

The Approximately Ideal, More or Less Free Distribution

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We present the minimum set of requirements necessary and sufficient to represent the foraging behaviour of an animal, and its utilisation of food, in order to explore the emergent properties of behaviour that allow animals to reduce their hunger. We present an individual-based model of foraging that provides a simple quantification of the requirements, which is sufficiently simple to yield some analytical results. Complex interactions beyond the scope of analysis have been explored through simulating animals foraging in regenerating patchy environments. In most cases the populations pass into equilibrium distributions which appear to be stable. The equilibria always approximate closely to the ideal free distribution, although typically with a small degree of undermatching. (Undermatching is the term applied to the departure from the ideal free distribution caused by a smaller proportion of the population than expected occupying areas with a higher than average regeneration rate). The model therefore implies that the distribution, hitherto accounted for in terms of ESSs may, in fact, be simply an effect of the animal's utilization of the food it collects to reduce its hunger. The model defines a specific feeling rate, v , the rate at which an animal can feed on a unit of food. This is a function of three parameters, v_1 , the specific feeding rate when alone, v_∞ , the rate, possibly zero, at which it can feed in the presence of an indefinitely large number of conspecifics, and $n_{1/2}$, the number of conspecifics that cause v to take the value $(v_1 + v_\infty)/2$. Exploitation competition in the absence of interference is represented by setting $v_1 = v_\infty$. Differences in competitive ability in exploitation have been represented by simulating animals with a range of values of v_1 , those with the larger values, feeding more rapidly, being the more effective competitors, and those with the lower values being the less effective. Interference competition is represented by setting $v_1 > v_\infty$ and social facilitation by $v_1 < v_\infty$. Individual differences in the strength of interaction are represented by different values of $n_{1/2}$. In competition, the animals with the larger values of $n_{1/2}$ are the more effective competitors: in facilitation, they are the less effective facilitators. The addition of physiological and behavioural detail makes very little alteration to the emergent equilibria, always close to the ideal free distribution, almost always showing undermatching. © 2001 Academic Press

INTRODUCTION

This paper shows how, in a patchy regenerating environment, hunger alone can produce distributions of animals that approximate closely to the ideal free distribution.

We present a minimal model of an individual forager, incorporating searching for, collecting, and utilizing food, and show how such animals distribute themselves. We then explore the sensitivity of the simple model to the addition of the biological properties of real animals, incorporating a realistic functional response and realistic

costs of metabolism. We then systematically explore the major predictions to be derived from modelling such individuals foraging in patchy environments. Finally, we show how these predictions differ from those derived from optimal models and identify the crucial data required to distinguish between the classes of models. We conclude that an account of the spatial distribution of foraging animals in patchy environments can be obtained without direct reference to evolutionary optimization.

Alternative Interpretations of the Ideal Free Distribution

Two different interpretations of the ideal free distribution are in common use: one assumes that the maximal rate of food intake is set by the standing stock of food and the other that it is set by the rate at which the food enters the environment (Weber, 1998). To discuss these different interpretations unambiguously it is necessary to define formally a specific environment and the ideal free distribution of the animals implied by such an environment.

Suppose that a heterogeneous environment contains n animals and p patches of food such that at time t there are n_α animals feeding at patch α , which contains F_α units of food, and which is regenerating at the rate $a_\alpha \geq 0$. Under the first interpretation, say Type I, the ideal free distribution of n animals at time t is taken to imply that $n_\alpha/n = F_\alpha(t)/\sum_{\beta=1}^p F_\beta(t)$, for $\alpha = 1, 2, 3, \dots, p$, and under the second interpretation, say Type II, to imply that $n_\alpha/n = a_\alpha(t)/\sum_{\beta=1}^p a_\beta(t)$. The Type I and Type II interpretations generally predict different distributions of foragers.

The Type I interpretation seems to imply that the environment contains food that does not regenerate but exists in such abundance that it is not depleted by the foragers; but without depletion there is no mechanism by which the animals can be distributed as predicted unless an alternative density-dependent mechanism such as direct interference is postulated. However, findings discussed in following sections suggest that the relationship between standing crop and rates of regeneration in the causation of equilibrium distributions of animals is likely to be more complex than it might, at first, appear to be.

The Type II interpretation assumes that the resources in the environment regenerate in some way. A feature of this interpretation that has led to confusion is that at equilibrium there may be no *net* depletion of the standing crop of food at each patch, and this has led to the conclusion that there is necessarily *zero* standing crop at each patch (Weber, 1998). This conclusion is questionable because the feeding rate of an individual animal is a

function of the standing crop of food. In the absence of food the animal is incapable of feeding.

Assumptions and Requirements

Any optimal theory that purports to explain the distribution of foraging animals must satisfy the following requirements: the environment must be sufficiently well characterised for an optimal solution to exist, and each animal must possess the properties that make the optimal solution accessible to it.

In order to derive the form of the ideal free distribution, a number of assumptions are made about the properties of the foragers. These are:

1. All animals are competitively equal.
2. All animals are free to search for food wherever they want, and the searching is free of costs.
3. All animals feed at their maximum possible rates.
4. The rate of feeding of an animal is a monotonically decreasing function of the density of animals.

This paper presents an alternative approach to modelling the foraging of a population of animals. It uses a *local* model to represent the dynamics of foraging that lead to the observed equilibria, and it provides an account not of the ideal free distribution of evolutionary theory, but of the observed distributions of approximately ideal, more or less free real animals. This approach is concerned not only with the collection of food, but also with the significance of feeding in the maintenance of life. Accordingly, the requirements given above may be replaced by the set that follows.

1. Animals eat food, part of which is incorporated into the animal (Requirement of Consumption).
2. To maintain itself an animal utilizes body tissue, the equivalent of stored food, and the rate of utilization is dependent on the mass of the animal (Requirement of Utilization).
3. An animal will reject food if the rate at which that food can be eaten is less than the rate of utilization of body tissue (Requirement of Hunger).
4. By eating, an animal depletes the standing crop of food (Requirement of Depletion).
5. The rate at which an animal feeds is a function of the standing crop of food (Requirement of Ingestion).
6. The rate at which an animal feeds is a function of the density of all of the animals feeding on same food (Requirement of Competition).

These requirements imply the following.

The Requirement of Consumption implies that there exists a function that maps food to body mass, the fundamental state variable in the system. Insofar as a currency is implied by this model that currency is body mass.

The Requirement of Utilization postulates that, other things being equal, big animals need more food for maintenance than small ones, explicitly recognizing that animals *use* food and implying that starving animals lose body mass by using their own reserves to maintain their vital processes.

The Requirement of Hunger is the fundamental physiological rule. While the animal is not feeding its mass decreases as it uses up incorporated food. Informally, when the animal is not feeding it gets hungry. The animal will reject food that does not reduce its hunger by increasing its body mass.

The Requirement of Depletion makes a clear distinction between the animal's feeding which depletes the standing crop of food and the state of a system of food and foragers in dynamic equilibrium where there may be no *net* depletion of food.

The Requirements of Depletion and Ingestion are sufficient alone to imply exploitation competition; the Requirement of Competition is added to admit interference competition.

Real animals vary in their competitive abilities and in their willingness to move in the environment. Standard ideal free theory can account for some of these less than ideal properties. In contrast, the model described here starts with the unideal animals and emphasises explanation, not of the process by which the ideal distribution arises, but of the consistently observed departures from it, and of the dynamic processes of competition that cause equilibrium distributions to arise. The following sections explore the distributions of individuals with a variety of unideal properties foraging more or less freely in a variety of regenerating environments.

THE MODELS

We consider two models: the first is a simple population dynamic model, concerned, for example, with the distribution of sessile animals invading a regenerating patchy environment, each population growing in its own patch, independently of the other populations; the second is a more complex behavioural model that ignores population dynamics, but which predicts how the decision-making of individual animals results in their disposition

approximating to the ideal free distribution, in timescales short with respect to the processes of natality and mortality. The population dynamics model is of interest because it provides a new mechanism, independent of the movement of individuals, which can cause the ideal free distribution of Type II to arise. This model can be expressed by the following:

$$\frac{dF}{dt} = a - vFN$$

$$\frac{dN}{dt} = bvFN \left(\frac{K - N}{K} \right),$$

where a is the constant rate of addition of food, b is the yield of animals per unit food eaten, F is the standing crop of food, v is the specific feeding rate of an individual animal, N is the standing crop of animals, and K is the maximum number that can be sustained indefinitely. The Requirement of Utilization implies that an equilibrium population of animals can be supported only by the continuous addition of food at a constant rate. Since food is being supplied at a rate a and since, at equilibrium, K animals are being supported, $K = a/m$, where m is rate of food consumption that is sufficient to maintain an individual. Since the size of the population in the patch is proportional to the rate of supply of food at the patch, the model defines a simple form of the Type II ideal free distribution. Solving this model for stationary states, \hat{F} and \hat{N} , it follows that

$$\hat{F} = \frac{m}{v}$$

and

$$\hat{N} = \frac{a}{m},$$

proving that for any rate of addition of food, the equilibrium standing crop of food, \hat{F} , is constant, and the equilibrium population size, $\hat{N} \propto a$, satisfying the definition of the ideal free distribution of Type II. In the context of what follows it is important to recognize that the population dynamic model satisfies all the requirements laid out above. Where it differs from the behavioural model to be discussed below is in the effect on the animals of the Requirement of Consumption. In the population dynamics model the result of consumption is a change in the numbers of individuals in the population, the individuals, by implication being of a fixed size, each

having a fixed constant maintenance requirement. In the behavioural model discussed below the result of consumption is bodily growth of a fixed number of individuals.

