COMMENTARIES 401

1977 Optimal Foraging: A Selective Review of Some Theory and Tests. Quarterly Review of Biology 52:137–154.

Rapport, David J.

1971 An Optimization Model of Food Selection. American Naturalist 105:575–587.

Real, L. A.

1981 Uncertainty and Pollinator-Plant Interactions: The Foraging Behavior of Bees and Wasps on Artificial Flowers. Ecology 62:20-26.

Rosenthal, Gerald A., and Daniel H. Janzen, eds.

1979 Herbivores: Their Interaction with Secondary Plant Metabolites. New York: Academic Press.

Schoener, Thomas W.

1971 Theory of Feeding Strategies. Annual Review of Ecology and Systematics 2:369–404.

1983 Simple Models of Optimal Feeding-Territory Size: A Reconciliation. American Naturalist 121:608–629.

Sih, Andrew

1980 Optimal Behavior: Can Foragers Balance Two Conflicting Demands? Science 210:1041-1043.

1984 Optimal Behavior and Density-Dependent Predation. American Naturalist 123:314–326.

Smith, Eric A.

1983 Anthropological Applications of Optimal Foraging Theory: A Critical Review. Current Anthropology 24:625–651.

Smith, James N. M., and Hugh P. A. Sweat-

1974 Food-Searching Behavior of Titmice in Patchy Environments. Ecology 55:1216-1232.

Stein, Roy A.

1977 Selective Predation, Optimal Foraging, and the Predator-Prey Interaction between Fish and Crayfish. Ecology 58:1237-1253.

Stephens, David W.

1981 The Logic of Risk-Sensitive Foraging. Animal Behaviour 29:628–629.

Townsend, Colin R., and Roger N. Hughes

1981 Maximizing Net Energy Returns from Foraging. In Physiological Ecology: An Evolutionary Approach to Resource Use. Colin R. Townsend and P. Calow, eds. Pp. 86–108. London: Blackwell Scientific Publications.

Werner, Earl E., and Donald J. Hall

1974 Optimal Foraging and the Size Selection of Prey by the Bluegill Sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

Werner, Earl E., Gary G. Mittelbach, and Donald J. Hall

1981 Foraging Profitability and the Role of Experience in Habitat Use by the Bluegill Sunfish. Ecology 62:116–125.

Werner, Earl E., Gary G. Mittlebach, Donald J. Hall, and James F. Gilliam

1983 Experimental Tests of Optimal Habitat Use in Fish: The Role of Habitat Profitability. Ecology 64:1525–1539.

Westoby, Mark

1974 An Analysis of Diet Selection by Large Generalist Herbivores. American Naturalist 108:290–304.

Zach, Reto, and J. Bruce Falls

1978 Prey Selection by Captive Ovenbirds (Aves: Parulidae). Journal of Animal Ecology 47:929–943.

Optimal Foraging Models and the Case of the !Kung

KRISTEN HAWKES JAMES F. O'CONNELL Department of Anthropology University of Utah

We concur with Sih and Milton that optimal foraging models "promise to be capable of providing valuable insights into the study of human foraging." Two important questions are raised by their comments: (1) How are optimal foraging models most usefully employed; and (2) Did we make a valid point about the !Kung? We address the general point first.

About Foraging Models

In our view, contrary to that of Sih and Milton, foraging models are not suited to describe the interaction of all, or even a large number of the variables that might affect subsistencerelated behavior. They are intended to simplify the complexity of the real world for purposes of analysis. They help one specify a set of hypotheses about the factors that most significantly shape subsistence behavior. These hypotheses lead to predictions that can be tested against real data. If the data are inconsistent with predictions, one or more of the hypotheses is wrong and must be revised. The nature of the mismatch between predicted and observed behavior should guide this revision. To interpret it efficiently, one must keep the number of variables under simultaneous consideration to a minimum.

