



## The Ideal Free Distribution with Kleptoparasitism

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(Received on 10 July 1996, Accepted in revised form on 17 January 1997)

We present a simple mechanistic model describing kleptoparasitic (food stealing) behaviour among a group of foragers. This behavioural model is used to produce an analytic expression for the food uptake rate (functional response) of individual foragers in the presence of kleptoparasitism. The parameters of this functional response can be interpreted in terms of the underlying behavioural model. We define intensity of interference as the rate at which obtained uptake rate, relative to that achieved without competitors, decreases with increasing forager density. The intensity of interference increases with increasing forager density and with decreasing food density. The functional response is used to find analytic expressions for the ideal free distribution of foragers among a range of habitats differing in food density. The model predicts that the proportion of foragers opting to use the richest patch will always be greater than the proportion of food there. The proportion of foragers using a patch depends not only on the proportion of food on that patch but on the distribution of food between the other patches in the system.

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### Introduction

Kleptoparasitism occurs when one individual steals food from another. Interspecific and intraspecific kleptoparasitism are widespread among vertebrates, and is particularly well documented for birds [see Brockman & Barnard (1979) and Furness (1987) for reviews]. Here we focus on intraspecific kleptoparasitism and how this affects the distribution of a foraging population between a group of discrete food patches.

The most common model used to describe the distribution of individuals in an environment with areas of different habitat quality is the ideal free distribution (Fretwell & Lucas, 1970). In one simple and commonly used form, this model assumes that each patch is held at a constant food density, and all foraging individuals are equal and are free to move to the habitat patch where their food intake rate is

maximised. At the ideal free distribution, no individual can increase its uptake rate by moving and, as a consequence, the intake rates for all individuals will be equal in all occupied habitat patches [see Kacelnik *et al.* (1992) and Milinski & Parker (1991) for reviews]. In the case where individuals have no effect on each other, all individuals will be predicted to feed in the best quality patch. However, if foraging efficiency decreases with forager density through some interference effect, such as kleptoparasitism, then lower quality patches may be utilised as a means of minimising interference. In order to investigate this phenomenon, we require an expression for the uptake rate of an individual in terms of the food and forager densities in its current patch: we term such an expression the functional response.

An early attempt to quantify the effect of interference between foragers was introduced by Hassell & Varley (1969). They suggested that the uptake rate of a forager ( $I$ ) could be related to the density of foragers ( $P$ ) though

$$\log(I) = \log(Q) - m \log(P),$$

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where  $Q$  is the intake rate achieved by a solitary forager in the absence of interference and  $m$  is the interference constant, which determines the strength of the density dependent reduction in intake rate. On logarithmic axes, the slope of the relationship between uptake rate and forager density determines, what we call generally, the intensity of interference. For the Hassell & Varley model, this slope has a constant gradient of  $-m$  over all forager densities.

Despite criticism of this relationship for not predicting that interference should be negligible at very low forager density (e.g. Free *et al.*, 1977), the use of this relationship, and in particular use of the constant  $m$  to describe the strength of interference, has become widespread. Further models by Rogers & Hassell (1972), Beddington (1975) and Ruxton *et al.* (1992) have derived functional responses from mechanistic models with interference between individuals. However, the interference interactions which take place in these models are not a good representation of kleptoparasitism where individuals handling a food item are attacked by others which are not handling food. This distinction is clear from the behavioural descriptions given in Beddington (1975) and Ruxton *et al.* (1992), where interference interactions can occur between two searching foragers neither of which is handling a food item. These models are a better description of time-wasting interactions whose costs relate to foraging time lost but whose benefits are not directly related to foraging, such as social interactions or grooming. In contrast, both the costs and benefits of kleptoparasitism relate directly to foraging, and hence previous formulisms of the functional response cannot be applied to kleptoparasitic interactions.

Ideal free distributions with kleptoparasitism have previously been investigated by Parker & Sutherland (1986) and Korona (1989). However, these models often produce contradictory results (Holmgren, 1995). In order to explore these differences, Holmgren presents and analyses a model based on a behavioural model of the processes of foraging and kleptoparasitism. His analysis concentrates on the effect which variation between individuals in foraging ability has on the distribution of foragers. Hence, the models presented by Holmgren are necessarily complex, are not amenable to analytic solutions and must be solved numerically. Here we present a behavioural model of the same foraging process, indeed our model can be obtained as a special case of Holmgren's model. By assuming that all individuals have equal competitive abilities, we are able to produce a novel analytic form for the functional response; in contrast to Holmgren

who explores his model numerically for a necessarily restricted set of parameter values.

In the next section, we set out a simple set of rules describing individual behaviour among a group of potentially kleptoparasitic foragers. These individual-level rules are then used to construct a population-level, simple (but justifiable) relation between forager and prey densities, and foragers' prey uptake rate; this relation is termed the functional response. The following section then explores the properties of this relation, relating it both to previous expressions representing other forms of interference between individuals, and to the underlying individual-level behavioural rules. The next section takes this functional response and uses it to provide analytic expressions for the ideal free distribution of kleptoparasitic foragers among a range of habitats differing in food quality. These distributions are compared with the results of a similar study into forager distributions in response to more conventional interference interactions (Moody & Houston, 1995). Differences in macroscopic population distributions between our model and theirs, are interpreted in terms of microscopic differences in the rules governing the behaviour of individuals in the two models.

