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Interference and the ideal free distribution: models and tests

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We review the assumptions and predictions of five competitive distribution models that predict how optimal foragers will be distributed across resource patches when gains are reduced by interference. This review revealed a number of previously ignored predictions and assumptions: in particular, there should be no change in relative patch use as competitor density changes. A new model is proposed in which interference results from the costs of encounters with other foragers and where the gains on a patch are independent of the costs of interference. This model predicts that as density increases, there will be increased proportional use of lower-quality patches. Past empirical studies of interference distributions are reanalyzed; none of the studies provides strong support for any of the existing ideal free-distribution models. We suggest that previous results are more consistent with the predictions of our new model. *Key words:* competition, ideal free distribution, interference. *[Behav Ecol 7:379-386 (1996)]*

The ideal free-distribution theory (Fretwell and Lucas, 1970; see also Orians, 1969; Parker, 1970) has proved to be a useful basis for explaining animal distributions in terms of individual decisions. This theory describes the distribution of animals that are "ideal," meaning that they are assumed to be equal in competitive ability, omniscient, and to consistently go to the patch where their intake rate is highest, and "free" in that they are able to enter any patch without restriction or costs. The key insight of the ideal free distribution (IFD) is that as the density of foragers on a patch increases, the suitability of that patch decreases. There have been many successful experimental tests of the original IFD theory, in which Fretwell and Lucas's "suitability" is substituted by some other fitness correlate such as food intake rate (see Parker and Sutherland, 1986, for a review). However, nearly all such tests have used continuous-input-type resources. "Continuous input" is a specific form of exploitation competition in which resources arrive on patches one item at a time. Each item can only be consumed by one animal, so any change in the number of competitors on a patch has a directly proportional effect on the average intake rate. This makes predicting the optimal distribution simple: the proportion of competitors on each patch should be equal to the proportion of resources arriving there in unit time. This situation, termed "input matching" (Parker, 1978) can be expressed as follows: an individual's payoff, W_H, in patch H depends on n_H, the number of competitors occurring there. If R_H equals the input rate into the patch, all individuals will obtain an equal and maximum payoff when:

$$W_H = R_H/n_H = \text{constant for all patches H,L, etc.} \quad (1)$$

Although continuous input is an excellent system for examining many aspects of the IFD, it may not be the most common type of natural foraging situation. Examples may be drift and filter feeders, and situations where males wait at particular sites for females and compete for matings. However, a more common scenario may be one in which animals search patches for dispersed prey that can be assumed to remain at constant density in the short term. The aims of the present paper are to review briefly the explicit predictions and assumptions of more recent IFD models designed to predict the optimal distribution in such situations. Then, through consideration of the strengths and weaknesses of existing models, we introduce a new approach to modeling the distribution of animals that interfere with each other in which fitness is an additive function of benefits and costs. Finally, the empirical evidence for and against interference IFD models is considered. In a companion paper (Tregenza et al., 1996) a specific test is made of observed and predicted distributions.

The ideal free distribution incorporating interference

IFD foraging models express hypothetical predictions about how animals will affect each other's choice of resource patch on which to forage. Any particular model is likely to be only one of a number of plausible hypotheses, and for this reason it is important that the predictions of each model are clear and testable. When, in contrast to the continuous input case, competing predators must forage in a patch for hidden prey items, a distribution of predators across the habitat can be achieved in the absence of depletion by some form of interference. "Interference" is defined as a short-term, reversible decline in intake rate as a result of the presence of others (Goss-Custard, 1980; Sutherland, 1983).

There has been a degree of confusion over the distinction between continuous input and interference IFD models (Tregenza, 1994). This confusion may have been partly due to the use of the interference constant (m) to model an exploitation process in the models of Sutherland and Parker (1985, 1992) and Parker and Sutherland (1986). Here, we consider only those models that explicitly consider interference as the density-dependent factor reducing habitat suitability.

Below, we review IFD models incorporating interference and outline their different assumptions and predictions.

Sutherland and Parker's interference IFD

The most widely cited ideal free models are those of Sutherland and Parker (see Milinski and Parker, 1991, for a review). Their models have incorporated unequal competitive abilities and consideration of how competitor density will affect animals of different phenotypes (Sutherland and Parker, 1985,

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1992; Parker and Sutherland, 1986). The basis for these models is Sutherland's original interference IFD formulation (Sutherland, 1983). Sutherland proposed that interference could be incorporated into the IFD by using Hassell and Varley's (1969) interference constant, m. He suggested that interference modifies the effect of competitor density such that the fitness of a competitor in patch H is:

$$W_H = Q_H / n_H^m = \text{constant} \qquad \text{for all patches H,L, etc.} \tag{2}$$

Q_H is the rate of resource uptake of a solitary forager in patch H, relating to both search efficiency and patch quality. The interference constant, m, determines the proportion of competitors on each patch. As m increases from zero, a greater proportion of competitors will be found on poorer patches.