This is one of the reasons we used energy as the measure of benefit. As Sih and Milton point out, other qualities of food are also important. Nevertheless, attempting to incorporate such potentially complicating factors at the beginning of analysis invites confusion, not clarification. Almost all successful (that is, informative) applications of optimal foraging models, including those cited favorably by Sih and Milton (e.g., Belovsky 1978, 1980) employ the "piecemeal" approach (Krebs, Stephens, and Sutherland 1983), initially identifying a few variables as critical, and adding others only as necessary to improve the fit between predicted and observed behavior. The alternate approach, beginning with large arrays of nutrients, involves complex models, which demand unrealistically precise estimates of nutritional requirements (e.g., Keene 1982). Predictions are very sensitive to small changes in these estimates, so that many fragile hypotheses come under simultaneous test, making it virtually impossible to tell which are at fault (Smith 1983; O'Connell and Hawkes 1984).

Sih and Milton are mistaken when they say that it is a "major prediction" of optimal foraging theory that food value be measured in calories (Charnov and Orians 1973; Krebs et al. 1983; Smith 1983). Still, there are good reasons for preferring energy in the early stages of analysis (Smith 1979, 1983; Schoener 1971; Winterhalder 1981a), especially over more complex measures of food value, which reduce the comparability of different applications and narrow the generality of any conclusions. Because nutritional needs are so poorly understood, decisions about which nutrients to include in an analysis and assessments of the implications of acquiring various fractions of each often lack empirical or theoretical justification. Moreover, complex measures require complex models that have additional drawbacks (see Krebs et al. 1983; O'Connell and Hawkes 1984; Smith 1983 for further discussion).

Sih and Milton also find unrealistic the assumption that human foragers know or can accurately estimate returns available from alternative resources, though they are apparently prepared to accept it for other organisms. We find this analytic simplification *least* unrealistic for human foragers, whose intimate familiarity with their local environments has long been noted. Modeling the cost of acquiring this information is, as Sih and Milton say, an area of current interest. Constraints other than the need to acquire information, including predator avoidance (e.g., Milinski and Heller 1978; Sih 1980), territorial defense

(e.g., Davies and Houston 1981; Martindale 1982), and minimizing the risk of starvation (e.g., Caraco, Martindale, and Whittam 1980; Stephens 1981; Stephens and Charnov 1982) may also be important. Nevertheless, keeping the analysis as simple as possible by studying only a few variables at a time allows the clearest assessment of results.

About the !Kung

The note (Hawkes and O'Connell 1981) that prompted Sih and Milton's comments was stimulated by the results of our analysis of the recent elimination of tree and grass seeds from the diet of the Alyawara of central Australia (O'Connell and Hawkes 1981, 1984). That analysis was guided by the optimal diet model (Charnov and Orians 1973; Charnov 1976), which drew our attention to the high processing costs of these resources relative to the returns they provide in energy and nutrients.

This led us to make two general points in our note:

- 1. The relative abundance and high nutrient content of many resources on which hunters rely has prompted the inference, now the conventional wisdom, that the costs of subsistence in hunting economies are very low. This inference fails to take account of the time required to process these resources. It takes five hours of cracking and pounding to produce 1 kg of mongongo nutmeats (Lee 1979:145), 4-6 hours to pick, winnow, and grind 1 kg of grass or tree seeds (O'Connell and Hawkes 1981; Simms 1984). In spite of their abundance and high nutrient content, these and other similar resources yield comparatively low returns on encounter-for example, approximately 1,300 kcal/hr for mongongo nuts (Lee 1979), 100-1,300 kcal/hr for certain species of central Australian and western North American grass seeds (O'Connell and Hawkes 1981; Simms 1984). In contrast, the available data suggest that returns on encounter with game animals in tropical and subtropical environments are in the range of 2500->15,000 kcal/hr (e.g., Hawkes, Hill, and O'Connell 1982; Hill and Hawkes 1983; Hill, Hawkes, Hurtado, and Kaplan 1984; Yost and Kelley 1983; Lee 1979; see Jones 1984 for a summary). The more heavily foragers rely on high cost/low return resources, the greater their subsistence costs, and the less legitimately they can be characterized as "affluent" (Sahlins 1968).
- 2. This observation has an important, but initially counterintuitive implication. If hunters seek to maximize their rate of food acqui-

COMMENTARIES 403

sition, then relatively high cost/low return resources like mongongo nuts and grass seeds may be eliminated from local diets, regardless of their quantitative importance, given a sufficient increase in the availability of resources that produce a better return relative to time invested in collecting and processing.

