Imperfectly Optimal Animals

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Summary. We consider models of behavior that apply to two different problems: when a predator should leave a foraging site and how a female should choose the best available male. In each case we derive rules for an optimal solution to the problem. We also derive models based on very simple, plausible rules of behavior that we suspect animals may actually use. Although the expected payoffs from optimality models always exceed the expected payoffs from our simpler behavioral models, under certain conditions the difference is not large. When good foraging sites last but a short time and when females' mobility in their habitat is limited, the results of simple models and optimal models are very close indeed.

Because of the difficulty of distinguishing between the results of each type of model and because natural selection will presumably provide a best mix of solutions to a range of problems rather than a best solution to any one problem, we suggest that behavioral ecologists expend more effort on simple, plausible models of animal behavior. Such models provide ready-made testable hypotheses about the animal's approximation to optimality and about the actual mechanisms of behavior.

Introduction

The use of simple rules-of-thumb for making decisions in a complex world has been an important subject in economic theory for some time (Simon 1959; Baumol and Quandt 1963). The rationale for such studies is that information that is accurate and complete enough to allow optimal decisions by a firm is costly to acquire and time-consuming to analyze. Consequently, simple but sufficient rules of behavior in the marketplace are important.

While biologists often recognize that similar limitations apply to animal behavior (Cowie and Krebs 1979; Charnov 1976b), models of behavior nearly always look for optimal solutions. This approach has obvious strengths (Cody 1974; Maynard Smith 1978, but see Gould and Lewontin 1979; Lewontin 1978).However, it leaves one with few clues as to how animals actually implement "strategic" decisions: i.e. what are the tactics of the animal? One would also like to know how far from the optimal solution simple tactics leave the animal.

In this paper, we shall present models for two different problems that many animals must face: when to leave a foraging site and how to select a mate. In each case, we shall present two solutions:

1. An optimal solution to the problem as presented, and

2. A model that yields a non-optimal solution but that is constructed around a simple and reasonable behavioral rule. The models are illustrative, but their comparison is illuminating. The difference between the solutions indicates how bad (or how good) simple, but nonoptimal mechanisms are likely to be. It also indicates the usefulness, from an experimenter's point of view, of constructing behavioral models around the tactics that an animal might actually use.

Methods and Results

When to Leave a Foraging Site

Charnov's marginal value theorem (1976b) gives a simple answer to this problem for an animal that depletes its food source in a patch: the animal should leave the patch when its rate of energetic return in that patch declines below the average rate of return of all patches in the environment. However, web-spinning spiders and other predators that do

not directly influence the rate of return at a foraging site face a slightly different problem (Janetos 1980b).

We assume that the environment consists of good foraging sites and poor foraging sites, at which a predator daily receives payoffs G and B, respectively $(G > B)$. A predator that moves from a site encounters a good site with probability p and a poor site with probability q $(p+q=1)$, and also incurs a cost C. G, B and C can be measured in any appropriate units, although the rate of net energy gain is usually preferred. We also assume that good sites have a constant lifespan, L, after which they become poor sites. Appendix 1 shows that a more realistic model in which the lifespan of good sites varies does not differ qualitatively from this conceptually and computationally simpler approach.

At the end of each day, the predator is assumed to decide whether to stay in its current foraging site or move to a new one. If the predator lands in a good site, it does not know how much of the lifespan of the site has already passed. The expected gain from moving to a new foraging site is the average value of a randomly chosen site less the cost of moving: $pG + qB - C$.

A Non-Optimal Predator

Our model for non-optimal behavior in the predator is very simple. The predator moves only after experiencing a poor day at a foraging site. We call such a predator a "tester". There is empirical evidence that orbweaving spiders are testers (Janetos 1980b, ms).

The average payoff for the tester is easy to calculate:

$$V_t = G(\text{avg. } T_R - 1) + B + pG + qB - C,$$

where T_R is the residence time at a foraging site.

