ship between behavior (e.g., patch residence time) and the distribution of food reward. Here, the effect of stochasticity is to require that we postulate (or measure) a second type of function; that is, we need not only relate behavior to food gains (Schoener's cost-benefit functions), but we must relate food gains to preference (utility functions).

Currency vs Expected Utility

There are two approaches to the problem of finding a forager's utility function. The conventional approach of utility theorists (cf. Raiffa 1968) is to allow the subject to specify its own utility function by giving it a series of preference tests. This approach has been adopted by Caraco et al. (1980) to make the important point that foraging animals have preferences over variance. The approach of deterministic foraging theory (cf. Pyke et al. 1977) has been to guess a reasonable currency based on our knowledge of the forager's natural hystory. These a priori currencies, with their connection to natural history, are one of the strengths of optimality analysis. Both approaches can be useful in the study of foraging behavior. But allowing the forager to specify its own utility function is, in a sense, the least satisfactory of the two alternatives because we want to know not only what a forager's preferences are, but why it has these preferences. We do not mean that these questions cannot be asked separately, but the second question is the biological one; utility theory, per se, sheds no light on the answer, only on the form the answer should take, i.e., a utility function.

Fitness and expected utility are both tautologically defined maximization criteria. To call them tautological is not a complete condemnation because they can both be interesting and helpful tautologies (see Maynard Smith 1969). Neither idea tells us much about the adaptive nature of foraging behavior. To say that selection has favored maximization of fitness or utility is simply too glib. We must go a step further and postulate how food and feeding are related to ultimate fitness. In the models we have presented, we postulated a simple connection between the forager's natural history and its risk-sensitivity: minimization of the probability of a short-fall. If our model fits natural foraging behavior, we can take satisfaction in having understood natural history well enough to have made an a priori guess about the appropriate utility, more so than if we had simply measured utility functions.

Description and Utility

The expected-utility hypothesis may fail; that is, no utility function may exist which describes the behavior. In economics there are famous examples of where humans show preferences which are inconsistent with the expected-utility hypothesis (e.g., Allais 1953). The reply of utility theorists is that their theory is prescriptive, not descriptive, of human behavior (Raiffa 1968). Utility theory tells us how rational human decisions *should be* made, not how human decisions are made. In foraging theory we do not want to prescribe animal preferences; we wand to describe them. We do not want to instruct animals in how to make better decisions. We want to describe the decisions they do make. Perhaps we should consider whether animal decisions are more likely to satisfy the criteria of the expected-utility hypothesis than human decisions. When we adopt techniques from other disciplines, we should look hard at their internal difficulties. In the case of utility theory there is a large body of literature on the pros and cons of its application (e.g., Raiffa 1968; Keeney and Raiffa 1978, who provide discussions).

Variance Discounting

The formal machinery of utility theory may not be necessary in practice, especially if food reward is normally distributed. While normality cannot be guaranteed, it is likely to be the most general food reward distribution; this is suggested by the results in section one and less restrictively by the central limit theorem itself. When normality does occur, the intuitive idea of a trade-off between a measure of central tendency (mean) and a measure of variability (variance) can be justified by rigorous mathematics because the mean and variance provide a complete specification of a normal distribution. If we take normality to be general, we then have the problem of trying to find some general way to combine mean and variance to provide a measure of quality. Section two proposed that the Z-score of the standard normal distribution is a sensible currency for the case of acquiring a threshold food requirement.

Many authors have proposed that a straightforward linear combination of mean and standard deviation may be a generally useful currency (Oster and Wilson 1978; Caraco 1980; Real 1980a, b). This currency has the form:

$$\max(\mu - k\sigma)$$

where μ is the mean and σ is the standard deviation of the reward distribution, and k is a constant measuring the forager's risk-sensitivity. We maximize the mean, discounted by a certain amount for 'undesirable' variability, because k is usually positive. While this formulation is recommended by its simplicity, its claim to generality may be strong as

well. Using arguments from utility theory, it has been shown that this formula is approximately correct under very general conditions using a series expansion argument (Oster and Wilson 1978; Real 1980a, b). It is exactly correct if the underlying distribution is normal and the utility function is a simple exponential function (Oster and Wilson 1978; Caraco 1980).