### The Functional Response

In this section, we aim to derive a novel analytic relation between predator and prey densities and foragers' uptake rate which captures the effects of kleptoparasitism. Consider a fixed density ( $F$ ) of food items distributed uniformly throughout an arena of fixed volume. Also contained within the arena is a fixed density ( $P$ ) of foragers. This population is divided into four subpopulations according to four activities in which a forager can be engaged. The density of the subpopulation which are actively searching for food is  $S$ ; the density of those that have found a food item and are handling it is  $H$ . Foragers may also be engaged in a kleptoparasitic interaction with a conspecific. We differentiate between the population density ( $W$ ) of those which will win their interaction and emerge with a food item, and those losers ( $L$ ) which will not. These activities are mutually exclusive so

$$S + H + W + L = P. \quad (1)$$

We will assume that each searching forager randomly explores a fixed volume  $v_F$  per unit time for food items, so that food items are found at a rate  $v_F SF$ . This is also the rate at which individuals leave the  $S$  population for the  $H$  (food handling) population.

Searching foragers are also assumed to explore a fixed volume  $v_H$  for other foragers that are handling a food item. Hence the rate at which handlers are discovered by searchers is  $v_H SH$ . For simplicity we assume that such encounters always lead to a food stealing attempt, hence  $v_H SH$  is the rate at which kleptoparasitic interactions begin, each causing an individual to leave both the  $S$  and  $H$  populations. One of these individuals joins the  $W$  population; the other joining the  $L$  population. Individuals remain in kleptoparasitic interactions for a time, which for algebraic convenience is drawn from an exponential distribution with mean  $t_k$ . After this time, losers join the searching population, and winners join the handling population. Similarly, handlers return to foraging after a time drawn from an exponential distribution with mean  $t_h$ . We can summarise these transition rates as a set of differential equations:

$$\frac{dS}{dt} = -v_F SF - v_H SH + \frac{H}{t_h} + \frac{L}{t_k} \quad (2)$$

$$\frac{dH}{dt} = v_F SF - v_H SH - \frac{H}{t_h} + \frac{W}{t_k} \quad (3)$$

$$\frac{dW}{dt} = v_H SH - \frac{W}{t_k} \quad (4)$$

$$\frac{dL}{dt} = v_H SH - \frac{L}{t_k}. \quad (5)$$

We wish to find intake rate ( $I$ ) per forager: since all food items found are consumed, this is equal to the rate per forager at which food items are found:

$$I = \frac{v_F \hat{S} F}{P}, \quad (6)$$

where  $\hat{\cdot}$  denotes an average or steady-state value of a population. Setting the rate equations to zero and using simple algebra, it is easy to show that there is only one positive steady-state value,

$$\frac{\hat{S}}{\hat{P}} = \frac{-1 - C + \sqrt{(1 + C)^2 + 8CD}}{4CD}, \quad (7)$$

where, for brevity, we have defined

$$C = v_F t_h SF \quad (8)$$

$$D = v_H t_k SP. \quad (9)$$

In the general case, the resulting functional response is rather unwieldy and unhelpful. If, however, we assume that kleptoparasitic interactions are not insignificant but are much less frequent or long-lived than food-handling bouts so that  $8CD \ll (C + 1)^2$ ,

then we can expand the square root to the second order of the Taylor series to obtain

$$\frac{\hat{S}}{\hat{P}} = \frac{1}{1 + C} - \frac{2CD}{(1 + C)^3}, \quad (10)$$

which, in this limiting case, is well approximated by

$$\frac{\hat{S}}{\hat{P}} = \frac{1}{1 + C + \frac{2DC}{1 + C}}. \quad (11)$$

This gives a functional response of the form

$$I(F, P) = \frac{I_{\max} F}{F + F_0 + \frac{\kappa FP}{F + F_0}} \quad (12)$$

where

$$I = \frac{1}{t_h} \quad (13)$$

is the maximum attainable uptake rate

$$F_0 = \frac{1}{v_F t_h} \quad (14)$$

is the ‘‘half-saturation’’ food density, when (at very low forager density)  $I = I_{\max}/2$ ; and

$$\kappa = \frac{2v_H t_k}{v_F t_h} \quad (15)$$

represents the strength of the kleptoparasitic effect. Even when kleptoparasitism is quite strong, and so the approximations used above are not strictly valid, eqn (12) still shows the same qualitative behaviour as the numerical solution of the full set of equations. Eventually, when kleptoparasitic interactions become very long-lived compared with the average time taken to find a food item, the solution of the full set of equations begins to deviate considerably from the simple analytic approximation. However, in this limit, it is difficult to justify our underlying behavioural assumption that searching foragers will always attempt kleptoparasitism when the opportunity arrives. An individual would do better to pass up the lengthy fight in order to concentrate on searching. Hence, neither the full set of equation nor the analytic functional response can be considered valid under these circumstances. Having dealt with the circumstances under which this functional response provides an accurate summary of the underlying behaviour of individuals in our microscopic model, the next section explores the properties of this particular form. We compare it with previously published functional responses representing other forms of forager–forager interactions, and interpret differences in terms of underlying individual behaviour.

### Properties of the Functional Response

In the limiting case where forager density is very low, the likelihood of a handling individual being disturbed by another forager before it has finished with a food item is very low. Hence in the limit  $P \rightarrow 0$ , the functional response reduces to the standard Holling disk-equation (Holling, 1959):

$$I(F) = \frac{I_{\max} F}{F + F_0} \quad (16)$$

with uptake rate being completely independent of forager density. As forager density increases, however, the incidence of kleptoparasitism will also increase. Thus, whereas the empirical model of Hassell & Varley (1969) produced a linear relation between  $\log(I)$  and  $\log(P)$ , our functional response produces a curvilinear response, with slope increasing with forager density up to a maximum value of one (see Fig. 1). Such a shape has been suggested by several authors (Hassell, 1971; Hassell & Rogers, 1972) to be more appropriate than that produced by Hassell & Varley's empirical model, since it suggests that interference becomes less strong as forager density decreases. Further, it has also produced by

other behaviour-based models of interference (Beddington, 1975; Ruxton *et al.*, 1992).