The first two terms derive from the fact that the total observable residence time will include the one poor period that is the stimulus for the predator to move. Since the average residence time in a good site for a predator using this rule will be half the length of the lifespan of a good foraging site, substitution gives

$$V_t = G(L/2 - 1) + B + pG + qB - C.$$

An Optimal Predator

An optimal predator maximizes its expected rate of gain during the next day. The optimal rule for moving from a foraging site is a mixed rule. If the predator experiences a day of poor rewards, it should move, as does the tester. However, there is

also a maximum residence time, $T_{\max}$, beyond which the predator will not stay at the foraging site.

In order to calculate $T_{\max}$, we must assume that the predator "knows" both L, the lifespan of good sites, and its own residence time at a site, T_R. We define $P(B|T_R)$ as the probability that a good foraging site becomes poor in the next day, given that the predator has been there for T_R days. Imagine that $T_R = L - 1$. Then the site must go bad on the next day: $P(B|T_R) = 1$. If $T_R = L - 2$, the site could go bad on the next day or the day after, depending on whether the predator arrived on the site's first or second day. Since either is equally probable, $P(B|T_R) = 1/2$.

The same reasoning applies for successively shorter residence times:

$$p(B|T_R) = 1/(L - T_R).$$

The optimal predator moves only when the expectation of doing better elsewhere tomorrow exceeds the expectation of gain from remaining, i.e. when

$$pG + qB - C > P(B|T_R) B + (1 - P(B|T_R)) G.$$

After substitution and rearrangement, the condition for moving becomes:

$$(G - B)(1/(L - T_R) - q) > C.$$

The critical point for a decision comes when the lefthand term equals C, implying a threshold rule. By solving for T_R, we find the optimal maximum residence time, $T_{\max}$:

$$T_{\max} = L - \frac{1}{C/(G - B) + q}.$$

The average payoff to a predator using this optimal rule is

$$V_{\text{opt}} = G(\text{avg. } T_R) + pG + qB - C.$$

The average residence time at a good site is a combination of the probability that the site lasts long enough for the predator to stay $T_{\max}$ days and the probability that the site does not last that long. Assuming that the predator's residence time is equally likely to start on any day in the lifespan of a good foraging site,

$$\text{avg. } T_R = \left(\frac{L - T_{\max}}{L}\right) T_{\max} + (T_{\max}/L)(T_{\max}/2)$$

$$= T_{\max}(1 - T_{\max}/2L).$$

By substitution,

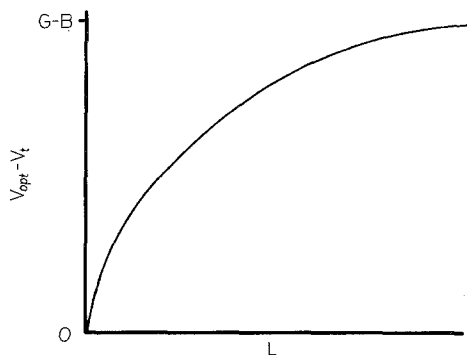$$V_{\text{opt}} = G(T_{\max}(1 - T_{\max}/2L)) + pG + qB - C.$$

Fig. 1. The difference between the payoffs of the optimal solution (V_{opt}) and the tester solution (V_t) as a function of the lifespan of a good site, L

We find the difference between the optimal predator's payoff and the tester's payoff by subtraction:

$$V_{opt} - V_t = G(T_{max}(1 - T_{max}/2L) - (L/2 - 1)) - B.$$

Substitution and extensive rearrangement gives

$$V_{opt} - V_t = (G - B) - \left(\frac{1}{2L(C/(G - B) + q)^2}\right) G.$$

Figure 1 shows the difference between the two payoffs as a function of L, the lifespan of a good site. The difference reaches an asymptote of $G - B$ as L gets large. The optimal behavior is, unsurprisingly, always more profitable than the tester. However, the magnitude of the difference depends on a collection of parameters: the ratio of the cost of moving to the difference between good and poor sites, the probability that a moving predator will encounter a poor site, and most importantly, the length of the lifespan of a good foraging site. When good foraging sites persist only a short time, the difference between the two models is very small. As the lifespan of good foraging sites increases, the difference between the optimal payoff and the tester payoff increases at a decreasing rate, eventually reaching an asymptote at the difference between good and poor sites.

