence of variation among foraging societies (Martin 1974). We thus face an unappealing choice: either to achieve generalizations that fail to explain much of the observed variation, or to give up the task of constructing general models and deal only with specific societies or regions. The first option is normative: diversity is explained away. The second option is particularist: diversity is accounted for in the aggregate but is not explained in a theoretically cohesive fashion.

The shifting anthropological views of hunter-gatherer society illustrate the continuing dominance of typological formulations. The previously accepted view of hunter-gatherer life as nasty, short, and brutish has given way to a new orthodoxy--expounded in the current crop of anthropology textbooks--that foraging represents the original affluent society (Sahlins 1972; Lee 1968). Lee's research on the !Kung San, demonstrating that in this foraging society a relatively small amount of foraging time secured ample food resources, played a major part in fostering the idea of hunter-gatherer affluence (Lee 1968 1969). Lee's analysis was based on a sample quite limited in size and duration, and his ethnographic fieldwork was with only one society. In light of this, the nearly complete reversal in anthropological orthodoxy that followed must have explanations more complex and subtle than Lee's empirical refutation of the earlier view. Not least is the persistent desire to make hunter-gatherers exclusively one thing or another, rather than capable of a range of life styles.

Recent ethnological research has employed statistical summaries to generate typological portraits which ostensibly take account of the diversity of foraging societies. Lee's (1968) statistical review of ethnographic information suggested that the relative affluence of hunter-gatherers was due to their primary reliance on plant foods. At least one "revisionist" interpretation has also used Murdock's *Ethnographic Atlas* (1967) and statistical summaries to question Lee's conclusions, along with other generalities about this form of subsistence (Ember 1978). Martin (1974) has used the same data to raise questions about the usefulness of *any* typological characterization of hunter-gatherer adaptations or lifeways.

In our view the value of typological characterizations or statistical summaries of ethnographic data is quite limited. None of the statistical analyses cited considers the severe problems in sampling methodology associated with the analysis of phylogenetically or historically related taxa or sociocultural groups (see Clutton-Brock and Harvey 1977: 1-8; Naroll 1970). Normative portraits can serve little enduring analytical purpose when--to our mind--the important questions are ones of ecological causation, diversity, and change. Ember (1978:447) recognizes this in a statement concordant with the goals of a socioecological approach: "We need to discover what predicts variation among recent hunter-gatherers. And then, using archeological indicators, we need to discover the past prevalence of those predictors and their presumed effects."

Along, then, with the difficulties raised by functionalism, we sense a dichotomy in hunter-gatherer studies between detailed empirical analyses which document variation and highly generalized models which by their nature must ignore it. The gap between these endeavors stymies the advance of both.

Archeological Research

Although we are outsiders to the subdiscipline, it is our impression that ecological approaches in archeology share parts of this twofold dilemma: (1) Can unsatisfactory aspects of functionalist arguments be mitigated? (2) Is there a heuristically attractive approach or perspective which avoids the dichotomizing effects of detailed study and highly general models?

Exciting recent advances in ethnoarcheology (R. Gould 1978; Binford 1978; Yellen 1977) and in experimental archeology (Tringham 1978) focus on analyzing how the archeological record is generated by human behavior, and how it is subsequently modified in its depositional environment. Deductive methods applied in this work enhance ability to infer behavior from artifacts and context, but usually with emphasis on how behavior causes the record rather than on what causes the behavior itself. This latter question, in our belief, is largely ecological. And here archeologists are bound by (and sometimes recreate on their own) the problematic aspects of ethnographic and ethnological studies of hunter-gatherers. It is not surprising then that archeologists and paleontologists are unsatisfied with the interpretive guidance offered by ethnography (Wobst 1978; Schiffer 1975:836-37; Plog 1975: 220-21; Jolly 1973:14) or even cultural ecology (Butzer 1975:108-9 1978a). The general state of ecological research in archeology is not well developed (cf. Hardesty 1980; Jochim 1979).

