Patterns of patch rejection in size-structured populations: beyond the ideal free distribution and size segregation

Frederick R. Adler,[1]* Shane A. Richards[2]‡ and André M. de Roos[2]

[1]*Department of Mathematics and Department of Biology, University of Utah, 155 South 1400 East, Salt Lake City, UT 84112–0900, USA and* [2]*Section of Population Biology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, Netherlands*

ABSTRACT

We examine optimal patch allocation strategies in a population structured by size or some other characteristic. By treating size-specific differences among patches as limiting factors, we create a single framework to analyse foraging for two resources, foraging in the presence of predators and foraging in the presence of competition. The ideal free distribution or size segregation are optimal only in restricted circumstances, among a range of other intermediate patterns of patch rejection. The predicted pattern can shift from an ideal free distribution to various forms of size segregation as resource renewal rates in patches become more different.

Keywords: foraging–predation trade-off, ideal free distribution, optimal foraging, size structure.

INTRODUCTION

When a population of foragers redistributes optimally among patches with different levels of resource availability, we might expect a correlation between the number and character of foragers present and the available resource. Under simple conditions, optimal foragers are predicted to redistribute themselves among patches so that no consumer would receive a different payoff if it moved to another patch, the ideal free distribution (IFD) (Fretwell and Lucas, 1970). When foragers differ in competitive ability, size or some other aspect of their state, the IFD is optimal only under particularly simple assumptions; for example, if foragers differ only in the rate at which they collect food (Parker and Sutherland, 1986; Sutherland and Parker, 1992). Ideal free distributions permit patches to be shared by all sizes of forager. Other differences among foragers can lead to segregation of foragers into different patches (Parker and Sutherland, 1986; Sutherland and Parker, 1992). For example,

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* Author to whom all correspondence should be addressed. e-mail: adler@math.utah.edu
‡ *Present address*: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101-5504, USA.

if some foragers are more susceptible to predation than others, they should often reject dangerous patches even if they are highly productive.

The distribution of organisms can be summarized in patterns of patch rejection. Some patches of poor quality might be rejected by all foragers, which we term universally rejected patches. In this case, the rejection pattern is not state-dependent. We refer to patches used by one or more foragers as accepted patches. In the ideal free distribution, no accepted patch is rejected by any state (Fig. 1a). At the other extreme, as in the predation example, different states reject different patches and thus segregate by state (Fig. 1b). In a model of dominance, Holmgren (1995) found an intermediate pattern he termed the semi-truncated distribution, where the most dominant foragers reject the poor patches, while the most subordinate foragers use all acceptable patches (Fig. 1c).

The risk of predation that leads to state segregation and the dominance hierarchy that leads to the semi-truncated distribution can both be thought of as limiting factors for the population in addition to the food resource itself (Levin, 1970). Many limiting factors, other than food, have been considered in models of patch selection, including predation (Ward *et al.*, 2000), competitive ability (Spencer *et al.*, 1995), interference (Moody and Houston, 1995) and dominance (Holmgren, 1995). In addition, a population could have two foods as limiting factors.

Some limiting factors, such as food, specialist predators and competition, respond to forager distribution. Others, such as generalist predators, available cover, optical clarity and temperature, may be fixed. We will show that the way that limiting factors respond to foraging determines the patterns of patch rejection, ranging from the IFD to segregation via several intermediate distributions.

We begin by reviewing models with a single limiting factor (thought of as a food), reiterating the conditions under which size-specific differences lead to segregation (Parker
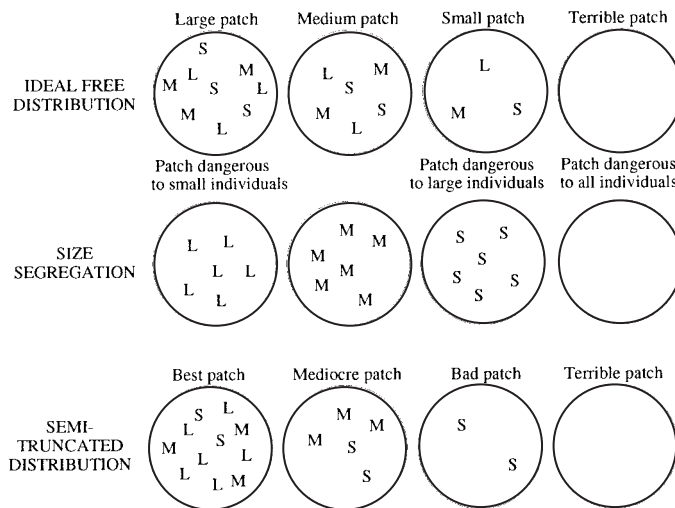

Fig. 1. Patterns of patch rejection illustrating the ideal free distribution, complete size segregation and the semi-truncated distribution. The letters S, M and L represent small, medium and large foragers respectively.

and Sutherland, 1986; Sutherland and Parker, 1992). For convenience, we discuss differences in size rather than state in general, although our results apply directly to the more general case. We then treat cases with two limiting factors: one a food and the other either fixed at different levels in different patches or responsive to forager number or size. Specifically, we consider the following cases:

1. Two food resources.

   (a) Filter feeders eat both foods upon encounter.
   (b) Perfect-preference feeders choose a single food in a given patch.
   (c) Optimal foragers choose the single food or combination of foods that maximizes intake rate.

2. One food resource and predation.

   (a) Generalist predators that do not respond to forager size and number.
   (b) Specialist predators that respond to forager size and number.

3. One food resource and competition.

   (a) Exploitation, where the interaction is mediated solely through food.
   (b) Interference, where the interaction depends on the ratio of sizes of foragers.
   (c) Dominance, where large individuals suppress small ones.

Our aims are to predict optimal patterns of patch rejection in these cases and to find commonalities among apparently different types of limiting factor.

MODELS WITH ONE LIMITING FACTOR

Although the case of one food resource has been modelled in detail (Parker and Sutherland, 1986; Sutherland and Parker, 1992), we include the analysis to introduce notation and to emphasize critical assumptions. Our models assume simple dynamics of the resources and track the standing crop (equilibrium level) of a resource rather than the input rate (Lessells, 1995; Frischknecht, 1996). We suppose that foragers redistribute quickly among patches relative to the speed of resource dynamics and ignore dynamical feedback (Kacelnik *et al.*, 1992; Abrams, 1999). Furthermore, we treat foragers as a density rather than as individuals, thus neglecting finite population size effects (Houston and McNamara, 1988; Ruxton and Humphries, 1999).

The basic model tracks a population of foragers that differ in size or some other state, indexed by s, which choose among a set of patches indexed by i. The total number (or density) of foragers of size s is a fixed function $N(s)$, meaning that the models treat foraging redistribution as fast relative to changes in population or forager size.