The result is intuitively satisfying. On the one hand, when L is small, both the optimal and tester models predict that predators will often be moving from one foraging site to another. The probability of finding a new good site, which is the same for both kinds of predators, dominates the payoff for each. On the other hand, as L increases, the ability of the optimal predator to leave at the right time becomes relatively more important in its average payoff, since it will pay the cost of enduring a poor foraging site for a day less often than will a tester.

Female Choice of Mates

We compare the results of two models that are optimal under different constraints on the female's behavior with the non-optimal results of a simpler model. The results that we compare will be the average fitness of males chosen by females that use a particular tactic of choice. Throughout, we shall assume that the genetic fitness of males is described by a uniform probability distribution over the interval (0–1). This assumption is reasonable; using other distributions affects the results quantitatively, but not qualitatively (Janetos 1980a).

Optimal Females

Best-of-n-Males. In this model, we assume that the female's freedom to choose males is limited only by time. She can remember all the males that she encounters and can return to any male that she has looked at previously. Clearly the best that a female can do under such circumstances is to examine all the males that time allows and then go back and mate with the best one. For any distribution of fitness among males, the expected value of the nth order statistic, $E(U_n)$, gives the average fitness of males chosen (Mosteller and Rourke 1973).

Optimal 1-Step. In this model we also assume that time limits a female to encounters with at most n males. However, we add a constraint on the female's mobility: she cannot go back to a male that she has previously encountered and left. Thus the female must decide at each encounter whether to mate and end her search, or to search further. Janetos (1980a) gives a simple verbal derivation of the model. Here we note one special aspect. The female uses sliding thresholds of acceptability. When the female has time to encounter at least n males, the first male that she sees must surpass an extremely high threshold for her to mate with him. If the first male does not surpass the high threshold, the threshold for the second male is a bit lower. The threshold for the third male encountered is lower still, and as the female runs out of time, her threshold for an acceptable male continues to drop, until she mates on her last chance regardless of the male's quality.

Non-Optimal Females

The non-optimal model is the fixed-threshold with last chance (FTLC) (Janetos 1980a). The female mates with the first male that she encounters whose fitness exceeds some fixed threshold, W_c. However, if she has not encountered a good enough male by her last opportunity to mate, she mates without regard
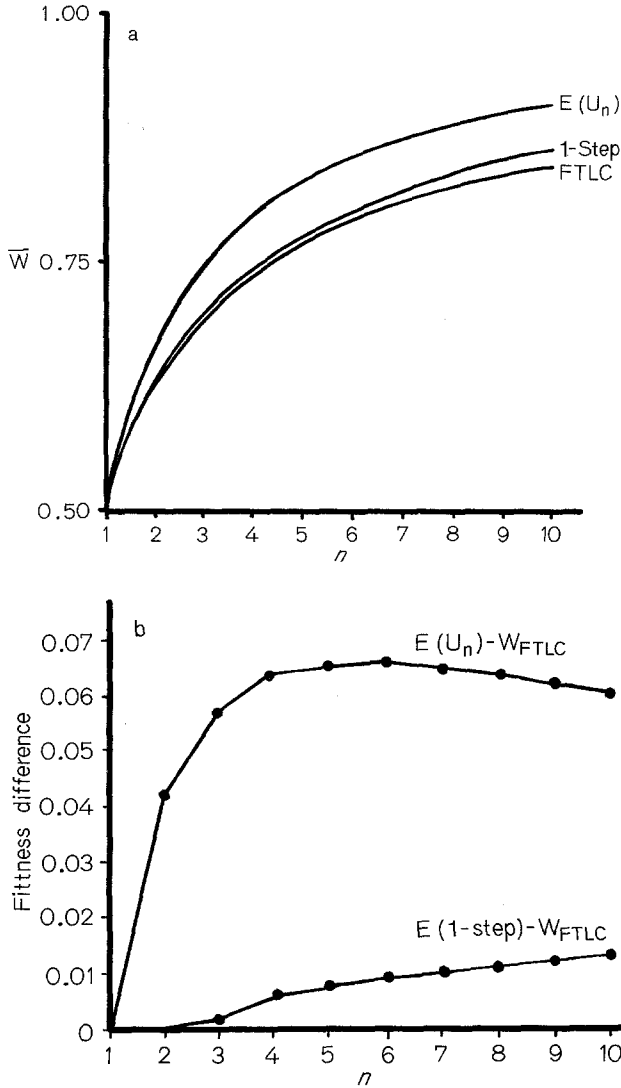
In order to find W_c^*, the optimal fixed threshold, we let $d\bar{W}_{ft}/dW_c = 0$. In general,