The term in the functional response representing kleptoparasitism,

$$\frac{\kappa F P}{F + F_0} \quad (17)$$

increases with increasing forager density, as one would expect. It also increases with increasing food density. As food becomes more easy to find, there will be more handlers for a searching individual to discover and upon whom to attempt kleptoparasitism. Notice too that this effect reduces in magnitude as food density increases. This is because at very high food density the increased availability of handlers is balanced by a decrease in the number of searching individuals and so the rate of kleptoparasitism does not increase. Although increasing food density can under some circumstances increase the proportion of time that an individual expends in kleptoparasitism, increasing food density has an even stronger effect on reducing the amount of time spent searching. Hence under all conditions, uptake rate increases with food density. At high food densities,

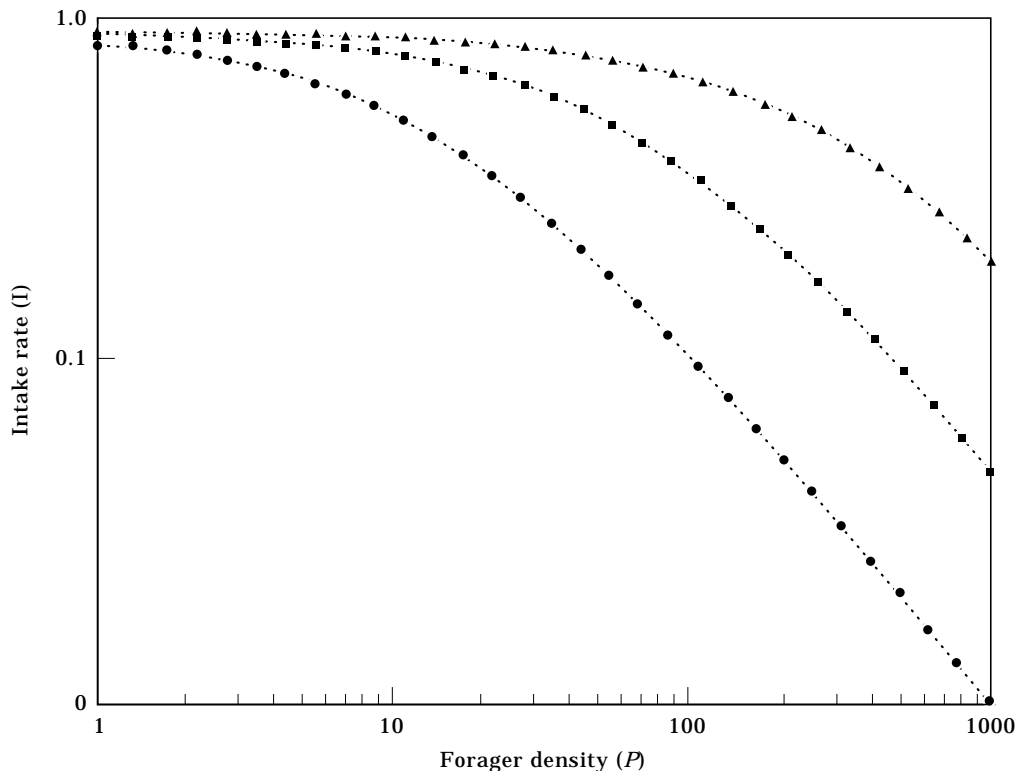


FIG. 1. The intake rate ( $I$ ) plotted as a function of forager density ( $P$ ) on logarithmic axes. The slope of the graphs represents Hassell & Varley's coefficient of interference ( $m$ ). At low  $P$ , this equals zero, since kleptoparasitism is negligible. However, the slope increases with  $P$ , and saturates at a value of one. Three values of  $t_k$  are considered: 0.1 (triangles), 1.0 (squares) and 10 (circles). The longer bouts of kleptoparasitism last (the higher  $t_k$ ), the more kleptoparasitism depresses the intake rate, and the lower the  $P$  values at which  $m$  reaches unity. Other parameter values:  $F = 100$ ,  $t_h = 1.0$ ,  $v_F = v_H = 0.1$ .

the intake rate increases at a faster rate than the increase in kleptoparasitism and so overall the intensity of interference decreases with increasing food density. This is illustrated in fig. 2 of Moody & Ruxton (1997) which shows that the slope of the uptake curves at high forager density decreases with increasing food density. The intensity of interference only increases with increasing food density for very low food densities, where the rate of increase in kleptoparasitism is high.

Another interesting feature of the model is the limit when individuals search very efficiently for both food and handlers. i.e.  $v_F \rightarrow \infty$  but

$$\frac{v_F}{v_H} \rightarrow C, \quad (18)$$

where  $C$  is a non-zero constant. In this (biologically rather implausible) limit, the model depends only on the ratio of foragers to food

$$I\left(\frac{F}{P}\right) = \frac{I_{\max}\left(\frac{F}{P}\right)}{\left(\frac{F}{P}\right) + \kappa}. \quad (19)$$

This is the type of “ratio-dependent” functional response first proposed by Arditi & Ginzburg (1989) and the subject of intense current debate (e.g. Abrams, 1994; Gleeson, 1994; Akcakaya *et al.*, 1995). There is a simple explanation why the functional response is ratio-dependent in this limit. Effectively no time is spent searching: as soon as an individual enters the searching state it immediately discovers either a handling forager or a food item. Which type is discovered in any one instance depends simply on the ratio of the abundance of food items and foragers.