The behavioural model requires a more explicit definition of the environment because the processes taking place at one patch are not independent of the processes taking place at the other patches. We therefore consider an environment that is composed of a number, p , of discrete patches. Throughout the text Greek subscripts will refer to food patches and Roman subscripts will refer to foraging animals. The patch α has a standing crop of food, F_α , which regenerates at a constant rate a_α . The patch contains n_α foraging animals which deplete the standing crop at a rate $\sum_{i=1}^{n_\alpha} R_i(F_\alpha)$, where we define $R_i(F_\alpha)$ to be the functional response of the i th animal. The functional response is currently assumed to be a function only of F_α , the standing crop. We consider the more complex case of the functional response depending also on n_α , the number of animals, below, in the section dealing with intraspecific interaction. (Notice that our use of the term functional response refers to the rate of ingestion of food only while the animal is feeding.) For the present the rate of change of the standing crop can be written as

$$\frac{dF_\alpha}{dt} = a_\alpha - \sum_{i=1}^{n_\alpha} R_i(F_\alpha). \quad (1)$$

Animals are composed of tissues belonging to two broad categories: structural tissue and reserve tissue. Structural tissue cannot be remobilised. Reserve tissue is more labile and is metabolised continuously to maintain physiological functioning. We assume that the forager is composed solely of reserve tissue and that the i th animal foraging on patch α contains $m_{i,\alpha}$ units of mass of such tissue. We also assume that the rate of assimilation of food is directly proportional to the rate at which it is ingested, and because the absolute rate of assimilation plays no part in the dynamics of the model, we assume that the rate of assimilation is equal to the rate of ingestion.

Food is ingested at a rate given by the functional response, $R_i(F_\alpha)$, and is metabolised at a rate given by the function $M(m_{i,\alpha})$. The rate of change of mass of the i th animal feeding at the patch α can therefore be written as

$$\frac{dm_{i,\alpha}}{dt} = R_i(F_\alpha) - M(m_{i,\alpha}). \quad (2)$$

To complete the model it is necessary to represent hunger formally. We assume that the i th animal will not

feed at a patch on arrival or will cease to feed at a patch when

$$\frac{dm_{i,\alpha}}{dt} \leq 0, \quad (3)$$

which means that an animal will not stay at a patch if its metabolic costs equal or exceed the return from feeding there.

The model is simplest when the functional response is a Holling Type I linear response,

$$R_i(F_\alpha) = vF_\alpha, \quad (4)$$

where v is the rate of feeding per unit standing crop of the i th animal at patch α . The rate of feeding per unit standing crop can vary between animals, but to simplify the notation the subscript i will be used only when necessary to avoid ambiguity. The metabolic cost is a linear function of the mass of tissue,

$$M(m_{i,\alpha}) = rm_{i,\alpha}, \quad (5)$$

where r is the metabolic rate per unit mass of tissue, the specific metabolic rate, of an animal; and the rate of change of the mass of the i th forager feeding at the patch α is expressed by the equation

$$\frac{dm_{i,\alpha}}{dt} = vF_\alpha - rm_{i,\alpha}. \quad (6)$$

If each patch of food regenerates at a constant rate, then the rate of change of the standing crop on patch α can be written as

$$\frac{dF_\alpha}{dt} = a_\alpha - V_\alpha F_\alpha, \quad (7)$$

where $V_\alpha = \sum_{i=1}^{n_\alpha} v$ is the total feeding rate of all the animals on the patch. This linear model was studied by Ollason (1987), who showed that Eqs. (6) and (7) could be solved explicitly to give

$$F_\alpha(t) = F_\alpha(\infty) + (F_\alpha(0) - F_\alpha(\infty)) e^{-V_\alpha t} \quad (8)$$

$$m_{i,\alpha}(t) = m_{i,\alpha}(\infty) + (m_{i,\alpha}(0) - m_{i,\alpha}(\infty)) e^{-rt} + \frac{v}{r - V_\alpha} (F_\alpha(0) - F_\alpha(\infty)) (e^{-V_\alpha t} - e^{-rt}), \quad (9)$$

where t is the time from first entering the patch, so that $t=0$ is the initial time when the animal arrives at the patch, and $F_\alpha(\infty) = a_\alpha/V_\alpha$, and $m_{i,\alpha}(\infty) = F_\alpha(\infty) v/r$ are the equilibrium values of the standing crop and reserve tissue, respectively, if the animal never leaves the patch. By calculating $dm_{i,\alpha}/dt$ and using the definition of hunger given by Eq. (3), the expected time spent foraging for the i th animal on the patch α , $t_{i,\alpha}$, is

$$t_{i,\alpha} = \frac{1}{r - V_\alpha} \left[\ln \left(\frac{r}{V_\alpha} \right) + \ln \left(1 - \frac{V_\alpha - r}{v} \right) \times \left\{ \frac{m_{i,\alpha}(\infty) - m_{i,\alpha}(0)}{F_\alpha(0) - F_\alpha(\infty)} \right\} \right], \quad (10)$$

which shows that the extremal staying time on patch α , $\hat{t}_{i,\alpha} = \ln(r/V_\alpha)/(r - V_\alpha)$, is a maximum if $(m_{i,\alpha}(\infty) - m_{i,\alpha}(0))(F_\alpha(0) - F_\alpha(\infty)) < 0$ and otherwise a minimum. For realistic scenarios we expect that $F_\alpha(0) > F_\alpha(\infty)$. Furthermore, if $F_\alpha(0) - F_\alpha(\infty) \approx |\varepsilon|$, where $\varepsilon \approx 0$, implying that the patch is close to its equilibrium, then any animal with $vF_\alpha(\infty) > rm_{i,\alpha}(0)$ is unlikely to leave the patch unless there is a change due to some external factor (for example more animals entering the patch). The model therefore predicts that if a patch is close to equilibrium, and the animals arrive with low mass, in other words, very hungry, only external factors will cause an animal to cease feeding.

The results presented in Eqs. (8–10) may be used to analyse the feeding behaviour of a single forager in an environment containing a finite number of patches visited and revisited in a fixed order, as on a closed trapline. Empirical evidence from simulation indicates that in such an environment the standing crop and the animal's foraging behaviour converge to equilibria that are independent of the initial conditions, such that at each point in time the animal arrives at any particular point in its circuit, all the patches are in the same state as they were when the point was last visited, as is the animal itself. The equilibrium properties of the system can be found by inferring the foraging behaviour that leaves the whole system unchanged after a forager has completed one circuit of the environment. This approach is used to calculate the equilibrium behaviour of one animal foraging in an environment composed of two patches, Patch 0 and Patch 1, replenished at the constant rates, a_0 and a_1 , and separated by a travelling time of t_t (Appendix 1). The single animal is indexed by i and is defined by Eqs. (6) and (7). It visits each patch in turn. The staying times at Patch 0 and Patch 1 converge to the equilibrium values of $t_{i,0}$ and $t_{i,1}$, respectively. The equilibrium behaviour

TABLE 1

The Behaviour of the Model Simulating One Forager in an Environment Containing Two Regenerating Patches under a Range of Travelling Times

t_t	$t_{i,0}$	$t_{i,1}$	$t_{i,0}/t_{i,1}$	$m_{i,1}(0)/m_{i,0}(t_{i,0})$
1	4.490	8.830	0.509	0.992
2	6.130	11.85	0.517	0.984
4	8.270	15.58	0.531	0.969
8	11.05	19.92	0.554	0.939
16	14.55	24.54	0.593	0.882
32	18.79	28.89	0.651	0.779
64	23.57	32.24	0.731	0.607
128	28.32	34.03	0.832	0.368
256	32.00	34.25	0.934	0.135
512	33.30	33.61	0.991	0.018
1024	32.95	32.96	1.000	3×10^{-4}
2048	32.59	32.59	1.000	1×10^{-7}

Note. $a_0 = 0.01$, $a_1 = 0.02$, $v = 0.08$, $r = 1/128$. t_t , travelling time; $t_{i,0}$, $t_{i,1}$ mean staying times at patch 0 and patch 1, respectively. For this choice of parameters the extremal staying time $\hat{t}_t = 32.23$. $m_{i,\alpha+1}(0)/m_{i,\alpha}(t_{i,\alpha})$ is the proportion of the body mass left after travelling.

can be determined exactly in three limiting cases. First, when the travelling time becomes large,

$$\lim_{t_t \rightarrow \infty} t_{i,0} = t_{i,1} = \hat{t}_t = \frac{1}{r - v} \ln \left(\frac{r}{v} \right), \quad (11)$$

where \hat{t}_t is the extremal staying time for one foraging animal. Hence, the animal spends equal times at each patch. So, as the travelling time becomes increasingly large, the model predicts an increasing degree of under-matching (Table 1). The ratio $m_{i,\alpha+1}(0)/m_{i,\alpha}(t_{i,\alpha})$ is the proportion of body mass remaining after travelling between patch α and $\alpha + 1$. The loss of a large proportion of the body mass is likely to be lethal to real animals. It is therefore likely that real animals will choose to forage in environments in which the average travelling time between patches is substantially less than $1/r$, the time required for the body mass to decay to $1/e$ of the mass on leaving the last patch. It is in such environments that the distribution will approximate reasonably closely to the ideal free distribution of Type II.

Second, when the metabolic costs become negligible, ($r \rightarrow 0$), it can be shown that

$$\lim_{r \rightarrow 0} \frac{t_{i,0} + 2t_t}{t_{i,1} + 2t_t} = \frac{a_0}{a_1} \quad (12)$$

and hence, third, as $t_t \rightarrow 0$, the staying times converge to those predicted by the ideal free distribution. The proofs

of these results are presented in Appendix 1. Finally, we show, for the special case of an indefinitely long trapline of patches of the same type, and when costs become negligible, that the time budget predicted by the model converges to the optimal time budget predicted by the marginal value theorem (Appendix 2).

Although this model is formally unchanged from that of Ollason (1987), the physiological interpretation, first introduced by Ollason and Lamb (1995), is different from the original interpretation, which was formulated in terms of learning. This paper extends the findings previously reported by additional analysis and by using the individual-based modelling approach to explore the emergent consequences of adding more realistic biological detail.

