A systematic error in tests of ideal free theory

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SUMMARY

Classical ideal free theory predicts that the distribution of consumers within a patchy environment should correspond to the distribution of resources. Tests of this prediction have inappropriately compared ratios of mean resource levels and mean consumer densities, rather than means of ratios. We show that this error, which has propagated through hundreds of studies, leads to a systematic bias: the theory will appear to underestimate the number of consumers occupying poor patches. We explain the correct way to test ideal free theory and apply it to published data; the classical model is then seen to yield far more accurate predictions than previously thought.

How will consumers distribute themselves within a patchy environment, given that each acts to maximize its own rate of resource acquisition? If all individuals know the whereabouts of resources and competitors, and if each is free to enter and exploit any patch on an equal basis with other residents, the result is what Fretwell & Lucas (1970) and Fretwell (1972) termed the 'ideal free distribution' (IFD): the distribution of consumers should match the distribution of resources within the habitat (general reviews of ideal free theory are given by Milinski & Parker (1991), Kacelnik *et al.* (1992), and Tregenza (1995)). In the simplest case, with only two patches, this can be expressed as

$$n_2/n_1 = r_2/r_1, \tag{1}$$

where n_i is the number of individuals and r_i the availability of resources in patch i. When consumer densities in the patches are balanced in this way, no individual can benefit by moving elsewhere (Milinski 1979; Pulliam & Caraco 1991; Fagen 1987).

Over the past 25 years, the habitat matching prediction has been subject to repeated tests (Milinski & Parker 1991; Kacelnik *et al.* 1992; Tregenza 1995; Abrahams 1986; Kennedy & Gray 1993). In a typical study, the experimenter calculates, based on a number of observations, the mean number of individuals in two or more patches that differ in resource availability (Milinski 1979, 1984; Harper 1982; Godin & Keenleyside 1984; Recer *et al.* 1987; Sutherland *et al.* 1988; Lamb & Ollason 1993; Utne *et al.* 1993; Tyler & Gilliam 1995). These mean values are then used in equation (1), and matching is said to occur if

$$\langle n_2\rangle/\langle n_1\rangle = \langle r_2\rangle/\langle r_1\rangle, \tag{2}$$

where angle brackets denote the expected value. In other words, the ratio of the mean number of individuals in patch 2 to the mean number in patch 1 must equal the ratio of the mean availability of resources in patch 2 to the mean availability in patch 1.

In practice, it is rare for equation (2) to be satisfied precisely. Most studies report a characteristic bias: patches with a greater than average proportion of resources tend to be underused (relative to the predictions of equation (2)), while those with a lower than average proportion of resources are overused (Abrahams 1986; Kennedy & Gray 1993). This phenomenon, known as 'undermatching', has prompted numerous modifications of the Fretwell & Lucas model, including the incorporation of individual differences in competitive ability (Parker & Sutherland 1986; Houston & McNamara 1988), varying levels of interference (Sutherland 1983), and perceptual constraints (Abrahams 1986), any or all of which might explain the observed bias.

But equation (2) is *not* predicted by IFD theory. This means that empirical studies have set out to test the wrong relationship. Before appealing to more complex models to explain undermatching, it is essential to consider more carefully the implications of the original ideal free theory.

Equation (1) specifies the relationship between resource availability and consumer density for any one observation. With N individuals in total, the expected number of individuals in patch i is given by

$$n_i = N\frac{r_i}{r_1 + r_2}\,. \tag{3}$$

The expected ratio of the mean number of individuals in patch 2 to the mean number in patch 1 is thus

$$\frac{\langle n_2\rangle}{\langle n_1\rangle} = \left\langle\frac{r_2}{r_1 + r_2}\right\rangle \Big/ \left\langle\frac{r_1}{r_1 + r_2}\right\rangle. \tag{4}$$

This reduces to equation (2) only under the implausible circumstance that the resource values of the patches exhibit no variation whatsoever, i.e. they are identical

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for all observations. To assume that equations (2) and (4) are equivalent would be to commit the 'fallacy of the averages' (a phrase first used in the ecological literature by Templeton & Lawlor (1981)). The fallacy is defined by Wagner (1969, p. 658): 'Given an arbitrary nonlinear function $f(x_1, \ldots, x_n)$ of random variables $x_1, \ldots, x_n$ it is usually erroneous to assume $E[f(x_1, \ldots, x_n)] = f(E[x_1], \ldots, E[x_n])$' where E is the expectation operator. In our case, the nonlinear function is $f(x_1, x_2) = x_1/(x_1 + x_2)$.