### Forager Distribution on Two Patches

We can understand how foragers might distribute themselves across a patchy environment by finding the distribution of foragers across these patches which gives all individuals the same uptake rate. By equating the uptake rates across patches the ideal free distribution is found. This is most clearly illustrated in the simple case of two patches. We will assume these two patches are of equal size so that the population densities can be considered as simple numbers. We denote the food population on one patch by  $F_1$ , similarly the food population in the second is  $F_2$ . We denote the total forager population as  $P_T$ , with  $P_1$  and  $P_2$  being the populations on the two patches, so

$$P_2 = P_T - P_1. \quad (20)$$

At equilibrium the uptake rates in each patch are the same,

$$I(F_1, P_1) = I(F_2, P_2). \quad (21)$$

Substituting explicit expressions for the functional responses and rearranging gives the number of foragers in the first patch as

$$P_1 = \frac{F_0(F_1 + F_0)(F_2 + F_0)(F_1 - F_2) + \kappa F_1 F_2 (F_1 + F_0) P_T}{\kappa F_1 F_2 (F_1 + F_2 + 2F_0)}. \quad (22)$$

If  $F_1$  is very low (relative to  $F_2$ ), then the calculated value of  $P_1$  will be negative. In this case, we assume that no individuals forage on this patch and the whole forager population is found on the second patch.

Figure 2(a) shows the relation between the proportion of food on patch one and the number of foragers predicted to use this patch, for various values for the total number of foragers. As one would expect, when all the food is in patch 1, so are all the foragers. As food is gradually moved from patch 1 to patch 2, there comes a critical point when a forager would do better leaving patch 1 for the relatively poorer patch 2, since although food will be harder to find, it will suffer less from kleptoparasitic interactions. As patch 2 gradually increases in quality, it is advantageous for more and more individuals to move there until, when the food is split 50:50 between the patches, so are the foragers. By the symmetry of the situation, the number of foragers in patch 1 when it has the poorer food load can be understood by considering the number of foragers in patch 2 when patch 1 was relatively rich. For example, the number of foragers in patch 1 when it has 30% of the food is the same as the number of foragers in patch 2 when patch 1 had 70% of the food. As the total number of foragers increases, so the number of kleptoparasitic interactions increases, hence the poorer patch becomes attractive at an even lower food density: as shown in Fig. 2(a). In the limit  $P_T \rightarrow \infty$ , the proportion of food in the first patch is given by,

$$\frac{P_1}{P_T} \rightarrow \frac{F_1 + F_0}{F_1 + F_2 + 2F_0}. \quad (23)$$

Hence, if the system is highly enriched so that  $F_1 \gg F_0$ , then we have a good approximation to “habitat matching”, where the proportion of foragers on a patch is equal to the proportion of food on that patch [see Milinski & Parker (1991) for further discussion of this term]. Notice that habitat matching is not a

