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Is satisficing an alternative to optimal foraging theory?

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Ward (1992; Oikos 63: 312–317) recently argued that optimal foraging theory suffers from a lack of alternative models and suggested that satisficing might serve as such an alternative. We disagree with both premises and argue that the optimal foraging approach generates multiple alternative and testable hypotheses within its own logical framework. Conversely, satisficing can only be defined in ways that are either trivial or a subset of optimal foraging. Satisficing fails as a coherent alternative to optimality because its predictions are not testable and therefore cannot be refuted. Ward also cited one result from our earlier work with ants as evidence for satisficing in nature. We show, however, that when our work is examined in its entirety, ant colonies actually forage in a manner that appears to maximize colony growth rather than to satisfy a minimum requirement.

In a recent paper, Ward (1992) sought to resurrect satisficing as a valid alternative model to optimization theory. In buttressing his arguments, Ward referred to our work (Nonacs and Dill 1990) as evidence that ants are satisficing in their foraging behavior rather than optimizing. In this paper we argue (1) that the behavior of the foraging ants was highly consistent with optimal foraging theory, and (2) that satisficing, itself, has little potential to generate testable predictions about foraging behavior. We respond to Ward's general arguments about the merits of satisficing, with specific emphasis on what our work with *Lasius pallitarsis* ants actually showed.

What is optimizing?

Given the immense literature on optimal foraging and similar optimality models, the need to define optimization yet again would seem to be unnecessary. However, Ward's (1992) paper clearly misses the point of the optimization approach. To suggest satisficing as an alternative to optimization implies that for any given problem there is only one optimization model. However, optimization is an *approach* to constructing models and not a model in and of itself. Thus, there can be several different "optimality" models to describe any behavioral activity.

An animal can be thought of as living in an n-dimensional activity space, the axes of which may be the time or effort devoted to foraging, finding mates, caring for young, avoiding predators, etc. Very often effort spent in one activity (along one axis) will detract from success in other activities. Because natural selection favors those individuals leaving the greatest number of viable offspring (Darwin 1859), it follows that organisms which correctly trade-off between all the conflicting demands will produce the most possible offspring. It can be argued that measuring the sum of all these trade-offs truly tests whether an animal is optimal. However, whether animals are globally optimal has never been tested. Nor should ecologists even *try* to test this prediction. The global-optimum model is not so much a predictor of nature as a definition of nature. It must be true that a perfectly adapted organism leaves the most possible offspring! The existence of a global-optimum point is what Stearns and Schmid-Hempel (1987) called a deep axiom: a tautology that guarantees logical consistency at the core of the theory.

Since an n-dimensional space for any organism is impossible to examine simultaneously, no optimality models are global in nature, but instead test for selection along a restricted number of axes. Thus, there is often no single model, but instead whole families of optimality models, with solutions and predictions varying according to their underlying assumptions. It is

