

Common misconceptions in applying the ideal free distribution

TOM TREGENZA

Population Biology Research Group, Department of Environmental and Evolutionary Biology, University of Liverpool, Liverpool L69 3BX, U.K.

*(Received 27 April 1993; initial acceptance 1 July 1993;
final acceptance 23 July 1993; MS. number: sc-887)*

One of the major aims of behavioural ecology is to explain the distribution of animals around their environment. Several authors (Brown 1969; Orians 1969; Fretwell & Lucas 1970; Parker 1970, 1974) have pointed out that a major influence on animal distribution will be competition between individuals. Fretwell & Lucas (1970) considered a situation in which all animals have equal competitive abilities, and are able to move anywhere without cost. If resources occur as patches of different prey density then initially the better quality patches will be preferred. However, as the density of competitors on better patches rises, interference will increase, reducing intake rates to the same level as can be achieved on lower quality patches. It will then pay some animals to leave the better patches, leading to intake rates equalizing across patches of different quality. Fretwell & Lucas termed this situation the 'ideal free distribution'.

In attempting to explain animal distributions, researchers have compared their observations with the predictions of the ideal free model. Although there have been several reviews explaining how the theory should be applied (most recently by Milinski & Parker 1991), a misunderstanding about the influence of resource distribution has led to several authors misinterpreting their results. These errors, and the difficulty in making quantitative predictions from even the simplest, equal-competitor, ideal free model, are the subject of this paper.

In the simplest ideal free scenario, patches consist of continuously arriving resources that are 'consumed' immediately. This might apply to fish feeding on food items drifting downstream towards them (e.g. Milinski 1979) or to males competing for females arriving at a patch (e.g. Parker 1970). In these situations interference, defined as the reduction of a given individual's intake rate as the result of competition, is the only factor other than input rate that influences the patch profitability. This means that any increase in competitor number causes an exactly proportional decrease in average

intake rate. Therefore, an individual's payoff, W_i in patch i depends on N_i , the number of competitors in the same patch. It is assumed that an evolutionarily stable state will prevail so that $W_i(N_i) = c$ (constant); i.e. all individuals attain an equal payoff.

Therefore, if Q_i = total input into patch:

$$W_i(N_i) = Q_i/N_i = c \quad \text{for all patches } i, j, k, \text{ etc.}$$

This gives the input matching rule: $N_i = Q_i/c$ (Parker 1978), which predicts that the number of competitors in a patch should be proportional to the total input received by that patch. Pulliam & Caraco (1984), despite clearly recognizing the unique nature of continuous input, restated this rule but called it the 'habitat matching rule' a name which gives no indication that it refers only to continuous input situations and which may have been one of the factors leading to some authors misapplying the theory.

Although continuous input is what most of us would associate with an ideal free distribution (add food twice as fast at one end of the tank and roughly twice as many fish forage there), it is only one type of foraging situation, and one that is probably relatively uncommon in the wild. In many environments, animals search patches for dispersed prey which remain at roughly constant density. In these situations there is no certainty that any competitors should be found in lower quality patches. The level of interference will only dictate the equilibrium distribution when time wasted in interacting with competitors reduces intake rate, reducing patch profitabilities and causing dispersal of competitors onto lower quality sites. Allowing for the effect of interference requires a term which modifies the influence of competitor density. Sutherland (1983) proposed that the 'interference constant', ' m ', be used such that:

$$W_i(N_i) = Q_i/N_i^m \quad \text{Where } 0 \leq m \leq \infty$$

The level of m has important consequences for competitor distribution. In contrast to continuous

input situations, and perhaps somewhat counter-intuitively, a patch with half the density of resources relative to the best patch is not automatically predicted to receive half the number of foragers. If m is zero it may remain completely unexploited by even a large population. If there is some interference but m is low then the patch will receive a small proportion of competitors but still less than the proportion of resources occurring there. At the other end of the scale, in animals with very high levels of mutual interference, a patch with high resource density will not support twice the number of individuals as another patch with half the resources, since interference wastes so much time on the better patch.

The main source of error in applying ideal free distribution theory to non-continuous input (or 'interference') situations appears to be in confusing the prediction that animals will have equal intake rates on all patches, with the input matching rule, which only applies to continuous input situations. Several examples illustrate the type of problems.

Fortier & Harris (1989) investigated whether post-larval fish were distributed as a result of competition or according to other factors such as predator avoidance. Because the percentage fish distribution corresponded to the percentage resource distribution they concluded that the fish are achieving an ideal free distribution. However, the planktonic food is not a continuous input resource, making this an unjustified conclusion. They cannot say whether or not there is an ideal free distribution without measuring intake rates. This is a potentially important error because the perceived fit to the ideal free distribution was the main piece of evidence for their conclusion that intraspecific competition is the most likely reason for the vertical distribution of fish larvae.

