



The Fallacy of the Traffic Policeman: A Response to Templeton and Lawlor

James F. Gilliam; Richard F. Green; Nolan E. Pearson

American Naturalist, Volume 119, Issue 6 (Jun., 1982), 875-878.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28198206%29119%3A6%3C875%3ATFOTTP%3E2.0.CO%3B2-L>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Naturalist is published by The University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

American Naturalist

©1982 The University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

THE FALLACY OF THE TRAFFIC POLICEMAN: A RESPONSE TO
TEMPLETON AND LAWLOR

Templeton and Lawlor (1981) have claimed that ecologists who build optimality models (in particular, optimal foraging models) are often guilty of the "fallacy of the 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 (G) per patch visited, and the time (T) per visit (including time between patches), may be considered to be random variables. Templeton and Lawlor claim that Charnov (1976) is guilty of the fallacy of the averages by assuming that $E(G/T) = E(G)/E(T)$. In fact, Charnov makes no such mistake.

Specifically, Templeton and Lawlor note that Charnov obtained his expression for the "average rate of energy intake" by dividing the average energy intake per patch by the average time required to obtain the energy per patch, arriving at the expression:

$$\frac{E(G)}{E(T)} = \frac{\sum_i p_i g_i(T_i) - tE_t}{t + \sum_i p_i T_i} \quad (1)$$

where

- T_i = time spent in a patch of type i ;
- $g_i(T_i)$ = net energy gained while foraging in a patch of type i for time T_i ;
- t = average travel time between patches;
- E_t = energy expended per unit time traveling; and
- p_i = fraction of patches that are of type i .

Equation (1) also describes the fine-grained case (foraging on individual prey items rather than in patches) if we consider prey types rather than patch types, handling time rather than time in a patch, and average search time between encounters with prey rather than average time traveling between patches.

Templeton and Lawlor indict (1) on the grounds that it is an example of the fallacy of the averages. They suggest that the proper formulation is:

$$E(G/T) = \sum_i p_i \left[\frac{g_i(T_i) - tE_t}{t + T_i} \right]. \quad (2)$$

The justification for (2) is that the expression in brackets represents the possible values of a random variable (call it X) describing the rate of energy intake available from a patch (or an item) of type i . Then (2) follows from the definition of expected value: $E(X) = \sum p_i x_i$, where the x_i 's are the possible values of the random variable X and the p_i 's are their probabilities of occurrence.

The formulation by Templeton and Lawlor, however, contains a conceptual flaw. The p_i 's used by them merely represent the relative patch frequencies, but not the proportion of time spent in patches of each type. If an animal spends twice as much time in each patch of type 1 as in each patch of type 2, then the probabilities of finding the animal in a given patch type should reflect this; the probabilities used by Templeton and Lawlor do not. We will illustrate this point with what we will call "the fallacy of the traffic policeman," after an old problem in a book of brain teasers. The problem is the following: A policeman observes that an automobile travels some distance at 30 miles per hour (mph) and then an equal distance at 60 mph, and concludes that the automobile was driven at an average rate of $(.5)(30) + (.5)(60) = 45$ mph. His error is that he failed to weight the activities by the time spent at each. Because the driver spent twice as much time at 30 mph as at 60 mph, some reflection should convince the reader that the relevant average rate is $(2/3)(30) + (1/3)(60) = 40$ mph. Both of the above calculations are averages, but the second is an accurate description of distance traveled per unit time because we can multiply the average speed by the total time and obtain an accurate value for the distance traveled. Similarly, a foraging model should accurately describe the energy gained per unit time by allowing us to multiply the average foraging rate by the time spent foraging and obtain the amount of energy gained. The Charnov model does this, whereas the alternative proposed by Templeton and Lawlor does not. The correct calculation of the expected net energy intake per unit time is performed in the Appendix. The result is precisely that of Charnov.