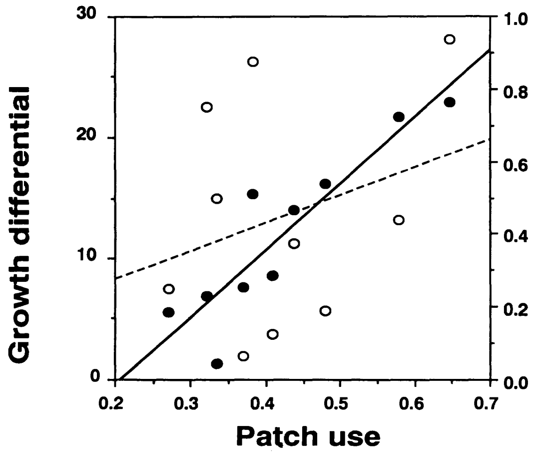

Fig. 1. Proportional use of the risky patch by *Lasius pallitarsis* ants as a function of the risky patch's higher caloric value (○) or greater potential for colony growth (●). Caloric value of a patch was defined by assigning the most concentrated diet a value of 1.0 and scaling the value of the other diets relative to their fractional dilution (1/2, 1/4, 1/8 or 1/16 of full strength). The caloric differential between the two patch choices was, therefore, the difference between their proportional values (handling times and energetic costs were identical for all choices). The change in brood biomass (in µg) per load of food returned by a forager was independently measured for *L. pallitarsis* colonies for each diet dilution (Nonacs and Dill 1990). Growth differential was thus the difference in expected brood biomass for a load of food brought back from the high-food, risky patch rather than from the poor-food, safe patch. The dashed line is the regression through the choices measured by caloric differential ($R^2 = 0.081$, $P > 0.05$), and the solid line is the regression through the choices measured by colony growth differential ($R^2 = 0.819$, $P = 0.003$).

through extensive testing of the predictions of these simplified representations of nature that the underlying logic of the optimization research program is validated (Mitchell and Valone 1990).

Ward (1992) isolated for criticism one such group of optimality models that predict behavior based on maximization of rate of net energy intake. He made much of the fact that increased food gathering does not always increase fitness in a monotonic fashion. To this end, he cited Nonacs and Dill (1990) as evidence that "one of the major assumptions of optimal foraging theory may not always be appropriate" (p. 314) and more specifically that ants' response to food "would truly be satisficing and not optimizing" (p. 315). Both conclusions are incorrect, as a more careful examination of our work reveals.

First, *L. pallitarsis* ant colonies were fed, ad libitum, on one of five artificial liquid diets that varied in dilution. The least concentrated solution was 16 times more dilute than the full-strength diet. The point that Ward emphasized was that the growth exhibited by colonies fed full strength solution was not significantly greater than that of colonies fed ½ strength solution (Nonacs and Dill 1990: Fig. 3). Ward then argued that ant colonies could "satisfice" by showing no preference between the diets. Ward neglected to mention that this is *not* what the colonies actually did! When given a choice between two patches that differed only in the dilution of food offered, the colonies consistently maximized their rate of net energy intake by always preferentially foraging at the more concentrated food source (Nonacs and Dill 1990: Fig. 4). Thus, when the ants' world varied along only one axis (the energy content of patches), the ants performed as predicted by optimal foraging theory.

In a similar vein, Nonacs and Dill (1988) showed that when food patches were equal in food quality, but varied in mortality risk, colonies preferentially foraged at the safer site. Therefore, ant colonies can be shown to maximize fitness under two different situations when faced with problems that vary along only a single ecological axis at a time.

The main goal of Nonacs and Dill (1990), however, was to test whether ants can optimize when faced with a trade-off between conflicting demands, i.e., when food quality and mortality risk in patches are inversely correlated. The non-linear relationship between food quality and colony growth suggested that a pure energy-maximizing strategy was unlikely to maximize fitness, given that forager mortality was now associated with the high-food quality patch. Rather, we hypothesized that colonies should make patch choices based on the consequences for overall colony growth (growth = brood production – adult deaths). Indeed, patch preferences were not significantly predicted by the differences in the rate of net energy intake between patches that also differed in mortality risk (Fig. 1: open circles and dashed line). However, patch preferences were strongly and significantly correlated with the expected colony growth differential per load of food returned to the colony (Fig. 1: closed circles and solid line). Most importantly, the point where colonies valued the risky, high-food patch equally to the safe, poor-food patch was such that the colony growth resulting from the better food approximately offset the biomass lost due to forager mortality (see calculations on p. 1891 in Nonacs and Dill 1990). Thus, the point at which colonies used safe and risky patches equally was also the point at which the patches had equal consequences for colony growth. Clearly this is an "optimizing" rather than a "satisficing" response.