Ethnographic analogs used in archeology unavoidably share limitations of the cultural ecology approach. In addition, highly generalized systems models of forager behavior sometimes represent a case of ecological "leapfrogging," to use Tringham's (1978) piquant term. Fundamental assumptions about ecological relationships are not tested. Two cases will illustrate. Williams's (1974:4-17) model of band society incorporates the assumption that hunter-gatherers are always territorial. In contrast, Dyson-Hudson and Smith (1978) use ethnographic evidence and evolutionary ecology models to show that the development of territoriality is contingent on specifiable environmental attributes, which may or may not be characteristic of particular hunter-gatherer habitats. In a second instance, Jochim (1976) has produced an elaborate and intuitively appealing systems model of settlement pattern and foraging behavior. His model incorporates optimal foraging concepts and predictions at an early stage. In an ethnographic evaluation of the same model, Winterhalder (1977) found that the relationships are commonly different from those assumed. For instance, Jochim assumed that search costs increase with mobility of the prey species. In fact, the Cree-Ojibwa hunters he cites often locate animals by tracks, and hence their search time costs decrease with the mobility of the prey species.

In each of these two cases an untenable assumption about specific socioecological relationships compromised the broader results of the procedure. Testing of middle-level socioecological hypotheses is a complementary and indispensible part of such systems-modeling efforts (Thomas, Winterhalder, and McRae 1979).

Prehistoric archeologists are creating detailed reconstructions of hunter-gatherer diet and behavior in space and time (Isaac 1976a,b; Walker, et al. 1978). Paleoecological studies are generating information about the environmental context of these people with equal ingenuity and detail (Livingstone 1975; Butzer 1977 1978b). But there is an essential socioecological link needed to unite these endeavors: the detailed and systematic study of the relationship between behavioral variability and environmental variability (cf. Wilmsen 1973). Evolutionary ecology models, ethnographically and archeologically confirmed, should assist in generating reliable predictions about behaviors not recoverable from or self-evident in the archeological record. They should also direct attention to new types of data, and assist in their interpretation.

In effect, then, we are proposing that socioecological research complements recent trends in archeological method, and provides a vital framework for analysis of prehistoric hunter-gatherer ecology. Heuristic qualities of the approach make ethnographic and archeological study directly relevant to one another. This should be evident in the mix of studies that constitute this volume.

Socioecology as a Field of Inquiry

History and Scope

The contributions in this volume share a socioecological perspective on human foraging. Socioecology is not a unified body of theory so much as a topical orientation: the ecological analysis of social behavior. Crook (1970b) defines socioecology as "the comparative study of social structure in relation to ecology," and stresses the focus on "correlations between social organization and contrasts in ecology." In biology, socioecology has drawn on extensive field research and on theory from evolutionary ecology. To a lesser extent it has been influenced by evolutionary genetics and classical ethology.

Several other syntheses of evolutionary and ecological theory concerned with animal behavior have been proposed. The currently most prominent one has been christened sociobiology (Wilson 1975). Contemporary sociobiology differs from the present studies, and from socioecology in general, in its emphasis on the genetics of social interactions in Mendelian populations. Some versions give attention to ecology (e.g., Clutton-Brock and Harvey 1978a), but human applications in particular suffer from an undue emphasis on putative genetic determinants of behavior (Smith 1979a; Washburn 1978; S. J. Gould 1978). The current confusion about the nature of sociobiology and its relationship to other areas of inquiry requires us to make a disclaimer here that would otherwise be obvious: evolutionary ecology models and optimization assumptions need not assume genetic causation of behavioral variation.

Evolutionary ecology had its origins about two decades ago in the work of MacArthur (1960 1961 1965; see Fretwell 1975), Hutchinson (1959 1965 1975 1978), and other population ecologists. This approach marks a self-conscious attempt to make ecology more theoretically rigorous. As a consequence it approaches ecological problems with a deductive orientation; emphasizes mathematical modeling; is often applied to behavioral aspects of ecology; and is guided always by the basic principles of natural selection. Brown (1963 1964), Crook (1965), Orians (1961 1969), and others initiated fieldwork evaluating the concepts and testing the hypotheses of evolutionary ecology, using models developed by such theorists as MacArthur (1972) and Levins (1968). This research, both theoretical and empirical, has continued and expanded. Several recent books give excellent overviews of this field (Pianka 1978; Emlen 1973; Cody and Diamond 1975; May 1976; Krebs and Davies 1978).