The forager strategy $N_i(s)$ is the number of foragers of size s foraging in patch i. Resources R_i in patch i obey

$$\frac{\mathrm{d}R_i}{\mathrm{d}t} = \rho_i - \left(\int a(s)N_i(s)\mathrm{d}s \right)R_i - \delta_i R_i \tag{1}$$

where ρ_i is the renewal rate and δ_i is the decay rate (see Table 1 for a complete description of notation). A non-zero decay rate guarantees that the resources will not increase without

Table 1. Variables, parameters and functions in
the single-resource model

s	size (or state) of forager
$N(s)$	density of foragers of a given size
$a(s)$	rate of resource collection by size s
i	index for patches
R_i	resource level in patch i
ρ_i	resource renewal rate in patch i
δ_i	resource decay rate in patch i
$N_i(s)$	number of foragers of size s in patch i

bound even in the absence of foragers. The collection function $a(s)$ describes the per capita rate of resource capture by foragers of size s. In the simplest model, this function does not depend on the patch i.

We suppose that foragers prefer patches where they can collect more resources. Because the collection function $a(s)$ does not depend on the patch, foragers of all sizes prefer the patch with the highest resource density. Thus, they deplete all patches to the same equilibrium (patches with a sufficiently low equilibrium in the absence of foragers are universally rejected).

More formally, resources in patch i reach an equilibrium of R_i^* given by

$$R_i^* = \frac{\rho_i}{\int a(s)N_i(s)\mathrm{d}s + \delta_i}$$

This equilibrium is evolutionarily stable if $R_i^* = R^*$ in each accepted patch. Such a solution does not uniquely determine the values of $N_i(s)$. Many distributions result in identical consumer pressure and resource densities in each patch (Houston and McNamara, 1988; Hugie and Grand, 1998; Ruxton and Humphries, 1999). The model makes no specific prediction about the distribution of size classes among patches because no size class is predicted to reject certain patches.

MODELS WITH TWO LIMITING FACTORS

The model with a single limiting factor can modify the ideal free distribution, but cannot lead to size-dependent patterns of patch rejection. In this section, we introduce two models that include two limiting factors, and show the patterns of size-dependent patch rejection that can occur. In the first, foragers cope with a depletable food resource and with a fixed limiting factor that does not change in response to forager pressure (e.g. a generalist predator, temperature or optical clarity). This fixed limiting factor acts as a patch-specific difference. In the second, foragers cope with two depletable food resources, each of which has its own dynamics.

One food and one fixed limiting factor

Foragers may segregate by size if patches differ in some way other than resource density. For example, some patches may have higher levels of predation on small foragers, or some may have resources that are easier for large foragers to collect. We generalize the basic

model (equation 1) by making the collection function $a(s)$ a function of the patch i with a subscript, $a_i(s)$.

Foragers of size s prefer patch i to patch j if

$$a_i(s)R_i > a_j(s)R_j$$

and are indifferent if

$$a_i(s)R_i = a_j(s)R_j$$

For a set of sizes to be indifferent to patches i and j (and to follow an IFD), all sizes s in that set must satisfy

$$\frac{a_i(s)}{a_j(s)} = \frac{R_j}{R_i}$$

This implies that the ratio of $a_i(s)$ to $a_j(s)$ must be size-independent. This is possible only if the functions $a_i(s)$ and $a_j(s)$ are proportional to each other, which we term perfect size scaling (Fig. 2).

If the curves $a_i(s)$ are not proportional, the model predicts size-dependent patterns of patch rejection. Figure 3 shows segregation of size classes into three patches, where large foragers are relatively best at foraging in patch 3, and choose that patch even though it has the lowest resource renewal rate. This reproduces the results of Parker and Sutherland (1986) and Sutherland and Parker (1992), except that we consider a continuum of size classes.

Two foods

Suppose patches contain two food resources, R and Q, which obey

$$\frac{dR_i}{dt} = \rho_i - (\int a(s)N_{iR}(s)ds)R_i - \delta_i R_i$$

$$\frac{dQ_i}{dt} = \sigma_i - (\int b(s)N_{iQ}(s)ds)Q_i - \zeta_i Q_i \qquad (2)$$

where σ_i is the renewal rate and ζ_i is the decay rate of resource Q in patch i (see Table 2 for a description of new parameters). $N_{iR}(s)$ and $N_{iQ}(s)$ represent the number of foragers of size s in patch i eating resources R and Q respectively, without excluding the possibility that some foragers consume both resources. The collection function $b(s)$ describes the per capita rate of capture of resource Q by foragers of size s and does not depend on the patch i because there are no other implicit limiting factors in the model.

Table 2. Additional variables, parameters and functions in the two-resource model

Q_i	level of resource Q in patch i
$b(s)$	rate of collection of resource Q by size s
σ_i	rate of renewal of resource Q in patch i
ζ_i	rate of decay of resource Q in patch i
$\upsilon(s)$	vulnerability of size s to predation
$\alpha(s, s')$	interference by one forager of size s' on one of size s

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a
Perfect size scaling: curves proportional

b
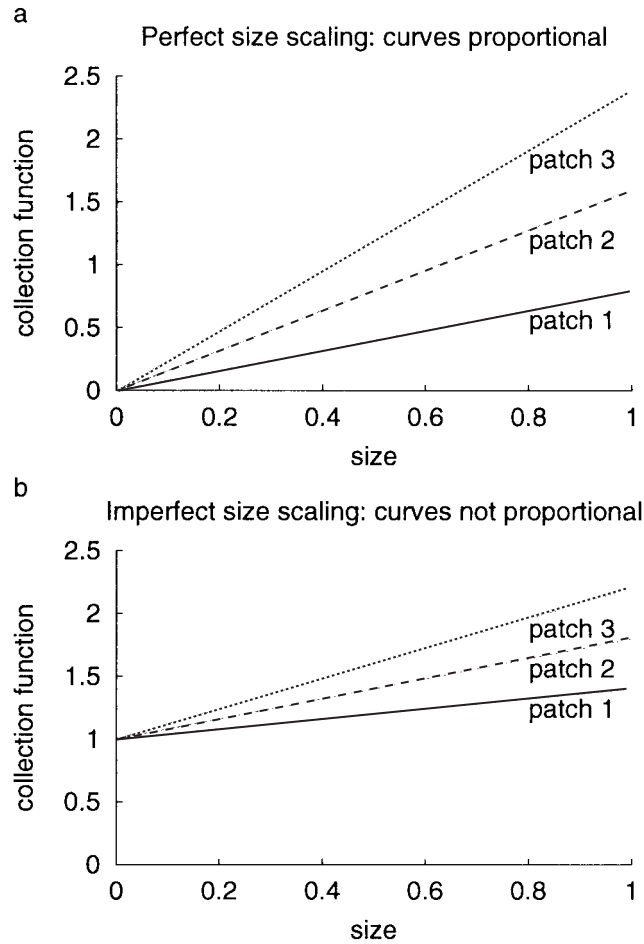### Imperfect size scaling: curves not proportional

Fig. 2. (a) Perfect size scaling with proportional collection functions $a_1(s) = 0.8s$, $a_2(s) = 1.6s$ and $a_3(s) = 2.4s$ in patches 1, 2 and 3 respectively. (b) Imperfect size scaling with non-proportional collection functions $a_1(s) = 1.0 + 0.4s$, $a_2(s) = 1.0 + 0.8s$ and $a_3(s) = 1.0 + 1.2s$ in patches 1, 2 and 3 respectively.