Uncertainty and Information in Patches

The marginal-value theorem (Charnov 1976a), a deterministic model finding optimal patch residence times, has been severely criticized because, according to Oaten (1977), sensible optimal leaving procedures 'must be based on a stochastic model'. Green (1980), Iwasa et al. (1981) and McNamara (in press) have all added mathematical weight to Oaten's criticism. It is unfortunate and misleading that Oaten and his colleagues have been so insistent in their campaign for stochasticity because the differences between Oaten's stochastic model and Charnov's deterministic model are not due to stochasticity per se.

Consider the following simple example. Imagine that a scientist is given two opaque urns, each containing different proportions of red to green balls, and is asked to obtain as many red balls as possible in some fixed number of draws, without replacement. If the scientist is told that the urn labelled A has initial proportion p_a of reds and the urn labelled B has reds in initial proportion p_b, the problem is closely analogous to Charnov's 'patch-use model where the urns are patches and the scientist is a forager. However, if the scientist is not told what the labels mean, he has Oaten's problem; because he cannot recognize patches he will do well to use knowledge gained while 'foraging' to improve his decisions. The difference here is not stochasticity. Both problems are stochastic. The difference is the amount of information the forager (scientist) is supposed to have. To call Oaten's model the stochastic case is to confuse the problems of risk and information.

Stochastic Rates

Pyke et al. (1977) have argued that maximization of the net rate of energy intake is the most sensible general currency of optimality in foraging because it subsumes both of the reasonable currencies proposed by Schoener (1971), energy maximization over a fixed time and time minimization to a fixed energy gain. Templeton and Lawlor (1981) have recently pointed out that in a stochastic world, maximization of the expected rate of energy intake is not necessarily equivalent to either of these strategies. In this case, what Templeton and Lawlor called the 'fallacy of averages' stems from the fact that the expectation of a quotient is not equal to the quotient of the expectations.

Let G be the random variable which specifies the net food gain over a random time T. Then each of following currencies of optimality is possible and generally distinct from the others.

1. Maximize $E(G/T)$.
2. Maximize $E(G)/E(T)$.
3. Maximize $E(G|T=t)$, where t is a fixed value.
4. Minimize $E(T|G=g)$, where g is a fixed value.

Currencies three and four are stochastic versions of Schoener's (1971) energy maximizer and time minimizer. However, a good deal of controversy surrounds the interpretation of currencies one and two (Templeton and Lawlor 1981; Gilliam et al., in press; Turelli et al., in press). Templeton and Lawlor claim that currency one is the average of energy intake and that models of optimal foraging which have claimed that currency two is the average rate of intake (specifically Charnov 1976b and Pulliam 1974) are wrong. Templeton and Lawlor are incorrect because both currencies are average rates of intake. The important question is which average is appropriate, not which is *the* average.

The precise meanings of these currencies depend on the definitions of G and T. If G is the amount of energy gained in time T, where T is the time from entering one patch until entering the next (Templeton and Lawlor's case), then as the number of patches visited becomes large, the average rate of energy intake *per patch* approaches $E(G/T)$ by the law of large numbers. By a similar argument, as the number of patches visited becomes large the average amount of energy gained *per unit of time* approaches $E(G)/E(T)$. These are both average rates. An animal using the $E(G/T)$ currency should choose foraging strategies where each patch yields the highest possible rate that particular patch can attain, regardless of the absolute amount of time spent in that patch. While the $E(G)/E(T)$ currency allows for the possibility that the rate attained within a particular patch might be less than the maximum possible if a higher overall rate can be had by moving on to better patches. There may be cases where $E(G/T)$ is a sensible currency: for example, if the forager is somehow limited to visiting only one patch per day (or whatever 'critical' period is applicable). However, we agree with Gilliam et al. (in press) that $E(G)/E(T)$ is a much better currency for nearly any forager.

Analysis and Simplicity

Our approach is to build simple models. Simple models are most useful because they allow us to see how the elements of the problem interact and to readily compare different conditions and assumptions. In a word, simpler models allow better analysis. The growing body of literature on stochasticity in foraging strongly argues that the additional complexities of stochastic models are worth it. But modelers should not lose sight of analysis. We have taken the time to discuss the controversies about stochastic rates and 'stochasticity' in patch use because we believe that these are cases where analysis has been lost in the shuffle. The cause of analysis is not well served by Templeton and Lawlor's (1981) surprising and self-contradictory statement that ecologists should be suspicious of 'conclusions that depend critically upon the precise form of the optimization criterion.' Not only are criteria critical by definition, if they are not they should have been removed from the model on the ground of parsimony inherent in the concept of analysis.