In contrast to evolutionary genetics, evolutionary ecology is well suited to analysis of the behavioral variability that is characteristic of hominids. Emlen (1979; see also Blurton Jones 1976; Mayr 1974:656) makes it clear that ecological models are of much greater relevance to behavioral research on vertebrates (especially primates) than are genetic ones, although the literature on the implications of human sociobiology has proceeded otherwise

(Smith 1979a). Evolutionary ecology combines the deductive features of selection theory and optimization concepts with the operational utility of quantifiable cost-benefit measures (see Winterhalder, chapter 2, below). It does not assume genetic causation of behavioral variability, only a capacity for adaptive decision making. Finally, it emphasizes behavioral plasticity and environmental variability, features crucial to the study of human adaptation.

The third research area, ethology, has recently shifted from phylogenetic studies of stereotypic and species-specific behavior (e.g., Lorenz 1950) to studies assessing the ecological and adaptive significance of the behavior of individuals as members of social groups (Callan 1970; Crook 1970a:xxiii-xxiv 1970b; Orians 1971:513-14). This change was encouraged by the primate field studies following World War II, which indicated that much social behavior was flexible, maintained by learning and tradition in complex groups, and closely related to features of the surrounding habitat (Crook 1970a:xxv 1970b; Clutton-Brock 1974; Eisenberg, et al. 1972; Jay 1968; Jolly 1972; Kummer 1971; Tuttle 1975). This work, and research on mammalian and avian social behavior (e.g., Bertram 1978; Caraco and Wolf 1975; Crook, et al. 1976; Emlen and Oring 1977; Geist and Walther 1974; Krebs 1973; Kruuk 1975), have demonstrated that ecological variables--the spatiotemporal distribution of food, predators, and potential mates and competitors--strongly affect the behavior patterns of species ranging from butterflies to baboons. The influences often operate in ways successfully predicted by optimality models (see reviews in Krebs and Davies 1978; Clutton-Brock and Harvey 1978b; Pyke, Pulliam, and Charnov 1977).

Advantages for Ecological Anthropology

The approach and subject matter of evolutionary ecology and socioecology have specific advantages for anthropological research with respect to difficulties cited earlier.

Functionalist shortcomings. Functionalism as practiced in anthropology suffers mainly from ambiguity in its postulates and assumptions. It pays little attention to the formulation of models, the development of realistic alternative hypotheses, or the provision of operational methods for testing hypotheses. These areas are strengths of evolutionary ecology models (see Maynard Smith 1978). Both functionalism and evolutionary ecology assume some kind of goal and optimization, but the latter makes these explicit aspects of the research methodology and considers quite specific topics (e.g., diet breadth). Evolutionary ecology compels detailed attention to the nature of the deductive argument and the testing procedures. Furthermore, it places the optimization assumption within neo-Darwinian theory, and, as a consequence, it generates sets of hypotheses about specific topics that are coherently related to one another and to evolutionary theory in general.

Middle-level hypotheses. Demonstrated diversity in foraging societies has left us skeptical about the validity or usefulness of general models of band society. At the same time, pursuit of the scientific goals of ecological anthropology requires that empirical studies not eschew the evaluation of theory. A research strategy emphasizing middle-level theory would seem to be the solution (see Thomas, Winterhalder, and McRae 1979). Middle-level models can be formulated with attention both to diversity and to generalizing goals. They can be applied in analysis of the detailed and varying nature of adaptive behavior without abandoning attempts to reach broader understanding of the process involved in producing that behavior.

Some vital socioecological questions have been little studied owing to the gap between descriptive ethnography or archeology and general models. These include: What resources in an environment should a forager use? Should the diet be broad or narrow? How should it change with fluctuations in resource abundance? If the environment is heterogenous, what parts of the mosaic should be harvested? How should a forager move among the patches being used? In what kinds of environment should we expect to find various systems of spatial organization such as territoriality, home ranges, or nomadic behavior? When should settlement systems be dispersed, and when should they be aggregated? How does ecological adaptation contribute to the size or composition of foraging groups? What is the relative importance of energy versus nutrients in foraging decisions? How does risk affect foraging behavior? These questions (and others that could be asked) imply that it is possible to specify aspects of foraging behavior based on costs and benefits associated with various alternatives. We believe that these are all questions amenable to socioecological analysis.