Foragers favoured with two food resources must make two choices: where to forage and what to eat. We consider three types of forager (as in Krivan and Sikder, 1999).

1. *Filter feeders* eat both resources simultaneously at rates proportional to resource densities.
2. *Perfect-preference foragers* consume only one resource at any one time, but can switch between resources.
3. *Optimal foragers* adjust their effort to consume either the single resource or the combination of resources that maximizes intake.
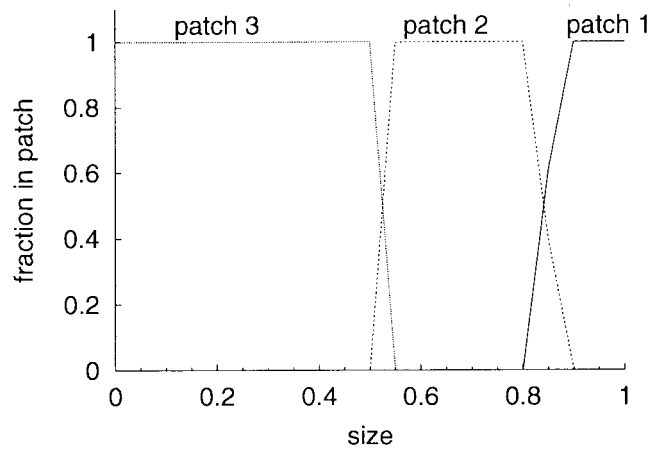
Fig. 3. Results of simulation of size segregation in three patches with non-proportional collection functions. The smallest foragers use patch 1 (solid line), the medium foragers use patch 2 (dashed line) and the largest use patch 3 (dotted line). The 21 size classes are evenly spaced and equally abundant, ranging from $s = 0$ to $s = 1$. The functions $a_i(s)$ are $a_1(s) = 1.0 + 0.4s$, $a_2(s) = 1.0 + 0.8s$ and $a_3(s) = 1.0 + 1.2s$, as in Fig. 2b. The parameter values are $\rho_1 = 1$, $\rho_2 = 2$, $\rho_3 = 3$ and $\delta_i = 1$. Simulations are done by allowing foragers of each size and strategy (here a patch choice) to reproduce at rates proportional to collection rates, normalizing the total population of each size class to its initial value after each time step, and repeating until values converge within a given tolerance.

Filter-feeders

Suppose that the profitability of patch i is a function of $a(s)R_i + b(s)Q_i$, the per capita rate of energy intake if R and Q are both measured in the same units. In this case, the resources are said to be perfectly substitutable (Tilman, 1982). Patch i is preferred over patch j if

$$a(s)R_i + b(s)Q_i > a(s)R_j + b(s)Q_j$$

When the collection functions $a(s)$ and $b(s)$ are proportional, all size classes share the same preference for the most resource-rich patch – that with the largest weighted sum of R and Q – and thus an IFD is the prediction.

There are two possible outcomes of the dynamics when $a(s)$ and $b(s)$ are not proportional. Patches might arrive at different equilibrium values of R and Q, resulting in size segregation of foragers. Alternatively, patches could achieve equal equilibria of R and equal equilibria of Q, which we term resource convergence.

To give some idea of how similar the input and decay rates must be for resource convergence to occur, we find the criteria for two patches. We find the set of input and decay parameters for which an equilibrium exists where $R_1^* = R_2^* = R^*$ and $Q_1^* = Q_2^* = Q^*$. The detailed calculations are presented in Appendix 1. Patches become identical if they are relatively similar to begin with, and remain different if they are somewhat more different (Fig. 4). One patch is universally rejected if it is too inferior. The region of resource convergence is larger when $a(s)$ and $b(s)$ are close to being proportional.
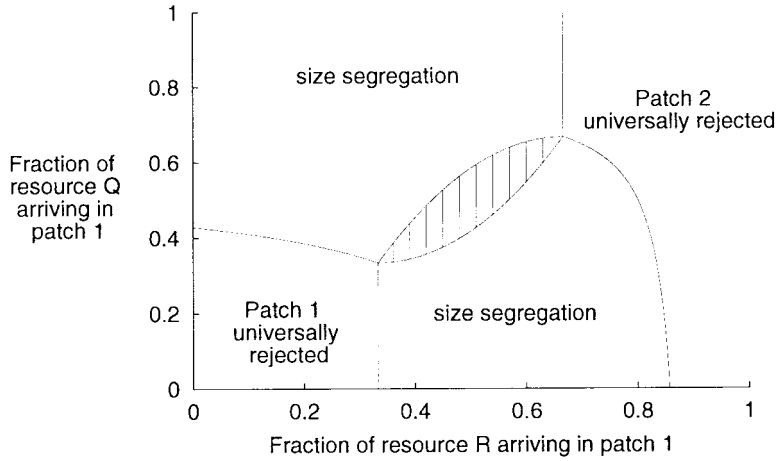
Fig. 4. Conditions under which a range of foragers in two patches achieve resource convergence (shaded region), universally reject one patch, or size-segregate into both patches. The axes show the proportion of total resource renewal rate in patch 1, given by $\rho_1/(\rho_1 + \rho_2)$ for resource R and by $\sigma_1/(\sigma_1 + \sigma_2)$ for resource Q. Foragers are distributed uniformly over the size range from $s = 0$ to $s = 1$; $a(s) = 1$, $b(s) = 2s$ and $\delta_i = \zeta_i = 1$ (see Appendix 1 for details).

With multiple patches, some pairs of patches converge to be identical, others remain unique and some are universally rejected. An example with five patches is depicted in Fig. 5. Patch 1 is universally rejected, patches 2 and 3 become identical, patch 4 is used exclusively by the smallest size classes, which are relatively most efficient at collecting resource R, and patch 5 is used exclusively by the largest size classes, which are relatively most efficient at collecting resource Q. The irregular lines for the intermediate size classes that use patches 2 and 3 result from the indeterminacy of the ideal free distribution, and depend on the particular choice of initial conditions. The equilibrium densities R^* and Q^* in accepted patches lie along a curve (Fig. 5b).

Perfect-preference foragers

These foragers consume only one food resource at a time, and must choose both a patch and a resource to consume. Resource R in patch i is preferred by size s if

$$a(s)R_i > a(s)R_j \quad \text{for all } j \neq i$$

and

$$a(s)R_i > b(s)Q_j \quad \text{for all } j$$

With a single patch, this model is formally identical to a two-patch version of the model with one food and one fixed limiting factor (see pp. 808–809).