There have been a number of attempts to apply IFD theory to interference situations. Unfortunately, most of these have been studies in which the theory has been used in an attempt to explain the observed distribution, without prior consideration of the type of data required (Tregenza, 1994, 1995) Nevertheless, several studies have claimed to show support for the theory, and several others were deemed to support unequal competitor versions by Parker and Sutherland (1986).

In reviewing the evidence for and against the IFD as applied to noncontinuous input situations, it is worth distinguishing between evidence that is simply consistent with an IFD (weak evidence) and evidence that can be considered to lend more concrete support (strong evidence). Results that could be considered strong evidence in favor of the theory need to show that at least one of the theory's predictions has been fulfilled that is distinct from the predictions of other models. There are a number of unique predictions made by the Sutherland-and-Parker–type IFD (hereafter referred to as the SP model) that could be considered to fall into this category.

Strong evidence for the SP ideal free interference model. According to the Sutherland (1983) model, in interference situations, the level of m dictates the type of distribution. Also note that Equation 2 is essentially a multiplicative formulation for payoffs and can be rearranged for patches H and L as:

$$Q_H / Q_L = n_L^{-m} / n_H^{-m} = (n_H / n_L)^m,$$

$$[\log(Q_H / Q_L)]/m = \log(n_H / n_L). \tag{3}$$

Since Q_H, Q_L, and m are constants, the IFD predicts that the ratio of number of animals on patches remains constant as the total number of competitors ($n_H + n_L$) increases. A graph of y = proportion of foragers using the better patch against x = the total number of foragers will have a gradient of zero and an intercept dependent on the strength of interference (m) and the relative (but not absolute) values of Q in the two patches. This is a prediction of the IFD that has proved to be accurate in continuous input studies, but it has yet to be tested in an interference situation, except in the companion paper (Tregenza et al., 1996).

Proponents of the SP model (e.g., Sutherland, 1983; Milinski and Parker, 1991) have pointed out that it can be used to predict the optimal distribution using gain-rate data, and this can then be compared to the observed distribution. This has been done on numerous occasions for continuous input studies, where the values of Q and m are known in advance (see Milinski and Parker, 1991, for review). However, it has never been applied to an interference situation because the intrinsic value of each patch and the effect of interference must be determined by observation of gain rates at different competitor densities (but see Tregenza et al., 1996).

The IFD for interference situations across two patches (H, L) can be predicted analytically after the parameters m and Q have been derived from the data. Note that from Equation 2, we have for patches H, L:

$$\log W_H = \log Q_H - m \log n_H = \log Q_L - m \log n_L. \tag{4}$$

If an observer measures intake rates in H and L at different equilibrium population densities, the plots of log gain rates (log W) against log competitor density (log n) for the two patches should have identical gradients (equal to m). Their intercepts on log W at $n = 1$ should equal the maximum log intake rates (log Q_H, log Q_L), achieved at $n = 1$ when there is no competition. Provided that the gradients m_H, m_L can be shown not to differ significantly, a pooled value for m can be calculated.

The values for m, Q_H, and Q_L thus derived can then be used to predict the IFD as follows. Let constant c = the calculated value of $[\log(Q_H / Q_L)]/m$, and let $N = n_H + n_L$ = the number of competitors in the two-patch system. From Equation 3, we obtain:

$$n_H = N/(10^{-c} + 1), \tag{5}$$

$$n_L = N/(10^{c} + 1). \tag{6}$$

The two-patch distribution thus predicted can be compared with the obtained distribution. In principle, the analysis can be expanded to more than two patches.

The Parker and Sutherland (1986) unequal competitor IFD predicts that if payoffs to one phenotype relative to those of other phenotypes vary between patches, then animals of that phenotype will be found in the patches in which their relative gain rate is highest (the truncated phenotype distribution). If relative payoffs are changed either experimentally or by some environmental disturbance, then competitors are predicted to change their distribution accordingly.

Weak evidence for the SP ideal free interference model. There are a number of less-specific results that have been used to demonstrate support for the IFD. Some of these test predictions and some test assumptions. These are distinct from the points above because they do not rule out other potential distributions. They are mainly useful if they are found not to have been fulfilled, since it is then clear that the distribution is not consistent with the model's predictions.

For equal competitors, competitor distribution is proportional to resource distribution. This would be strong evidence for an IFD in a continuous input situation because it can be assumed that mean intake rates are then equal across patches. However, in an interference situation, without measuring individual intake rates, we cannot be sure that intake rates are the same across patches.

For equal competitors, intake rates are the same across patches of different value. This is consistent with an interference or continuous input IFD, but could also be due to intake rate being limited by factors other than interference. To be sure that interference is responsible, gain rates at different competitor densities need to be equal in different patches, and the interference constant, m, must not differ across patches.

For unequal competitors, average gain rate is higher in better patches. This has been used in support of an unequal competitor IFD, or where territoriality is obvious, in support of an ideal despotic distribution (Fretwell, 1972). However, because this evidence is consistent with several IFD models, it cannot be considered strong support for any one.