Simulations involving several patches of food and small numbers of foragers can display apparently pathological behaviour: an animal can come to settle in a patch α and, provided that circumstances do not change, it will stay at that patch indefinitely with a rate of growth which, although positive, asymptotically approaches zero. Other animals visiting other patches can attain much greater masses and on visiting or revisiting patch α leave immediately, being unable to feed at the minimum expected rate. Consequently the population can divide into a group of animals that are small, grow slowly, and are fixed in one of the patches, say α , and a group of animals that are larger, that grow more rapidly, and that visit all patches, but feed only in the patches other than α . The initial conditions for such simulations where this behaviour was observed were as follows. Each animal was assigned at random to one of the patches. The initial values of $m_{i,\alpha}$ were small and randomly perturbed so that no two animals had the same value of $m_{i,\alpha}$. Some of the individuals assigned to the poorest patch left it, fed at one of the other patches, and upon revisiting the poorest patch left without feeding. Only animals that were initially present in the poorest patch stayed feeding there. This behaviour depends only on initial conditions and is independent of the number of foragers simulated. It is most unlikely to be observed in populations of real animals in which stochastic processes, unrelated to foraging, will cause the individuals to move away from such patches. In the simulations that follow the staying times of animals, $t_{i,\alpha}$, are constrained to lie in the range $0 \leq t_{i,\alpha} \leq t_{max}$, where $t_{max} = 1000$ time units. This avoids the subdivision of the population. All results presented below were obtained with staying times potentially constrained in this fashion, although, in fact, it was very seldom necessary to apply the upper bound to the staying times.

All simulations converged towards equilibria, and the simulations were concluded and the data recorded when

the staying times for all animals on any patch changed by no more than 1% over 100 consecutive visits. In the simulations involving two patches a standard set of initial conditions was chosen: the value of $m_{i,\alpha}$ for each individual was set to a small value, randomly perturbed, and all the individuals were placed at one of the patches, chosen at random. We chose these initial conditions to represent the usual initial experimental conditions of placing of food-deprived animals into the environment and observing their behaviour. Except where noted below, at the beginning of the experiments the patches all contained the same amount of food, but the rates of regeneration of each patch were varied as the simulation required. The detailed results of a quantitative investigation of the influence of initial conditions are presented below, in the section describing the distribution of many animals in many patches. The results we have chosen to report are those usually reported in observational or experimental studies of the distributions of foraging animals. In general we have chosen not to report the standing crop of food at the patches, because of the difficulty of assessing this variable in the laboratory or the field while the animals are foraging.

For small travelling times, such as are observed when animals are foraging over limited geographical areas, and spending much more time foraging than searching, the mean distributions of foragers approximated closely to the ideal free distribution of Type II but undermatched it to a small degree. ("Undermatching" is the term applied to the observation that a smaller proportion of the population occupies the areas that have a higher than average regeneration rate than that predicted by the Ideal Free Distribution.)

ONE ANIMAL FORAGING IN TWO PATCHES

Consider an environment composed of two patches, Patch 0 and Patch 1, replenished at constant rates a_0 and a_1 , and separated by a travelling time of t_t . A single animal, indexed by i and defined by Eqs. (6) and (7) visits each patch in turn. The staying times at Patch 0 and Patch 1 converge to $t_{i,0}$ and $t_{i,1}$, respectively. The equilibrium behaviour in this system is described by Eqs. (11) and (12). The results shown in Table 1 of the simulations of the foraging behaviour defined by Eqs. (6) and (7) show that the degree of undermatching increases with travelling time as predicted.

In real animals the functional response is unlikely to be linear and the specific metabolic rates are unlikely to be

constant; it is therefore of interest to explore the consequence of including more biological detail. In one simulation we replaced the linear functional response with a Holling Type II response, and in another we scaled the specific metabolic rate as a power of body mass.

We assumed that the functional response had the form

$$R_i(F_\alpha) = \frac{vF_\alpha}{S_i + F_\alpha}, \quad (13)$$

where S_i is the half-saturation constant (the standing crop of food that enables the i th animal to feed at half the maximum possible rate). When $S_i = 0$ the functional response is constant. When $S_i \gg F_\alpha$ then R_i is linear. If the standing crop is much greater than S_i the rate of feeding becomes almost independent of the standing crop, and if this circumstance should arise, the occupancy of the patches would depart significantly from the ideal free distribution. We explored the effect of S_i , the half-saturation constant, on the staying times of one animal foraging in the environment containing two patches with S_i in the range $0.1 \leq S_i \leq 10$, and the results are shown in Table 2.

TABLE 2

The Effect of a Holling Type II Functional Response, $R_i(F_\alpha)$, on the Equilibrium Staying Times, $t_{i,0}$ and $t_{i,1}$, of a Single Animal Feeding in an Environment Containing Two Patches, 0 and 1

S_i	$t_{i,0}$	$t_{i,1}$	$t_{i,0}/t_{i,1}$	$F_0(t_{i,0})$	$F_1(t_{i,1})$
10	4.703	9.247	0.509	0.389	0.391
5	3.239	6.297	0.514	0.195	0.196
4	2.868	5.548	0.516	0.156	0.156
3	2.448	4.697	0.521	0.117	0.117
2	1.954	3.697	0.529	0.078	0.078
1	1.320	2.420	0.545	0.039	0.039
0.5	0.885	1.555	0.569	0.019	0.020
0.333	0.697	1.190	0.586	0.013	0.013
0.25	0.590	0.985	0.599	0.010	0.010
0.1	0.335	0.530	0.632	0.004	0.004

Note. $R_i(F_\alpha) = vF_\alpha/(S_i + F_\alpha)$, where F_α is the standing crop of food on patch α , v is the maximum specific feeding rate, and S_i is the half-saturation constant. $F_0(t_{i,0})$ and $F_1(t_{i,1})$ are, respectively, the standing crops of food at Patch 0 and Patch 1 at the time the animal leaves. The other values of the parameters in the simulations are as follows: $v = 0.8$, $t_i = 1$, $a_0 = 0.01$, and $a_1 = 0.02$, implying that the expected value of $t_{i,0}/t_{i,1} = 0.5$. Note that in every case the equilibrium standing crop is much less than the corresponding value of S_i , implying that saturation has only a very small effect on the feeding behaviour of the animal and that there is an increasing degree of undermatching as S_i approaches 0. This may be explained by the fact that as $S_i \rightarrow 0$, t_i becomes large with respect to $t_{i,0}$ and $t_{i,1}$.

Except when S_i is very small, the Type II functional response makes little change to the ratio of the staying times of the animal: the system shows a degree of undermatching characteristic of the behaviour of the model with the Type I functional response. As S_i decreases the undermatching increases, because as S_i decreases the overall feeding rate increases. The faster the animal feeds, the faster the standing crop is depleted and the shorter the staying time. When S_i is very small, staying times are small compared with the travelling times, converging to the limit defined in Eq. (11), producing undermatching.

Empirical evidence suggests that the specific metabolic rate is not constant; rather it approximates to an allometric scaling of body mass which may be represented as

$$M(m_{i,\alpha}) = rm_{i,\alpha}^z, \quad (14)$$

where z is the allometric exponent ($z = 1$ gives the linear case of Eq. 5). To explore the influence of z , simulations were carried out for values of z in the range $0.5 \leq z \leq 1.5$ and the results are shown in Table 3.

With increasing values of z the equilibrium staying times decrease, because with a larger value of z the animal will reach its break-even point ($dm_{i,\alpha}/dt = 0$) earlier than an animal with a lower value of z . However, despite the fact that the staying times of the animals vary by a factor of approximately 3, the proportions of the population feeding at the two sites remain approximately constant, indicating that the distribution of the foragers between the patches is not strongly dependent upon z .

TABLE 3

The Influence of Making the Metabolic Costs Proportional to $m_{i,\alpha}^z$, Where $m_{i,\alpha}$ is the Mass of the i th Animal on Patch α

z	$t_{i,0}$	$t_{i,1}$	$t_{i,0}/t_{i,1}$
0.5	8.460	17.019	0.497
0.6	6.990	13.910	0.503
0.7	6.030	11.930	0.505
0.8	5.360	10.568	0.507
0.9	4.870	9.580	0.508
1.0	4.496	8.831	0.509
1.1	4.201	8.241	0.510
1.2	3.965	7.770	0.510
1.3	3.766	7.373	0.511
1.4	3.603	7.048	0.511
1.5	3.463	6.771	0.511

Note. The behaviour of a single animal has been simulated and the parameters of the simulation are $a_0 = 0.01$, $a_1 = 0.02$, $v = 0.08$, $r = 1/128$. The equilibrium staying times at Patch 0 and Patch 1 are, respectively, $t_{i,0}$ and $t_{i,1}$. Over the range of z encountered in nature the ratio of staying times is relatively independent of z . $t_{i,0}$ and $t_{i,1}$ are the mean staying times of individuals at Patch 0 and Patch 1, respectively.

TABLE 4

The Distribution of the Animals Approximates to the Ideal Free Distribution Independently of the Number of Animals Foraging

n	$t_{i,0}$	$t_{i,1}$	$t_{i,0}/t_{i,1}$	n_t	n_0	n_1	n_0/n_1
1	4.49	8.830	0.509	0.131	0.293	0.576	0.509
2	6.72	13.860	0.490	0.179	0.600	1.222	0.491
4	9.21	18.152	0.508	0.272	1.255	2.472	0.508
8	14.51	29.636	0.490	0.347	2.515	5.138	0.490
16	19.46	38.557	0.505	0.533	5.188	10.279	0.505
32	33.27	67.853	0.490	0.621	10.323	21.056	0.490
64	50.22	100.210	0.501	0.840	21.084	42.076	0.501
128	46.14	92.157	0.501	1.825	42.093	84.082	0.501
256	87.60	174.179	0.503	1.941	85.192	169.040	0.504

Note. The parameters used in the simulations were $v = 0.08$, $r = 1/128$, $t_i = 1$, $a_0 = 0.01$, $a_1 = 0.02$. The entries in the table are n , the total number of animals; $t_{i,0}$, $t_{i,1}$, the mean staying times; n_0 , n_1 , the mean numbers at Patch 0 and Patch 1, respectively; and n_t , the mean number of animals travelling between patches.

The distribution is weakly dependent on z , however, the equilibria arising with the lower values of z showing overmatching, and the higher values undermatching.

In view of the insensitivity of the model to z , and to S_i , the remaining simulations have been carried out using the simple linear version of the model.