In fact, relative to equation (2), the ideal free hypothesis *predicts* undermatching. If patch 2 has the greater resource value, we show in Appendix 1 that (assuming noise is generated by the same process in each patch),

$$\langle n_2 \rangle / \langle n_1 \rangle < \langle r_2 \rangle / \langle r_1 \rangle, \tag{5}$$

i.e. the ratio of the mean number of individuals in patch 2 to the mean number in patch 1 will be less than the ratio of the mean availability of resources in patch 2 to the mean availability in patch 1.

Even a cursory survey of tests of the IFD reveals that most report significant variance in the numbers of consumers exploiting patches. If the observed distributions are to be interpreted in terms of ideal free theory, this variation in numbers must reflect variation in resource values. Experimenters typically attempt to reduce the variance in input rates to an insignificant level (although this is not always possible, e.g. Lamb & Ollason (1993)); however, even if input rate variation is somehow entirely eliminated, resource availability will necessarily vary as a consequence of individuals depleting the resource. The source of the variation makes no difference to the effect: any study that looks at the mean numbers of consumers in different patches should not expect—even if the assumptions of Fretwell & Lucas's model are satisfied—to find that they match the mean resource values of those patches (as specified by equation (2)).

The precise degree of undermatching (of means) predicted by Fretwell & Lucas's model depends on the degree of variation in underlying resource availability. In practice, however, resource variation is usually very difficult, if not impossible, to measure directly, especially if it arises largely due to depletion. In the rare instances when it can be measured (e.g. Lamb & Ollason 1993) experimenters should report the resource variance in each patch (not just the means). Otherwise, it is necessary to estimate both resource variation and the predicted degree of undermatching using the standard deviation, σ_n, in the observed proportion of individuals occupying either patch (see Appendix 2 for further discussion of this point).

To quantify the degree of undermatching, we use the index proposed by Fagen (1987) and Kennedy & Gray (1993),

$$K \equiv \log \frac{\langle n_2 \rangle}{\langle n_1 \rangle} \Big/ \log \frac{\langle r_2 \rangle}{\langle r_1 \rangle}, \tag{6}$$

where a value of $K = 1$ represents perfect matching of means, while $K < 1$ represents undermatching. Assuming noise is generated by the same process in both patches, a very good fit to the predicted relationship between K and σ_n is

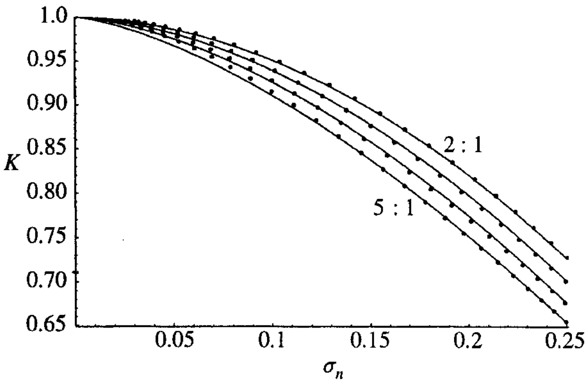

Figure 1. The matching index K of Fagen (1987) and Kennedy & Gray (1993), defined in equation (6), as a function of σ_n, the standard deviation in the observed proportion of individuals occupying either patch, for four different values of the ratio $\langle r_2 \rangle : \langle r_1 \rangle$ (2:1, 3:1, 4:1 and 5:1). The plotted points show the precise values of K predicted by the original Fretwell & Lucas (1970) IFD, assuming log-normal noise. The solid curves show our estimates of K obtained from equation (7). In the past, experimenters have implicitly assumed that the Fretwell–Lucas model always predicts $K = 1$, independent of σ_n.

$$K \simeq 1 - a\sigma_n^b, \tag{7a}$$

where

$$a = 4.317 - 0.327\langle r_2 \rangle / \langle r_1 \rangle, \tag{7b}$$

$$b = 2.138 - 0.132\langle r_2 \rangle / \langle r_1 \rangle, \tag{7c}$$

and $\sigma_n \lesssim 0.25$.

