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Commentaries

On the Logic and Application of Optimal Foraging Theory: A Brief Reply to Martin

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Optimal foraging theory is that part of evolutionary ecology developed over the last two decades as a tool for analyzing animal subsistence behavior (Pyke et al. 1977; Krebs 1978). A collection of articles (Winterhalder and Smith 1981) that gives foraging models a central role in the analysis of archeological and ethnographic data on hunter-gatherers is the subject of a lengthy review by John Martin ("Optimal Foraging Theory: A Review of Some Models and Their Applications," *AA* 85:612–629, 1983). As editors of this volume (*Hunter-Gatherer Foraging Strategies*, hereafter, HGFS), we wish to note some of the serious flaws in Martin's piece.

Along with its demonstrated heuristic value, there are some genuine difficulties in optimal foraging theory (review in Krebs et al. 1983) and limitations on its applicability to humans (reviews in Smith 1983; Winterhalder 1983). Some of these are known; we presume that some are unrecognized. One of the central virtues of foraging theory is that it provides a coherent set of concepts and models that can be subjected to criticism, debate, and revision. However, the criticisms should be informed, the debate rigorous, and the proposed revisions carefully constructed to ensure that they truly offer improvements in clarity, scope, or anthropological utility. Because Martin's review fails by these criteria, a critique is in order.

A careful response to a 10,000-word essay packed with technical commentary would involve a critique of at least equal length, especially since Martin has misunderstood or misinterpreted fundamental aspects of evolutionary ecology and foraging theory. The editorial policy of this journal severely restricts the length of replies, so here we simply list Martin's more serious errors and briefly discuss two of them. Readers interested in the fuller evaluation may write us for a copy.

Martin's review is replete with basic misunderstandings of the theory, models, and applications. They include:

1. Martin distorts the optimization postulate by portraying it as a form of unconstrained maximization that has no counterpart in either economics or evolutionary ecology (p. 613).

2. Martin exhibits a faulty grasp of fundamental aspects of neo-Darwinian theory and population biology, as evinced by the following (all p. 613): (a) selection for efficient foraging is confused with long-term population-level effects on prey availability and amounts harvested; (b) the relative fitness of individual behaviors ("foraging strategies") is conflated with the average fitness of a population; and (c) the growth rates of populations removed in time and space are used improperly to deduce conclusions about the adaptiveness or fitness of different foraging strategies, and of foraging relative to agriculture. Both b and c represent extreme forms of group selectionism which have no basis in evolutionary theory.

3. Martin's depiction of the marginal value theorem (pp. 615–616) omits various elements of this model and his criticisms of it depend on these omissions.

4. Martin expresses a similarly faulty but more convoluted misunderstanding of the optimal diet breadth model, leading him to (a) use it in cases not meeting its stated assumptions; (b) misconstrue the definition of a "prey type" (p. 619); (c) misunderstand how the model can be applied to situations in which parameter values (e.g., marginal costs or benefits) are changing (pp. 618–619); (d) misuse or even overlook the search cost/pursuit cost distinction that is central to the structure of the model (pp. 617, 619); (e) incorrectly claim that a verbal version of the model given in HGFS (HGFS, p. 84; cf. MacArthur 1972: 62) is in conflict with the mathematical version (p. 617); and (f) misunderstand the manipulations to which the graphical version of the model is suited (p. 627, n. 2; cf. MacArthur and Pianka 1966).

In addition to such technical failings, Martin's style of argument also presents problems.

He usually begins a topic by presenting a faulty or exaggerated description of a postulate, model, or argument. He then elaborates or exemplifies the contradictions that arise from his flawed depiction. On occasion he eventually discovers the source of the problem, but fails to recognize that he is exposing and correcting his own interpretive errors, not those of optimal foraging theory. The exercise built around his Table 1 (pp. 617–618) is an example.

Due to space limitations, we can discuss only two of the less complicated items listed above. We have chosen one of a general, conceptual nature (the "maximization postulate") and one to represent Martin's more technical errors (his discussion of the marginal value theorem).