MANY ANIMALS FORAGING IN TWO PATCHES

Simulations of differing numbers of foragers in an environment containing just two patches of food were carried out to determine whether the equilibria were dependent on the numbers of foragers. The results, shown in Table 4, indicate that the model's predictions are independent of the number of animals simulated.

MANY ANIMALS FORAGING IN MANY PATCHES

The equilibrium distribution of many foragers, among many patches, approximates to the ideal free distribution. An example of the simulation of animals foraging in a two-dimensional environment is given below. The environment is a square lattice containing nine nodes in all. A patch of food could be placed at each node. The nodes are separated from their nearest neighbours by a travelling time, $t_t = 16$ units. In the simulation there are three patches of food, located at the three corners with the coordinates $x = 0, y = 2$, $x = 2, y = 2$, and $x = 2, y = 0$. The regeneration rates of the patches are, respectively, 0.01, 0.02, and 0.04. Sixty foragers are introduced into the

system. On leaving a patch a forager is free to move to any neighbouring node, including those on the diagonals, and chooses its destination at random. If the animal moves diagonally the travelling time is adjusted accordingly. When an animal leaves, the destination node is chosen at random. The foragers are all similar, their parameters having the following values: $r = 1/512$, $v = 0.01$. At the

TABLE 5

The Mean Distribution of 60 Foragers Searching for Food in a Square Lattice Containing Nine Nodes at Three of Which Patches of Food Are Regenerating

Coordinate x, y :	0, 2	2, 2	2, 0
$a_{x,y}$:	0.01	0.02	0.04
Initial conditions			
0.1, 0.2, 0.4	0.161	0.299	0.540
0.1, 0.4, 0.2	0.165	0.298	0.537
0.2, 0.1, 0.4	0.160	0.292	0.548
0.2, 0.4, 0.1	0.163	0.295	0.542
0.4, 0.1, 0.2	0.168	0.302	0.532
0.4, 0.2, 0.1	0.161	0.296	0.543
4.0, 2.0, 1.0	0.167	0.300	0.533
40.0, 20.0, 10.0	0.165	0.295	0.540

Note. The entries in the table show the mean proportions of the feeding animals at each patch. The initial conditions list in order the masses of food present at each patch at the start of the simulation. The patches regenerate at the rates $a_{x,y}$. The travelling time from node to node is 16 units. The entries in the upper part of the table provide evidence that all possible permutations of the same initial standing crops generate the same equilibrium distributions. The entries in the lower part show that the equilibrium distributions are independent of the absolute masses of the initial standing crops. The parameters of the animals are $v = 0.01$ and $r = 1/512$. The simulation ran for 40,000 events. The means were computed after discarding the results from the first 20% of the duration of the simulation.

beginning of the simulation each animal has $m_{i,\alpha} = 2 + \delta m$, where δm is a small random perturbation to ensure that each animal is slightly different in mass from all the others. Table 5 shows the results of the simulation run over 40,000 visits by individual animals. The results in the first 20% of the simulation are neglected to avoid any transient effects due to the initial conditions.

Table 5 shows that the distribution of foragers is almost exactly as the Type II ideal free distribution predicts, the degree of undermatching being very small. The equilibrium standing crops in the simulations were not recorded because their close approximation to equality is logically entailed by the model. By definition the rate of removal of food by an animal is proportional to the standing crop (Eq. 4). The equilibrium number of animals is proportional to the rate of supply of food. Each of the feeding animals everywhere must therefore be feeding at approximately the same rate, and therefore each animal must be feeding at a patch of food containing the same mass of food. This implies that the distribution of the animals departs from that predicted by the Type I model, except in the case where the rate of supply of food is the same at each patch. More complex interactions involving nonlinear dependence of rate of feeding on standing crop, and direct interactions among individuals, are considered in the following sections.

In order to confirm that the behaviour of the simulations is independent of the initial conditions, the simulations were replicated with different initial masses of food at the three patches. These were 0.1, 0.2, and 0.4 units, and, as shown in Table 5, all permutations of the food and the regeneration rates were explored. The proportion of time spent at a patch was unaffected by the amount of food present at the beginning of the simulation. The observed variation in the proportions lying within the range of variability was caused by the stochastic process governing the choice of destinations. The effect of much larger initial amounts of food was explored by supplying initial masses of 4.0, 2.0, and 1.0 and 40.0, 20.0, and 10.0 units of food. Table 5 indicates that the proportions of the population occupying the patches are independent of the initial masses of food.

MIXTURES OF FREE AND SITE-FAITHFUL ANIMALS FORAGING IN TWO PATCHES

The settlement and continued feeding of animals at a particular site has no significant effect on the mean proportions of the population feeding at each patch if the

TABLE 6

The Influence of Animals That Stay Feeding at One Patch on the Overall Mean Distributions of Foragers in an Environment Containing Two Patches

No. stayers	n_0	n_1	n_0/n_1
0	10.326	21.062	0.490
5	10.248	21.093	0.486
10	10.341	21.093	0.490
15	10.357	21.093	0.491
20	10.341	21.093	0.490
25	6.705	25.000	0.268

Note. The simulation involved 32 foragers in all. The patches regenerated at the rates $a_0 = 0.01$ and $a_1 = 0.02$. The travelling time between patches was $t_i = 1$. The parameters of the foragers were $v = 0.08$ and $r = 1/128$. The simulation ran for 8000 time units; the means were calculated after discarding the results for the first 20% of the duration of each simulation. The ideal free ratio is $n_0/n_1 = 0.5$.

proportion that is settled is less than or equal to the proportion of the total regeneration of food taking place at that patch, such that at patch α , $n_\alpha/n < a_\alpha/\sum_{\beta=1}^p a_\beta$, where n_α is the number of settled, site-faithful, animals at patch α , and $n = \sum_{\alpha=1}^p n_\alpha$ is the total number of animals in the environment containing p patches of food, of which the patch β is regenerating at the rate a_β . An example of the effects of site-fidelity is shown in Table 6. Thirty-two animals foraging in two patches were simulated. Different numbers of settled animals were placed at Patch 1. The expected average occupancy was 1/3 of the population at Patch 0 and 2/3 at Patch 1. Table 6 shows that the presence of stayers has hardly any effect on the overall distribution until more than 2/3 of the foragers are settled at Patch 1.

THE EFFECT OF INTRASPECIFIC INTERACTION

Depletion of food and hunger cause the animals to move from patch to patch. As well as competing by exploitation, animals may also interact directly, altering each other's access to the food, typically reducing it; but for some species the feeding rate of the individual is *increased* as the number of conspecifics in the feeding area increases: among flock-feeding wading birds the cost per individual of vigilance may be reduced as the flock increases in size, enabling individuals to feed faster in larger flocks than in smaller ones. The simple case in which the standing crops at patches were not depleted by the feeding animals, but where the rate of feeding of

an individual was inversely proportional to the number of individuals feeding at the patch, was discussed by Ollason (1987). It was shown that in this case the distribution of animals approximated closely to the ideal free distribution of Type I. More complex interactions among animals may be modelled by making $R_i(F_\alpha)$, the functional response, a function of n_α , the number of animals in patch α , competition being represented by a decreasing function of n_α and facilitation by an increasing function. A simple representation of this effect is provided by the function

$$v(n) = (v_1 - v_\infty) e^{-u(n-1)} + v_\infty$$

$$R_i(F_\alpha, n) = v(n) F_\alpha$$

$$u = \frac{1}{(n_{1/2} - 1)} \ln(2),$$

where n is the number of animals at the patch, v_1 is the specific feeding rate when the animal is alone, v_∞ is the specific feeding rate of the animal in the presence of an infinite number of conspecifics, and $n_{1/2}$ is the number of animals at a patch that causes the specific feeding rate to take the mean of the maximum and minimum feeding rates, $(v_1 + v_\infty)/2$. If the animals are competing $v_1 > v_\infty$ and if facilitating $v_1 < v_\infty$. Such interaction could also have a similar effect on metabolic costs. This too could be modelled by making r within the patch a function of the number of occupants. An example of the effects of interference by suppression of feeding rate is shown in Table 7.

TABLE 7

The Influence of Interference Competition of Differing Intensities on the Mean Distributions of Foragers in an Environment Containing Two Patches

$n_{1/2}$	n_0	n_1	n_0/n_1
3	2.271	57.145	0.040
4	5.279	54.103	0.098
5	11.231	48.110	0.233
8	17.770	32.381	0.549
15	18.795	31.654	0.594
30	18.173	33.720	0.539
60	18.192	33.748	0.539
120	18.180	33.740	0.539

Note. The simulation involved 60 foragers in all. The patches regenerated at rates $a_0 = 0.001$ and $a_1 = 0.002$. The travelling time between patches was $t_r = 25$. The parameters of the foragers were $v_1 = 0.008$, $v_\infty = 0$, and $r = 1/128$. The simulation ran for 8000 time units; the means were calculated after discarding the results for the first 20% of the duration of each simulation. Except when interference is very severe ($n_{1/2}$ small), it has little effect on the mean distribution of the foragers. The ideal free ratio is $n_0/n_1 = 0.5$.

The expected proportion for large n is 1/3 of the feeding population at Patch 0 and 2/3 at Patch 1. Except when $n_{1/2}$ is very small, the population is distributed almost exactly in the ideal free distribution, implying that interference is unimportant in determining the equilibria unless extremely intense.

An example of the consequence of facilitation of feeding is shown in Fig. 1.

Thirty foragers were simulated foraging at two patches, regenerating at the rates, $a_0 = 0.001$, $a_1 = 0.002$, $v_1 = 0.008$, $v_\infty = 0.016$, and $n_{1/2} = 5$. The ideal free distribution therefore predicts that the proportion of feeding animals at Patch 0 will be 1/3 and at Patch 1 will be 2/3. Although the numbers of foragers at the patches fluctuates greatly, the mean number of animals occupying Patch 0 was 9.845, and Patch 1 was 16.504, making the proportion of the feeding animals feeding at Patch 0 equal to 0.374 and the proportion at Patch 1 equal to 0.626. In contrast interference, simulated by setting $v_1 = 0.008$, $v_\infty = 0.004$, and $n_{1/2} = 5$, produces only very small departures from the ideal free distribution of Type II (Fig. 2).