As long as some foragers consume R and some consume Q, all accepted patches must achieve equal equilibria R^* and Q^*. Patches break into four categories:
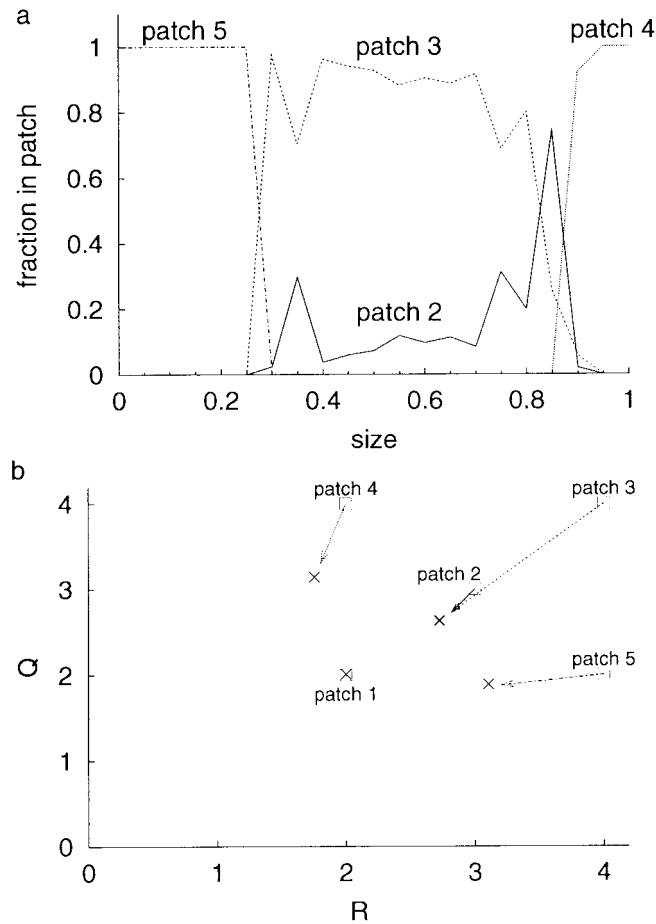
Fig. 5. Results of simulation with the filter-feeding strategy. (a) Distribution of foragers in five patches. Patch 1 is universally rejected and does not appear, foragers of intermediate size use patches 2 (solid line) and 3 (dashed line), the largest foragers use patch 4 (dashed line) and the smallest use patch 5 (dot-dashed line). (b) Equilibrium levels R and Q with and without foragers in the five patches. Boxes show the equilibrium without foraging; crosses show the equilibrium with foragers. The parameters values are: $\rho_1, \ldots, \rho_5 = 2, 3, 4, 2, 4; \sigma_1, \ldots, \sigma_5 = 2, 3, 4, 4, 2; a(s) = 1, b(s) = 2s$ and $\delta_i = \zeta_i = 1$.

1. Those with $R_i = R^*$ and $Q_i = Q^*$ are used for both resources.
2. Those with $R_i < R^*$ and $Q_i = Q^*$ are used for Q only.
3. Those with $R_i = R^*$ and $Q_i < Q^*$ are used for R only.
4. Those with $R_i < R^*$ and $Q_i < Q^*$ are used for neither.

   Typically, size classes specialize on a food resource but not on a single patch, which we refer to as a dual IFD. In Fig. 6, large foragers specialize on resource Q, and reduce equilibria of that resource to equal values in patches 2, 3 and 4, rejecting patches 1 and 5. Small foragers specialize on resource R, and reduce equilibria of that
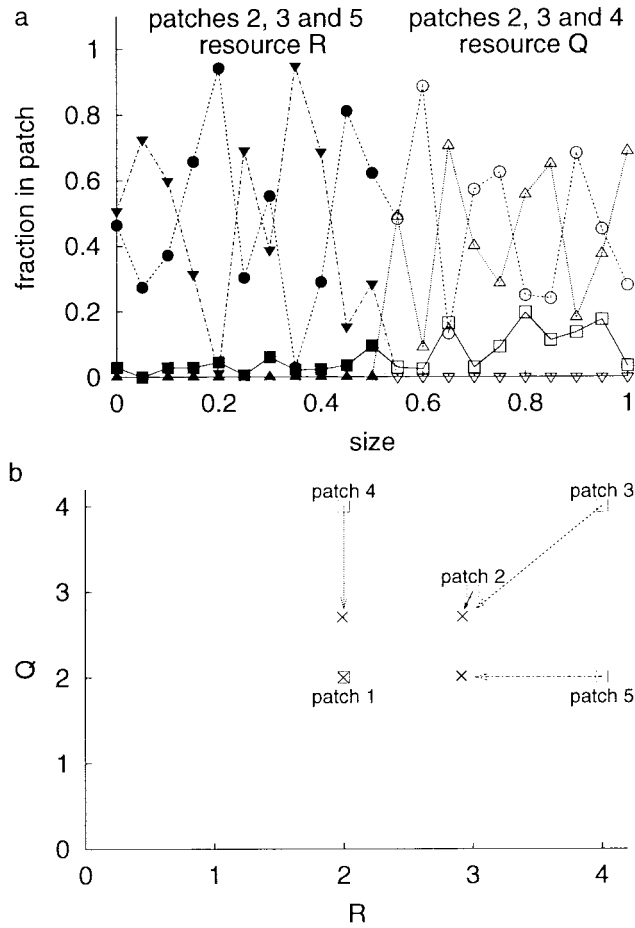
Fig. 6. Results of simulation with the perfect-preference strategy (parameters and methods as in Fig. 5). (a) Distribution of foragers in five patches. Patch 1 is universally rejected and does not appear. Small foragers use resource *R* (solid symbols) in patches 2 (solid line, squares), 3 (dashed line, circles) and 5 (dot-dashed line, inverted triangles). Large foragers use resource *Q* (open symbols) in patches 2, 3 and 4 (dashed line, triangles). Simulations done as in Fig. 3 except that strategies now include a resource in addition to a patch choice. (b) Equilibrium levels of *R* and *Q* with and without foragers in the five patches (as in Fig. 5b).

resource to equal values in patches 2, 3 and 5, rejecting patches 1 and 4. As before, the irregular lines result from the indifference foragers have among accepted patches. The equilibrium densities R^* and Q^* in accepted patches lie along a corner rather than a curve (Fig. 6b).

Optimal foragers

A detailed model of optimal foragers would include handling times, encounter rates and the energy values of the two resources as functions of forager size (Stephens and Krebs, 1986).

To indicate the qualitative results, we present a simple scenario where foragers choose a patch-specific parameter γ that represents their specialization on resource Q in that patch.