Lacking generalized ecological approaches to such middle-level questions, and faced with the great diversity of hunter-gatherer behaviors, anthropologists have developed few systematic concepts of what constitutes the *effective environment* of a forager--the variables of an ecosystem which the forager or foraging group adapts to or influences. We know little about how foraging decisions are adjusted to recurrent and nonrecurrent environmental variability to build up patterns or strategies of adaptive responses. Reconstruction of hominid history, and understanding of foraging adaptations as well as of shifts to alternative subsistence systems, are limited by this deficiency. The studies in this volume suggest one route to answering these questions.

In effect we are after a set of theoretically coherent but individually simple and topically limited insights. What, for instance, is the relationship between the population density of a prey species and the likelihood of its being included in an efficient forager's diet? This type of query is preferable to "What did group X eat?" and to "What is the ecological nature of band society?" because it promises a kind of insight which spans both questions.

Variability. Variation in hunter-gatherer socioecology should be celebrated--as a fact, and as a central preoccupation of theory and explanation. Generalizations can still be developed and evaluated through the use of models and hypotheses that are comparative and that explicitly allow one to incorporate variance in environmental and behavioral parameters. Socioecology has these qualities (see Winterhalder, chapter 2, below). It is not an overstatement to say that variability--its origin, its fate under selection, and its relationship to adaption--is the central concern of evolutionary theory (Lewontin 1974a), a prerequisite to and a fundamental quality of evolutionary change and adaptation.

There is a second reason that ecological anthropologists and prehistorians should make the relationship between behavioral and environmental variability a preeminent concern. Human behavior is the product of the interaction of jointly interdependent factors--on short- and long-term time scales. The respective influence of these must be demonstrated through comparative analysis of the contribution each makes to behavioral *variance*. Without a focus on variability the relative influences of interacting causes cannot be discerned (see Haldane 1936 1947; Hebb 1953; and Lewontin 1974b, for discussion of the analogous problems in developmental and behavioral genetics).

Mutual relevance to ethnography and prehistory. Finally, socioecological analysis is equally at home in ethnographic or prehistoric study. While the kinds of data available from contemporary or prehistoric studies are different, they are complementary. Ethnographic study provides direct access to detailed information on socioecological parameters and behavior; prehistoric archeology is limited in this respect but expands the temporal and spatial information to evolutionarily appropriate scales. This gives the two types of study a joint relevance and a mutual need of each other (Terrell and Fagan 1975). We believe that this is demonstrated in the chapters in this volume. As anthropologists we find that kind of interaction a worthwhile result.

The Studies

The combination of a socioecology subject matter and an evolutionary ecology approach or methodology gives the studies contained here their unique qualities. The optimal foraging models used are derived primarily from evolutionary ecology; complementary economic theory plays a more limited role. Evolutionary genetics scarcely figures, except as background to the predominant focus on individual advantage and in the attempt by the authors of several of the studies to specify how specific cost-benefit functions may ultimately be related to fitness.

The individual studies can be categorized by four attributes: the research problem (e.g., group size or diet choice); the theoretical source (e.g., optimal foraging theory or economic optimization theory); the cost-benefit currency employed (e.g., energy, time, nutrients, or risk); and the modeling techniques (e.g., graphical analysis or linear programming). As such, they exemplify possible combinations of topics and analytic procedures, but only hint at the potential flexibility of socioecology as a research tool.

In chapter 2, Winterhalder summarizes the general framework of optimal foraging theory. He outlines the assumptions and logical format of this research approach, and describes models dealing with optimal patch choice, prey choice, and time allocation. The chapter notes analytic decisions faced by an anthropologist using this theory, and identifies models and hypotheses that are particularly appropriate for anthropological applications. Winterhalder also considers the areas in which significant amounts of empirical information are required to apply foraging strategy models reliably. The chapter considers how this theory can be adapted for research on human behavior. Similar topics have been addressed by Pulliam, writing on the application of optimal foraging theory to humans (1978), and more generally to species in which learning is the basis for strategic adaptive choices (1981).