In the latter simulation the mean number of animals occupying Patch 0 was 9.907, and at Patch 1 the mean

TABLE 8

The Foraging Behaviour of 30 Similar Individuals Was Simulated in an Environment Containing Two Patches of Food, Each Patch Regenerating at a Constant Rate

$n_{1/2}$		$pa_0 = 1/2$	$pa_0 = 1/3$	$pa_0 = 1/5$	$pa_0 = 1/9$
5	pn_0	0.499	0.319	0.174	0.103
	pF_0	0.499	0.148	0.04	0.018
10	pn_0	0.500	0.340	0.204	0.108
	pF_0	0.500	0.323	0.20	0.151
20	pn_0	0.500	0.334	0.203	0.112
	pF	0.500	0.41	0.344	0.304
40	pn_0	0.498	0.336	0.205	0.111
	pF_0	0.50	0.456	0.41	0.402

Note. In the four different environments shown, Patch 0 regenerates at a_0 , Patch 1 at a_1 . The rate of regeneration at Patch 1 was always the same ($a_1 = 0.04$), and the regeneration of Patch 0 was $a_0 = 0.005$, 0.01, and 0.04. For all animals the maximum specific feeding rate, $v_1 = 0.08$, and the minimum specific feeding rate was $v_\infty = 0$ and $r = 1/128$. The proportion of the total rate of regeneration at Patch 0 is denoted by pa_0 , the proportion of the feeding foragers at Patch 0 is denoted by pn_0 , and the proportion of the standing crop of food at Patch 0 is denoted by pF_0 . The rows of the table shows the equilibrium proportions of food and foragers when all the foragers are equal competitors, and the presence of conspecifics decreases the feeding rate. The smaller the value of $n_{1/2}$, the more intense the competition. Notice that under the Type II interpretation, the distribution is close to the ideal free distribution, while under the Type I interpretation it departs increasingly as the intensity of the interference decreases.

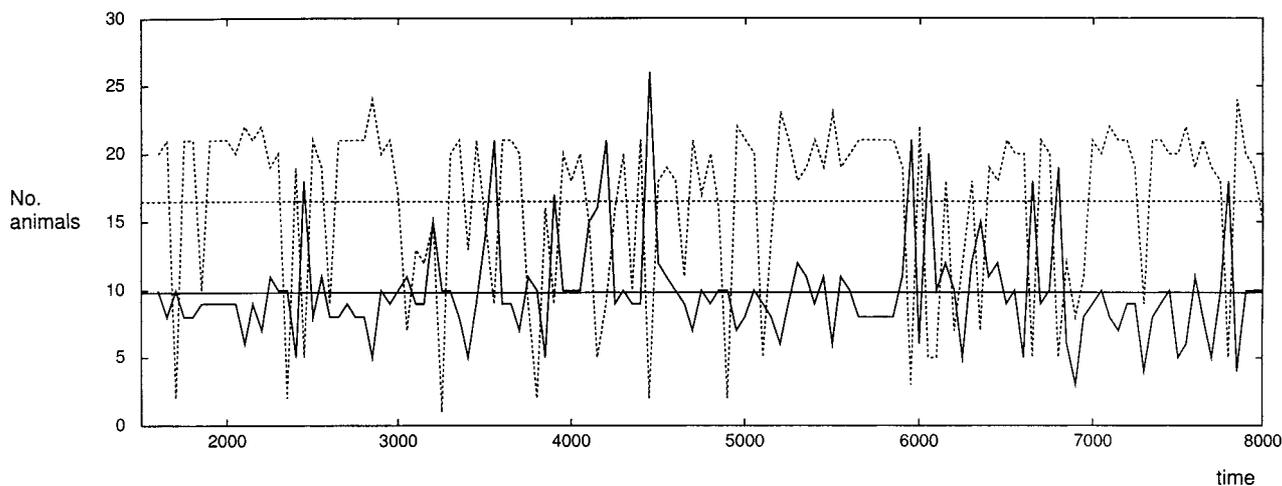


FIG. 1. The numbers of foragers searching for food at Patch 0, regenerating at rate 0.01 (solid lines), and Patch 1, regenerating at rate 0.02 (dotted lines). The straight lines indicate mean numbers of occupants over the duration of the simulation. Consecutive points in the curves are sampled at intervals of 50 time units. The constant lines indicate the mean numbers of animals feeding at the patch, calculated after transient behaviour has decayed to insignificance. The animals facilitate each other's feeding rate. The large variance in the numbers occupying the patches is caused by the fact that as one individual leaves a patch the feeding rates of the remaining animals are reduced, causing others to leave almost immediately. The expected proportion of feeding animals feeding at Patch 0 is $1/3$ and at Patch 1 is $2/3$; the observed mean proportions were 0.3736 and 0.6264 at patches 0 and 1, respectively. This represents a small degree of undermatching ($v_1 = 0.08$, $v_\infty = 0.016$, $n_{1/2} = 5$, $r = 1/128$).

number was 19.845. In facilitation, the departure of an individual depresses the feeding rate of the other individuals at the patch, causing more individuals to leave almost immediately (Fig. 1). In competition, the departure of one individual increases the rate of feeding at the patch, and this reduces the likelihood that others

will leave (Fig. 2). Despite the marked differences in the dynamics the mean distributions of animals in the two simulations are very similar.

The effect of the intensity of interference manifested by otherwise equal competitors has been investigated by simulating populations of animals of the same type, but

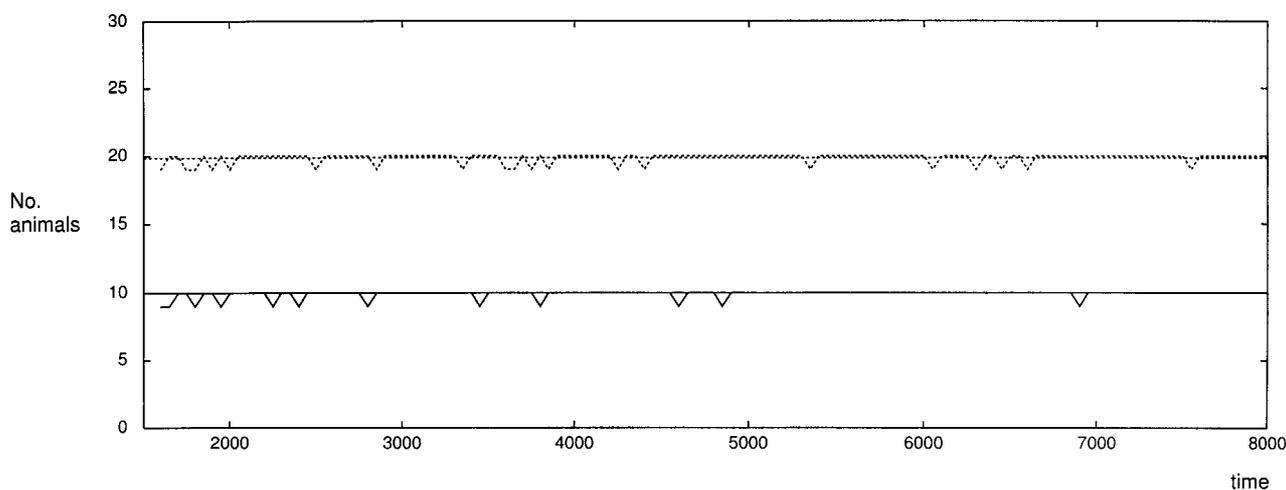


FIG. 2. The numbers of foragers searching for food at Patch 0, regenerating at rate 0.01 (solid line), and Patch 1, regenerating at rate 0.02 (dotted line). Consecutive points in the curves are sampled at intervals of 50 time units. The constant lines indicate the mean numbers of animals feeding at the patch, calculated after transient behaviour has decayed to insignificance. The animals interfere reducing each other's feeding rate. The small variance in the numbers occupying the patches is caused by the fact that as one individual leaves a patch the feeding rates of the remaining animals are increased, causing the others to remain feeding. The expected proportion of feeding animals feeding at Patch 0 is $1/3$ and at Patch 1 is $2/3$; the observed mean proportions were 0.3330 and 0.6670 at Patches 0 and 1, respectively ($v_1 = 0.008$, $v_\infty = 0.004$, $n_{1/2} = 5$).

with different values of $n_{1/2}$. Table 8 indicates that the intensity of the interference has very little effect on the proportions of the population foraging at the different patches, the distribution being close to the ideal free distribution of Type II, and that as competition becomes intense ($n_{1/2}$ becoming small), there is some suggestion that the distribution approaches that predicted by the Type I interpretation. The exact form of interaction function may be very important in determining the overall equilibrium distributions. The function we chose to represent interaction was chosen to have the following general properties: it is strictly monotonic and depending on the relationship between v_1 and v_∞ can be either increasing or decreasing, representing both facilitation and interference, respectively. The parameter $n_{1/2}$ is a convenient index of the intensity of interaction. For most normal cases of interference v_∞ will be equal to 0. However, in cases of facilitation it is likely that v_∞ would take some finite positive value.

MANY UNIDEAL ANIMALS (UNEQUAL COMPETITORS) FORAGING IN TWO PATCHES

Inequality may be simulated by assigning a different value of the functional response to each animal of the population of foragers, and in the linear case this is a different value of v , the specific feeding rate. Animals with

larger values of v will feed faster than those with smaller values, implying that animals with the larger values of v are the more effective competitors. An example of the results of allowing such unequal individuals to forage in two patches follows. The environment contained two patches of food separated by a travelling time, $t_i = 1$, Patch 0 with a regeneration rate $a_0 = 0.01$, and Patch 1 with a regeneration rate $a_1 = 0.02$. The animals possessed the same value of r , the metabolic rate, with $r = 1/128$. Each of 32 foragers had its own rank $i = 1, 2, \dots, 32$ and corresponding v_i , and $v_i = v_1 + (i - 1) \delta v$, where $v_1 = 0.08$ and $\delta v = 0.05$. (Note that in this simulation v is independent of the number of animals present at a patch, implying that the animals come into exploitation competition only).

