WHAT SHOULD OPTIMAL FORAGERS MAXIMIZE? A RESPONSE TO TEMPLETON AND LAWLOR

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Templeton and Lawlor (1981) have claimed that ecologists who build optimization medels (in particular, optimal foraging models) are often guilty of the "fallacy of averages", that is, of confusing the expected value of a function with the function of the expected values. For animals foraging in patches the energy gained per patch visited, G, and the time per visit (including time between patches), T, may be considered to be random variables. Templeton and Lawlor claim that Charnov (1976) and Pulliam (1974) are guilty of the "fallacy of averages" by assuming that $E(G/T) = EG/ET$. In fact, Charnov and Pulliam make no such mistake, but Templeton and Lawlor themselves are mistaken, both mathematically and biologically.

Charnov's (1976) "marginal value theorem" tells when a forager should leave a patch if it is to maximize its average energy intake per unit time. Templeton and Lawlor confuse intake per unit time with intake rate per visit, and thus claim that Charnov should have tried to maximize $E(G/T)$. However, average intake per unit time is found by averaging over many units of time. Such an average is approximated by $\sum G/\sum T$, which goes to EG/ET by the law of large numbers. It is this EG/ET which Charnov seeks to maximize. Templeton and Lawlor are correct in pointing out that $E(G/T) \neq EG/ET$, but no one claims any different. The difference is that Charnov claims that the average intake per unit time is

EG/ET, while Templeton and Lawlor claim it is E(G/T). Mathematically, Charnov is right and Templeton and Lawlor are wrong.

Templeton and Lawlor do not claim that it is better to maximize E(G/T) than EG/ET. Indeed, they should not do so because it is easy to see that such a claim would be wrong. Consider, for example, an animal that forages in patches, half of which are good and half bad, but the animal must search them each a bit to know whether they are good or bad. Assume that the animal finds no prey in bad patches, but finds one prey per unit time (including time between patches) in good patches. Assume that the animal can spend any amount of time from 1 to 10 units in each patch. Then, no matter how much time the animal spends in each patch he would find prey at rate $G/T = 0$ in the bad patches and rate $G/T = 1$ in the good patches. Therefore, $E(G/T) = 1/2$, no matter what strategy the animal uses. However, an animal seeking to maximize EG/ET would do better to stay in good patches and leave bad patches.

There certainly is a problem in extending Charnov's marginal value theorem to the stochastic case, as Oaten (1977) has pointed out in general and I have shown in particular (Green 1980). But Templeton and Lawlor seem to miss the point of this criticism. The point is not what should be maximized (everyone, except Templeton and

Lawlor, agree that it is EG/ET), but how the maximization is to be achieved. The problem is that the marginal value theorem tells us when an animal should leave a patch, but it does not tell how the animal should decide when to leave a patch. It may well be impossible to find a leaving rule which satisfies the marginal value theorem. In fact, in my version of Oaten's model the best strategy does not satisfy the marginal value theorem. It is only in this extension to the stochastic case in which the forager must assess patch quality that the marginal value theorem breaks down. The marginal value theorem as stated by Charnov and criticised by Templeton and Lawlor is correct.

Templeton and Lawlor seem to think that it is a criticism of optimization theory that when different optimization criteria are used different conclusions are reached. If the question of what is optimized is of interest, then it is to be hoped that different optimization criteria would lead to different conclusions. If all models lead to the same conclusions then there is no way to choose between models. This point is illustrated by the example I gave above. Animals maximizing E(G/T) as suggested by Templeton and Lawlor should be indifferent between good patches and bad patches while animals maximizing EG/ET as suggested by Charnov should prefer good patches. Perhaps some experimental biologist could test which conclusion, and therefore which optimization criterion, is correct.

LITERATURE CITED

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Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theor. Popul. Biol. 18:244-256.

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Pulliam, H. R. 1974. On the theory of optimal diets. Am. Nat. 108:59-74.

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For evidence that animals do, in fact, sometimes prefer to maximize E(G/T) rather than EG/ET, see:

Killeen, P. R. 1968. On the measurement of reinforcement frequency in the study of preference. J. exper. Anal. Behav., 11:263-269.