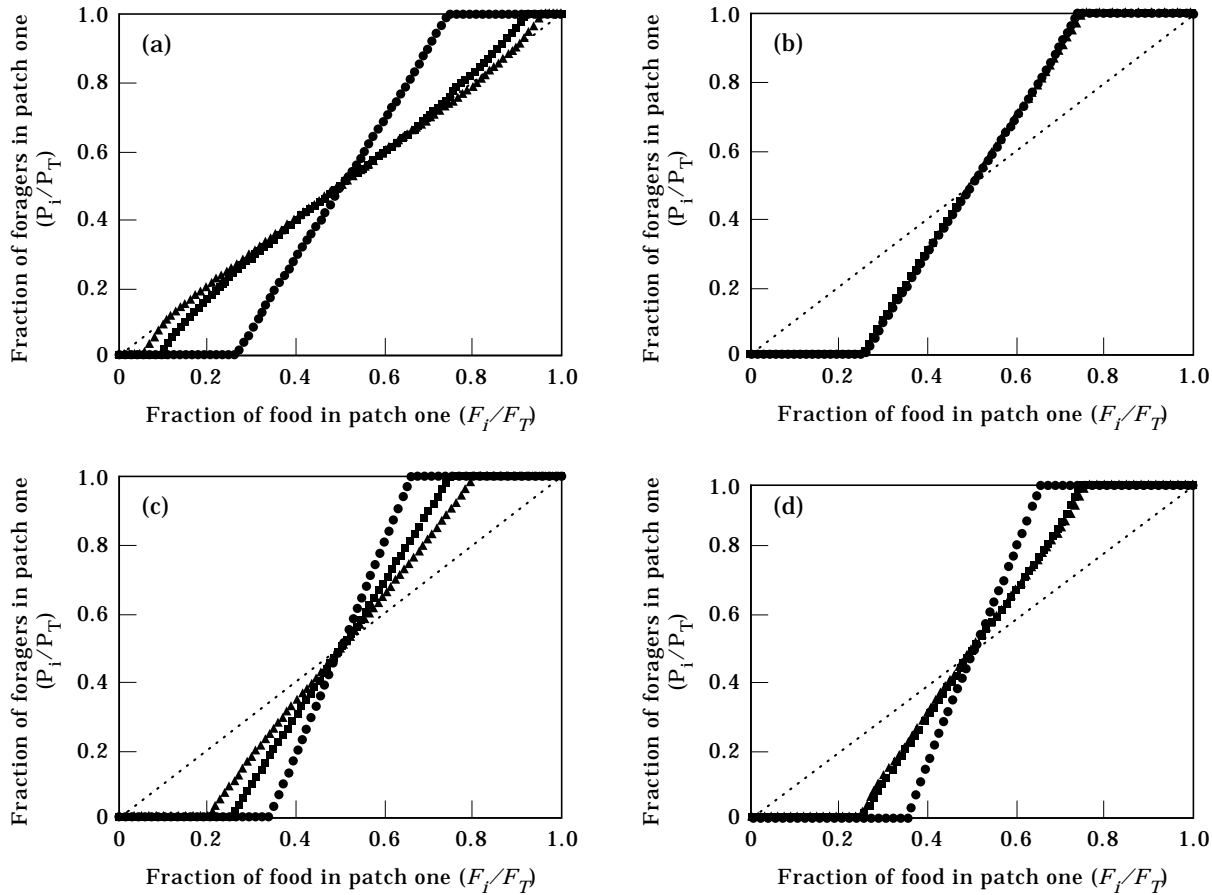


FIG. 2. The proportion of foragers in patch one as a function of the proportion of food in that patch. Part (a) shows the relation when total forager number is 10 (circles), 50 (squares) and 90 (triangles). Part (b) shows the relation when total food density ( $F_T$ ) is 10 (circles) and 1000 (squares). Part (c) shows the relation when  $t_k = 0.5$  (circles), 1.0 (squares) and 1.5 (triangles). Part (d) shows the relation when  $t_h = 0.1$  (circles), 1.0 (squares) and 10 (triangles). The broken line shows the distribution of foragers predicted by simple habitat matching. Default parameter values:  $P_T = 10$ ,  $F_T = 100$ ,  $t_h = t_k = 1.0$ ,  $v_F = v_H = 0.1$ .

guaranteed result of the ideal free distribution being achieved (Tregenza, 1994).

Figure 2(b) shows that increasing the total amount of food in the system has very little effect on the distribution of foragers. Although it makes the poorer patch more attractive to foragers, the reward obtained in the rich patch also increases. It is trivial to show that as the total amount of food tends to infinity, the forager distribution depends only on the relative richness of the patches and is independent of the total amount of food.

If the mean length of kleptoparasitic contests ( $t_k$ ) is increased, then this increases the intensity of interference caused by kleptoparasitism and hence reduces the threshold amount of food that the poorer patch must hold before being occupied, as shown in Fig. 2(c). In the limit  $t_k \rightarrow \infty$ , the proportion of foragers in the first patch is given by,

$$\frac{P_1}{P_T} \rightarrow \frac{F_1 + F_0}{F_1 + F_2 + 2F_0}. \quad (24)$$

Hence, if the system is highly enriched so that  $F_1 \gg F_0$ , then we have a good approximation to habitat matching. At the opposite extreme, when  $t_k \rightarrow 0$ , kleptoparasitism is unimportant and so all foragers utilise the richer of the two patches. For all values of  $t_k$  between these two extremes, we find “over-matching” (Milinski & Parker, 1991): i.e. the proportion of foragers in the richer patch is greater than the proportion of food in this patch. Clearly, from the definition of  $\kappa$ , varying the rate at which handlers are found ( $v_H$ ) has exactly the same effect on the distribution of foragers as varying  $t_k$ .

Figure 2(d) shows the effect of varying the time taken to handle a food item ( $t_h$ ). As this increases, the likelihood of being affected by kleptoparasitism whilst handling rises, and hence the poorer patch will be

utilised more readily. However, increasing  $t_h$  also causes the amount of time spent searching to drop and hence this reduces the strength of kleptoparasitism. As  $t_h$  becomes very large, these two effects cancel and the distribution of foragers becomes unaffected by change in  $t_h$ . Increasing  $v_F$  has exactly the same effect on the distribution.

If we investigate the limiting case where the functional response is ratio-dependent then it is trivial to show that perfect habitat matching is predicted:

$$P_1 = \frac{F_1}{F_1 + F_2}. \quad (25)$$

### Forager Distribution on Three or More Patches

When there are three patches in the system, we wish to find the distribution of foragers which gives

$$I(F_1, P_1) = I(F_2, P_2) = I(F_3, P_3). \quad (26)$$

Substituting explicit expressions for the functional response and rearranging [see Moody & Houston (1995) for an equivalent manipulation] gives the forager population in the three patches as

$$P_1 = \frac{Q + \kappa P_T F_1 F_2 F_3 (F_1 + F_0)}{\kappa F_1 F_2 F_3 (F_T + 3F_0)}, \quad (27)$$

where

$$Q = F_0(F_1 + F_0)[F_2(F_3 + F_0)(F_1 - F_3) + F_3(F_2 + F_0)(F_1 - F_2)], \quad (28)$$

$P_2 =$

$$\frac{F_0(F_1 + F_0)(F_2 + F_0)(F_2 - F_1) + \kappa P_1 F_1 F_2 (F_2 + F_0)}{\kappa F_1 F_2 (F_1 + F_0)} \quad (29)$$

and

$$P_3 = P_T - P_1 - P_2. \quad (30)$$

If any of the forager populations are negative then the population on the poorest patch is set to zero and the remaining two patch system is solved. This process is repeated until there are no negative forager populations.

Figure 3(a) shows an example of the distribution of foragers in response to varying distributions of food among three patches. The total amount of food was held constant and 50% of the food was always distributed to patch 1. At the extreme left of the figure, food is distributed so that the remaining 50% is in patch 3, with patch 2 containing no food. As one would expect, the foragers are divided equally between patches 1 and 3. As we

move across the graph, we effectively move food from patch 2 to patch 3. At first, the increased food load in patch 2 is not sufficient to sustain a forager population, however, the reduction in the richness of patch 3 causes foragers to leave this patch for patch 1. This process continues until the population in the food density in patch 3 becomes large enough to sustain a forager population. As more food is moved from patch 2 to patch 3 then the forager population on patch 3 increases at the expense of both that on patch 2 and, to a much lesser degree that on patch 1. This difference is not surprising since the food quota on patch 2 is falling but that on patch 1 remains constant.