In chapter 3, Smith reviews evolutionary and ecological theories of group formation and focuses on the diverse, foraging-related determinants of group size. Smith proposes a four-level scheme of group organization in human foragers (foraging, resource-sharing, information-sharing, and coresident groups). The theoretical discussion considers sets of hypotheses relating size variation at each group level to variation in resource harvesting conditions. Smith then tests one of these hypotheses with data on contemporary Eskimo (Inuit) foraging. The hypothesis proposes that foraging group size in this society varies among alternative hunt types so as to maximize the net energy captured per individual per unit foraging time. The test results are positive but indicate that simple models sometimes have to be modified to accommodate the complexities of human foraging behavior. This process itself can provoke insights about human adaptive strategies.

In chapter 4, Winterhalder uses three optimal foraging models to analyze contemporary Cree hunting behavior as a response to resource characteristics of the boreal forest. Detailed description of resource qualities in this patchy environment is combined with quantitative measures of Cree foraging efficiency. Optimal diet and patch choice models, plus Charnov's (1976a) marginal value theorem, are used to predict prey choice, patch utilization, and patterns of time allocation within patches. Historical trends in diet breadth are analyzed, and are shown to be congruent with those predicted on the basis of changing search-time/pursuit-time ratios. Winterhalder notes that ethnographic testing can determine which models are reliable in those circumstances where supporting information is incomplete.

The fifth chapter, by O'Connell and Hawkes, analyzes the foraging behavior of the Alyawara, people living in the central desert of Australia. The study centers on the gathering of plant resources. An energy currency and models of optimal diet and patch choice are applied to explain changes in the exploitation of native vegetable foods, especially seeds, and lizards. Although the models and hypotheses used here are similar to those analyzed by Winterhalder in chapter 4, confirmation and results are reached by a somewhat different approach. In particular, O'Connell and Hawkes make detailed comparisons of within-trip foraging decisions based mainly on the energy costs of harvesting and preparing various species. In doing so they not only confirm the appropriate hypotheses, but highlight the important role that "pursuit and handling" costs have in foraging decisions. Further, although the evidence is limited, hypotheses based on the patch choice model seem to be both more appropriate and more accurate in this environment and population than Smith (chapter 3) or Winterhalder (chapter 4) found in the Arctic and boreal forest, respectively. O'Connell and Hawkes use the results of their analysis to offer tentative explanations for geographic variation in resource use among Australian natives, and for the pattern of prehistoric colonization of Australia.

In chapter 6 Heffley employs a model, first proposed by Horn (1968), to account for the diversity of sociospatial arrangements exhibited by three northern Athapaskan societies. Horn's model is concerned with the adaptive advantage of different forms of social spacing in relation to the predictability and dispersion of key prey species; it predicts maximum aggregation of the foraging population when resources are unpredictable and concentrated, and dispersal when resources are predictable and evenly spaced. Heffley's argument, then, takes Athapaskan prey choices as given, and asks how hunters should disperse or aggregate in order to minimize the time or distance involved in locating these prey. The role of information exchange and food storage is also explored, and related to resource characteristics and variation in coresident group sizes. Heffley's work is a preliminary application of the model (following Wilmsen's [1973] suggestion) to group sizes and settlement patterns, using a comparative (cross-cultural) approach.

In chapter 7 Yesner presents an analysis of Aleut foraging which combines archeological information with an optimal foraging approach. Yesner takes an indirect route to confirmation of an optimal prey choice hypothesis. He observes that those species within the optimal diet breadth (determined by a systematic interaction of resource pursuit and handling times with abundances) should be harvested in proportion to their natural density. Using a careful reconstruction of prey densities in the Aleut ecosystem, and data on the prehistoric diet of the Aleuts, he is able to show that in most instances this is the case. His approach to the confirmation of diet breadth models is well suited to data that are archeologically recoverable. A set of secondary hypotheses is examined to refine the original optimization hypothesis.