$$d\bar{W}_{ft}/dW_c = (1 - F(W_c)^{n-1}) dK/dW_c$$
$$- (n-1) F(W_c)^{n-2} K dF(W_c)/dW_c$$
$$+ \mu(n-1) F(W_c)^{n-2} dF(W_c)/dW_c.$$

For a uniform distribution of male fitness on the interval (0–1), $\mu = 1/2$,

$$F(W) = W, \quad \text{and} \quad K = \frac{1 - F(W_c)}{2} + W_c = 1/2 + 1/2(W_c).$$

Substitution and considerable algebra yield

$$d\bar{W}_{ft}/dW_c = 1/2(1 - W_c^{n-1} - (n-1) W_c^{n-1}),$$

and thus

$$d\bar{W}_{ft}/dW_c = 0 \quad \text{when} \quad 1 - W_c^{n-1} = (n-1) W_c^{n-1},$$

i.e.

$$W_c^* = n^{1/(1-n)} = {}^{1-n}\!\sqrt{n}.$$

We can substitute W_c^* into the expression for $\bar{W}_{ft}$ in order to find the average fitness of males chosen by females that use the FTLC. Figure 2a compares the results of both optimal models with the results of the FTLC. The differences between each optimal model and the FTLC model are graphed in Fig. 2b as a function of n, the number of males that a female has time to examine. The shape of the curve in Fig. 2b is the same as the shape of the curve in Fig. 1, the difference between the payoffs of the optimal predator model and the tester. When n is small, the difference between an optimal and non-optimal solution is small. When a female has time to look at several males (n large), the difference between the models increases. However, the difference soon becomes relatively independent of n.

The Selective Advantage of Optimality

Just how large a selective disadvantage do our non-optimal animals labor under? One more simple model will illustrate the advantages that optimal animals have over our more constrained creatures. We shall use the mate choice models as the example, although the foraging models could in principle be just as easily used.

Assume the simplest possible genetic model: the tactic that a female uses to choose males is controlled at one locus. At first, the population consists

Fig. 2. a Average fitness ($\bar{W}$) of males chosen by females that use best-of-n-males ($E(U_n)$), optimal 1-step and fixed-threshold with last chance. b Differences in the average fitness of males chosen by females that used either optimal tactic and the non-optimal fixed-threshold rule

for the male's quality (hence the last chance). We allow natural selection to set an optimal fixed threshold, W_c^*. In other words, we allow our hypothetical females to do the best they can with a non-optimal tactic.