With equation (7), we have now recast the prediction of the Fretwell–Lucas model in terms that are directly relevant to the data collected in empirical studies. Our approximation (7) was calculated as a least-squares fit assuming log-normal noise; for noise with a specified origin it may be possible to calculate precisely the associated distribution function, but for our purposes this is not important because our approximation (7) appears to be insensitive to the particular noise distribution assumed. In figure 1, we compare equation (7) with the precise predicted value of K as a function of σ_n for several different values of the ratio $\langle r_2 \rangle : \langle r_1 \rangle$.

To test the Fretwell–Lucas model correctly using equation (7), an experimenter needs to measure the standard deviation σ_n in addition to the means $\langle r_1 \rangle$, $\langle r_2 \rangle$, $\langle n_1 \rangle$ and $\langle n_2 \rangle$. Then, rather than inserting means into equation (2), the means should be inserted in equation (6) to obtain the observed degree of undermatching K_{obs}, and the means and σ_n should be inserted in equation (7) to obtain the predicted degree of undermatching K_{pred}. Any discrepancy between theory and experiment is then quantified by the difference between K_{pred} and K_{obs}.

A review of two-patch, continuous input tests of the IFD revealed 15 experiments for which sufficient information was reported to estimate the standard

Table 1. *Observed and predicted values of the matching index K for a sample of two-patch, continuous input tests of the IFD*

(We are unaware of any other published studies that report the data necessary to compute the predicted K. Observed K values are based only on the stable distribution of consumers, excluding the initial approach period (as defined by the authors in each case). Where authors report several equivalent experiments, we have pooled data to obtain one result for each input ratio. (In some cases, we therefore obtain slightly different K values from Fagen (1987) and Kennedy & Gray (1993), who combined data from all input ratios to obtain a single estimate.) Note that the table is divided into two parts. The first comprises those studies for which the standard deviation in the proportion of individuals in either patch (σ_n) could be calculated directly from published data and graphs. The studies listed in the second part (where σ is marked with an asterisk) all involved several trials, in each of which many observations were made. While the standard deviation (or standard error) of trial means was given, the amount of variation among observations within each trial was not reported. Consequently, to calculate the predicted values of K, we were forced to estimate σ_n crudely as the standard deviation in trial means multiplied by the square root of the number of observations in each trial. More accurate tests are possible only with full access to experimental data. In the future, it would be helpful if experimenters made a point of publishing numerical values for the quantities given in each column of this table.)

study	$\langle r_2\rangle/\langle r_1\rangle$	$\langle n_2\rangle/\langle n_1\rangle$	observed K (equation (6))	σ_n	predicted K (equation (7))
Harper 1982	2	1.91	0.93	0.07	0.98
Lamb & Ollason 1993	2.17	2.05	0.93	0.07	0.98
	3.28	2.67	0.82	0.05	0.98
Milinski 1979	2	1.70	0.77	0.12	0.93
	5	4.36	0.91	0.11	0.90
Milinski 1984 'regular prey'	2	1.71	0.77	0.17	0.87
'irregular prey'	2	1.42	0.51	0.23	0.78
Recer *et al.* 1987	2	1.92	0.94	0.05	0.99
Tyler & Gilliam 1995	3	2.47	0.82	0.07	0.97
Godin & Keenleyside 1984	2	1.74	0.80	0.19*	0.84
	5	2.28	0.51	0.19*	0.79
Sutherland *et al.* 1988	2	1.38	0.46	0.14*	0.91
Utne *et al.* 1993	2	1.98	0.99	0.14*	0.91
	5	3.81	0.83	0.13*	0.88
	8	3.66	0.62	0.15*	0.80

*Estimated.