Figure 3 shows that the mean proportions of the population approximate closely to the ideal free distribution of Type II, 0.327 and 0.673 (expected 1/3 and 2/3), but the occupancy of the patches varies with time and the degree of variation is a function of the difference between the most dominant (fastest feeding) and the least dominant (slowest feeding) individuals. The mean specific feeding rate, \bar{v} , is $(v_1 + v_n)/2$, and the mean rank, \bar{r} , is $(1 + n)/2$. If the animals are assorting themselves randomly, the mean rank per individual occupying either patch will approximate to \bar{r} , but if the animals collect together in a nonrandom way, the mean rank of the individuals at a patch will be a function of the number of animals occupying the patch.

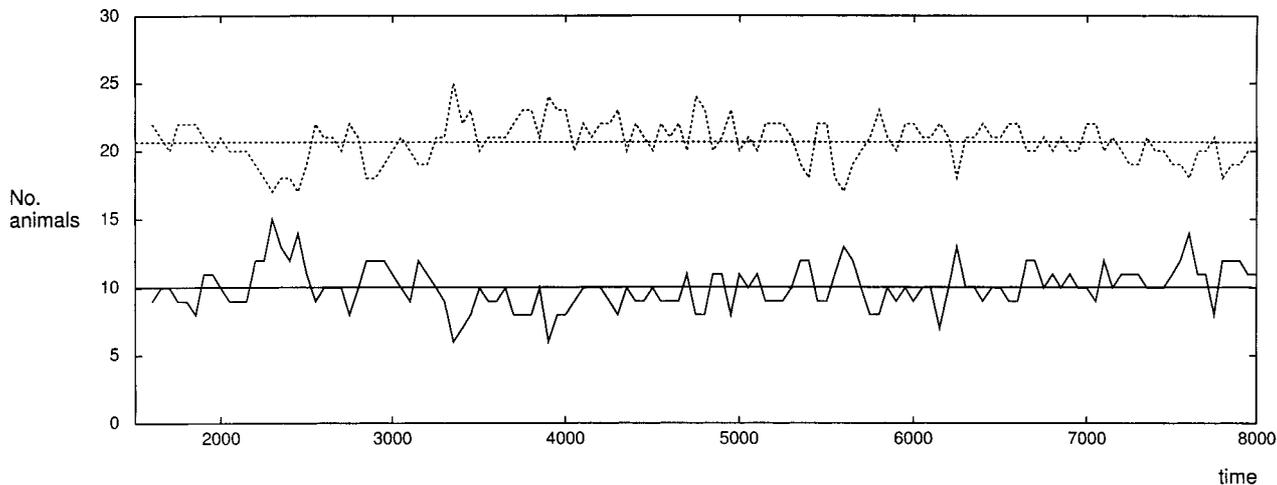


FIG. 3. The numbers of foragers searching for food at Patch 0, regenerating at rate 0.01 (solid line), and Patch 1, regenerating at rate 0.02 (dotted line). Consecutive points in the curves are sampled at intervals of 50 time units. The constant lines indicate the mean numbers of animals feeding at the patch, calculated after transient behaviour has decayed to insignificance. The foragers are linearly ranked in dominance, and this dominance is expressed through exploitation competition. The large variance in the numbers occupying the patches is caused by the fact that the dominant individuals collect together, and as they move from patch to patch they drive subordinates out and the subordinates travel to the other patch. The expected proportion of feeding animals feeding at Patch 0 is 1/3 and at Patch 1 is 2/3; the observed mean proportions were 0.3267 and 0.6731 at Patches 0 and 1, respectively.

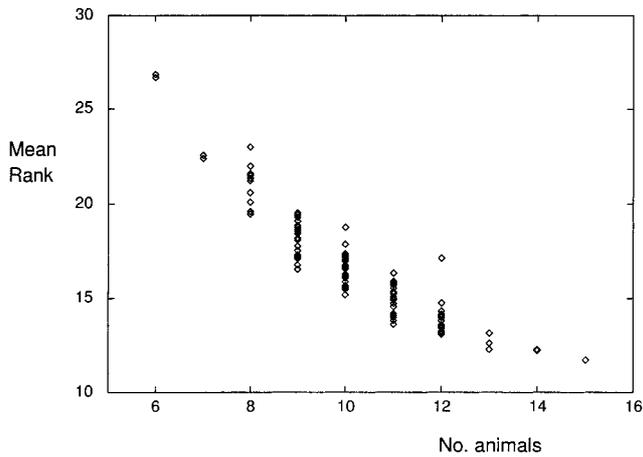


FIG. 4. The relationship between the mean rank of the individuals at Patch 0 and the number of animals occupying the patch. The strong negative correlation between the variables indicates that the animals are assorted such that animals with large ranks indicating large values of the specific feeding rate v drive others from Patch 0. The expected number of animals feeding at Patch 0 is 10.4574. The mean rank is 16.5.

Figure 4 shows the relationship between mean rank of individuals at Patch 0 as a function of the number of animals present. There is a strongly negative relationship between the mean rank of the occupying animals and the number occupying the patch. This shows that the dominant animals collect together and implies that their feeding activities drive the subordinates to the other patch.

Suppose, alternatively, that all the animals share the same value of v_1 , the specific feeding rate when foraging alone, and v_∞ , the specific feeding rate in the company of an indefinitely large number of conspecifics, with $v_1 > v_\infty$, and that the animals possess different values of $n_{1/2}$, the number of conspecifics at the patch that reduce the feeding rate to $(v_1 + v_\infty)/2$. A large value of $n_{1/2}$ implies that the feeding rate of an individual is reduced relatively little as the number of foragers at the patch increases. Dominant animals are therefore those with large values of $n_{1/2}$ and subordinates those with small values. The parameters used in this simulation were as above, but with the following exceptions: for all animals v_1 was set to 0.08 and v_∞ to 0.02, for the i th animal,

$$n_{1/2,i} = n_{1/2,1} + (i-1)\delta n, \quad (15)$$

where $\delta n = 0.5$. This simulation can therefore be interpreted as representing interference competition between unequal individuals.

In contrast to the first simulation, this one passed rapidly to equilibrium in all cases investigated, the equilibria undermatching the relative rates of supply

and dominant individuals occupying the more rapidly regenerating patch preferentially. The mean number of animals at Patch 0 was 12.085 and at Patch 1 was 18.803, the proportions being 0.390 (expected 1/3) and 0.609 (expected 2/3). If the animals were assorted exactly by rank the expected mean ranks are $(1 + 12)/2 = 6.5$ and $(13 + 32)/2 = 22.5$. The mean rank of animals at Patch 0 was 9.000 and at Patch 1 was 21.6316, indicating that the observed distribution of animals by rank is close to that predicted if the dominant animals were always found at Patch 1 and the subordinates at Patch 0.

Under exploitation competition the ideal free distribution of the animals implies that each one gets the same proportion of its food from either patch, but that the dominant animals feed, overall, faster than the subordinates; under interference competition all animals feed at the same rate, and the interference causes the observed distribution to depart from the ideal free distribution and assort the individuals into the different patches. This assortment process has some intriguing properties that are revealed by exploring the consequences of gradients of the intensity of intraspecific competition.

A series of simulations was carried out in an environment containing two patches of food regenerating at rates a_0 and a_1 , $a_1 = 0.04$, and $a_0 = 0.005, 0.01, 0.02$, and 0.04 in different simulations. The patches were separated by a travelling time, $t_t = 1$. The simulation used 30 foragers each with different specific feeding rates, v_i , set as defined by Eq. (15), but with differing values of δn , the gradient of the competitive abilities of the animals. If δn is large, this implies that the specific feeding rate of high ranking animals is reduced relatively little by the presence of conspecifics feeding at the same patch. The results of the simulations are shown in Table 9.

When the gradient of competitive ability is steep (δn large), the presence of conspecifics greatly reduces the average feeding rate of the individuals, the standing crop of food builds up at the patch, and the ideal free distribution arises, seemingly with respect to standing crop (the Type I interpretation), rather than with respect to the relative rates of regeneration (the Type II interpretation). This explains the close agreement between the mean proportion of standing crop at patch 0, pF_0 , and the mean proportion of foragers at patch 0, pn_0 , below the diagonal of Table 9. Where the gradient of competition is shallow pn_0 agrees more closely with the proportion of total regeneration rate at patch 0, pa_0 , (entries above the diagonal in bold type). In the absence of interference the proportion of animals feeding at a patch is independent of the standing crop of food at the patch and, indeed, the standing crop of food at each patch in the system will be the same, the distribution of the foragers being

TABLE 9

The Result of Simulating Populations of 30 Foragers Coming into Interference Competition for Food at Two Patches

δn		$pa_0 = 1/2$	$pa_0 = 1/3$	$pa_0 = 1/5$	$pa_0 = 1/9$
0	pn_0	0.498	0.318	0.174	0.103
	pF_0	0.499	0.148	0.050	0.017
0.25	pn_0	0.499	0.468	0.327	0.227
	pF_0	0.498	0.462	0.277	0.151
0.5	pn_0	0.503	0.474	0.337	0.236
	pF_0	0.502	0.479	0.335	0.214
1.0	pn_0	0.500	0.474	0.318	0.220
	pF_0	0.500	0.479	0.37	0.273

Note. The parameters of the simulations are the rate of regeneration of food at Patch 0, $a_0 = 0.040, 0.020, 0.010,$ and $0.005,$ and at Patch 1, $a_1 = 0.04$. The proportion of the total rate of regeneration that takes place at Patch 0 is denoted by pa_0 . The mean proportion of the foragers at Patch 0 is denoted by pn_0 . The patches are separated by a travelling time $t_t = 1$. The specific metabolic rate $r = 1/128$. Each animal has a numerical rank $i, i = 1, 2, 3, \dots, 30,$ and a specific feeding rate v_i . The feeding rate of each animal alone, $v_1 = 0.08,$ and $v_\infty = 0,$ and for $n_{1/2,1} = 5$. (This means that feeding at a patch with five conspecifics the specific feeding rate of that animal of rank 1 is reduced to half of that of v_1 .) For the animal of rank $i, n_{1/2,i} = n_{1/2,1} + (i - 1) \delta n,$ where δn takes the values shown above. The feeding rate of individuals of higher rank is reduced less by the presence of a given number of conspecifics than is the feeding rate of individuals of lower rank. In other words, the larger the value of $\delta n,$ the more extreme is the difference between the competitive ability of the individuals. When the gradient of competitive ability is steep, the presence of conspecifics reduces the average feeding rate of the individuals to the extent that food builds up at the patch, giving the appearance of the ideal free distribution under the Type I interpretation, and this is the cause of the close agreement between pF_0 and pn_0 below the diagonal of the table. Where the gradient of competition is less, pn_0 agrees more closely with pa_0 (entries above the diagonal in bold type).

determined only by the relative rates of regeneration of the patches.