Letting $\bar{W}_{ft}$ be the average fitness of males chosen by females using the FTLC tactic, $F(W)$ be the cumulative probability distribution of fitness over males, μ be the average fitness of all males, and K be the average fitness of males that exceed W_c, the payoff to females from the FTLC is:

$$\bar{W}_{ft} = (1 - F(W_c)^{n-1}) K + \mu F(W_c)^{n-1}.$$

Table 1. Form of a simple genetic model for the spread of a dominant mutation that allows females to choose males optimally in a population of non-optimal females. We have ignored all second-order terms, as well as the terms $E_1 X/2$ and $E_2 Y/2$, which are both much less than $X/2$

♂	♀	#Off-spring	Avg.# of each genotype in a family		Frequency of mating type
			♂	♀	
aa × aa	X	$X/2$ (aa)	$X/2$	1
Aa × aa	X	$X/4$ (Aa)	$X/4$	E_1
aa × Aa	Y	$Y/4$ (Aa)	$Y/4$	E_2

entirely of females that use the FTLC, i.e. all females use a non-optimal, but simple tactic.

Now suppose that a dominant mutation arises at a very low frequency in the population. Females that possess the mutation choose males according to one of the two optimal tactics (which one is not important yet). There is no effect in males. Will the mutation spread?

Females that use an optimal tactic for choosing a mate will, on average, select males with higher fitness than will females using the FTLC. This fitness difference is translated into an increase in the number of offspring that survive to breed in the next generation: females using the FTLC have X offspring and females using an optimal tactic have Y offspring, $Y > X$. Table 1 shows the form of the genetic model. We are considering the behavior of the allele A at very low frequencies, so the frequencies E_1 and E_2 are very small, and we can safely ignore all second-order terms.

We can write the equations for the frequencies of different mating types in the next generation, E_1' and E_2':

$$E_1' = (E_1 X/4 + E_2 Y/4)/(X/2) = 1/2(E_1) + 1/2(Y/X) E_2$$
$$E_2' = (E_1 X/4 + E_2 Y/4)/(X/2) = 1/2(E_1) + 1/2(Y/X) E_2.$$

It is now a simple matter to write the transition matrix and solve its characteristic equation to find the growth rate of the gene in the population.

$$\begin{pmatrix} 1/2 & 1/2(Y/X) \\ 1/2 & 1/2(Y/X) \end{pmatrix} \begin{pmatrix} E_1 \\ E_2 \end{pmatrix} = \begin{pmatrix} E_1' \\ E_2' \end{pmatrix}$$

$$\lambda^2 - \lambda(1/2 + 1/2(Y/X)) = 0$$

$$\lambda = 1/2(1 + Y/X).$$

If Y and X are proportional to the expected fitnesses of males chosen by females that use an optimal strategy and the FTLC, respectively, then we can substitute the values from Fig. 2a to find the

relative advantage of the optimal tactic. The selective advantage of the optimal 1-step over the FTLC is a relatively constant 0.6%, while the selective advantage of the best-of-n-males over the FTLC is approximately 4%.

Discussion

We have presented two different kinds of models:

1. Strategic models that describe the optimal behavior that the animal could use, and

2. Tactical models that are based on simple behavioral rules that animals might be expected to use, but that yield non-optimal solutions to the problems.

Optimal solutions are, unsurprisingly, better than solutions from models based on simple behavioral rules for both foraging and mate choice problems. However, the analysis of the fate of a mutant gene shows that the selective advantage of an optimal solution may be quite small. A useful question to ask is whether the small gain from attaining the optimal solution to a problem is worth the cost of maintaining the machinery necessary to attain the optimum. This is simply the question of satisficing restated in biological terms, rather than economic.

We again call attention to the premise that natural selection acts, not just on one behavior, but on the adaptation of the whole organism to its environment. Because problems arise simultaneously, not sequentially, there is a trade-off between attaining the best possible solution to each problem and attaining the best possible mix of solutions.

There is no simple answer to this question. The behavior that parasitoid wasps (Waage 1979), great tits (Krebs et al. 1974; Krebs et al. 1977; Smith and Sweatman 1974), web-spinning spiders (Riechert 1976; Janetos 1980b) and sunfish (Werner and Hall 1974) employ in diet choice and patch use approximate the formulations of optimal foraging theory (Charnov 1976a; Pulliam 1974; Schoener 1971; MacArthur 1972; Cook and Hubbard 1977). Likewise, the behavior of mottled sculpins (Brown 1978; Downhower and Brown 1979, 1980), lark buntings (Pleszczynska 1978) and blackbirds (Searcy 1979) approximates the optimal strategies for the choice of the proper male (Orians 1969; Emlen and Oring 1977; Trivers 1972).