Templeton and Lawlor do not claim that it is better to maximize (2) than (1). Indeed they should not, because such a policy can be shown to lead to bizarre foraging behavior. Consider, for example, an animal that forages in patches, of which half are good and half are 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 ($G/T = 0$), but in good patches finds one prey per unit time ($G/T = 1$, including time traveling between patches). Therefore, using equation (2), $E(G/T) = (.5)(0) + (.5)(1) = .5$, no matter how much time the animal spends in each patch, implying that under Templeton and Lawlor's criterion, foraging in good patches is not necessarily preferred to foraging in bad patches. On the other hand, an animal seeking to maximize $E(G)/E(T)$, as suggested by Charnov, should remain in good patches and leave bad patches immediately. Other examples are easily constructed in which Templeton and Lawlor's criterion leads to the biologically absurd conclusion that an animal should forage longer in patches of net negative value than in patches of high positive value, whereas Charnov's formulation would not permit foraging in negative-valued patches.

Although Templeton and Lawlor's criticism of Charnov's model is incorrect, his model is vulnerable to the criticism that it is a deterministic representation of a process that is fundamentally stochastic. Charnov's marginal value theorem tells us when an animal should leave a patch if the animal knows its future foraging rates in the patch and the environment, but the theorem does not tell us how an animal should estimate those rates. The stochastic models of Oaten (1977) and

Green (1980) explicitly consider this problem, and their "leaving rules" use information on previous prey encounters more completely than Charnov's suggested use of the "giving-up-time" rule. Nonetheless, the theorem cannot be faulted, as Templeton and Lawlor have tried to do, on the grounds of internal inconsistency or flaws in logic. The conclusion of the theorem does indeed "follow from the stated assumptions" (Templeton and Lawlor 1981, p. 391). Furthermore, despite its deterministic character, Charnov's theorem has true worth in setting a standard of foraging behavior for the consummate energy-maximizer, and of serving as a basis for the interpretation of data and the construction of more realistic models.

ACKNOWLEDGMENTS

James MacMahon, Gordon Orians, Earl Werner, Gary Mittelbach, and Andy Sih made useful comments on earlier versions. This work was supported in part by grants DEB78-24271 and DEB79-04534 from the National Science Foundation. The order of authorship is alphabetical.

APPENDIX

The probability of finding an animal in or traveling to patch type i at a given instant depends not only on the frequency (p_i) of the patch type in the habitat, but on the time ($t + T_i$) associated with that patch type. The probability is given by:

$$p'_i = \frac{p_i(t + T_i)}{\sum_j p_j(t + T_j)} \quad (\text{A1})$$

The expected rate of energy intake is then (cf. eq. [2]):

$$\sum_i p'_i \left[\frac{g_i(T_i) - tE_t}{t + T_i} \right] = \frac{\sum_i p_i [g_i(T_i) - tE_t]}{\sum_j p_j(t + T_j)} = \frac{\sum_i p_i g_i(T_i) - tE_t}{t + \sum_i p_i T_i} \quad (\text{A2})$$

where we have made use of the fact that $\sum p_i = 1$, and in the last step have replaced the dummy index j by i .

This is Charnov's result (see eq. [1]). This derivation shows that Charnov's result can be obtained either as a ratio of expected values (Charnov's original method), or as a single expected value if the probabilities reflect the proportion of time spent in each patch (above method).

LITERATURE CITED

- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9:129-136.
 Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theor. Popul. Biol.* 18:244-256.
 Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. *Theor. Popul. Biol.* 12:263-285.

Templeton, A. R., and L. R. Lawlor. 1981. The fallacy of the averages in ecological optimization theory. *Am. Nat.* 117:390-393.

JAMES F. GILLIAM

W. K. KELLOGG BIOLOGICAL STATION
DEPARTMENT OF ZOOLOGY
MICHIGAN STATE UNIVERSITY
HICKORY CORNERS, MICHIGAN 49060

RICHARD F. GREEN

DEPARTMENT OF MATHEMATICAL SCIENCES
UNIVERSITY OF MINNESOTA
DULUTH, MINNESOTA 55812

NOLAN E. PEARSON*

DEPARTMENT OF BIOLOGY AND ECOLOGY CENTER
UTAH STATE UNIVERSITY
LOGAN, UTAH 84322

Submitted June 1, 1981; Accepted December 1, 1981

*Present address: Division of Mathematics-Science, University of Maine, Presque Isle, Maine 04769.