IFD for competition arising by pairwise interactions

As an alternative to the SP models, Korona (1989) has suggested that an unequal competitor IFD can be modeled by considering that randomly chosen pairs of individuals from the same patch compete over resource items. However, if we consider equal competitors, the model is identical to the original IFD model and cannot be readily applied to interference situations where intake rate is limited by search time as well as by competitor density.

Kleptoparasitic models

In many animals, one of the main sources of interference is loss of prey items to conspecifics. Parker and Sutherland (1986) modeled this situation using a system in which there is a dominance hierarchy of phenotypes and competitors steal food from their subordinates. An individual's payoffs increase with the number of subordinates and decrease with the number of dominants in a patch. The model does not account for reduction in average prey intake rate due to competition; prey are reallocated according to dominance, but average intake remains constant. Parker and Sutherland (1986) could obtain no stable distribution with this model (see also Pulliam and Caraco, 1984).

IFD-based rates of transition between behavioral states

Holmgren (1995) and Moody and Houston (1995) suggest models that make predictions about distribution between patches by seeking an equilibrium dictated by the number of foragers engaged in three activities: searching, handling, and interacting with competitors. In Holmgren's model, the rate of transition between activities is a function of the density of predators engaged in each activity, the time taken to handle each item of prey or to engage in an interaction, and the rate of encounters with prey. Moody and Houston (following Ruxton et al., 1992) base their model on an analogy with chemical-reaction kinetics in which the reactants are the group of foragers and their prey. Holmgren's model assumes that competitors differ in their relative abilities, whereas Moody and Houston restrict consideration to equal competitors. Although Holmgren does not discuss the underlying predictions of his model when competitors are equal, both models predict that at low densities all competitors occupy the better patch; as density increases, an increasing proportion of competitors use the poorer patch.

The ideal despotic distribution

The ideal despotic distribution (IDD) was proposed by Fretwell (1972) to describe any distribution in which animals guard resources. The IDD assumes that the profitability of a patch to a newcomer is a function of the profitability of the patch to incumbent individuals multiplied by a density-dependent factor that reflects the advantage of holding a territory. Several authors investigating animal distributions have found evidence of despotic behavior and higher gain rates for competitors on better patches. Often these results have been deemed to be evidence in favor of the IDD, but similar effects are generated by the unequal competitor IFD.

Benefit–cost model for competitive distribution

We now suggest a model that assumes that interference manifests itself through a cost incurred when two competitors meet. It is essentially an additive formulation for payoffs. As in the previous models, the environment consists of two patches for computational simplicity, although more patches could be considered without affecting the qualitative predictions of the model. Individuals are considered to be competitively equal. Individual intake on a patch, W_i, is determined by the resource density on the patch, the predator's searching efficiency, and costs incurred through encounters with other foragers. Costs are in undefined units, equivalent to lost prey items. The basis of the model can be expressed algebraically:

$$W_H = SD_H - ZI_H(n_H), \tag{7}$$

where W_H = individual gain rate on patch H, D_H = resource density on patch H, S = search efficiency (rate at which predator would encounter the prey if just one prey item were present on the patch), I_H (n_H) = rate of interference interactions per individual on patch H, a function of n_H, and Z = cost of each interaction measured in terms of equivalence to prey items. Note that SD_H is formally equivalent to Q_H (as in Equation 2); we separate resource density and search efficiency so that they can be measured directly in empirical studies. Therefore, with two patches, H and L, at the evolutionarily stable state:

$$W_H = SD_H - ZI_H(n_H) = SD_L - ZI_L(n_L),$$

thus

$$S(D_H - D_L) = Z[I_H(n_H) - I_L(n_L)]. \tag{8}$$

Because S and Z are positive constants, if $D_H > D_L$, then $I_H > I_L$: there must be more encounters in H than in L (greater interference, as expected). At equilibrium, the difference in interaction rate in the two patches must be constant, whatever the population density. The difference in rate of gain between the two patches must equal the difference in rate of loss due to interference.

A linear relationship between competitor density and interference. The equilibrium values for n_H, n_L depend on the form of $I(n)$. If there is a linear relationship between competitor number and the rate of encounters, then $I_i(n_i) = Kn_i$, where K is a constant:

$$S(D_H - D_L) = ZK(n_H - n_L)$$

$$(S/Z)K(D_H - D_L) = n_H - n_L. \tag{9}$$

Hence, since S, Z, K, D_H, and D_L are all constants, the absolute difference in numbers $(n_H - n_L)$ is constant and proportional to the difference in prey densities between patches, whatever the total competitor density, $n_H + n_L$.