It is important to note that in our experiments (Nonacs and Dill 1990, 1991) the ants could have either: maximized energy intake rate by always preferring the high-food patch, minimized adult mortality by always preferring the low-food patch, or traded-off between the two patches to maximize colony growth. All three of these possible outcomes are predicted by different optimization models with differing assumptions about what is being maximized or minimized. The rejection of the simplistic optimality models (maximize energy or minimize mortality) in favor of one that more accurately estimates fitness (maximize colony growth) belies

Ward's argument that there are no alternative models in optimal foraging theory. We therefore stand by our earlier conclusion that selection has acted strongly over evolutionary time on ants to respond efficiently to environmental variation in both food quality and predation risk (Nonacs and Dill 1990, 1991).

Ward gives Ritchie's (1988) work with ground squirrels as a second example supporting satisficing. Curiously, Ward's rationale was that Ritchie showed that only 63% of the population foraged optimally. Even though the remaining 37% had lower reproductive success, Ward proclaimed a failure of the optimality model because genes for optimal foraging had not gone to fixation. One response to Ward's argument is that, although the mean value of any behavioral trait may be expected to be near the optimal value, it is very likely that variation in the trait will remain, particularly if the environment is temporally variable (Lande 1975, 1980). A second, more testable response to Ward's conundrum is that, if the ground squirrels' habitat remains unchanged, the percentage of optimally foraging squirrels should increase over time. However, if eventually 99% of the squirrels forage optimally, would this still be evidence for satisficing rather than optimizing? The fact that satisficing can only be defined as being non-optimal, and cannot be rejected if even a single animal fails to behave optimally, is a most serious deficiency. In contrast, Ritchie's optimal diet choice model would have been rejected if a low percentage of the squirrels had foraged as he predicted and if there were no variation in reproductive success across foraging strategies. For satisficing to be a valid alternative to optimizing, it must likewise be defined in a way that allows for rejection.

What is satisficing?

Satisficing in its most trivial sense means doing just enough of whatever is required to survive and reproduce. Therefore, all living organisms are at least presently satisficing and had ancestors which also at least satisficed. Conversely, species extinction is a result of a failure of all individuals of that species to satisfice. Such a universal truism has little practical application, and if satisficing is to produce testable predictions, it must be more rigorously defined. Ward (1992) attempts to do so in two ways, but both ultimately fail.

Minimum requirements

One definition of satisficing is that it is equivalent to pursuing a behavior until some minimum requirement is met. Unfortunately, as Ward himself points out, this aspect of satisficing "has little heuristic value to ecologists" (p. 313). The problem is similar to the trivial definition above – this definition too easily fits with observation. As examples, any animal that declines a feeding opportunity may have done so because it has satisfactorily fed in the recent past. Any rate of feeding of offspring by parents is satisfactory as long as the offspring do not actually starve to death!

If satisficing is to produce a testable prediction, then there must be a rational way to define the criterion of "minimum requirements" which is not simply synonymous with staying alive. Rather than do so, Ward instead proposes that optimization models fall victim to the same problem of being too easily adapted to explain any possible result. The logic of this argument appears to be that if both optimization and satisficing are equally flawed then they must be equally valid alternative hypotheses. However, as argued above, the optimality research program produces a family of models generated by different assumptions as to which variables are optimized. Therefore, a well-constructed research program can test (and reject) more than one model. In contrast satisficing, defined as meeting minimum requirements, cannot ultimately be falsified.

Time and information constraints

This definition of satisficing is more subtle. Animals are proposed to be satisficing if they cannot find the optimal solution due to either time or information constraints. Unfortunately, this argument collapses because it either predicts an outcome that is unlikely to be evolutionarily stable or describes a subset of existing optimality theory.

Ward argues that under time or information constraints a satisficer may use "rules of thumb" rather than optimal algorithms. Such rules of thumb could vary from being very ineffective to being very good (i.e., close to optimal). Let us suppose a population consists of animals using a poor rule of thumb. Such a population would be extremely vulnerable to being invaded by animals using any more efficient rule. Therefore, it is difficult to see how satisficing could be evolutionarily stable when competition is possible with substantially superior decision rules.