In particular, we set the total resource collection in patch i to be

$$a(s)f(1 - \gamma)R_i + b(s)f(\gamma)Q_i$$

where $f(\gamma) = (1 + \theta)\gamma - \theta\gamma^2$. The function f describes the trade-off between collection of the two resources. When $\gamma = 0$, collection of resource R ceases, corresponding to a perfect preference for resource Q. When $\gamma = 1$, collection of resource Q ceases, corresponding to a perfect preference for resource R. The optimal value of γ depends on the ratio of the abundances of the resources and the efficiencies of resource collection (Fig. 7a). When one resource is much more common, the optimal strategy is to reject the other. The parameter θ controls the benefit of using an intermediate strategy. If $\theta = 0$, there is no incentive to use an intermediate strategy, and foragers always pick $\gamma = 0$ or $\gamma = 1$. For other values of θ, some foragers choose to utilize both resources when the two resources are roughly comparable in profitability for their size class (Fig. 7b).

Depending on the initial distribution of patch parameters and on the value of θ, results can resemble those with filter feeders (if all foragers choose intermediate values of γ), those with perfect preference (if all foragers choose $\gamma = 0$ or $\gamma = 1$), or a combination of the two. Figure 8 shows an example where some patches are occupied by specialists (patch 5 used for resource R by small foragers and patch 4 used for resource Q by large foragers), and patches 2 and 3 are used by generalists of intermediate size.

APPLICATION TO OTHER TYPES OF LIMITING FACTOR

Limiting factors that differ in their dynamics (fixed or responsive) or in how they are encountered (filter feeders, etc.) create different patterns of patch rejection. We now apply these methods to predation and competition, finding that the patterns found in models with two food resources often, but not always, carry over to these biologically distinct situations.

Predation

Predation risk may also be thought of as a limiting factor. Suppose prey seek to minimize the ratio of predation risk to food resource encountered (Gilliam and Fraser, 1987). In our notation, foragers minimize

$$\frac{v(s)Q_i}{a(s)R_i}$$

where $v(s)$ is the rate at which size s individuals succumb to predation, and Q_i is the predator abundance in patch i. We now consider two types of predator, generalists and specialists.

Generalist predators may not respond to forager abundances and the Q_i may be thought of as fixed. On the other hand, specialist predators may respond to forager abundances, and Q_i responds to patch rejection decisions made by foragers. For both generalists and specialists, nonetheless, the patches exhibit perfect size scaling and the prey are predicted to obey an IFD. However, perfect size scaling may not occur if predators respond differently to prey of different sizes, in which case we predict size segregation. Moody *et al.* (1996) provide
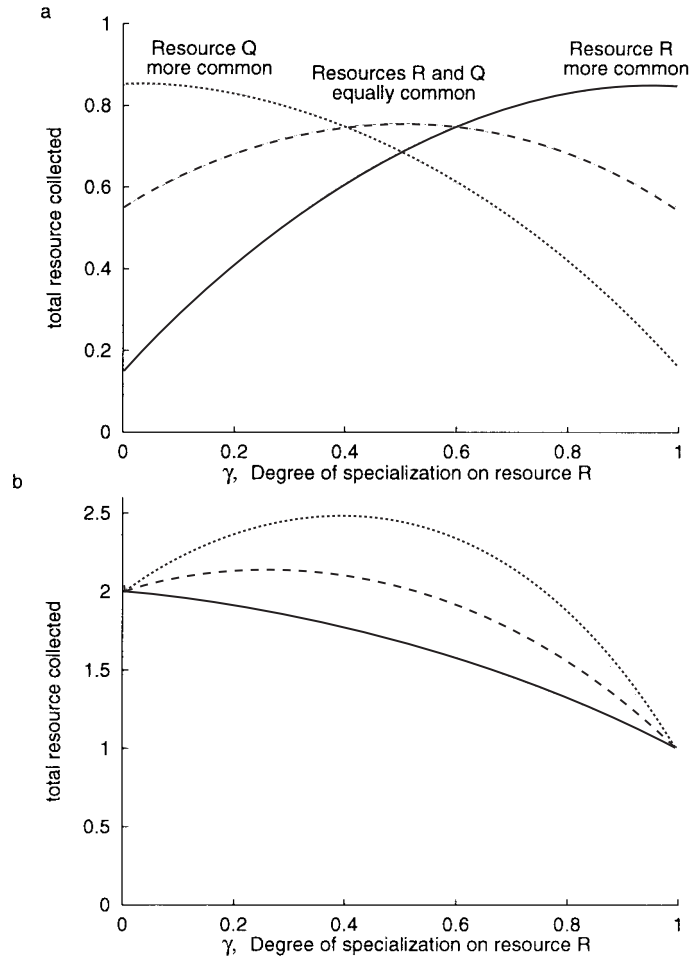
Fig. 7. Effects of parameters on simple model of optimal foraging. (a) Behaviour of the function $a(s)f(1 - \gamma)R + b(s)f(\gamma)Q$ for three different values of $(a(s)R, b(s)Q)$: resource R more common (0.85, 0.15), resource Q more common (0.15, 0.85), resources R and Q equally common (0.55, 0.55). The optimal value of γ produces the maximum on the curve. The parameter θ is set to 0.75 in each case. (b) Behaviour of the function $f(1 - \gamma) + 2f(\gamma)$ for three different values of θ: 0.25 (solid line), 0.75 (dotted line) and 1.25 (dashed line). Small values of θ tend to produce optima at the endpoints, while large values tend to produce optima at intermediate values of γ.

a discussion of state-based approaches to deriving fitness functions from the two currencies of food and predation, not all of which lead to perfect size scaling as in this example.

Competition as a limiting factor

Forager size can also influence patch selection through various modes of competition, which also acts as a limiting factor. Suppose that the rate at which a forager of size s collects resources in patch i is
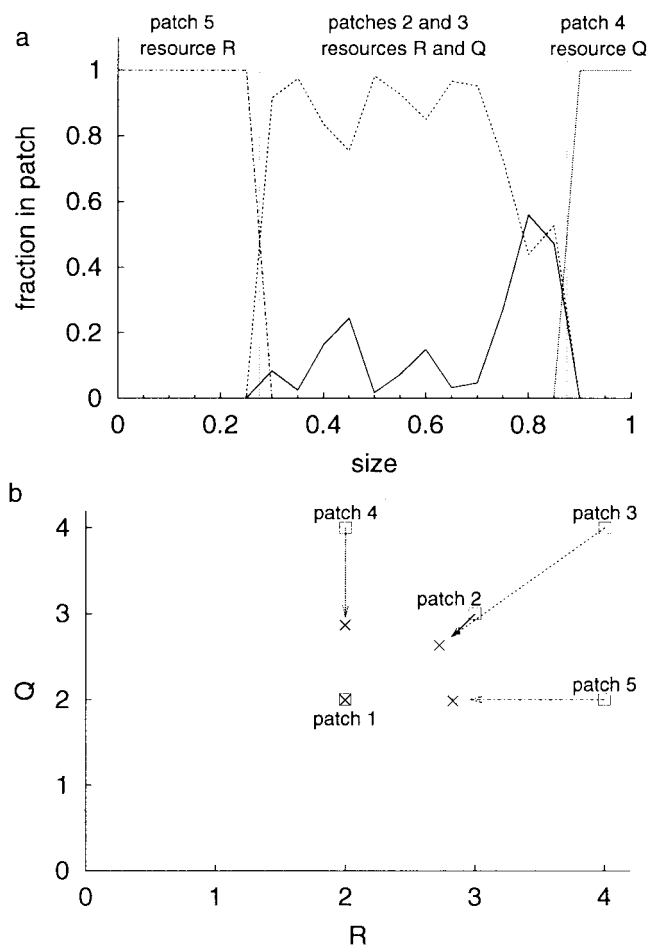
Fig. 8. Results of simulation with the optimal foraging strategy (other parameters and methods as in Fig. 5). (a) Distribution of foragers in five patches. Patch 1 is universally rejected and does not appear, foragers of intermediate size use resources R and Q in patches 2 (solid line) and 3 (dashed line), the largest foragers use resource Q in patch 4 (dashed line) and the smallest use resource R in patch 5 (dot-dashed line). Simulations done as in Fig. 3 except that strategies now include a value of γ (degree of specialization on resource Q) in addition to a patch choice. (b) Equilibrium levels of R and Q with and without foragers in the five patches (as in Fig. 5b).