DISCUSSION

Despite the fact that the model makes no explicit reference to optimality theory, its predictions depart only slightly from the ideal free distribution of Type II, and indeed for a single animal foraging in an environment containing two patches, if travelling time and metabolic costs are negligible, the equilibrium distribution is exactly as predicted by the ideal free model. In general the model predicts distributions that undermatch the ideal free distribution, and undermatching has been widely observed in nature (Kennedy and Gray, 1997). An important feature of the model is that the distribution of

animals predicted arises as a result of the distribution of staying times of the individuals. Other models accounting for the ideal free distribution are necessarily silent about the detailed processes causing the equilibria to arise.

For a few experimental systems, it has been discovered that the distribution of foragers, for example wood-ants (*Formica aquilonia*), approximated very closely to the ideal free distribution (Lamb and Ollason, 1993). When the behaviour of the ants had established the equilibrium, at each patch there was a pool of solution at which the ants fed. Had there been no pools, there would have been no feeding ants. Other studies of the foraging behaviour of animals in systems containing two regenerating patches include those of Milinski, (1979, 1984) and Harper, (1982), but these differ from the work of Lamb and Ollason because the food was added as discrete particles, rather than continuously, and because of this, the standing crop of food fluctuated as an item was added and was ingested almost, but not exactly, immediately by a feeding animal. The consequence of this is that in these experiments also there was, on average, a finite nonzero standing crop of food, contrary to the assumption of zero standing crop.

The model is an extreme simplification of the physiology of an animal, but it can be refined as required. The simple extensions of the model, allometric scaling of the specific metabolic rate, incorporation of the Holling Type II functional response, had little effect, the equilibrium distributions departing only a little from those generated by the simple model. If the model is to be applied to the prediction of the distribution of populations of particular animals, other biological properties are likely to be important: The gut of an animal is finite and, when filled, the animal may stop feeding. There is also a maximum of reserve tissue that an animal can embody. Finally, there is a lower limit to the reserves that allow an animal to survive. The processes of ingestion, digestion, and incorporation and the katabolism of resources can all be modelled and will play their part in determining the set of conditions in which the animal will become hungry.

The model in Eq. (2) has already been elaborated upon to incorporate aspects of the known physiology of the kittiwake, *Rissa tridactyla*. The physiological model represents the adult bird as two compartments, a gut, into which food passes and is digested, and a body of reserve tissue, from which metabolic costs are met. There is an additional mass of structural tissue, skeleton, etc., which imposes a fixed maintenance cost, but which is never available for maintenance. This elaborated version

has been applied, in preliminary studies, to predict the spatial distribution of foraging kittiwakes over the North Sea caused by the heterogeneous distribution of their food (Ollason *et al.*, 1997).

In homoiotherms, smaller animals have higher specific metabolic rates than larger ones (Peters, 1983). The model, dependent on the specific metabolic rate, implies that the degree of undermatching ought to increase with increasing specific metabolic rate and therefore with decreasing body mass in these animals. Such predictions are unique to this model and open up new areas of empirical inquiry.

The representation of interference and facilitation is very crude: the dependence on exponential processes has a distant connection to notions about random search in an increasingly crowded environment, but there is no empirical justification for the choice of the specific function. The simulations show that the study of the effects of competition is complicated by the qualitatively different effects of interference and exploitation which will almost certainly be operating to different degrees from time to time as populations of real animals search for food in the real environment.

Perhaps the most interesting result to arise from the simulation of interference competition is the feedback from the behaviour of the animals to the standing crop of food. The results provide a mechanism by which, for certain ranges of parameters, interference between competing foragers can lead to equilibria that appear to be close to those predicted by the Type I interpretation, even though two fundamental requirements of the Type I interpretation (no depletion and no regeneration) do not apply. The correct interpretation is that the interference causes the equilibrium to depart widely from the predictions of the Type 2 interpretation. This finding is intriguing because it provides evidence that approximation to the Type I interpretation need not imply that its underlying assumptions are satisfied.

The mapping from food to body mass may be complicated and difficult to evaluate, but is, in principle, evaluable. The dependence on body mass offers an escape from one of the conceptual problems implicit in conventional optimization theory, its dependence on the identification, *a priori*, of a single currency. The process of metabolism is the cause of changes of behaviour and the value of an item of food can be measured in terms of its contribution to the replacement of metabolic reserves.

Finally, we propose that the same processes of physiology and behaviour will apply in *all* circumstances in which animals forage. Other forms of foraging behaviour, such as central place foraging, and the selection of a diet

(Ollason and Lamb, 1995), can be modelled using the same principles, and when the parameters are evaluated for a particular animal its foraging behaviour can be predicted in all conceivable circumstances.

It is, perhaps, surprising that the interplay of physiology and behaviour alone, without explicit reference to natural selection, should provide so comprehensive an account of the origin of the approximately ideal more or less free distribution, but in view of the centrality of evolutionary arguments to other accounts, it is worthwhile discussing the elements of the model that might be amenable to evolutionary explanation.

On the basis of the results we suggest that undermatching is to be expected from the physiological consequences of metabolism. From the perspective of optimisation modelling these consequences could be regarded as constraints imposed by physiology on natural selection which would otherwise optimise the behaviour. From the point of view of the physiological model it is absurd to regard the specific metabolic rate, a fundamental necessity for the maintenance of life, as a constraint, preventing natural selection from instantiating the optimal foraging that would be observed if the animal possessed the optimal zero-specific metabolic rate.

Despite these reservations, the behaviour of the model is adaptive and may not be so very far away from optimisation models of foraging. Clearly, the model predicts behaviour that in the view of many biologists has been satisfactorily accounted for by the Ideal Free Distribution. The locality of the physiological model is the fundamental distinguishing feature that sets it apart from optimisation models. The physiological model makes no assertion about the ontological status of the environment; it depends on no characterisation of the environment from an omniscient point of view; instead, it derives the behaviour of the foraging animals from an assessment of their physiological needs and the behaviour by which they satisfy their needs, taking into account both the local availability of food and the local density of the other animals feeding on it. To the extent that the animal is doing "the best it can," its behaviour could be regarded as optimal, but among the infinity of ways that the animal could do the best it can, no single way can be identified as the best of all. What is interesting is not that animals forage more or less optimally, but that it is possible to account, using extraordinarily simple rules, for the small, consistent departures of the behaviour of animals from that predicted by optimisation methods. In broader terms still, the physiological model might be seen as an account epistemologically detached from the theory of evolution by natural selection. No animal,

however it was brought into existence, would be able to survive long enough to reproduce if it was unable to determine whether or not the food it chose to eat was satisfying its hunger. Foraging behaviour approximating closely to optimal foraging emerges automatically from the behaviour that satisfies hunger. Therefore, optimal foraging is not necessarily connected to natural selection, because there could never have been animals that foraged suboptimally, and therefore, no mutant optimal forager could ever have invaded the suboptimal population.

The model, by representing the utilisation of food as well as its collection, provides an account, not of the evolutionary game that leads to the ideal free distribution, but of the physiological processes that lead to the approximately ideal, more or less free distribution of real animals.

APPENDIX 1

The time budget of one animal foraging in an environment containing two patches of regenerating food

Here we present the proofs of the analytical results (Eqs. 11 and 12) for the simple model at equilibrium, where only one animal, indexed by i , is present in an environment containing only two patches. Equation (11) shows that large travelling times result in undermatching and in the limit $t_t \rightarrow \infty$ the forager has no preference for either patch. Equation (12) shows that approximation of the solution to the Type II interpretation of the ideal free distribution becomes exact in the limit $r \rightarrow 0$ and $t_t \rightarrow 0$. Equations (1), (2), (4), and (5) give the dynamical equations for the model which can be solved for each visit to a patch to give the general solution for the model *not necessarily at equilibrium* (Eqs. 6a and 6b). We use Eqs. (8) and (9) together with the requirement of equilibrium to obtain the behaviour of the model at equilibrium.

The patches are labelled 0 and 1 and have regeneration rates a_0 and a_1 , respectively. The method could be extended to more than two patches, although the algebra becomes very unwieldy. Note that in the following arguments, each time the animal arrives at patch 0 it stays $t_{i,0}$ time units feeding, then it travels t_t time units to patch 1, staying at patch 1 for $t_{i,1}$ time units, and then travelling t_t time units back to patch zero. Hence the total time spent on one circuit of both patches is $t_{i,0} + t_{i,1} + 2t_t$. The quantities ΔF_0 and ΔF_1 denote the changes in the standing crop of food between the arrival and the departure of the animal at Patch 0 and Patch 1,

respectively. When the system is at equilibrium, ΔF_0 and ΔF_1 are constants. In the following arguments, we continuously rescale time, so that $t = 0$ at the instant of arrival at a patch. The equations dealing with feeding are evaluated separately from the equations dealing with travelling.