If we let the constant $(S/Z)K\ (D_H - D_L) = d$ and let total competitor number again be $N = n_H + n_L$, then

$$d = n_H - n_L,$$

and

$$n_H = (N + d)/2, \tag{10a}$$

$$n_L = (N - d)/2, \tag{10b}$$

and the ratio of numbers,

$$n_H/n_L = (N + d)/(N - d). \tag{11}$$

As N increases, Equation 11 clearly implies a progressive increase in use of the poorer patch; ultimately, when $N \gg d$, the ratio approaches 1:1 (Figure 1). It is worth noting that this model is functionally equivalent to the SP model, except that it assumes a simple linear relationship between competitor density and net intake rate, rather than the log relationship employed in the SP model.

A relationship between competitor density and interference based on random movement. Clearly, the assumption that the likelihood of encounter will rise linearly with density is likely to be unjustified in many situations. If foragers move randomly, a more realistic assumption would be that as the density increases, the number of encounters increases according to the Poisson distribution. For a given number, n, of competitors in a patch of size P spatial units, the probabilities of getting 0, 1, 2 . . . n individuals together in the same spatial unit is given by the Poisson distribution with mean n/P. It is assumed that the number of encounters per individual in a spatial unit equals the number of individuals present, thus the weighted mean number of encounters per individual can be calculated. Because encounters rise exponentially with com-

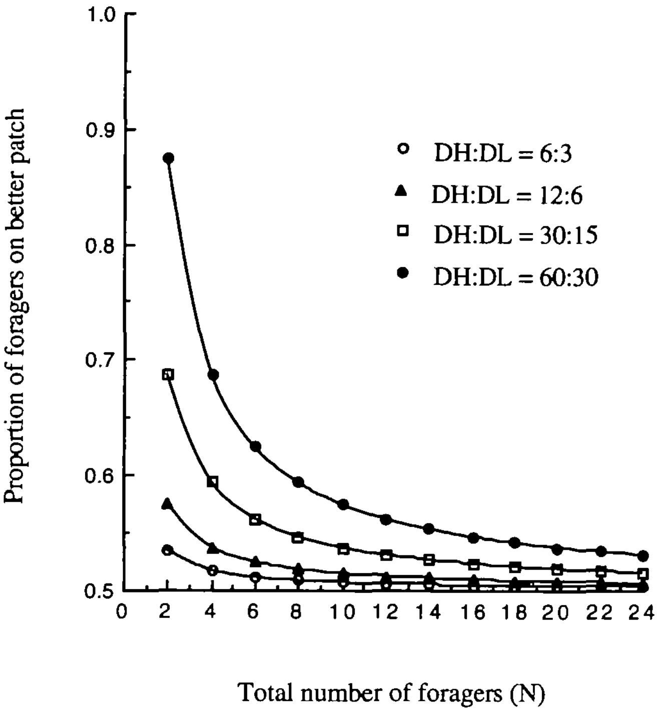

Figure 1
Predictions of the benefit–cost interference model with a linear relationship between encounter rate and competitor density. The graph shows the equilibrium proportion of foragers choosing to use the better patch at different overall forager densities and different absolute patch qualities when S = 0.005, Z = 0.1.

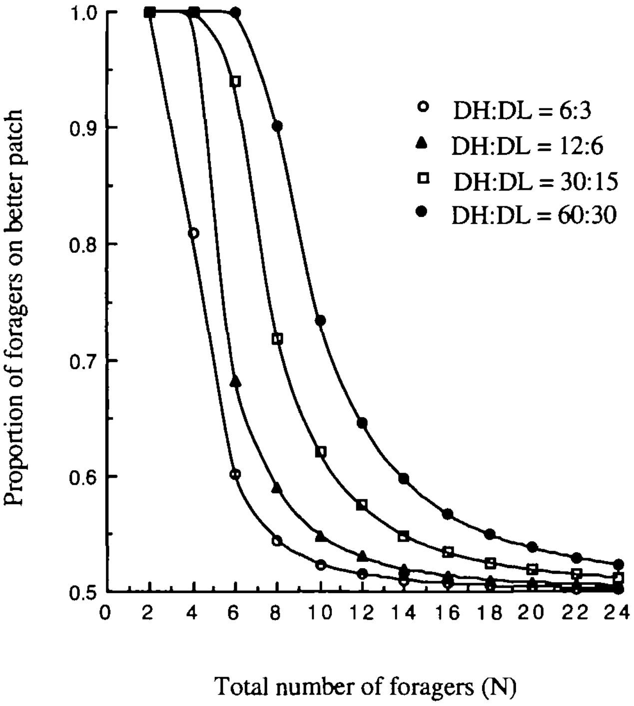

Figure 2
Predictions of the benefit–cost model with the relationship between encounter rate and competitor density according to the Poisson distribution (see text). The graph shows the proportion of foragers choosing to use the better patch at different overall densities and different absolute patch qualities (but equal relative patch qualities) when S = 0.005, Z = 0.1.

petitor density, *d* is no longer a constant. The equilibrium (net gains on both patches equal) must now be solved iteratively.