Suppose, however, that the population consists of animals using a reasonably effective, but not entirely optimal, rule of thumb. Ward argues that such rules could have a great advantage over optimality when decisions must be made with great dispatch. We agree that this may be often true, but this is not comparing a satisficing model to an optimizing model. Instead, it is comparing two different optimizing models! Constraints do not disprove optimality, they just add new factors into the mix. Given a time constraint such as "the animal must make a decision in less than a second", a quickly employable and largely effective rule of thumb will also be the optimal thing to do (see Stephens and

Krebs (1986) for extensive discussions of optimization models with biological constraints).

Such convergence to optimality-type arguments is a common failing of the satisficing approach. For example, Ward discusses a managerial technique that responds primarily to immediate crises ("putting out fires": Radner 1975) and suggests that it could be applied in predicting activities that "minimize detrimental effects on long-term fitness" (p. 314). However, is this really a satisficing model or an optimization model that assumes the currency to be maximized is long-term fitness? The difference here is truly only semantic. The key point is that, whatever the constraint, a satisficing model still must make arbitrary assumptions about the organism's goals and what the minimum acceptable requirements are. In an optimizing framework, such assumptions must be clearly defined and subject to refutation, but in a satisficing framework it appears to suffice to simply say that behavior is predicted to be less than optimal.

The inability of satisficing to be coherently defined as separate from optimization, ultimately makes it a superfluous concept. To test the proposition that animals satisfice requires first determining the optimal response itself, or else it would be impossible to conclude that a given response merely satisfices. Satisficing is therefore just another name for the null hypothesis. As such it deserves no special consideration and serves no real function other than reminding researchers that the underlying assumptions of optimization models may not always hold.

Optimization and parsimony

Ward also argues that when the data are equivocal, satisficing may be a better explanation than optimization because it is the simpler, more parsimonious, explanation. We, however, challenge the proposition that satisficing models are intrinsically simpler than optimization models.

Consider our foraging experiments with *L. pallitarsis*. An optimizing model requires that foragers are sensitive to both food quality and level of predation risk and balance both to maximize colony growth. A satisficing model might be constructed along the following lines: colonies forage enough to keep growing and avoid predators enough to keep worker numbers from declining. The optimization model has two behavioral parameters, and so does the satisficing model (both models require reactions to food and predators). The difference is that the parameters are explicit in the optimizing approach and implicit for the satisficing model. However, ambiguity should not be mistaken for either simplicity or generality.

Ultimately, satisficing is a simpler model only if behaving satisfactorily is physiologically less costly (e.g., fewer neurons need to be used to perform a given task). However, there is no a priori reason to expect that foraging behaviors that only meet a minimum requirement will require less physiological complexity than those that optimize. Mathematical complexity cannot be assumed to translate inevitably into an equivalent amount of biological complexity.

Conclusions

Satisficing is not a coherent alternative to optimization theory for explaining animal foraging behavior. Satisficing can be defined only by what it is not: it is not dying (or failing to reproduce) and it is not behaving optimally. Any definition more specific than this requires assumptions that organisms meet some arbitrarily determined minimum requirements. In contrast, optimization theory also requires assumptions about what maximizes fitness, but these assumptions derive from rational constructs and are readily testable. The warnings Ward raises about the fascination with optimality models should be well heeded, but they are not new. The assumptions of any model should be closely examined and the sensitivity of predictions to small variations in the details of the models should be carefully examined (see Gladstein et al. 1991). Researchers should not selectively use or collect data that support pet theories and they should be willing to allow their models to be disproved. We all should be wary of post hoc explanations of why a model "works" even though the data suggest otherwise. However, is the use of satisficing the shining path leading from a quagmire of optimality models? The answer is no. Foraging theory will be better advanced if care is taken to produce better and more realistic optimization models, rather than embracing untestable concepts as alternative hypotheses.

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