Sih and Milton disagree with this inference, arguing that "energy based rankings do not appear relevant for the !Kung." They suggest that protein may be the more critical measure of food value, although they cautiously observe that "the data are insufficient to evaluate the appropriateness" of these alternatives. The data are indeed limited, but suggest that Sih and Milton are wrong: energy is apparently a more critical resource than protein for the !Kung. Lee (1968), for example, reports a very high protein but just sufficient calorie intake at Dobe. He also documents a pattern of seasonal weight loss (Lee 1979; see also Wilmsen 1982). The extensive medical assessment of Truswell and Hansen (1976:194) leads them to conclude that "the only nutritional weakness in the San's diet is a shortage of energy (calories) usually in the spring dry season.

There is a more basic issue. Sih and Milton argue that "If protein rankings are indeed appropriate, then contrary to Hawkes and O'Connell's (1981) assertion that mongongos should be near the bottom of the list, they should be strongly preferred (see Lee's 1979 appendix D and table D.1)." The point of our note was to underline the importance of counting the costs of resources. We were concerned to show the difference between the value of a resource as measured only by its nutritional constituents, and its net value, counting processing costs. Mongongo nuts are a rich source of both calories and protein, but they also have high processing costs. These costs remain high regardless of whether energy or protein is chosen as the measure of food value. Mongongo nuts are expensive resources.

The table to which Sih and Milton refer reports the nutritional constituents of an array of !Kung plant resources. Surprisingly, the correlation between protein and calories in these resources is extremely high (r = 0.93). If game animals were added to the list, the correlation would be even higher. This means that the ranking of !Kung resources would be very similar using calories or protein. Either way, mongongo nuts are low ranked because of their processing requirements, and are thus likely to be eliminated given a sufficient increase in the availability of higher-ranked resources.

A final point about resource distribution: an assumption of the optimal diet model is that

resources are encountered at random. This is often untrue in the real world, and certainly untrue for the !Kung. Sih and Milton suggest that the patch choice model may be more appropriate, especially because its predictions may differ radically from those of the optimal diet model. We definitely agree that the patch choice model is a useful tool in anthropological analysis (see O'Connell and Hawkes 1981, 1984; Hawkes et al. 1982; Winterhalder 1981b; Smith 1980 for examples of its application). Like the diet breadth model, it entails an unrealistic, but useful simplifying assumption: that resources are encountered in perfectly discrete patches separated by unproductive space. Picking one or the other of these models depends on the question of interest. Even if we consider mongongo groves as a patch, their value as a resource still depends on processing costs.

Summary

The major issue here is not the utility of foraging models, but how they are most productively employed. Sih and Milton advocate an approach that incorporates many complicating variables from the beginning of an analysis. This makes it very difficult to formulate quantitatively testable predictions about behavior or to tell which, if any, of the multiple hypotheses are *not* at fault when predicted and observed behavior fail to match. The alternative approach, in which the number and complexity of hypotheses simultaneously under consideration is kept to a minimum, has served students of foraging well in the past and should continue to do so in the future.

Sih and Milton conclude with the comment that foraging models have clarified the importance of quantifying not just energy, but also its cost. This is the point that prompted our note on affluent hunters.

Acknowledgments. We thank N. Blurton Jones, E. Charnov, D. Grayson, R. Hames, D. Metcalfe, E. Smith, J. Speth, and B. Winterhalder for useful comments.

References Cited

Belovsky, G. E.

1978 Diet Optimization in a Generalist Herbivore: The Moose. Theoretical Population Biology 14:105–134.

1980 Optimal Activity Times and Habitat Choice of Moose. Oecologia 48:22-30.
 Caraco, T., S. Martindale, and T. S. Whittam
 1980 An Empirical Demonstration of Risk-Sensitive Foraging Preferences. Animal Behavior 28:820-830.

Charnov, E. L.

