The Ecology of Human Subsistence

Hunter-Gatherer Foraging Strategies. Ethnographic and Archeological Analyses. BRUCE WINTERHALDER and ERIC ALDEN SMITH, Eds. University of Chicago Press, Chicago, 1982. x, 268 pp., illus. Cloth, $18; paper, $7.50. Prehistoric Archeology and Ecology.

The papers in this collection use models drawn from evolutionary ecology to explore the foraging strategies of human hunter-gatherers. They reflect a recent trend within human ecology toward greater use of formal models, systematic hypothesis testing, and the explicit application of biological ecology to studies of human behavior. The problems addressed are familiar concerns to students of foraging societies and include the determinants of diet choice, group size, and the effect of the spatial distribution of resources on foraging behavior and settlement pattern. The authors, however, attempt to move beyond the plausibility arguments and functionalist analyses that characterized much of the earlier work to more rigorous testing of hypotheses drawn from evolutionary ecology. Although the results are sometimes inconclusive, they do generate insights and help to integrate anthropological theory and data into the mainstream of ecological theory.

The theoretical arguments in this book draw principally from optimal foraging theory and rest upon the principle of adaptation. It is assumed that animals will forage in a manner that maximizes fitness at the individual level. Although the validity of this assumption is a matter of dispute, so much of animal ecology seems to make sense in the context of such models that they are difficult to ignore. The situation is complicated further where variation in foraging behavior is learned rather than genetic. However, since learning itself evolved, there is reason to believe that people will adopt most readily those behaviors that contribute to their survival and reproductive success. The application of optimal foraging theory to humans rests on this latter assumption.

Three of the papers in this volume consider the question of optimal diet and patch use, using models developed initially by MacArthur and Pianka. Like most optimal foraging models, these assume that individuals forage so as to maximize their energetic efficiency. In the diet choice model, for example, it is hypothesized that animals choose food types that maximize their net rate of energy intake; the optimal diet is determined by considering the caloric value of each item, search time, and the time spent capturing the item after it has been encountered. As the papers by O'Connell and Hawkes, Winterhalder, and Yesner show, these models yield interesting insights into the behavior of contemporary and prehistoric foragers.

O'Connell and Hawkes, in explaining diet choices made by the Alyawara of Australia, note that seeds were not collected by the individuals they observed, although seeds are plentiful and are reported to be a traditional Alyawara food item. Data on the calories per "handling" hour of various resources enable these authors to conclude that seeds are an inefficient source of food and are not worth collecting unless the average returns for a patch are very low. Why were seeds apparently taken in the past? It is a property of the optimal diet model that, as the abundance of highly ranked resources increases, the number of food types in the optimal diet set decreases. O'Connell and Hawkes suggest that the Alyawara are now using more European foods than in the past and that because such foods are highly ranked resources for the Alyawara their use has been associated with the deletion of seeds from the diet.

This result illustrates that exposure to European foods and technology does not make optimal foraging theory inapplicable to human foragers, but rather can be used as a natural experiment in which new foraging options may lead to changes in optimal behavior. This is also demonstrated by Winterhalder's study of optimal diet and patch choice among the Cree. The optimal diet model separates foraging costs into search time and pursuit (or handling) time and predicts that an increase in the efficiency of searching should constrict the breadth of the optimal diet. Winterhalder cites evidence that suggests just such a process in Cree foraging history, where the decrease in search time brought about by snowmobiles and outboard motors in recent times has been associated with a more specialized diet.

Another interesting application of optimal foraging theory is Smith's analysis of foraging group size among the Inuit. As in the models discussed above, it is assumed that the optimal strategy—in this case, the optimal group size—maximizes the per capita rate of energy return. Smith's data relating modal and optimal group sizes for ten types of hunts provide strong, though not perfect, support for his model.

As with all models, those discussed above have many simplifying assumptions. Perhaps the most troubling to anthropologists is the assumption that people will act so as to maximize their rate of energy capture per unit time. Although there are cogent reasons, nicely reviewed by Smith and Winterhalder, for using an energy rate measure as the cost-benefit currency, anthropologists can easily think of situations where some other optimization goal might be more appropriate (for example, protein per unit energy expended, energy per unit area, reliability of energy capture). The paper by Keene in this volume makes the danger of this assumption clear. Keene is concerned with diet choice among prehistoric (Archaic) foragers in southern Michigan, but, unlike the authors discussed above, he uses a linear programming model that allows him to consider various needs besides energy. The optimal diet predicted by his model shows energy to be a binding constraint during only part of the year, those during remaining months being calcium, ascorbic acid, thiamine, and hides.

Ethnographic discussions in this volume and elsewhere suggest that an overriding concern of many human foragers, in fact, may be to minimize risk (maximize the reliability of food procurement) rather than to maximize the efficiency with which any food nutrient is acquired. Risk is not well handled in optimal foraging theory, and anthropologists could make a significant contribution by incorporating their insights into formal models that would have general relevance. An excellent start in this direction is made by Durham, in an overview chapter that concludes the book. Durham enlarges upon Smith's model of optimal group size and presents a graphical analysis showing the effects of maximizing the reliability, rather than the efficiency, of energy capture. According to Durham's model, a criterion of reliability leads to a larger optimal group size than one predicted by energetic efficiency. He suggests the possibility that the larger-than-optimal seal hunting groups reported by Smith may be part of a risk aversion strategy of resource procurement.