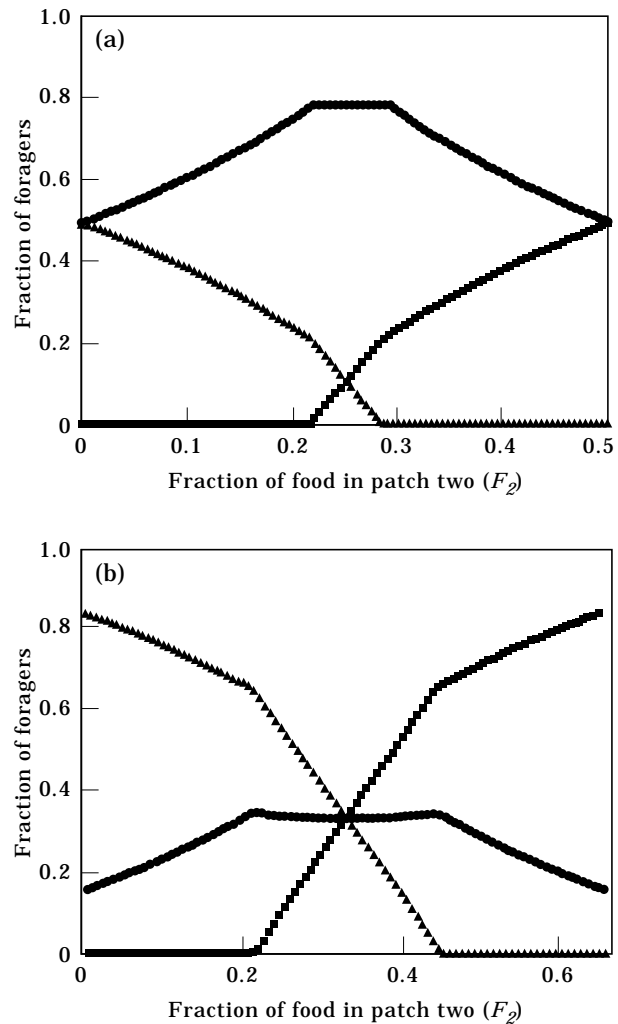


FIG. 3. The distribution of foragers on a system of three patches as a function of the food distribution among the patches. The population on the patch 1 is denoted (circles), on patch 2 (squares), and on patch 3 (triangles). In part (a), the proportion of food in patch 1 is held constant at 0.5; in part (b) it is held constant at 0.333. Other parameter values:  $P_T = 10$ ,  $F_T = 100$ ,  $t_h = t_k = 1.0$ ,  $v_F = v_H = 0.1$ .

Eventually, when the food quotas are equal on patches 2 and 3, so are the forager populations. The right side of the graph can be understood by considering the symmetry of the situation. Notice that the proportion of foragers in patch 1 is always greater than the proportion of food held there (50%). This is a further demonstration of the habitat over-matching observed in the two-patch system.

Figure 3(b) shows the results of a similar set of calculations where the proportion of food held in patch 1 is kept constant at 0.333. Now on the extreme left-hand edge, most of the foragers are in patch 3 which has 0.667 of the food, a smaller number are in patch 1 and none in patch 2 where there is no food. The proportion of foragers in the richest patch is greater than the proportion of food there, once again demonstrating the habitat-overmatching. When the food is shared evenly throughout the three patches, so are the foragers. When foragers are present in all of the patches then the uptake rate (at the ideal free distribution) is maximised when the patches are equally rich. This can be seen in Fig. 3(b) by the forager density in patch one (where food is held constant) being at a minimum at this point. This effect occurs because kleptoparasitic interactions increase in frequency at high food and forager densities. Hence, they can be minimised by distributing these evenly. Moody & Houston (1995) investigated a similar model where interference was produced by time wasting interactions occurring only between pairs of searching individuals. In this case, increasing food density causes a reduction in the amount of time each individual spends searching and hence a reduction in interference. Hence, in this case, interference is minimised when most of the foragers are distributed on a patch with a high food density. For the model of Moody & Houston, distributing the food evenly among the patches minimises the uptake rate for ideal free distributions where all patches are occupied.

It is possible to obtain a general expression for the number of foragers in the  $i$ th patch of an  $N$  patch system:

$$P_i = \frac{Q + \kappa P_T (F_i + F_0) \prod_{m=1}^N F_m}{\kappa (F_T + N F_0) \prod_{m=1}^N F_m}, \quad (31)$$

where

$$Q = \sum_{k=1}^N \left[ F_0 (F_i - F_k) (F_i + F_0) (F_k + F_0) \times \prod_{m=1}^N, m \neq i, m \neq k F_m \right]. \quad (32)$$

A similar method of successive elimination to that used in the three patch model must be adopted to produce a final solution without negative populations.

## Discussion

Recently, Dolman (1995) has criticised model predictions based on Hassell & Varley's empirical relation on the grounds that it assumes that food density has no effect on the intensity of interference, in contrast to his own and other experimental studies. He calls for behaviour-based functional responses, such as the one presented here, to be developed in order to better represent this effect. In agreement with Dolman's observations, the model presented here predicts that interference will increase with increasing food density when food density for all but very low food densities [see Moody & Ruxton (1996) for a fuller discussion of the interpretation of several forms of the functional response arising from comparison with Dolman's data]. Another behavioural model was presented in Ruxton *et al.* (1992) which also predicts that interference changes with food density. In this case, increasing food density always causes a decrease in interference. Although the behavioural model used to generate the functional response used in this paper is only very slightly different from that used to generate the functional response of Ruxton *et al.* (1992), the resulting change in the functional response leads to qualitatively different predictions for the distribution of individuals across habitat types.