1976 Optimal Foraging: Attack Strategy of a Mantid. American Naturalist 110:141-151.

Charnov, E. L., and G. L. Orians

1973 Optimal Foraging: Some Theoretical Explorations. Manuscript on file, Department of Biology, University of Utah.

Davies, N. B., and A. I. Houston

1981 Owners and Satellites: The Economics of Territory Defence in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157–180.

Hawkes, K., K. Hill, and J. F. O'Connell

1982 Why Hunters Gather: Optimal Foraging and the Ache of Eastern Paraguay. American Ethnologist 9:379–398.

Hawkes, K., and J. F. O'Connell

1981 Affluent Hunters? Some Comments in Light of the Alyawara Case. American Anthropologist 83:622–626.

Hill, K., and K. Hawkes

1982 Neotropical Hunting among the Ache of Eastern Paraguay. In Adaptive Strategies of Native Amazonians. R. B. Hames and W. T. Vickers, eds. Pp. 139–188. New York: Academic Press.

Hill, K., K. Hawkes, A. Hurtado, and H. Kaplan

1984 Seasonal Variance in the Diet of Ache Hunter-Gatherers in Eastern Paraguay. Human Ecology 12:145–180.

Iones, K

1984 Hunting and Scavenging by Early Hominids: A Study in Archeological Method and Theory. Ph.D. dissertation, Department of Anthropology, University of Utah.

Keene, A. S.

1982 Prehistoric Foraging in a Temperate Forest: A Linear Programming Model. New York: Academic Press.

Krebs, J. R., D. W. Stephens, and W. J. Sutherland

1983 Perspectives in Optimal Foraging.
In Perspectives in Ornithology. A. H.
Brush and G. A. Clark, Jr., eds. Pp. 165–216. Cambridge: Cambridge University Press.

Lee, R. B.

1968 What Hunters Do for a Living, or, How to Make Out on Scarce Resources. *In* Man the Hunter. R. B. Lee and I. DeVore, eds. Pp. 30–48. Chicago: Aldine.

1979 The !Kung San: Men, Women, and Work in a Foraging Society. Cambridge: Cambridge University Press.

Martindale, S.

1982 Nest Defense and Central Place Foraging: A Model and Experiment. Behavioral Ecology and Sociobiology 10:85–90.

Maynard, Smith J.

1978 Optimization Theory in Evolution. Annual Review of Ecology and Systematics 9:31–56.

Milinski, M., and R. Heller

1978 Influence of a Predator on the Optimal Foraging Behavior of Sticklebacks (Gasterosteus aculeatus L.). Nature 175:642-644.

O'Connell, J. F., and K. Hawkes

1981 Alyawara Plant Use and Optimal Foraging Theory. *In* Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses. B. Winterhalder and E. A. Smith, eds. Pp. 99–125. Chicago: University of Chicago Press.

1984 Food Choice and Foraging Sites among the Alyawara. Journal of Anthropological Research 40:504–535.

Sahlins, M.

1968 Notes on the Original Affluent Society. In Man the Hunter. R. B. Lee and I. DeVore, eds. Pp. 85–89. Chicago: Aldine.

Schoener, T.

1971 Theory of Feeding Strategies. Annual Review of Ecology and Systematics 2:369–404.

Sih, A.

1980 Optimal Foraging: Can Foragers Balance Two Conflicting Demands? Science 210:1041–1043.

Simms, S. R.

1984 Aboriginal Great Basin Foraging Strategies: An Evolutionary Analysis. Ph.D. dissertation, Department of Anthropology, University of Utah.

Smith, E. A.

1979 Human Adaptation and Energetic Efficiency. Human Ecology 7:53–74.

1980 Evolutionary Ecology and the Analysis of Human Foraging Behavior: An Inuit Example from the East Coast of Hudson Bay. Ph.D. dissertation, Department of Anthropology, Cornell University.

1983 Anthropological Applications of Optimal Foraging Theory: A Critical Review. Current Anthropology 24:625–651.

Stephens, D. W.