Optimization and Maximization

Martin's discussion of the maximization postulate common to optimal foraging models serves as another example of his general approach. His initial version—unbridled maximizing—is so extreme that after a full page of refinement he is able to refute it by noting that elephants eat more than dik diks (p. 613). After another page he concludes that the postulate can only be interpreted as the result of erroneously imbuing "the blind processes of evolution with a purpose or entelechy" (p. 614). Thus, a central premise of two unreservedly mechanistic disciplines—evolutionary biology and microeconomics—supposedly is unmasked as an Aristotelian vitalism.

Martin's object of criticism and foraging theory are quite different propositions. Martin begins correctly by stating that the theory's "basic postulate" is that "foragers maximize their net rates of energy intake while foraging" (p. 612), but shortly he restates this as an empirical claim that "organisms—in particular humans—forage at maximum rates" (p. 613). Such a claim as Martin's, if "taken literally," is indeed "either false or trivial" (p. 613), but it is not advanced in HGFS nor is it a valid conception of the maximization assumption guiding optimal foraging theory. That theory argues that under specified conditions selection is likely to favor from among the set of available strategies and choices those that maximize the net rate of energy capture while foraging (HGFS, pp. 15–16, 20–22, 27–38, 51–52, 67, 174–175, 230–231).

Martin's conception is unlike that of foraging theory in a second way as well. To foraging theorists, maximization refers to constrained maximization, to a choice of an "optimal" strategy *in comparison to all strategies in some fea-*sible set. Thus, Martin's points about diminishing returns due to prey depletion or population growth, or the constraints imposed by body size or forager capabilities (pp. 613–614) are superfluous. Such factors already are incorporated into defining and measuring the feasible set of options.

The general point, that efficiency maximization in optimal foraging theory must be defined "in terms of some set of capacities and conditions" (p. 613), is one that Martin reaches after lengthy criticism of his initial and irrelevant version of the concept. The pedagogical or critical value of the exercise is unclear, as anyone knowledgeable about evolutionary ecology or microeconomics is familiar with the point and should have no trouble with its explicit reiteration (e.g., p. 22) in HGFS.[2]

The Marginal Value Theorem

The marginal value theorem (Charnov 1976) has been independently derived (Parker and Stuart 1976), extended to central place foraging (Orians and Pearson 1979), and tested with mixed results (Krebs et al. 1983) and with striking quantitative success (Kramer and Giraldeau 1984). Stochastic analogs to the model have been developed by Oaten (1977), McNamara (1982), and Stephens and Charnov (1982). Until Martin's review (pp. 615–616) it has not been found "incoherent," "impossible," or "beset with circularity." We note Martin's basic technical errors; most of his criticism simply compounds these.

1. The impossible situation of averages above the average (p. 615) is due to Martin's misreading of both Winterhalder and Charnov. In particular, he omits mention of movement of the forager between utilized patches, thus failing to note that overall foraging intake for a habitat includes (averages in) search time "lost" to unproductive interpatch movement, as well as the productive time spent foraging within patches.

2. Contrary to Martin's claim, Oaten (1977) does not refute the marginal value theorem (see Stephens and Charnov 1982). Oaten starts with different assumptions and arrives at a somewhat different outcome, a common procedure in evolutionary ecology where one goal is to determine clearly the consequences of alternative premises.

3. In a note (p. 627) Martin compares Charnov's and Winterhalder's different labeling of the graphical form of the model and pronounces Winterhalder's a misrepresentation. However, a line in a plane that is read as net intake on the vertical axis and time on the hor-

izontal axis will have a slope that is a net rate of intake. Charnov's label calls attention to the vertical axis; Winterhalder's to the slope. Both are correct; both are consistent with the model.

4. The attribution of circularity to the model is likewise spurious. Martin (p. 615) states:

> Further, there cannot be one absolute or theoretical mean return for a habitat; the value of the habitat mean is dependent on how far the forager goes out on the marginal cost curve for each patch, and derivatively, its total production. The theorem is beset with circularity.

If by "absolute" Martin means maximal, then the first clause of the first sentence is incorrect; the second clause is correct but significantly incomplete. The concluding sentence is wrong.