The relative merits of an energy/time analysis versus a more complete consideration of hunter-gatherer nutrient and nonfood needs are addressed by Keene (chapter 8). The optimization problem analyzed concerns prey choice by prehistoric temperate forest foragers in the Late Archaic period. Keene shows how foraging strategy models can play an important role in the reconstruction of prehistoric economies in cases where archeological preservation is poor. He predicts an optimal diet for the study population using linear programming analysis--a tool developed originally by economists but recently employed in several foraging strategy studies (Altmann and Wagner 1978; Pulliam 1975; Belovsky 1978; Reidhead 1976; Glander, 1981). Keene's analysis highlights how predictions generated by energy efficiency models may differ from those produced by more complex nutrient models. It also raises the issue of the modeler's dilemma--how to achieve a balance among realism, precision, and generality (see Winterhalder, chapter 2, below). In foraging populations relying substantially on vegetable foods, analytical techniques which are capable of simultaneously evaluating the role of multiple nutrient factors are likely to be crucial. Keene's use of linear programming is exemplary in this regard.

The optimal foraging models developed in biology, and used as the basis for most of the analyses in this volume, do not explicitly consider regional interactions or information exchanges between foragers. In chapter 9 Moore analyzes the effects of information gathering and exchange on the spatial distribution of hunter-gatherers, using theory developed by ecologists and geographers. Moore points out that hexagonal patterning of boundaries between foraging units does not necessarily indicate efficient use of space. By assuming that foragers do not have access to the perfect information implied in geographic locational theory, Moore analyzes the cost of acquiring the information and of arranging nonoverlapping seasonal movements and settlement patterns. Moore uses optimal foraging models to argue that groups will attempt to position themselves without overlap in their foraging ranges. He then uses computer simulation techniques to assess the group-level costs of efficient spatial organization given various degrees of knowledge about the distribution of resources and other groups, and various ways of acquiring the relevant information. His analysis points up the need to consider regional processes affecting the adaptations of individuals and local groups.

In the final chapter, William Durham places these studies in a general biocultural context, and discusses the rationale for using ecological optimization theory to study the adaptive significance of cultural behavior. He evaluates the research presented in this volume in light of four general questions: (1) What are the optima predicted by foraging strategy models? (2) To what extent do human foragers conform to these predictions? (3) How and why do hunter-gatherers optimize, if and when they do? and (4) To what extent do these optimization approaches help us understand hunter-gatherer diversity? Durham concludes that ecological foraging theory will undoubtedly be modified to take into account more of the unique properties of human behavior, and he expresses optimism that this approach can compass the terrain.

Finally, we should note that most of the cases presented here come from arctic, subarctic or temperate North American populations (chapter 5 by O'Connell and Hawkes is the exception). This is a coincidence, unrelated to theory or to guidelines used to choose authors. Hames (pers. comm.; Hames and Vickers, in preparation) notes that data on diet breadth and central place foraging behavior gathered in studies of Amazonian Indians support appropriate optimal foraging hypotheses. We expect the theory to be enriched and changed as it is extended to analyses from this and additional ecozones and populations.

Conclusion

Evolutionary ecology and socioecological research provide an approach and set of models which should prove well suited to the investigation of human adaptation--current, historic, and prehistoric. The models represent heuristic tools for analyzing the evolution of social behaviors as diverse as mating systems, foraging strategies, predator avoidance, and demographic (life history) strategies. Some of these models, in particular those concerned with foraging, are potentially of great usefulness for research on hunter-gatherers. These models are general and realistic, and are designed to predict the behavioral patterns expected to evolve or develop in response to specific patterns and features of the environment. In many instances they generate reliable hypotheses about foraging behavior, some of which are not otherwise evident. They have the further advantage of presenting hypotheses with clear operational significance; that is, the models generate predictions amenable to confirmation or refutation.

If carefully applied, socioecological models may alleviate some shortcomings of the predominantly empirical and functional approaches of anthropological research on foraging. Populations of active hunter-gatherers are rapidly disappearing and with them the basis for ethnographically expanding our knowledge of the major part of human history. As direct fieldwork opportunities dwindle, attention will necessarily shift more to interpretation of historical, prehistoric, and paleontological records. Evolutionary ecology will assist with this interpretation, but to date it has developed almost exclusively from the study of nonhuman species. While ethnographic testing is still possible, it is important for ethnographers and archeologists to work together to determine the applicability of evolutionary ecology theory in studies of human foraging behavior.