This change in the influence of density on the likelihood of encountering another forager leads to very different quantitative distributions, as shown in Figure 2. Because S/Z acts as a single constant (see Equations 8 and 9), it is the ratio, not the absolute values, of S and Z that determine the distribution. Changing the value of S/Z has the same qualitative effect on the predicted distribution as changing absolute patch qualities, as can be seen in Figures 2 and 3. Increased forager density always leads to greater relative use of the poorer patch if I increases with n in this additive model, whether this relationship is linear or exponential.

Comparison of the benefit–cost model and the SP model

Because the IFD is the result of individual behavior, the choice of model to apply to a particular system will depend on the underlying behavior of the species concerned. The lack of specifically designed experiments on interference distributions makes it difficult to suggest which species will be best described by any particular formulation.

There are a number of important differences in the assumptions and predictions made by the SP model and by our additive benefit–cost model. The benefit–cost model does not predict that there will be a constant ratio of competitors between patches as in SP. At low density, the poorer patch may be ignored completely. It would be possible to generate such effects within the SP model by allowing m to vary with competitor density. However, this would greatly complicate empirical determination of m, making quantitative predictions much more difficult.

In the SP model, m dictates implicitly how changes in competitor density affect intake rate. In the benefit–cost model,

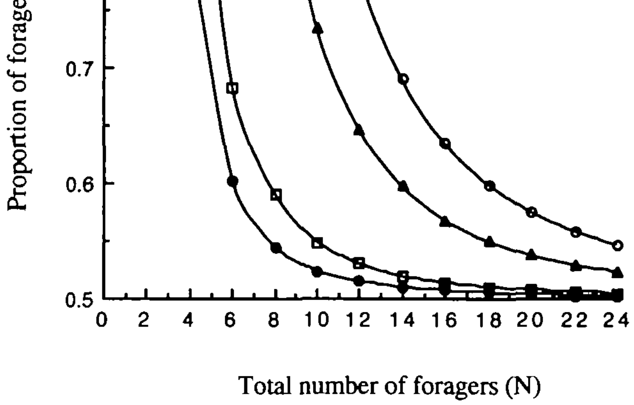

Figure 3
The proportion of foragers choosing to use the better patch at different overall forager densities and different encounter costs (Z) in the Poisson model when S = 0.001. The two patches are of the same size and one contains twice the resources of the other (D_H = 60, D_L = 30).

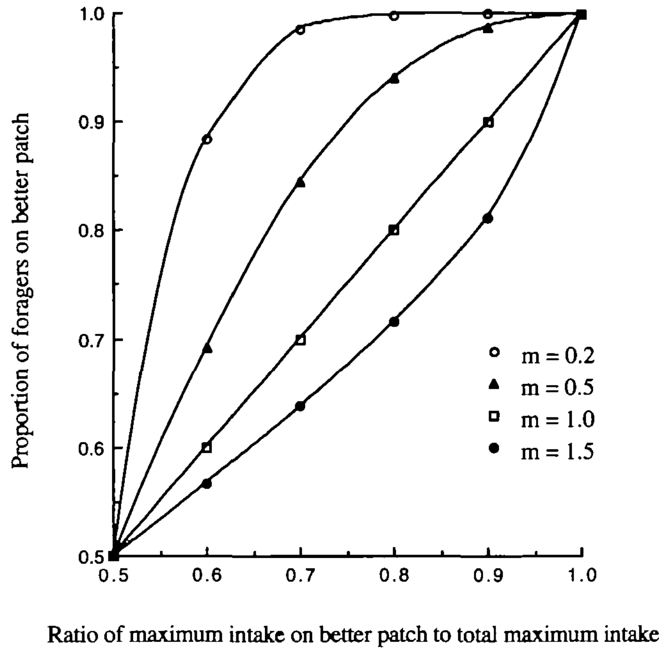

Figure 4
The proportion of foragers on the better patch in relation to the proportion of total maximum intake achievable there, $Q_H/(Q_H + Q_L)$, as predicted by the SP model.

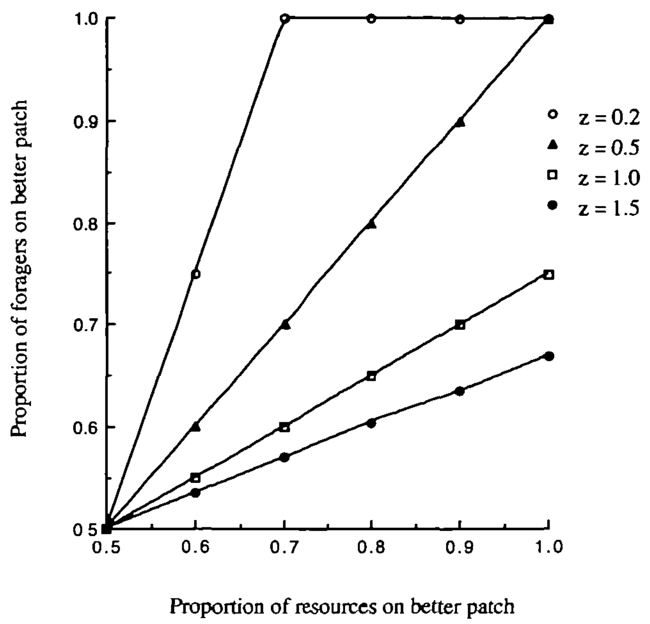

Figure 5
The proportion of foragers on the better patch in relation to the proportion of total resources occurring there, $D_H/(D_H + D_L)$, as predicted by the benefit–cost IFD model with a linear relationship between forager density and encounter frequency, when S = 0.005.

the effect of interference is explicit (here by using either a linear relationship between density and costs or a Poisson distribution). If the Poisson distribution is used, because each successive competitor entering a patch has more impact on intake rate than the last, our model is analogous to an SP model in which $m > 1$.