Perusse & Lefebvre (1985) made the same mistake in applying continuous input theory to a non-continuous input situation. In the introduction to their experiments on feral pigeons, *Columba livia*, they predicted that 'resource matching' will occur in interference situations. This has implications for the analysis of their results. They found that when patches of food were very small, competition forced many pigeons to feed on the poorer patch. When the patches contained dispersed food all the pigeons initially went to one patch and then left for the next one as it depleted. They described the dense food patch situation as fitting the ideal free prediction whereas the dispersed food result was seen as

deviating from it. Unfortunately, the predictions of the ideal free distribution are much more difficult to come by than Perusse & Lefebvre realized, requiring measures of interference at the patches. In fact, with some allowance for the benefits of aggregation, their results might both be in agreement with an ideal free distribution. When food is in small, dense patches, interference is higher, reducing patch profitability and causing more birds to use the poorer patches. On the other hand, patches of more dispersed food lead to drastically reduced interference and hence more birds feed on the same patch.

Other papers have shown the same error in applying the ideal free distribution, although it has not had such profound implications for their results. Korona (1990) seems to have failed to appreciate the unique nature of the continuous input situation. In his laboratory study of the flour beetle, *Tribolium confusum*, he predicted that numbers of individuals in different patches of a resource should be linearly related to the profitabilities of these patches. Again, this is only the case for continuous input. His subsequent discussion showed that increased travel costs led to a departure from his predicted distribution. However, since some measure of the level of interference is required to predict the distribution from the ideal free model, it is impossible to say whether travel time has caused departures from it and hence his conclusions are less valid. Similarly, Jakobsen & Johnsen (1987), in their study of the distribution of *Daphnia*, claimed that individuals distributed themselves in close approximation to patch profitabilities when food was limiting. This is unjustified since patch profitabilities, in terms of the intake rate of the *Daphnia* occurring there, were not determined. Although this was possible using their results it does not support their conclusion, which is based on the patch qualities, their intrinsic value before exploitation. Jakobsen & Johnsen may have mistakenly assumed that their experiment was an example of continuous input because food flows through the system. However, this is not the case because each food item was not immediately consumed upon arrival, so the unique feature of continuous input, that an increase in competitor density produces a directly inverse proportional decrease in average intake rate, was not present.

I believe that the main reason for errors being made in applying ideal free distribution theory is that it does not readily lend itself to quantitative explanations of non-continuous input competitor distributions. It highlights the complexity of these

situations and makes qualitative predictions about how competition will determine animals' decisions about where to forage. However, determining whether an ideal free distribution is occurring requires measurement of individual intake rates, since m cannot be determined independently except in the continuous input case. Measuring intake rates is time consuming in the laboratory and difficult in the field. Several studies have successfully described non-continuous input ideal free distributions (e.g. Sutherland 1982; Sibly & McCleery 1983; Goss-Custard et al. 1984). However, researchers trying to quantify competitive distributions must realize that this has been possible only through careful observation of individual gain rates, bearing in mind the measurements required by the theory.

I thank G. A. Parker, D. J. Thompson and M. Kennedy for valuable comments on the manuscript and NERC (grant GT4/91/TLS/30) for funding.

REFERENCES

- Brown, J. L. 1969. The buffer effect and productivity in tit populations. *Am. Nat.*, **103**, 347–354.
- Fortier, L. & Harris, R. P. 1989. Optimal foraging and density-dependent competition in marine fish larvae. *Mar. Ecol. Prog. Ser.*, **51**, 19–33.
- Fretwell, S. D. & Lucas, H. J., Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.*, **19**, 16–36.
- Goss-Custard, J. D., Clarke, R. T. & Durell, S. E. A. Le V. Dit. 1984. Rate of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *J. Anim. Ecol.*, **53**, 233–245.
- Jakobsen, P. J. & Johnsen, G. H. 1987. Behavioural response of the water flea *Daphnia pulex* to a gradient of food concentration. *Anim. Behav.*, **35**, 1891–1895.
- Korona, R. 1990. Travel costs and the IFD of ovipositing female flour beetles, *Tribolium confusum*. *Anim. Behav.*, **40**, 186–187.
- Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. *Z. Tierpsychol.*, **51**, 36–40.
- Milinski, M. & Parker, G. A. 1991. Competition for resources. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 137–168. Oxford: Blackwell Scientific Publications.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.*, **103**, 589–603.
- Parker, G. A. 1970. The reproductive behaviour 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, G. A. 1974. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. IX. Spatial distribution of fertilization rates and evolution of mate search strategy within the reproductive area. *Evolution*, **28**, 93–108.
- Parker, G. A. 1978. Searching for mates. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 214–244. Oxford: Blackwell Scientific Publications.
- Perusse, D. & Lefebvre, L. 1985. Grouped sequential exploitation of food patches in a flock feeder, the feral pigeon. *Behav. Proc.*, **11**, 39–52.
- Pulliam, R. H. & Caraco, T. 1984. Living in groups, is there an optimal group size? In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 122–147. Oxford: Blackwell Scientific Publications.
- Sibly, R. M. & McCleery, R. H. 1983. The distribution between feeding sites of herring gulls breeding at Walney Island, U.K. *J. Anim. Ecol.*, **52**, 51–68.
- Sutherland, W. J. 1982. Spatial variation in the predation of cockles by oystercatchers at Traeth Melynes, Anglesey. II. The pattern of mortality. *J. Anim. Ecol.*, **51**, 491–500.
- Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. *J. Anim. Ecol.*, **52**, 821–828.