1981 The Logic of Risk-Sensitive Foraging Preferences. Animal Behavior 29:628-629.

Stephens, D. W., and E. L. Charnov

1982 Optimal Foraging: Some Simple Stochastic Models. Behavioral Ecology and Sociobiology 10:251–263.

Truswell, A. S., and J. D. L. Hansen

COMMENTARIES 405

1976 Medical Research Among the !Kung. In Kalahari Hunter-Gatherers: Studies of the !Kung San and Their Neighbors. R. B. Lee and I. DeVore, eds. Pp. 166–194. Cambridge, MA: Harvard University Press.

Wilmsen, E.

1982 Studies in Diet, Nutrition, and Fertility among a Group of Kalahari Bushmen in Botswana. Social Science Information 21:95–125.

Winterhalder, B.

1981a Optimal Foraging Strategies and Hunter-Gatherer Research in Anthropology: Theory and Models. *In* Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses. B. Winterhalder and E. A. Smith, eds. Pp. 13–35. Chicago: University of Chicago Press.

1981b Foraging Strategies in the Boreal Environment: An Analysis of Cree Hunting and Gathering. In Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses. B. Winterhalder and E. A. Smith, eds. Pp. 66–98. Chicago: University of Chicago Press.

Yost, J. A., and P. J. Kelley

1983 Shotguns, Blowguns, and Spears: The Analysis of Technological Efficiency. In Adaptive Responses of Native Amazonians. R. B. Hames and W. T. Vickers, eds. Pp. 189–224. New York: Academic Press.

Agricultural Intensification and Women's Work

DAVID A. CLEVELAND Center for People, Food and Environment Tucson, AZ

Ember's analysis in "The Relative Decline in Women's Contribution to Agriculture with Intensification" (AA 85:285–304, 1983) of changing women's roles in agricultural labor organization is unconvincing. She fails to adequately define concepts, which leads to inappropriate comparisons, and she takes an ahistorical, synchronic approach which leads to viewing the process of change in isolation from the larger world. I offer the following four comments in an attempt to further discussion of this important issue.

1. The lack of a critical, comparative evaluation of the definitions, methods, and time

frames used in the various studies she uses in her analysis makes the tables, each with different numbers of different cases from different surveys, very confusing. The only evidence offered in support of her central argument, that there is a relative decline in women's labor contribution to agriculture and an increase in their domestic work with intensification, is given in Table I. This table consists of a sample of 13 groups taken from a previous review (Minge-Klevana 1980). In subsequent sections she supports proposed causes for this change in women's roles by drawing on three additional cross-cultural surveys: the HRAF Probability Sample, the Ethnographic Atlas (Murdock 1967), and Nag's (1962) survey of factors affecting fertility. Mixing data from these surveys together, often in the same table, and using different sets of groups in each table (none of the five subsequent tables uses the same groups used in Table I to establish the condition to be explained) makes the argument unconvincing.

2. Although the concept of agricultural intensification is central to Ember's argument, it is never explicitly defined. She does imply, however, that intensification is to be equated with "having the plow or irrigation" (p. 287). This is not the usual definition of intensification, which centers on the increasingly frequent use of land (Boserup 1965:43), although it can include increased technical and labor inputs (Netting, Cleveland, and Stier 1980; Cox and Atkins 1979:139-140; Ruthenberg 1980:15–16). Thus, while the use of the plow or irrigation may be associated with intensification, it does not define it. Ember also states, in explanation of her assignment to categories in Table I, that people practicing hoe agriculture are probably nonintensive, although she "cannot be sure" (p. 287). While "hoe agriculture" is often equated in the anthropological literature with "slash and burn" techniques, which of course are relatively nonintensive, many people using the hoe as the major tool of cultivation have quite intensive systems. Ember does not, however, even follow her own definition. For example, the Tallensi and Ashanti are both classified as intensive agriculturalists in Tables II and IV even though neither use irrigation and neither depend on the plow. Although the plow was introduced to the Tallensi in the 1930s, it has not replaced the hoe as the primary tool in their intensive system of cultivation centered on continuous cropping of manured fields. Puzzlingly, in Table VI the Ashanti have become horticulturalists. They are in fact nonintensive, cropping a plot for three years and then fallowing from two to ten times as long (Allan