It is a trivial point that for survival, animals need not be optimal but only good enough. However, survival alone does not imply a selective advantage. Implicit in many studies is the notion that the optimal solution to a problem will be of such overwhelming selective advantage that it will be the one
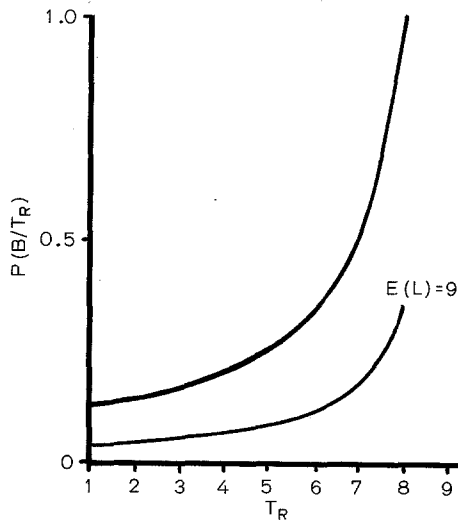
Fig. 3. The probability that a good foraging site will go bad on the next day, given a residence time for the deterministic case (upper curve, $L=9$) and probabilistic case (lower curve, $E(L)=9$)

that ultimately appears. We show that this is not the case; solutions of quite different forms than the optimum may carry very small selective disadvantages. Such simple tactics may be the ones that actually appear.

Appendix 1

We will show here that our assumption of a constant lifespan, L, for good foraging sites makes no qualitative difference to our argument. Recall that in the most general case, the optimal predator moves when

$$pG + qB - C > P(B|T_R) + (1 - P(B|T_R)) G,$$

which reduces to the condition: $P(B|T_R) > (C/(G-B)) + q$. As long as $P(B|T_R)$ is an increasing function of T_R, there will be a maximum residence time which the optimal predator should not exceed.

Imagine that instead of good sites having a constant lifespan, L, foraging sites may be either good or poor, and may change in quality at the end of each day. Poor sites become good with probability b; good sites become poor with probability a. At equilibrium, good sites occur with frequency $p = b/(a+b)$, and poor sites with frequency $q = a/(a+b)$ (Janetos 1980b, ms).

When is a good foraging site likely to turn poor for the first time? If we consider the sequence of qualities of the site as a sequence of Bernoulli trials (Hoel et al. 1971), with a constant probability of "success" (i.e. the site goes bad), then the probabili-

ty of a good site first going bad on day i is geometrically distributed.

P (site going bad on day i) $= a(1-a)^i$.

In the deterministic case, we assumed that the predator "knew" both its own residence time, T_R, and L, the lifespan of a good site. In this case, we shall assume that the optimal predator knows both T_R and $E(L)$, the expected lifespan of the site. The reasoning for calculating $P(B|T_R)$ is exactly the same as in the deterministic case, except that the probability must be weighted by the probability that the site's lifespan is at least $E(L)$, i.e. a weighting of $1 - \sum_{i=0}^{E(L)} a(1-a)^i$. For a geometric distribution, $E(L) = (1-a)/a$, and thus

$$P(B|T_R) = \frac{1 - \sum_{i=0}^{E(L)} a(1-a)^i}{E(L) - T_R} = \frac{\sum_{i=1/a}^{\infty} a(1-a)^i}{1/a - 1 - T_R}.$$

Figure 3 shows $P(B|T_R)$ as a function of T_R for $a=0.1$, which gives $E(L)=9$. It also shows $P(B|T_R)$ for the deterministic case of a constant lifespan of 9 days for good sites. Notice that the effect of letting L vary is to reduce the certainty of one's guess that the site will go bad tomorrow. However, the shape of the curve does not change.

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