$$\frac{a(s)R_i}{1 + \int \alpha(s, s')N_i(s')\mathrm{d}s'}$$

where the function $\alpha(s, s')$ describes the per capita interference created by a forager of size s' (the interferer) on one of size s (the recipient). This is a simple treatment of a time budget analysis (Ruxton *et al.*, 1992; Vandermeer and Ens, 1997). We consider three cases: competitive weights (Parker and Sutherland, 1986), interference (Ruxton *et al.*, 1992; Vandermeer and Ens, 1997) and dominance (Korona, 1989; Holmgren, 1995).

Competitive weights

First, suppose that the amount of interference depends only on the interferer and is independent of the size of the recipient. Mathematically, $\alpha(s, s') = c(s')$ for some function c depending only on s'. The rate of resource collection in patch i is then

$$\frac{a(s)R_i}{1 + \int \alpha(s, s')N_i(s')\mathrm{d}s'} = \frac{a(s)R_i}{1 + \int c(s')N_i(s')\mathrm{d}s'} = \frac{a(s)R_i}{1 + \bar{N}_i}$$

where $\bar{N}_i = \int c(s')N_i(s')\mathrm{d}s'$. Whatever the size scaling of resource collection or competitiveness, foragers of all sizes share the same ranking of patch quality and the same patch rejection strategy. These results match those in the original model with competitive weights (Parker and Sutherland, 1986).

Size-ratio dependent competition

Second, suppose that the amount of interference is given by the ratio

$$\alpha(s, s') = \frac{c(s')}{c(s)}$$

for some function $c(s)$. Time wasted depends on the ratio of the competitiveness of the interferer to that of the recipient. Therefore,

$$\frac{a(s)R_i}{1 + \int \alpha(s, s')N_i(s')\mathrm{d}s'} = \frac{a(s)R_i}{1 + \dfrac{\int c(s')N_i(s')\mathrm{d}s'}{c(s)}} = \frac{a(s)c(s)R_i}{c(s) + \bar{N}_i} \tag{3}$$

where $\bar{N}_i = \int c(s')N_i(s')\mathrm{d}s'$ as before. This resembles the filter-feeder example (see pp. 811–812). As long as the function $c(s)$ is not constant, the evaluation of a patch with particular values of R_i and $\bar{N}_i$ depends on the size of the forager. Foragers of different sizes may rank patches differently.

  Alternatively, patches may converge to have identical values of both R and $\bar{N}$. Using the functional form $c(s) = 1 + ks$, we can find criteria for when two patches converge (as in the filter-feeder case illustrated in Fig. 4). We find parameters for which a solution exists of $R_1^* = R_2^*$ and $\bar{N}_1 = \bar{N}_2$. The detailed calculations are presented in Appendix 2. Patches become identical if they are relatively similar to begin with, and remain different if they are somewhat more different. In that case, the superior patch is used by the superior competitors. One patch is universally rejected by all sizes if it is too inferior (Fig. 9). With more than two patches, similar patches can still converge to have identical values of R and $\bar{N}$, although the algebraic conditions are not identical.

Dominance

A simple model of dominance sets

$$\alpha(s, s') = \begin{cases} 0 & \text{if } s > s' \\ 1 & \text{if } s < s' \\ 0.5 & \text{if } s = s' \end{cases}$$

This model is akin to models of seed competition, where larger seeds dominate smaller seeds (Geritz *et al.*, 1998). Because each size experiences a different level of net interference,
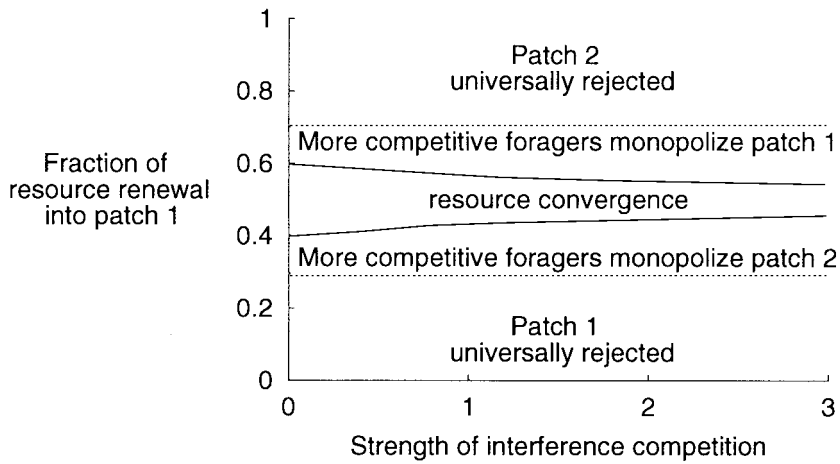
Fig. 9. Conditions under which a range of foragers in two patches achieve resource convergence, universally reject one patch or size-segregate into both patches when there is interference competition given by the ratio $\alpha(s, s') = c(s')/c(s)$ with $c(s) = 1 + ks$. The horizontal axis gives the value of the parameter k and the vertical axis shows the proportion of total resource renewal rate in patch 1, $\rho_1/(\rho_1 + \rho_2)$. Foragers are distributed uniformly over the size range from $s = 0$ to $s = 1$; $a(s) = 0.5 + 4.5s$ and $\delta_i = \zeta_i = 1$ (see Appendix 2 for details).
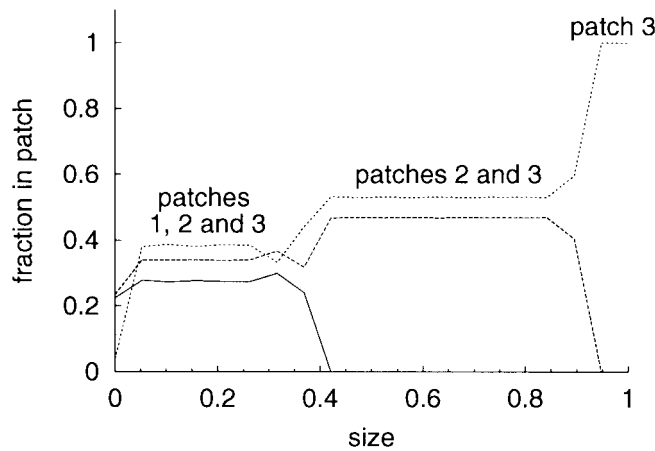