As portrayed in the model, the average efficiency of a forager moving in a patchy environment is a function of the marginal intake (derivately, of the time spent) in any given patch (Figure 1). For simplicity, the present graph considers the case of a set of patches with *identical* return rate curves (cf. Charnov 1976; HGFS, pp. 28–29; and Krebs 1978, Fig. 2.7a, for more complex versions). The *average* return rate over all patches utilized, including interpatch travel time, is represented by a straight line (A-B). The maximum value for this average or overall return rate is defined by the steepest line originating at A that is tan-
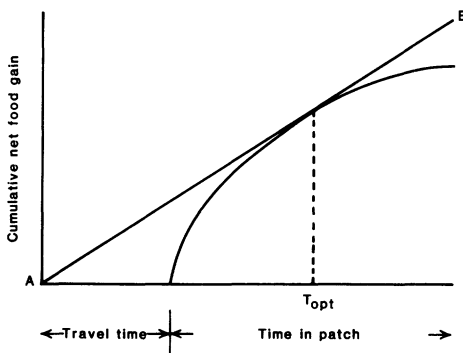
gent to the within-patch depletion curve. Behaviorally, foraging returns are optimized by allocating time T_{opt} to each patch, where T_{opt} is the time at which the marginal return rate from a patch equals the average return rate for the patch set.

Martin fails to note (see 1, above) that the average efficiency also includes unproductive time spent moving *between* patches. This linkage, the tradeoff between decreasing rates of return within a patch and the travel costs and subsequent benefits of moving to a richer locality, establishes a unique maximal rate of intake for the habitat. As a consequence, the model predicts a singular optimal patch residence time. The forager that spends less or more time in the patch will be foraging at lower than possible efficiencies, and it is a reasonable hypothesis that selection will act to create organisms capable of adjusting this variable.

Figure 1 also shows how badly Martin has misunderstood foraging theory when he claims (p. 613) that "the basic postulate" of optimal foraging theory is that "the forager operates at the highest point on the marginal return curve." As long as there is more than one patch, the optimal time allocation is always less than this point (at which the net return rate falls to zero).

Conclusions

Although space allows only these two examples, Martin's critique of the applications in HGFS is vitiated by his persistent failure to grasp the theory or models underlying the analyses presented in the book.

HGFS gives the basics of a new theoretical approach to hunter-gatherer ecology, with illustrative field studies. The book emphasizes that the theory is incomplete, the models partial, and that the standard methods and data of ecological anthropology are not always sufficient to inform the issues being addressed. For these reasons it is an exciting area of research. Optimal foraging theory is dedicated to producing a family of relatively simple and (taken individually) relatively modest models, using consistent premises. The initial results have been highly productive, partly because those problems that do arise can be addressed within a coherent theoretical framework, one that can expand cumulatively. Extensions of the models to include stochasticity, opportunity costs, social interactions, and other factors, promise comparably valuable insights. We repeat that optimal foraging theory is "rich in the need for empirical verification" (HGFS, p. 34). If Martin's review inhibits

Figure 1
The marginal value theorem. This model depicts the optimal time allocation to a set of foraging areas or "patches." It assumes a standard or mean interpatch travel time and a monotonically-declining within-patch return rate (i.e., net food gain per unit of time spent foraging within a patch).

people from undertaking that effort, then by its carelessness and overstatement it will be a disservice not only to this book but to ecological and economic anthropology as well.

Notes

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[1]Authorship was shared equally; the order established alphabetically.

[2]Martin himself has constructed a model of hunter-gatherer local-group size (cited in HGFS, p. 46) with the central assumption that Pai Indian foragers "were disposed to seek the highest net material (subsistence) return for their labors" (Martin 1973:1449). He goes on to clarify this in a note:

> This theory does not claim that Pai consciously and rationally pursued the highest net return. The claim is much more limited: it is that they moved towards optimal solutions. [1973:1464, n. 2]

He further comments that "the optimal size for the task groups" is equal to the minimum necessary to carry out "the most efficient technique in the group's repertory" and that "efficiency is defined in terms of net material reward per man hour of work" (1973:1449). It is not evident how one is to reconcile his critique of optimization assumptions in optimal foraging theory with these statements.

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