The additive model exposes the influence of a wider set of biological parameters. In the SP model, only relative patch qualities and m are considered, whereas in the benefit–cost model, the total population size, absolute patch values, encounter costs, patch sizes, and search efficiency all explicitly influence the optimal solution. However, the weakness in the SP model is also one of its main strengths. An important reason the original ecological models (on which SP is based) were structured after Equation 2 is that by considering only the relative values of patches, it is possible to apply the theory without measuring absolute patch qualities, something that it is extremely difficult to do.

The additive model is narrower in applicability than the multiplicative model because only interference due to encounters is modeled. Continuous input situations, which can be modeled using the same equations as interference with the SP model, are explicitly not considered. However, different types of competitive situations will have different implications for distribution, and each will require a different explicit theoretical treatment. It is likely that the main reason current IFD theory works well for continuous input and less well for other situations is that continuous input is modeled explicitly by m = 1 in Equation 2. Other situations have not been the subject of exact models.

Even the more sophisticated version of the benefit–cost model in which encounters occur with a frequency dictated by the Poisson distribution is likely to be an oversimplification in many situations. Animals incurring costs upon encountering conspecifics are likely to avoid interactions, so the relationship between density and encounter rates will be complex and difficult to predict. However, it might be possible to measure such parameters experimentally.

The proportion of foragers on the better patch relative to the proportion of maximum intake per capita on that patch has a different relationship in the two models. This is illustrated in Figures 4–6.

Two important differences between the models can be seen in Figures 4–6. First, it is apparent that when all the resources occur on one patch in SP, because costs are manifested only

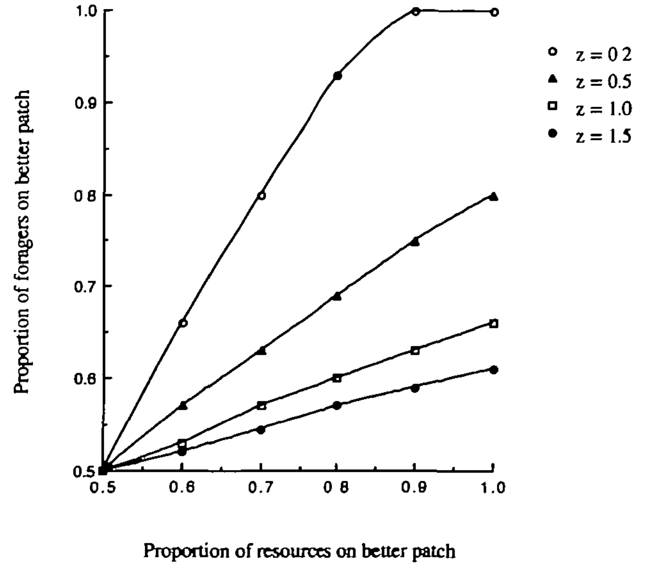

Figure 6
The proportion of foragers on the better patch in relation to the proportion of total resources occurring there, $D_H/(D_H + D_L)$, as predicted by the benefit–cost IFD model with relationship between forager density and frequency of encounters according to the Poisson distribution when S = 0.005.

Table 1

Summary of noncontinuous input studies of competitive distribution, with consideration of whether each provides evidence for or against any ideal free distribution (IFD) model