Modeling is just figuring out the implications of a set of assumptions. Templeton and Lawlor (1981) and Oaten (1977) seem to have elevated assumptions to the realm of metaphysics by insisting on right and wrong assumptions. Maximizing $E(G)/E(T)$ has different implications than maximizing $E(G/T)$, and a discussion of the these differences has proved helpful, despite Templeton and Lawlor's error (Gilliam et al., in press; Turelli et al., in press). Similarly, Oaten's important work has shown that foragers which cannot recognize patches should act differently from those which can. But this does not show that 'published strategies are not optimal,' as Oaten claims.

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References

Allais M (1953) Le comportement de l'hommme rationnel devant le risque: critique des postulats et axioms de l'ecole americaine. Econometrica 21:503–546

Caraco T (1980) On foraging time allocation in a stochastic environment. Ecology 61:119–128

Caraco T (1981) Energy budgets, risk and foraging preferences in Dark-eyed juncos. (*Junco hymelais*). Behav Ecol Sociobiol 8:213–217

Caraco T, Martindale S, Whittam TS (1980) An empirical demonstration of risk-sensitive foraging preferences. Anim Behav 28:820–830

Charnov EL (1973) Optimal foraging: some theoretical explorations. PhD dissertation. University of Washington

Charnov EL (1976a) Optimal foraging: the marginal value theorem. Theor Popul Biol 9:129–136

Charnov EL (1976b) Optimal foraging: the attack strategy of a mantid. Am Nat 110:141–151

Cox DR (1962) Renewal theory. Methuen, London

Gilliam JF, Green RF, Pearson NE (in press) The fallacy of the traffic policeman: a response to Templeton and Lawlor. Am Nat

Green RF (1980) Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theor Popul Biol 18:244–256

Herrnstein RJ (1964) Aperiodicity as a factor in choice. J Exp Anal Behav 7:179–182

Hey JD (1979) Uncertainty in Microeconomics. New York University Press, New York

Holling CS (1959) Some characteristics of simple types of parasitism. Can Entomol 16:385–398

Iwasa Y, Higashi M, Yamamura N (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. Am Nat 117:710–723

Keeney RL, Raiffa H (1976) Decisions with multiple objectives: preferences and value trade-offs. Wiley, New York

Krebs JR, Erichsen JT, Webber MI, Charnov EL (1977) Optimal prey selection in the great tit (*Parus major*). Anim Behav 25:30–38

Leventhal AM, Morrell RF, Morgan EF, Perkins CM (1959) The relation between mean reward and mean reinforcement. J Exp Psychol 57:284–287

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

Maynard Smith J (1969) The status of neo-darwinism. In: Waddington CH (ed) Towards a theoretical biology. 2. Sketches. University Press, Edinburgh. pp 82–89

Maynard Smith J (1974) Models in ecology. Cambridge University Press, Cambridge

McNair JN (1979) A generalized model of optimal diets. Theor Popul Biol 15:159–170

McNair JN (in press) Energy reserves and the risk of starvation: some foraging strategies. Am Nat

McNamara J (in press) Optimal patch use in a stochastic environment. Theor Popul Biol

McNamara J, Houston AI (in press) Short-term behaviour and life-time fitness. In: McFarland DJ (ed) Functional ontogeny. Pitmans, London

Oaten A (1977) Optimal foraging in patches: a case for stochasticity. Theor Popul Biol 85:673–690

Oster GF, Wilson EO (1978) Caste and ecology and the social insects. Princeton University Press, Princeton, New Jersey

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, Ohio. pp 155–177

Paloheimo JE (1967) On the theory of search. PhD dissertation. University of Toronto

Paloheimo JE (1971) On the theory of search. Biometrika 58:61–75

Pearson NE (1974) Optimal foraging theory. Quan Science Paper No 39, Center of Quan Science in forestry, fisheries and wildlife. University of Washington, Seattle, Washington