Several previous models of the distribution of kleptoparasitic individuals (e.g. Sutherland, 1983; Korona, 1989) assume that the uptake rate of individuals on a patch (and hence their distribution over patches) is determined only by the ratio of the forager and food densities and not by their absolute values. In contrast there is experimental evidence that the number of foragers has an effect on uptake rates and population distribution (Gillis & Kramer, 1987). Our model clearly predicts that increasing forager density will increase the use of lower-quality patches. This is in general agreement with the observation of Goss-Custard *et al.* (1992) that oystercatchers made more and more use of poorer-quality mussel beds as oystercatcher numbers increased. Another important prediction of our model is that the proportion of the



foraging population using one particular site depends not only on the proportion of the total food available which can be utilised from that site, but on how the remainder of the food is distributed among the remaining patches.

There has been much interest in empirical functional responses which depend only on the ratio of foragers to food (Arditi & Ginzburg, 1989; Akcakaya *et al.*, 1995). These functional responses have been criticised (Abrams, 1994) for not having a behavioural basis which allows easy interpretation and estimation of parameter values. Hence, it may be of interest to the proponents of such expressions that a ratio-dependent form can be obtained in a limiting case of the behaviour-based model presented here. There has also been some controversy over how to test the utility of ratio-dependent function responses (e.g. Arditi *et al.*, 1991; Ruxton & Gurney, 1992). Both the results presented here and those presented (for a different density-dependent functional response) in Moody & Houston (1995) predict that foragers will be over-represented in richer areas of habitat, whereas ratio-dependent models predict that there will be close matching between food and forager densities. Hence, analysis of field and experimental feeding distributions may provide an effective opportunity to test the utility of the ratio-dependent functional response.

A similar study to that presented here is presented in Moody & Houston (1995). These authors do not consider interference between individuals to occur through kleptoparasitism but through time-wasting "face-offs" which occur whenever two searching individuals meet. This small change in the rules of the underlying behavioural model feeds through to a small change in the form of the functional response. This in turn causes different predictions at community level. Consider the case where all patches are used. This study predicts that uptake rates can be maximised if the quality of all the patches are identical; Moody & Houston predict that this situation minimises uptake rate. This difference can be understood in terms of the different behavioural rules of the models. However, this result illustrates the importance of basing the functional response on a clear behavioural mechanism, since the choice of the appropriate mechanism for a given system can have an important bearing on model predictions at a community level.

A reduction in uptake rate with increased forager density can occur for reasons other than time-wasting confrontations such as those which underlie the model presented here. One possibility is that dominant individuals occupy the richest food patches

and exclude others. As the population increases, subdominants must use less-rich patches and so the uptake rate averaged across the whole population declines. This is the pseudo-interference effect described by Free *et al.* (1977) and observed experimentally by Dolman (1995). There is evidence in wading birds that individuals alter their search patterns so as to avoid other individuals (Vines, 1980), and increase vigilance (and so decrease foraging time) when other individuals are nearby (Ens & Goss-Custard, 1984). Where food items can take some anti-forager action (e.g. fleeing, crypsis, or retreating into a shell or burrow) in response to forager detection, it is likely that foragers could suffer reduced uptake rates as their numbers increase and so more food becomes inaccessible. All these mechanisms should be open to the explicit behaviour-based modelling approach used here. As we have already demonstrated, small changes in the rules of the underlying behavioural model, can lead to important changes in its predictions of the distribution of foragers. Hence, in modelling any system where interference effects are expected to be important, it is essential to identify which of various possible interference mechanisms have a dominant effect.

In order to construct an analytically tractable expression for the functional response, the rules defining the behaviour of individual foragers used in our model are very much simplified. One aspect of behaviour where our rules may sometimes be an over-simplification is the assumption that a searching individual will always attempt to steal food from a handling individual, if the opportunity presents itself. This may be realistic when the time investment in such a tussle is much less than the searching individual's expectation of the time required for it to find a food item of its own. However, there will be other circumstances where the searcher might do better to turn down opportunities to steal. Hence, one useful extension of this work would be to explore the consequences at population level of allowing individuals to act "optimally" when choosing whether or not to initiate kleptoparasitic interactions. Adding this refinement will certainly make the model considerably more complex, and much of the algebraic analysis performed here would become impractical. However, the results provided here may still provide a useful guideline.

The model presented here assumes that all individuals have an equal ability to find, handle and fight for food. There are, however, several examples of systems where individuals do not all have equal foraging abilities: e.g. Harper (1982), Ens & Goss-Custard (1984), Sutherland *et al.* (1988). Using

a simple model based on the Hassell & Varley interference model, Sutherland & Parker (1985) have shown that a distribution of foraging ability can have important effects on the spatial distribution of foragers. This work was expanded using a behavioural-based model akin to the one presented here by Holmgren (1995). However, unlike this study, Holmgren was unable to obtain any analytic results and was required to explore his model numerically for a range of "plausible" parameter values. It seems likely that introducing between-individual variation will generally lead to this difficulty. Hence, it seems that further modelling studies would benefit from a hybrid approach where a model like Holmgren's is investigated numerically but simplified limiting cases are investigated using analytic techniques such as those presented here. This analysis should allow general rules to be formulated, whose relevance to the full model can be tested numerically. The general rules can then be tested against experimental data. It is essential that we produce models which can be tested in this way and we believe that construction of appropriate behaviour-based functional responses are a worthwhile step towards that goal.