Reference	Species	Result	Strong evidence for or against any model?	Consistent with any model? (weak evidence)
Andren (1990)	Jay	Jays in dense forest showed highest success; territoriality results in unequal resource partitioning	No	Consistent with ideal despotic distribution, but evidence is nonquantitative
Buxton (1981)	Shelduck	Spent less time feeding in areas of dense prey	Conflicts with all models	No
Fortier and Harris (1989)	Marine fish larvae	Post-larval stages of copepod feeders distributed in direct proportion to resources	No	Consistent with equal competitor IFD
Goss-Custard et al. (1984)	Oystercatcher	Average intake differs consistently between mussel beds	No	Consistent with unequal competitor IFD
Goss-Custard et al. (1992)	Oystercatcher	Greater spreading out across patches occurred as forager density increased	Conflicts with Sutherland's model, since density affects patches used	No
Jakobsen and Johnsen (1987)	*Daphnia pulex*	Both patches depleted to same level. Proportionally more use of better patch at lower food density	Conflicts with Sutherland's model, since density affects patches used	No
Korona (1990)	Flour beetles	With low travel costs, the number of ovipositing beetles corresponded to the amount of flour on each patch	No	Consistent with equal competitor IFD, but intake rates not measured
Messier et al. (1990)	Muskrat	Different survival rates between patches. Some individuals gained higher fitness via resource monopolization	Conflicts with Sutherland's model, since density affects patches used	Consistent with ideal despotic distribution
Monaghan (1980)	Herring gull	Average intake about five times higher in better areas of rubbish tip	No	Consistent with unequal competitor IFD
Morris (1989)	White-footed mice	Fitness of mice was not significantly different between three habitats	No	Consistent with equal competitor IFD, but individual differences not measured
Nishida (1993)	Coreid bugs	Males in bigger aggregations were more successful despite identical competitive ability	No	No; may be due to perceptual constraints
Perusse and Lefebvre (1985)	Feral pigeons	Smaller food patches led to greater dispersal across patches. Large patches led to grouped sequential exploitation	Conflicts with Sutherland's model, since not all food patches are used	Small food patch experiment is consistent with equal competitor IFD
Power (1984)	Loricariid catfish	Growth rate of algae in sunny and shaded pools was equal as a result of foraging by catfish	No	Consistent with equal competitor IFD
Sibly and McCleery (1983)	Herring gull	Average intake consistently higher on open tip than elsewhere	No	Consistent with unequal competitor IFD
Sutherland (1982)	Oystercatcher	Average intake differed between parts of cockle bed	No	Consistent with unequal competitor IFD
Talbot and Kramer (1986)	Guppies	Proportion of fish in a habitat correlated with food suply, but no fit to IFD	No	No; may be due to perceptual constraints
Thompson (1981)	Shelduck	Time spent feeding similar between areas with different prey densities	No	No; may be due to perceptual constraints
Thompson (1984)	Lapwing and golden plover	Rate of intake greater in fields where prey was most abundant. Increase in density led to a change in proportional use of patches	Conflicts with Sutherland's model, since density affects patches used	No
Zwarts and Drent (1981)	Oystercatcher	Intake constant in years of different mussel availability	No	Consistent with equal competitor IFD

as a reduction in intake rate, all the competitors must be found on that patch. In the benefit–cost model, because costs are independent, they can theoretically exceed benefits on either patch. Hence, when encounter costs are high, increasing population density could theoretically lead to negative gains on patches. In practice, at the point of zero gains, further increases in density of competitors on the patch would cease, and further increases simply add to the off-patch population. At equilibrium, some competitors would remain off patches and all would receive equal (zero) payoffs. This commonly occurs in territorial species in which some individuals do not hold territories and, as a result, may be unable to reproduce (e.g., Smith and Arcese, 1989). This situation can be explained if gains achieved as a result of being on the patch are bought at the expense of future costs, such as shorter life span. In this case, those animals not using the patch are effectively waiting to do so.

Second, in the benefit–cost model, if encounter rates rise linearly with forager density, then there is also a linear relationship between proportion of individuals on the good patch and the proportion of resources occurring there. If encounter rates rise increasingly with forager density, as predicted by random encounters, then the proportion of competitors using the better patch always rises more slowly than in the linear model. In comparison, in SP the shape of the curve relating proportion of total maximum intake achievable on the good patch to the proportion of competitors occurring there is a function of the strength of interference, m.

Review of empirical tests of interference IFD

The predictions and assumptions of IFD models have been tested in many experiments. Those prior to 1985 are reviewed by Parker and Sutherland (1986: Table 1), whose table we have modified by including comment on which model explains the results of experiments and observations. We have also added the results of work published after 1985.

Table 1 shows that, so far, no experiment or field study has produced results that fulfil any of the unique predictions of the interference IFD models outlined. It is important to note that although no specific support for an ideal free interference model has been found, there have not been any studies to date that have been designed to test the specific predictions of the various interference IFD models, and hence the necessary data have not been collected. However, of the six experiments that conflict with Sutherland's (1983) model, five do so due to a lack of agreement with the prediction that changes in competitor density would not lead to changes in proportional patch use. This suggests that this prediction, which is an intrinsic feature of the model, may not apply to many systems.

Our benefit–cost formulation illustrates that an equally plausible model can be constructed that generates an alternative prediction: the proportion of competitors on poorer patches rises with increasing population density. This pattern is seen (Table 1) in several empirical tests.

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REFERENCES

Andren H, 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. Ecology 71:1706–1803.

Buxton NE, 1981. The importance of food in the determination of the winter flock sites of the shelduck. Wildfowl 32:79–87.

Fortier L, Harris RP, 1989. Optimal foraging and density dependent competition in marine fish larvae. Mar Ecol 51:19–33.

Fretwell SD, 1972. Populations in a seasonal environment. Princeton; New Jersey: Princeton University Press.

Fretwell SD, Lucas HJ Jr, 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor 19: 16–36.