Prys-Jones RP (1977) Aspects of reed-bunting ecology with comparisons with the yellowhammer. D Phil thesis, University of Oxford

Pubols BH (1962) Constant versus variable delay of reinforcement. J Comp Physiol Psychol 55:52–56

Pulliam HR (1974) On the theory of optimal diets. Am Nat 108:59–74

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev. Biol. 52:137–154

Raiffa H (1968) Decision analysis. Addison-Wesley, Reading, Massachussetts

Real LA (1980a) Fitness, uncertainty and the law of diminishing returns in evolution and behavior. Am Nat 115:623–638

Real LA (1980b) On uncertainty and the law of diminishing returns in evolution and behavior. In: Staddon JER (ed) Limits to action: the allocation of individual behavior. Academic Press, New York, pp 37–64

Real LA (1981) Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps on artificial flowers. Ecology 62:20–26

Schoener TW (1969) Models of optimal size for solitary predators. Am Nat 103:277–313

Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecol Syst 2:379–404

Smith WL (1955) Regenerative processes. Proc. R Soc Lond [A] 232:6–31

Stephens DW (1981) The logic of risk-sensitive foraging preferences. Anim Behav 29:628–629

Templeton AR, Lawlor LR (1981) The fallacy of the averages in ecological optimization theory. Am Nat 117:390–383

Turelli M, Gillispie JH, Schoener TW (in press) The fallacy of the fallacy of the averages in ecological optimization theory. Am Nat

Waddington KD, Allen T, Heinrich B (1981) Floral preference of bumblebees (*Bombus edwardsii*) in relation to intermittent versus continuous rewards. Anim Behav 29:779–784

Werner EE, Hall DJ (1975) Optimal foraging and the size-selection of prey by bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052

ERRATA LITERATURE CITED

The following references are cited in the text and are missing from the literature cited:

Bond, A. B. (1981) Giving-up as a Poisson process: the departure decision of a green lacewing. Anim. Behav. 29: 629-631.

Caraco, T. (1980) Stochastic dynamics of avian foraging flocks. Am. Nat. 115: 262-275.

Charnov, E.L. (1982) The theory of sex allocation. Princeton University Press, Princeton.

Davison, M. (1969) Preference for mixed-interval vs. fixed interval schedules. J. Exp. Anal. Behav. 12: 247-252.

Horn, H. S. (1978) Optimal tactics of reproduction and life-history. In: Krebs, J. R. & Davies, N. B. (eds.) Behavioural Ecology: an evolutionary approach. Blackwells, Oxford.

McNamara, J. & Houston, A. (1980) The application of statistical decision theory to animal behaviour. J. theor. Biol. 85: 673-690.

Orians, G. H. (1969) On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-603.

Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat? Am. Nat. 119: 151-178.

Parker, G. A. and Stuart, R. A. (1976) Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Am. Nat. 110: 1055-1076.

Pulliam, H.R. (1973) On the advantages of flocking. J. theor. Biol. 38: 419-422.

Real, L. A. (1981) Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps on artifical flowers. Ecology 62: 20-26.

Rechten, C. Krebs, J. R. & Houston, A. I. (1981) Great tits and conveyor belts: a correction for non-random prey distribution. Anim. Behav. 29: 1276-1277

Schoener, T. W. (1969) Models of optimal size for solitrary predators. Am. Nat. 103: 277-313.

Waage, J. K. (1979) Foraging for patchily distributed hosts by the parasitoid Nemeritis canescens. J. Anim. Ecol. 48: 353-371.

Wilson, E. O. (1980a) Caste and division of labor in leaf-cutter ants. (Hymenoptera: Formicidae: Atta) I. The overall pattern in A. sexdens. Behav. Ecol. Sociobiol. 7: 143-156.

Wilson, E. O. (1980b) Caste and division of labor in leaf-cutter ants. (Hymenoptera: Formicidae: Atta) II. The ergonomic optimization of leaf-cutting. Behav. Ecol. Sociobiol. 7: 157-165.

Winterhalder, B. (1981) Foraging strategies in the boreal forest: an analysis of Cree hunting and gathering. In: Winterhalder, B. & Smith, E. A. (eds.) Hunter-gatherer foraging strategies. Univ. of Chicago Press, Chicago.