At equilibrium, the depletion of the standing crop while the animal is foraging on the patch is equal to the regeneration of the standing crop while the animal is foraging elsewhere. This can be expressed by

$$\Delta F_0 = F_0(t_{i,0}) - F_0(0) = -a_0(t_{i,1} + 2t_t) \quad (1.1a)$$

$$\Delta F_1 = F_1(t_{i,2}) - F_1(0) = -a_1(t_{i,0} + 2t_t). \quad (1.1b)$$

Similarly, at equilibrium the value of reserve tissue of an animal entering patch 1 is equal to the value of reserve tissue when the animal left patch 0, discounted by the metabolic cost of travelling between the patches,

$$m_{i,0}(0) = m_{i,1}(t_{i,1}) e^{-rt_t} \quad (1.1c)$$

$$m_{i,1}(0) = m_{i,0}(t_{i,0}) e^{-rt_t}, \quad (1.1d)$$

where t_t is the travelling time between the patches, r is the specific metabolic rate of the animal, and at Patch 0, $t_{i,0}$ is the time spent foraging, $F_0(0)$ is the standing crop, $m_{i,0}(0)$ is the mass of the animal's reserve tissue when it starts feeding, and $m_{i,0}(t_{i,0})$ is the mass of the animal's reserve tissue when it leaves. The variables with the subscript 1 refer to the corresponding variables with respect to Patch 1.

In the case of large travelling times Eqs. (1.1c) and (1.1d) give

$$\lim_{t_t \rightarrow \infty} m_{i,0}(0) = 0 \quad (1.2a)$$

$$\lim_{t_t \rightarrow \infty} m_{i,1}(0) = 0. \quad (1.2b)$$

Substituting these results into Eq. (10) gives

$$\lim_{t_t \rightarrow \infty} t_{i,0} = t_{i,1} = \frac{1}{r-v} \ln \left(\frac{r}{v} \right) = \hat{t}_i, \quad (1.3)$$

where v is the specific feeding rate of the animal. So, as the travelling time increases, the time spent foraging on any patch approaches the extremal possible staying time. By simply extending the above argument it can be shown that Eq. (1.3), with \hat{t}_i given by the extremal value of Eq. (10), is true for any number of foragers on any number of patches.

Next to be considered is the case when metabolic costs become negligible, ($r \rightarrow 0$). By dividing Eq. (1.1a) by Eq. (1.1b) we obtain

$$\frac{\Delta F_0}{\Delta F_1} = \frac{a_0(t_{i,1} + 2t_t)}{a_1(t_{i,0} + 2t_t)}. \quad (1.4)$$

It will be shown that in limit, as $r \rightarrow 0$, $\Delta F_0/\Delta F_1 \rightarrow 1$, which implies the result given in Eq. (12).

We rewrite Eq. (10) as

$$\begin{aligned} F_\alpha(0) - F_\alpha(\infty) \\ = \frac{r}{v} \frac{v-r}{g(t_{i,\alpha})} (m_{i,\alpha}(0) - m_{i,\alpha}(\infty)) e^{-rt_{i,\alpha}} \end{aligned} \quad (1.5)$$

where $g(t_{i,\alpha}) = r \exp(-vt_{i,\alpha}) - v \exp(-rt_{i,\alpha})$, $F_\alpha(\infty) = a_\alpha/v$, and $m_{i,\alpha}(\infty) = a_\alpha/r$. Substituting Eq. (1.5) into Eq. (9) gives an expression for $m_{i,0}(0)$:

$$\begin{aligned} Am_{i,0}(0) = m_{i,1}(\infty) g(t_{i,0})(g(t_{i,1}) + (r-v) e^{(r-v)t_{i,0}} \\ - m_0(\infty)(r-v) e^{-(r-v)t_{i,1}-rt_t} \\ \times (g(t_{i,0}) + (r-v) e^{-(r-v)t_{i,0}}), \end{aligned} \quad (1.6)$$

where $A = g(t_{i,0}) g(t_{i,1}) \exp(rt_t) - (v-r)^2 \exp(-rt_t) \exp(-(r+v)(t_{i,0} + t_{i,1}))$. Similarly, an expression for $m_{i,1}(0)$ can be calculated to have the same form as Eq. (1.6), but with the indices 0 and 1 reversed.

In the limit, as $r \rightarrow 0$, Eq. (1.6) can be written as

$$\begin{aligned} Am_{i,0}(0) = m_{i,0}(\infty) rve^{-vt_{i,0}}(e^{-vt_{i,1}}(1 - vt_{i,1}) - 1) \\ + m_{i,1}(\infty) rve^{-vt_{i,1}}(e^{-vt_{i,0}}(1 - vt_{i,0}) - 1) \\ + O(r^2) \end{aligned} \quad (1.7)$$

and similarly for $m_{i,1}(0)$. Because the right-hand side of Eq. (1.7) remains the same when the indices 0 and 1 are exchanged, it follows that

$$\lim_{r \rightarrow 0} m_{i,0}(0) = m_{i,1}(0), \quad (1.8)$$

and substituting this result into Eqs. (1.1c) and (1.1d) also gives

$$\lim_{r \rightarrow 0} m_{i,0}(t_{i,0}) = m_{i,1}(t_{i,1}). \quad (1.9)$$

Finally, by substituting this result into the solutions for F_α and $m_{i,\alpha}$ (Eqs. 8 and 9), it follows that

$$\lim_{r \rightarrow 0} \Delta F_0 = \Delta F_1, \quad (1.10)$$

which can be used in Eq. (1.4) to arrive at the result

$$\lim_{r \rightarrow 0} \frac{t_{i,1} + 2t_t}{t_{i,0} + 2t_t} \frac{a_0}{a_1} = 1, \quad (1.11)$$

which after rearrangement gives the result presented in Eq. (12).

APPENDIX 2

One animal foraging in an environment containing more than two patches all regenerating at the same constant rate

An investigation of the relationship between the local model developed above and optimal foraging theory indicates that in the special case of foraging around a closed trapline containing patches of food regenerating at the same constant rate, each patch separated from the next one visited by the same constant travelling time t_t , as $r \rightarrow 0$, if the number of patches in the trapline becomes indefinitely large, the behaviour of the model approaches that predicted by the marginal value theorem. Suppose that the environment contains p patches, that each patch regenerates at rate a , and that each patch is separated from its neighbour by a travelling time of t_t . Each patch is assigned an index $\alpha = 0, 1, 2, \dots, p-1$ and arranged in the form of a closed trapline, such that on the n th visit the animal is at patch $n \bmod p$.

Since the patches all regenerate at the same rate, it will be assumed that the behaviour of the animal will come to an equilibrium such that it spends the same time at each patch. Numerical simulations discussed in the body of the paper provide evidence that such equilibria, while perhaps not unique, do arise. In this case Eqs. (1.1a-d) can be rewritten as

$$\begin{aligned} \Delta F_\alpha &= F_\alpha(t_{i,\alpha}) - F_\alpha(0) \\ &= -a \left(\sum_{\beta=0}^{p-1} t_{i,\beta} - t_{i,\alpha} + pt_t \right) \end{aligned} \quad (2.1a)$$

$$m_{i,\alpha}(0) = m_{i,\alpha}(t_{i,\alpha}) e^{-rt_t}, \quad (2.1b)$$

where α and $\beta = 0, \dots, p-1$, r is the animal's specific metabolic rate, $t_{i,\alpha}$ is the time spent feeding at patch α , $F_\alpha(0)$ is the standing crop and $m_{i,\alpha}(0)$ the mass of the animal's reserve tissue when it starts foraging at patch α , and $F_\alpha(t_{i,\alpha})$ and $m_{i,\alpha}(t_{i,\alpha})$ are, respectively, the mass of food remaining at the patch and the mass of its reserve tissue when the animal leaves patch α .

By substituting Eq. (2.1b) into the general solution for $m_{i,\alpha}(t)$ (Eq. 9), discarding the patch subscripts because each patch will be identical when the animal arrives to feed, and rearranging, it follows that

$$\frac{v-r}{g(t_i)} (m_i(0) - m_i(\infty)) e^{-rt_i} = \frac{m_i(\infty)(v-r)(e^{rt_i} - 1)}{(e^{r(t_i+t_i)}(ve^{-vt_i} - re^{-rt_i}) - (v-r)e^{-vt_i})} \quad (2.2)$$

where $g(t_i) = r \exp(-vt_i) - v \exp(-rt_i)$.

The left-hand side of Eq. (2.2) can be replaced by $F(0) - F(t_i)$ using Eqs. (1.5), (8), and (2.1a) to give

$$(p-1)t_i + pt_i = \frac{v-r}{v} \frac{(e^{-rt_i} - 1)(1 - e^{-vt_i})}{((v-r)e^{-vt_i} - e^{-r(t_i+t_i)})(ve^{-vt_i} - re^{-rt_i})}. \quad (2.3)$$

In the limit as $r \rightarrow 0$, Eq. (2.3) becomes

$$\lim_{r \rightarrow 0} \left(\frac{p-1}{(p-1)t_i + pt_i} \right) = \frac{ve^{-vt_i}}{1 - e^{-vt_i}}. \quad (2.4)$$

In the limit, as $p \rightarrow \infty$, Eq. (2.4) yields the optimal solution obtained from the marginal value theorem (Charnov, 1976). This can be shown by considering the feeding rate of one animal on one type of patch:

$$vF(t_i) = vF(0) e^{-vt_i}, \quad (2.5)$$

where $F(0)$ is the standing crop of food when the animal first started feeding at the patch, and t_i is the time spent feeding. Using this rate of feeding, \bar{F} , the mean rate of intake of food in the absence of metabolic costs may be expressed as

$$\bar{F} \propto \frac{\int_0^{t_i} vF(t) dt}{t_i + t_i}. \quad (2.6)$$

The marginal value theorem states that the optimal solution is the one that maximizes \bar{F} . By differentiating

Eq. (2.6) with respect to t_i and equating the derivative to zero, the maximum rate of intake of food occurs when the staying time t_i satisfies

$$ve^{-vt_i} = \frac{1 - e^{-vt_i}}{t_i + t_i}, \quad (2.7)$$

which is also the limit of Eq. (2.4). Notice, however, that the mathematics implies implausible biology. At equilibrium each patch of an indefinitely long trapline will contain the same indefinitely large amount of food by the time the animal revisits a given patch, and in the presence of such an amount of food, the requirement that v , the specific feeding rate, is constant will not be even approximately true for a real animal. Furthermore, the specific metabolic rate of a real animal cannot approach zero. The value of the approach is that it implies the physiological conditions of the animal that are necessary for the animal to produce the optimal behaviour, and it predicts the expected departures as a function of the physiological properties of the animal and its responses to the local properties of the environment in which it finds itself.

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