As these examples show, the analyses in this book suggest interesting and nonobvious insights into the foraging strategies of hunter-gatherers. The volume's most important contribution is the evaluation of general ecological models in a human context. Most of these models were developed in the context of animal ecology, but they also seem to provide a useful perspective for understanding subsistence behavior in humans. Yet the editors' claim that the volume emphasizes "adapting, rather than simply adopting, models and approaches developed in evolutionary ecology" is somewhat misleading. Of the papers in this book, only Moore's is principally concerned with building rather than evaluating theory. Most of the authors adopt ecological models without modification, and discord between predictions and observations is resolved via ad hoc interpretations more often than by any attempt to extend existing models or to develop new ones. This problem is also apparent in the biological literature and is certainly not unique to the papers in this book. Nonetheless, the discrepancies between data and predictions often point to assumptions that are inappropriate in the human context, and incorporation of these insights into new general models would be a welcome next step.

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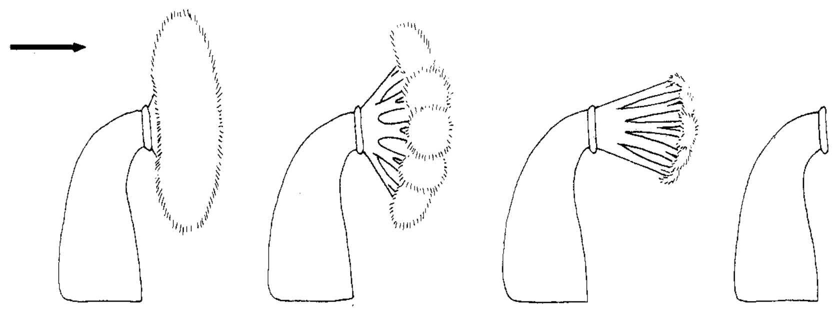


Changes in the shape of a large sea anemone, *Metridium*, exposed to currents of increasing speed. In low-speed currents (far left), the anemone extends into the flow, bends just beneath the oral disk, and extends its tentacles for filter feeding. As the current gets faster, the oral disk separates into lobes and is eventually retracted in strong currents (far right). The changes in shape reduce the rate of increase in drag that would otherwise be proportional to the square of the current speed. [From *Life in Moving Fluids*]

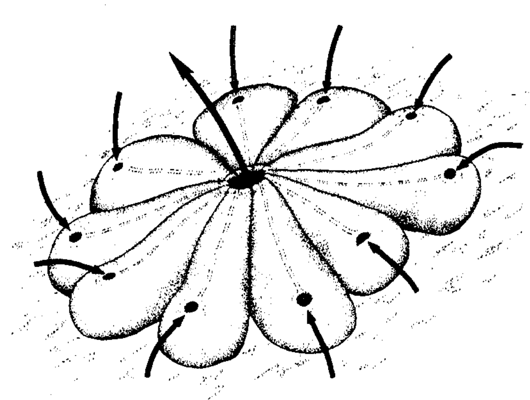
Organisms and Flow

Life in Moving Fluids. The Physical Biology of Flow. STEVEN VOGEL. Illustrated by Sally A. Schrohenloher. Willard Grant Press, Boston, 1981. xvi, 352 pp. $23.50.

Steven Vogel's book has grown out of many years of experience with organisms and flow. The book evolved as a course textbook, but it should be required reading for students of biology at all levels of career development. Flow, whether natural or induced, in the aquatic medium or in air, is important in some facet of the lives of all organisms, and Vogel demonstrates that fluid mechanics offers a viable and rewarding way to understand a multitude of biological adaptations.

The book emphasizes essentially open systems, of flow around or through organisms. Flow in closed systems receives limited treatment, and non-Newtonian fluids (such as mucus) and fluid with inclusions (such as blood) are outside the scope. Concepts of fluid mechanics are carefully developed, and each step is artfully illustrated with biological applications. For example, definitions and properties of fluids are used to illustrate how temperature-viscosity relationships influence the shape of water fleas. Laws of continuity and conservation and energy concepts are related to numbers of arteries, veins, and capillaries in humans, to the ventilation of sponges, worm holes, and prairie dog burrows, to the movement of sap in trees, and to the air bubbles that surround submerged beetles. Drag and its consequences for organisms of various sizes are discussed in detail. Aspects relevant to swimmers and fliers have been well reviewed elsewhere. Here, sessile organisms (ranging from forest trees to intertidal algae and hydroids) receive equal treatment for the first time. The discussion of life in boundary layers (that region of flow where solids and fluids meet) will be especially welcome to benthic ecologists. More discussion of the transport of gases and nutrients through boundary layers would have been welcome, especially in the context of tradeoffs with drag for aquatic organisms. Vogel also explains how the boundary layer can be a barrier to dispersal, for example of spores, and how some organisms overcome the problem. Lift forces and their exploitation by flying and gliding organisms are shown with reference to seeds, sand dollars, insects, birds, and mammals. Fish, which swim using lift forces, receive relatively little attention. Fish swimming has been treated at a rate in excess of one review per year for several years, but Vogel's iconoclastic approach could have brought a new and valuable perspective to the subject. Induced flows are important in small animals and many filter feeders. These are described as part of the discussion of flow dominated by viscosity, which includes ideas on seed and spore dispersal and how interstitial fauna can manipulate their habitat. Flow in pipes is put in the context of the life of trees and worms. Finally, Vogel has done great service to experimental biologists by describing methods and including an invaluable list of suppliers.

Vogel's underlying philosophy is clearly stated in the preface. It is one advocating an approach to biological problems by way not of elaborate mathematics but of "insight into the operative physical processes." This has been the common approach for most biologists who have backed into fluid mechanics to tackle some specific problem; most become too fascinated to wish to back out again. However, the applications rest on advances in fluid mechanics by workers



Flow patterns through a colony of sea squirts, or ascidians (*Botryllus*), to show the combination of incurrent flow into a single relatively high-speed excurrent, effluent jet. This flow pattern ensures that colonies will not reingest water from which they have already removed food and oxygen and which contains their own excretions. [From *Life in Moving Fluids*]