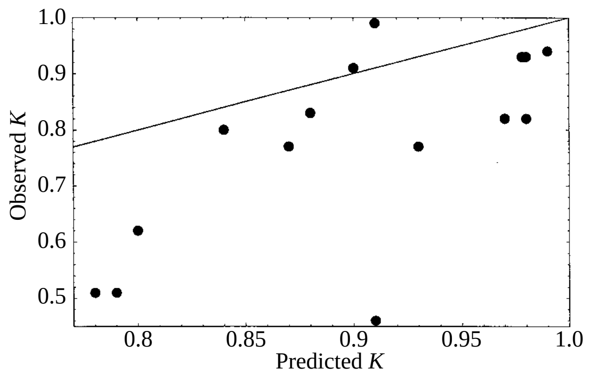

Figure 2. The matching index K predicted by the Fretwell–Lucas model (equation (7) or figure 1) versus the observed value of K, for each of the studies listed in Table 1. If observations agreed perfectly with the prediction of the Fretwell–Lucas model, then the corresponding points would lie precisely on the line of slope 1 shown in the graph. Some of the plotted points lie sufficiently close to this line that the Fretwell–Lucas model is adequate to explain the published observations. In most cases, the plotted points lie below the plotted line, indicating undermatching relative to the Fretwell–Lucas model (much less undermatching, however, than previously reported relative to the prediction of $K = 1$ valid only for $\sigma_n = 0$). Observed and predicted values of K are correlated at the 99% level (see text), showing that more noise does indeed lead to more undermatching, as our analysis of the Fretwell–Lucas model predicts.

deviation σ_n, and hence to predict the matching index K. In table 1, we list the observed and predicted values of K for these tests. Both the linear and Spearman rank correlations between observation and prediction are positive and highly significant ($r = 0.68$, $t = 3.35$, d.f. $= 13$, $p < 0.006$; $r_s = 0.65$, $t = 3.05$, d.f. $= 13$, $p < 0.01$; see figure 2*b*). In most cases, the effects of variation do not account for all of the observed undermatching. However, they frequently account for most of the observed undermatching, and greater variation is associated with greater undermatching, as our analysis predicts.

Although we have focused only on the original IFD, similar considerations are essential when testing any ideal free model, e.g. Sutherland's (1983) interference model, Parker & Sutherland's (1986) analysis featuring differences in competitive ability, or models incorporating imperfect information (Abrahams 1986). Many of these models predict undermatching even in the absence of variance, but this does not imply that the effects of resource variation can be ignored. When testing any IFD model, one cannot take the relationship it yields and insert mean values of the relevant variables; doing so will result in undermatching relative to the model's predictions.

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APPENDIX 1. PROOF OF UNDERMATCHING OF MEANS

Undermatching of means is defined by equation (5). Noting that

$$\frac{r_2}{r_1+r_2} = 1 - \frac{r_1}{r_1+r_2}, \tag{8}$$

and using equation (4), it is easy to see that the inequality in equation (5) is equivalent to

$$\left\langle \frac{r_1}{r_1+r_2} \right\rangle > \frac{\langle r_1\rangle}{\langle r_1\rangle + \langle r_2\rangle}, \tag{9}$$

i.e. the proportion of individuals in patch 1 is greater than expected if inserting patch means in equation (1) could be justified. This is what we shall prove.

To make our argument precise, we write $r_i = \langle r_i\rangle(1+x_i)$, where x_i, $i=1,2$, are independent and identically distributed random variables with mean $\langle x_i\rangle = 0$ and lower bound $x_i > -1$ (to ensure r_i is always positive). If we define

$$\alpha \equiv \frac{\langle r_1\rangle}{\langle r_1+r_2\rangle},\ U(\alpha) \equiv \left\langle \frac{1+x_1}{1+\alpha x_1 + (1-\alpha)x_2} \right\rangle, \tag{10}$$

we can then write

$$\left\langle \frac{r_1}{r_1+r_2} \right\rangle = \alpha U(\alpha). \tag{11}$$

Our goal is therefore to show that if $0<\alpha<1/2$, i.e. patch 2 is better than patch 1, then $U(\alpha) > 1$.

It is convenient to change variables to $u = x_1 + x_2 + 2$ and $v = x_1 - x_2$. Since $x_i > -1$, $u > 0$ and $u = v + 2(1+x_2) > v$ for all x_1 and x_2. Since x_1 and x_2 are identically distributed, $v = x_1 - x_2$ and $-v = x_2 - x_1$ are equally probable. Hence, the joint probability distribution $p(u, v)$ is even in v, i.e. $p(u,v) = p(u, -v)$ for all $u > 0$ and $v \in \mathbb{R}$.