Fig. 10. Distribution of foragers in three patches with dominance (equation 4). Parameter values for ρ and δ as in Fig. 3. The equilibrium resource levels in the three patches are 0.89, 1.09 and 1.24 respectively. The curves are averaged to eliminate a sawtooth pattern generated by discretization of sizes.

some size segregation must occur. We observe what Holmgren (1995) calls a semi-truncated distribution. The most dominant foragers use the patch with the highest equilibrium of resources, leaving subordinates to choose between a low equilibrium or high competition (Fig. 10).

DISCUSSION

In this paper, we provide a framework that unifies models of patch choice and patch rejection by foragers structured by size (the results apply equally well to other differences in state). We do so by considering size-specific differences among patches as limiting factors. Limiting factors fall naturally into two classes: those that are fixed (like optical clarity or generalist predators) and those that respond to the forager distribution (like food or specialist predators). If only one limiting factor is responsive, different levels of the fixed limiting factor act like differences between patches. With perfect size scaling (parallel response of different sizes to the non-responsive limiting factor in different patches), an IFD of foragers is optimal and the model makes no predictions as to which size classes occupy particular patches. If size scaling is not perfect, then we predict size segregation and a unique optimal distribution of foragers in patches.

When both limiting factors are responsive, foragers are predicted to exhibit patch rejection strategies between the IFD and complete size segregation. Some size classes reject all but one patch, while others accept several patches, meaning that the distribution of foragers can only be partially predicted. The details of the interaction between foragers and the two limiting factors determine the precise pattern of patch rejection.

When both limiting factors are food resources, the way that foragers gather food in a patch determines optimal patch rejection strategies. Filter feeders that consume both resources in proportion to encounter rate achieve an ideal free distribution only if the collection functions for the two resources are proportional. Otherwise, we predict truncated distributions with foragers of different sizes segregated into different patches. The equilibrium levels of the two resources follow a trade-off curve, with a high equilibrium of one implying a low equilibrium of the other. However, resource convergence, where some subsets of patches achieve equal equilibria of both resources, is possible when patches have sufficiently similar resource input or decay rates (Fig. 5). In particular, segregation might not be observed between two sufficiently similar patches even when collection functions are not proportional (Fig. 4).

Perfect-preference foragers can choose to consume one, but not both, of the resources in a given patch. In general, they achieve a dual ideal free distribution, with sharp size segregation by resource type consumed. Patches that are used by foragers consuming one particular resource have matching equilibria of that resource (Fig. 6). As with filter feeders, pairs of patches can have matching equilibria of both resources. We observe similar results when foragers may choose to eat one or both resources to maximize their consumption rate. In this case, foragers tend to size segregate by diet. Those patches used by perfect-preference foragers follow a dual ideal free distribution, those used by foragers with a mixed diet follow a trade-off (as with filter feeders) and sufficiently similar patches can show resource convergence (Fig. 8).

We also treat predation as a limiting factor. Generalist predators (modelled as a patch-specific vulnerability to predation) act like patch-specific differences, and produce size segregation when the functions relating vulnerability to size are not proportional in different patches. Specialist predators respond to the availability of their forager prey and create a model similar to that of filter feeders because prey cannot choose whether to eat or be eaten (Levin *et al.*, 1977).

Finally, we consider interference competition as a limiting factor, finding that the results depend on the mechanism of competition. If the effect of one competitor on another

depends only on the size of the first, then competition can be modelled using 'competitive weights' (Parker and Sutherland, 1986). In this case, there is perfect size scaling because patches with different numbers of foragers have proportional consumption functions. This leads to an ideal free distribution where competitive weights adjust to equalize the equilibrium level across patches. If the effect of one competitor on another depends on the ratio of the competitive weights (a simple model of interference), the results are similar to those with two food resources, non-proportional consumption functions and filter feeding foragers. Sizes segregate with more competitive foragers in the superior patch, unless patches are sufficiently similar to show resource convergence (Fig. 9). Finally, if the effect of one competitor on another depends on an interaction between sizes, as in a dominance hierarchy, then we observe the semi-truncated distribution (Holmgren, 1995) where the most competitive foragers deplete the best patch, leaving the least competitive foragers to choose between low resource patches and patches with severe competition (Fig. 10).

The models presented here are highly simplified and ignore many of the factors that Kennedy and Gray (1993) hypothesized lead to deviations from the ideal free distribution. Missing components of forager behaviour include explicit modelling of decision rules (Cezily and Boy, 1991; Houston *et al.*, 1995; Farnsworth and Beecham, 1997; Hugie and Grand, 1998; Abrams, 1999; Bernstein *et al.*, 1999), the effects of history and settlement order (Spencer *et al.*, 1995; Houston and Lang, 1998), imperfect perception (Gray and Kennedy, 1994; Spencer *et al.*, 1996; Cartar and Abrahams, 1997), memory (Milinski, 1994) and exploitation of heterogeneity within the patch (Brown and Mitchell, 1989). In addition, we consider only a snapshot, thus ignoring resource dynamics (Abrams, 1999; Van Baalen and Sabelis, 1999) and growth (Tyler and Rose, 1997). Finally, we ignore any effects of finite population size (Houston and McNamara, 1988; Ruxton and Humphries, 1999).

Even with these many simplifications, the modelling approach presented here has the potential to unify studies of rather different systems. Here we categorize studies where there are at least two limiting factors, one of which is a food resource, and say whether ideal free distributions are predicted by our modelling approach.

Abiotic factors. Abiotic factors, or other fixed patch differences, are expected to lead to size segregation if there is non-proportional scaling of effects. Tyler and Gilliam (1995) found that the energy costs of foraging in different flow regimes have important effects on distributions of fish, but that there is no apparent interaction of energy costs with size, and thus no reason to expect size segregation. Hughes and Grand (2000) did find size segregation when temperature affected different sizes differently.

Predation and cover. Grand and Dill (1999) present a special case of the results in this paper, showing that size segregation is expected when predation risk does not scale identically in different patches. Earlier results (Grand and Dill, 1997) indicated that predation risk scaled nearly, but not exactly, with competitive weight. Utne *et al.* (1997) found that fish of different sizes evaluate predation risk differently and thus might be expected to segregate by size. Predation can interact with crowding through a selfish herd mechanism (Krause, 1994), where foragers of distinctive size are at higher risk, or foragers of smaller size are forced to the edges of the shoal. Alternatively, dilution of predation risk can lead to segregation (Grand and Dill, 1999). Both of these cases would be thought of as models of three limiting factors (food, predation and crowding) within the framework of this paper. Giannico and Healey (1999) explored the effects of cover on ideal free distributions. Interestingly,

they found ideal free distributions only when patches were similar, in accord with the predictions made here regarding resource convergence in the presence of interference competition.