We thank an anonymous referee for helpful comments.

## REFERENCES

- ABRAMS, P. A. (1994). The fallacies of ratio-dependent predation. *Ecology* **75**, 1842–1850.
- AKCAKAYA, H. R., ARDITI, R. & GINZBURG, L. (1995). Ratio-dependent predation—an abstraction that works. *Ecology* **76**, 995–1004.
- ARDITI, R. & GINZBURG, L. R. (1989). Coupling in predator-prey dynamics: ratio-dependence. *J. theor. Biol.* **139**, 311–326.
- ARDITI, R., PERRIN, N. & SAIH, H. (1991). Functional responses and heterogeneities: an experimental test with cladocerans. *Oikos* **60**, 69–75.
- BEDDINGTON, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* **44**, 331–340.
- BROCKMAN, H. J. & BARNARD, C. J. (1979). Kleptoparasitism in birds. *Anim. Behav.* **27**, 487–514.
- DOLMAN, P. M. (1995). The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia* **102**, 511–514.
- ENS, B. J. & GOSS-CUSTARD, J. D. (1984). Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *J. Anim. Ecol.* **53**, 217–231.
- FREE, C. A., BEDDINGTON, J. R. & LAWTON, J. R. (1977). On the inadequacy of simple models of mutual interference for parasitism and predation. *J. Anim. Ecol.* **46**, 543–554.
- FRETWELL, S. D. & LUCAS, (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta biotheor.* **19**, 16–36.
- FURNESS, R. W. (1987). Kleptoparasitism in seabirds. In: *Seabirds: Feeding Ecology and Role in Marine Ecosystems* (Croxall, J. P., ed.). Cambridge: Cambridge University Press.
- GILLIS, D. & KRAMER, D. L. (1987). Ideal interference distributions: population density and patch use by zebrafish. *Anim. Behav.* **35**, 1875–1882.
- GLEESON, S. K. (1994). Density-dependence is better than ratio-dependence. *Ecology* **75**, 1834–1835.
- GOSS-CUSTARD, J. D., CALDOW, R. W. G. & CLARKE, R. T. (1992). Correlates of density of foraging oystercatchers *Haematopus ostralegus* at different population size. *J. Anim. Ecol.* **61**, 159–173.
- HARPER, D. G. C. (1982). Competitive foraging in mallards: 'ideal free' ducks. *Anim. Behav.* **30**, 575–584.
- HASSELL, M. P. (1971). Mutual interference between searching insect parasites. *J. Anim. Ecol.* **40**, 473–486.
- HASSELL, M. P. & ROGERS, D. J. (1972). Insect parasite responses in the development of population models. *J. Anim. Ecol.* **41**, 661–676.
- HASSELL, M. P. & VARLEY, G. C. (1969). New inductive model for insect parasites and its bearing on biological control. *Nature* **223**, 1133–1136.
- HOLLING, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–398.
- HOLMGREN, N. (1995). The ideal free distribution of unequal competitors: predictions from a behaviour-based functional response. *J. Anim. Ecol.* **64**, 197–212.
- KACELNIK, A., KREBS, J. R. & BERNSTEIN, C. (1992). The ideal free distribution and predator-prey populations. *Trends Ecol. Evol.* **7**, 50–55.
- KORONA, R. (1989). Ideal free distribution of unequal competitors can be determined by the form of competition. *J. theor. Biol.* **138**, 347–352.
- MILINSKI, M. & PARKER, G. A. (1991). Competition for resources. In: *Behavioural Ecology* (Krebs, J. R. & Davies, N. B., eds) pp. 137–168. Oxford: Blackwell Scientific.
- MOODY, A. L. & HOUSTON, A. I. (1995). Interference and the ideal free distribution. *Anim. Behav.* **49**, 1065–1072.
- MOODY, A. L. & RUXTON, G. D. (1996). The intensity of interference varies with food density: support for behaviour-based models of interference. *Oecologia*, **108**, 446–449.
- PARKER, G. A. & SUTHERLAND, W. J. (1986). Ideal free distributions when individuals differ in competitive ability: phenotype limited ideal free models. *Anim. Behav.* **34**, 1222–1242.
- ROGERS, D. J. & HASSELL, M. P. (1972). General models for insect parasite and predator searching behaviour: interference. *J. Anim. Ecol.* **43**, 239–253.
- RUXTON, G. D. & GURNEY, W. S. C. (1992). The interpretation of tests for ratio-dependence. *Oikos* **65**, 334–335.
- RUXTON, G. D., GURNEY, W. S. C. & DE ROOS, A. M. (1992). Interference and generation cycles. *Theor. Pop. Biol.* **42**, 235–253.
- SUTHERLAND, W. J. (1983). Aggregation and the ideal free distribution. *J. Anim. Ecol.* **52**, 821–828.
- SUTHERLAND, W. J. & PARKER, G. A. (1985). Distributions of unequal competitors. In: *Behavioural Ecology* (Silby, R. M. & Smith, R. H., eds) pp. 255–273. Oxford: Blackwell Scientific.
- SUTHERLAND, W. J., TOWNSEND, C. R. & PATMORE, J. M. (1988). A test of the ideal free distribution with unequal competitors. *Anim. Behav.* **44**, 345–355.
- TREGENZA, T. (1994). Common misconceptions in applying the ideal free distribution. *Anim. Behav.* **47**, 485–487.
- VINES, G. (1980). Spatial consequences of aggressive behaviour in flocks of oystercatchers, *Haematopus ostralegus* L. *Anim. Behav.* **28**, 1175–1183.