Figure 1. Two extreme fitness functions ($f(N)$) used in the computer simulation of group stability. Both have optima at a group size of 5. Note how the $dW/dN$ changes on either side of the optimum. The stable group size for each function is indicated by the stars, the open star for the dashed line $f(N)$, and the closed star for the solid line $f(N)$.

each of five different $f(N)$. The $f(N)$ were designed such that while $N_{\text{opt}}$ remained constant at five the $dW/dN$ at $N < N_{\text{opt}}$ was changed in relation to $dW/dN$ at $N > N_{\text{opt}}$. Two extreme examples of the $f(N)$ used are presented in Fig. 1.

The simulations confirm that $N_s$ can never be smaller than $N_{\text{opt}}$, a result derived analytically by Pulliam & Caraco (1984). Our simulations indicate, however, that Sibly's conclusion that $N_{\text{opt}} < N_s$ is incorrect since in some cases $N_s = N_{\text{opt}}$ (Fig. 1). This occurs when the fitness of joining a group of optimal size is less than that of remaining alone (see Fig. 1). The generality of both Clark & Mangel's (1984) and Pulliam & Caraco's (1984) conclusion that individuals will more often be in groups larger than $N_{\text{opt}}$ because $N_{\text{opt}}$ is unstable resides in the generality of $f(N)$ for which $N_{\text{opt}} < N_s$. At present, there is no reason to believe that this type of $f(N)$ is more common than any other. In fact, when competition is important, we would expect $f(N)$ to be of the shape that stabilizes $N_{\text{opt}}$. This is because competition could add costs to joining supra-optimal group sizes. These costs could be the result of harassment, aggression or even exclusion from the group. Spotted hyaenas for instance, establish dominance hierarchies that exclude lower-ranking individuals from having access to smaller carcasses (Tilson & Hamilton 1984). The costs of joining groups of supra-optimal size for lower-ranking individuals may be greater than the costs of joining groups of sub-optimal size.

When lions hunt Thompson's gazelle in the Serengeti, $N_{\text{opt}}$ (two lions) provides the maximum attainable harvesting rate (Caraco & Wolf 1975). Groups larger than the optimum could not provide the minimum daily food requirement of adult lions (Caraco & Wolf 1975). It is clear that lions joining a group in excess of $N_{\text{opt}}$ would reduce their fitness considerably such that $N_{\text{opt}}$ would be stable. Contrary to Sibly's conclusions therefore, one should not assume that $N_s$ and $N_{\text{obs}}$ are greater than $N_{\text{opt}}$ before investigating the shape of the fitness functions.

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Luc-Alain Giraldeau*
Darren Gillis

References


* Present address: Department of Psychology, University of Toronto, Toronto, Ontario, Canada M5S 1A1.

Department of Biology,
McGill University,
1205, Avenue docteur Penfield,
Montreal, Canada H3A 1B1.

How Important are Partial Preferences?

In the recent international conference on foraging behaviour, two speakers (G. H. Pyke & R. Gray) concluded that the existence of partial preferences is a major empirical failing of optimal diet theory (Pulliam 1974; Charnov 1976). I disagree, because under any reasonable statistical model of preference, it is practically impossible to observe anything but partial preferences, even if optimal diet theory is correct. Moreover, I argue that the

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literature's pre-occupation with partial preferences (per se) has been counter-productive (see Krebs & McCleery 1984 for a list of proposed explanations).

A typical prediction of optimal diet theory might be that 'above encounter rate $\lambda^*$, only large (more profitable) mealworms should be taken, and below $\lambda^*$, both small (less profitable) and large mealworms should be taken' (where $\lambda^*$ is the threshold encounter rate). 'Absolute' preferences would occur if at every encounter rate below $\lambda^*$, all small mealworms encountered were eaten, and at every encounter rate above $\lambda^*$ none of the small mealworms encountered were taken (see Fig. 1A). Instead of this 'step function' experimentalists usually observe a smooth 'S-shaped' relationship (Fig. 1B) between encounter rate and the proportions of small mealworms taken. This is what is meant by 'partial preferences'.

Suppose that $\lambda^*$ is the predicted time spent in a patch, instead of the predicted threshold. An experiment could be designed in which many patch-residence times (in identical patches) would be observed. The observed frequency distribution of patch-residence times (containing information about mean and variance) could then be compared with the predicted time. A statistical test of the hypothesis that the mean patch-residence time is equal to the predicted patch-residence time could be performed, and statements about the significance of such a hypothesis could be made. Obviously, it would be unreasonable to expect that no variance would be observed around the predicted patch-residence time.