Goss-Custard JD, 1980. Competition for food and interference amongst waders. Ardea 68:31–52.

Goss-Custard JD, Caldow RWG, Clarke RT, 1992. Correlates of the density of foraging oystercatchers *Haemotopus ostralegus* at different population sizes. J Anim Ecol 61:159–173.

Goss-Custard JD, Clarke RT, Durell SEA, 1984. Rate of food intake and aggression of oystercatchers *Haemotopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. J Anim Ecol 53:233–245.

Hassell MP, Varley GC, 1969. New inductive model for insect parasites and its bearing on biological control. Nature 223:1133–1136.

Holmgren N, 1995. The ideal free distribution of unequal individuals: predictions from a behaviour-based functional response. J Anim Ecol 64:197–212.

Jakobsen PJ, Johnsen GH, 1987. Behavioural response of the water flea *Daphnia pulex* to a gradient of food concentration. Anim Behav 35:1891–1895.

Korona R, 1989. Ideal free distribution of unequal competitors can be determined by the form of competition. J Theor Biol 138:347–352.

Korona, R, 1990. Travel costs and the IFD of ovipositing female flour beetles, *Tribolium confusum*. Anim Behav 40:186–187.

Messier F, Virgl JA, Marinelli L, 1990. Density-dependent habitat selection in muskrats: a test of the ideal free distribution model. Oecologia 84:380–385.

Milinski M, Parker GA, 1991. Competition for resources. In: Behavioural ecology: an evolutionary approach, 3rd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 137–168.

Monaghan P, 1980. Dominance and dispersal between feeding sites in the Herring gull (*Larus argentatus*). Anim Behav 28:521–527.

Moody AL, Houston AI, 1995. Interference and the ideal free distribution. Anim Behav 49:1065–1072.

Morris W, 1989. Density dependent habitat selection: testing the theory with fitness data. Evol Ecol 3:80–94.

Nishida T, 1993. Spatial relationships between mate acquisition probability and aggregation size in a gregarious coreid bug (*Colpula lativentris*): a case of the ideal free distribution under perceptual constraints. Res Popul Ecol 35:45–56.

Orians GH, 1969. On the evolution of mating systems in birds and mammals. Am Nat 103:589–603.

Parker GA, 1970. The reproductive behavior and the nature of sexual selection in *Scatophaga stercoraria* L. II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. J Anim Ecol 39:205–228.

Parker GA, 1978. Searching for mates. In: Behavioural ecology: an evolutionary approach, 1st ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 214–244.

Parker GA, Sutherland WJ, 1986. Ideal free distributions when individuals differ in competitive ability: phenotype limited ideal free models. Anim Behav 34:1222–1242.

Perusse D, Lefebvre L, 1985. Grouped sequential exploitation of food patches in a flock feeder, the feral pigeon. Behav Proc 11:39–52.

Power ME, 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. J Anim Ecol 53:357–374.

Pulliam HR, Caraco T, 1984. Living in groups: is there an optimal group size? In: Behavioural ecology: an evolutionary approach, 2nd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 122–147.

Ruxton GD, Gurney WSC, Roos AM, 1992. Interference and generation cycles. Theor Popul Biol 42:235–253.

Sibly RM, McCleery RH, 1983. The distribution between feeding sites of herring gulls breeding at Walney island, U.K. J Anim Ecol 52: 51–68.

Smith JNM, Arcese P, 1989. How fit are floaters? Consequences of alternative behaviors in a nonmigratory sparrow. Am Nat 133:830–845.

Sutherland WJ, 1982. Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. J Anim Ecol 51:491–500.

Sutherland WJ, 1983. Aggregation and the "ideal free" distribution. J Anim Ecol 52:821–828.

Sutherland WJ, Parker GA, 1985. Distribution of unequal competitors. In: Behavioural ecology—ecological consequences of adaptive behavior (Sibly RM, Smith RH, eds). Oxford: Blackwell; 255–274.

Sutherland WJ, Parker GA, 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. Anim Behav 44:345–355.

Talbot AJ, Kramer DL, 1986. Effects of food and oxygen availability on habitat selection by guppies in a laboratory environment. Can J Zool 64:88–93.

Thompson DBA, 1981. Feeding behavior of wintering shelduck in the Clyde Estuary. Wildfowl 32:88–98.

Thompson DBA, 1984. Foraging economics in flocks of plovers and gulls (PhD dissertation). Nottingham: University of Nottingham.

Tregenza T, 1994. Common misconceptions in applying the ideal free distribution. Anim Behav 47:485–487.

Tregenza T, 1995. Building on the ideal free distribution. Adv Ecol Res 26:253–307.

Tregenza T, Thompson DJ, Parker GA, 1996. Interference and the ideal free distribution: oviposition in a parasitoid wasp. Behav Ecol 7:387–394.

Zwarts L, Drent RH, 1981. Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: Feeding and survival strategies of estuarine organisms (Jones NV, Wolff WJ, eds). London: Plenum; 193–216.