In terms of u and v we find

$$\begin{aligned} U(\alpha) &= \left\langle \frac{u+v}{u-(1-2\alpha)v} \right\rangle \\ &= \left\langle \frac{(u+v)(u+(1-2\alpha)v)}{u^2-(1-2\alpha)^2v^2} \right\rangle. \end{aligned} \tag{12}$$

Now,

$$\begin{aligned} &(u+v)(u+(1-2\alpha)v) \\ &= [u^2-(1-2\alpha)^2v^2] + 2(1-\alpha)[uv+(1-2\alpha)v^2]. \end{aligned} \tag{13}$$

Hence,

$$U(\alpha) = 1 + \left\langle 2(1-\alpha)\frac{uv+(1-2\alpha)v^2}{u^2-(1-2\alpha)^2v^2} \right\rangle. \tag{14}$$

Since $u>v$ and $0<\alpha<1$, the denominator of the quantity whose expected value is sought here is always positive, and the coefficient $2(1-\alpha)>0$. The uv term is an odd function of v; since $p(u,v)$ is even in v, the mean of this term is zero for any $\alpha \in (0, 1/2)$. Finally, if $\alpha<1/2$ then the v^2 term is always positive, hence so is its mean. Thus, $U(\alpha)>1$ if $0<\alpha<1/2$, as required.

APPENDIX 2. PREDICTING THE DEGREE OF UNDERMATCHING

The undermatching index K is defined by equation (6). To predict K based on ideal free theory, we use equation (3), which relates predicted patch occupancy to resource availability for individual observations. From equation (3), the predicted mean value of n_1 is

$$\langle n_1\rangle = \mathcal{N}\left\langle \frac{r_1}{r_1+r_2} \right\rangle, \tag{15}$$

where $\mathcal{N} = n_1 + n_2$ is the (constant) total number of individuals. Assuming noise is generated by the same process in both patches, we can write $r_i = \langle r_i\rangle(1+x_i)$, with x_1 and x_2 identically distributed, as in Appendix 1. Then, in terms of α and $U(\alpha)$ defined in equation (10), we find

$$\langle n_1\rangle = \mathcal{N}\alpha U(\alpha), \tag{16}$$

where $U(\alpha)$ depends on the probability distribution of the noise variables x_i.

Let ν_r denote the standard deviation of x_i (or, equivalently, the coefficient of variation of resource availability in either patch). If we specify the noise distribution function, then for given α and ν_r, equation (16) gives us the corresponding $\langle n_1\rangle$ predicted by the Fretwell–Lucas model, and a similar expression exists for $\langle n_2\rangle$. These expressions can then be inserted in equation (6) to obtain the predicted undermatching index K_{pred}. Assuming log-normal noise, for example, the relationship between K_{pred} and ν_r is approximately

$$K(\nu_r) \simeq \frac{1+\nu_r+0.50\nu_r^2}{1+\nu_r+1.17\nu_r^2}. \tag{17}$$

This approximation is accurate to within 2% for $\nu_r < 3$ and $\frac{1}{6} \leqslant \alpha \leqslant \frac{1}{3}$, the range within which most experiments fall. (Note that, unlike the approximation, the precise value of K_{pred} is influenced by α, but only to a very slight degree.)

As we have emphasized in the main text, resource variation is rarely possible to measure directly (particularly if it arises largely due to depletion). Fortunately, patch occupancy variation is usually easy to monitor. Let σ_n denote the standard deviation in $n_i/\mathcal{N}$, the proportion of individuals occupying either patch (since $\mathcal{N}$ is fixed, this value is the same for both patches). If we specify the noise distribution function, then for given α and ν_r, we can use equation (3) to calculate σ_n just as we did to calculate $\langle n_1\rangle$ and $\langle n_2\rangle$. The predicted relationship between σ_n and K, to which a very good approximation is given by equation (7) in the main text, can then be used to test the Fretwell–Lucas model (while equation (7) was obtained as a least-squares fit assuming log-normal noise, the approximation appears to be insensitive to the particular noise distribution assumed).

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