The central problem is that a threshold ($\lambda^*$) cannot be directly observed. If the forager ignores a small mealworm at $\lambda'$ then all that can be inferred is that $\lambda^*$ is less than $\lambda'$. According to the absolute preferences view, $\lambda'$ must always be above $\lambda^*$, but if $\lambda^*$ is a random variable it is possible (in fact expected) that $\lambda'$ will sometimes be above and sometimes be below the threshold $\lambda^*$. Absolute preferences can only occur if the threshold ($\lambda^*$) has no variance. Observed thresholds will have some variance for a number of reasons: incomplete experimental control, within- and between-subject variability, and possible intrinsic variability.

Suppose that an experiment was designed to test diet theory by controlling the encounter rate. Four levels of encounter rate are chosen $\lambda_4 > \lambda_3 > \lambda_2 > \lambda_1$. $\lambda^*$ (the predicted threshold) is between $\lambda_2$ and $\lambda_3$ (see Fig. 1). According to the 'absolute preferences' view of diet theory, small mealworms must be taken on 100% of the encounters with small mealworms in treatments $\lambda_1$ and $\lambda_2$, and never taken in treatments $\lambda_3$ and $\lambda_4$. Suppose that the underlying distribution of the threshold is normal (with mean equal to $\lambda^*$ and unknown variance), and that a different realization of the threshold is 'drawn' from one encounter to the next (in the same way that a forager's patch residence time will vary from patch to patch even if the patches are identical). Because of the underlying stochasticity, $\lambda_3$ is usually above the threshold (more than 50% of the time), but sometimes below it. Specifically, it will be above the threshold (predicting that small mealworms should be ignored) on $\Phi((\lambda_3-\lambda^*)/\sigma)$ of the encounters. In an experiment like this, one can only observe the cumulative distribution function of the randomly-distributed threshold. The cumulative distribution function of the normal (\Phi) is sigmoid, and this is why a sigmoid dose–response relationship is not surprising.

A number of statistical techniques can be used to estimate the mean and variance of a threshold. The most widely known technique is probit analysis (Finney 1962), which uses transformed response scores and weighted linear regression. This technique allows tests of the hypothesis: is the observed threshold significantly different from the predicted threshold? Finney discusses the problems of, and appropriate experimental designs for the study of these dose–response relationships. Although the conventional use of probit analysis is to estimate
the toxicity of drugs and poisons, Finney points out that the technique was originally used for behavioural preference testing.

I anticipate the following two objections. (1) It may be argued that the analysis I propose presupposes the existence of a threshold, which is one of the predictions of diet theory. This is true enough. However, this is the way statistical tests always work. Significance is a measure of error given that the underlying hypothesis is correct. The way around this difficulty is to test alternative hypotheses. A clear statement of the statistical implications of threshold predictions should help rather than hinder this process. One problem is that there is little observable difference between a graded sigmoid response to dose, and a randomly-distributed threshold. However, diet theory provides an a priori way to predict one of the dose–response curve’s parameters (the mean; the variance must be estimated from the data), while the graded response view requires the estimation of two parameters from the data.

(2) It may be argued that the presence of variance is an apology for optimal diet theory, and worse, that it hides many of the interesting phenomena which a science of foraging behaviour ought to address. Admitting that observed partial preferences are the result of variance enhances, rather than diminishes, attempts to understand them by providing a focus for further study. Five out of six of Krebs & McCleery’s (1984) explanations of partial preferences can be viewed as components of variation (the sixth, simultaneous encounters, can be ruled out in any well-controlled experiment). The empirical support for diet theory would, of course, be most impressive if the variance about the threshold were small, but the variance must be measured before one can conclude that it is inordinately large. It is ironic that the literature’s obsession with partial preference has prevented students of foraging from measuring how partial the preferences are.

The simple existence of partial preferences is no more damning for optimal diet theory than the existence of variance is for the hypothesis that the sex ratio of mammals is one to one. Probit analysis can be used to test whether the data are systematically different from predictions. Optimal diet theory has not been allowed the luxury of such tests because of the pre-occupation with partial preferences. Using these techniques the phenomena which must be accounted for by the theoretical successors to optimal diet theory can be accurately and succinctly described.

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D. W. Stephens

Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A.

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