Competitive ability. Sutherland *et al.* (1988) provided the original test, showing that competitive weights predict the distribution of foragers more accurately than simple numbers. Other studies have found that the situation is more complicated. Tregenza and Thompson (1998) found that competitive weights are unstable over time, a situation not considered in our models. Grand (1997) found some evidence that competitive weights are patch-dependent, and might thus be predicted to produce some degree of size segregation. Krause (1994) found an interaction between crowding and size, with the competitive effect of large fish depending on the number of fish in the shoal. Tregenza *et al.* (1996) hypothesized that there is a switch from contest competition at low density to scramble competition at high density, leading to different patterns of size-dependent success.

Testing the predictions

The field implications of different mechanisms of competition have been reviewed by Dolman and Sutherland (1997). Our explicit consideration of multiple limiting factors leads to the following specific predictions in a controlled two-patch experiment.

1. If patches differ in predation risk or some other fixed effect, we predict size segregation if the effects on different sizes are not proportional.
2. For foragers with two foods, one could manipulate the fraction of renewal of the two resource types in the two patches. We make the following predictions:

   (a) If foragers are filter feeders and eat both resources in proportion to encounter rates, we predict an ideal free distribution of foragers when patches are very similar, size segregation when patches are less similar, and the use of a single patch when patches are very different.
   (b) If foragers feed on only a single resource at a time, we predict size segregation onto different food types, but equal equilibria of the two resources in the two patches.
   (c) If foragers choose an optimal diet, consisting of one or both resources, we predict size segregation by diet. If patches have similar input rates, we predict resource convergence and no segregation by size class or patch. As input rates become more different, we predict size segregation into different patches and different diets.

3. If foragers compete for a single food resource, we treat competition as another limiting factor. Depending on the mechanism of competition, we predict different patterns as the fraction of input into one of the patches increases.

   (a) In scramble competition, where foragers interact only through their ability to deplete the resource (competitive weights), we predict an ideal free distribution.
   (b) When interference decreases foraging efficiency by a ratio of a function of the sizes (large foragers affect small foragers a lot, but small foragers still affect large foragers a bit), we predict an ideal free distribution when patches have similar input rates. When input rates are more different, we predict segregation, with larger individuals in the patch with a higher equilibrium level of resources.

(c) When interference decreases foraging efficiency through a dominance hierarchy (large foragers affect small foragers, small foragers do not affect large foragers), we predict a semi-truncated distribution (Holmgren, 1995) with the largest foragers using the patch with higher equilibrium and small foragers using both patches.

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REFERENCES

Abrams, P.A. 1999. The adaptive dynamics of consumer choice. *Am. Nat.*, **153**: 83–97.

Bernstein, C., Auger, P. and Poggiale, J.C. 1999. Predator migration decisions, the ideal free distribution, and predator–prey dynamics. *Am. Nat.*, **153**: 267–281.

Brown, J.S. and Mitchell, W.A. 1989. Diet selection on depletable resources. *Oikos*, **54**: 33–34.

Cartar, R.V. and Abrahams, M.V. 1997. Predicting the distribution of organisms among a few patches: problems with detecting departures from the ideal free distribution. *Oikos*, **78**: 388–393.

Cezilly, F. and Boy, V. 1991. Ideal free distribution and individual decision rules – a Bayesian-approach. *Acta Oecol.*, **12**: 403–410.

Dolman, P.M. and Sutherland, W.J. 1997. Spatial patterns of depletion imposed by foraging vertebrates: theory, review and meta-analysis. *J. Anim. Ecol.*, **66**: 481–494.

Farnsworth, K.D. and Beecham, J.A. 1997. Beyond the ideal free distribution: more general models of predator distribution. *J. Theor. Biol.*, **187**: 389–396.

Fretwell, S.D. and Lucas Jr., H.L. 1970. On territorial behavior and other factors influencing habitat distribution of birds. 1. Theoretical development. *Acta Biotheor.*, **19**: 16–36.

Frischknecht, M. 1996. Predators choosing between patches with standing crop: the influence of switching rules and input types. *Behav. Ecol. Sociobiol.*, **38**: 159–166.

Geritz, S.A.H., Van der Meijden, E. and Metz, J.A.J. 1998. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.*, **55**: 324–343.

Giannico, G.R. and Healey, M.C. 1999. Ideal free distribution theory as a tool to examine juvenile coho salmon (*Oncorhynchus kisutch*) habitat choice under different conditions of food abundance and cover. *Can. J. Fish. Aquat. Sci.*, **56**: 2362–2373.

Gilliam, J.F. and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.

Grand, T.C. 1997. Foraging site selection by juvenile coho salmon: ideal free distributions of unequal competitors. *Anim. Behav.*, **53**: 185–196.

Grand, T.C. and Dill, L.M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory. *Behav. Ecol.*, **8**: 437–447.

Grand, T.C. and Dill, L.M. 1999. Predation risk, unequal competitors and the ideal free distribution. *Evol. Ecol. Res.*, **1**: 389–409.

Gray, R.D. and Kennedy, M. 1994. Perceptual constraints on optimal foraging: a reason for departures from the ideal free distribution? *Anim. Behav.*, **47**: 469–471.

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

Houston, A.I. and Lang, A. 1998. The ideal free distribution with unequal competitors: the effects of modelling methods. *Anim. Behav.*, **56**: 243–251.

Houston, A.I. and McNamara, J.M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Anim. Behav.*, **36**: 166–174.

Houston, A.I., McNamara, J.M. and Milinski, M. 1995. The distribution of animals between resources: a compromise between equal numbers and equal intake rates. *Anim. Behav.*, **49**: 248–251.

Hughes, N. and Grand, T.C. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. *Environ. Biol. Fishes*, **59**: 285–298.

Hugie, D.M. and Grand, T.C. 1998. Movement between patches, unequal competitors and the ideal free distribution. *Evol. Ecol.*, **12**: 1–19.

Kacelnik, A., Krebs, J.R. and Bernstein, C. 1992. The ideal free distribution and predator–prey populations. *Trends Ecol. Evol.*, **7**: 50–55.

Kennedy, M. and Gray, R.D. 1993. Can ecological theory predict the distribution of foraging animals – a critical analysis of experiments on the ideal free distribution. *Oikos*, **68**: 158–166.

Korona, R. 1989. Evolutionarily stable strategies in competition for resource intake rate maximization: I. The model. *Behav. Ecol. Sociobiol.*, **25**: 193–200.

Krause, J. 1994. The influence of food competition and predation risk on size-assortative shoaling in juvenile chub (*Leuciscus cephalus*). *Ethology*, **96**: 105–116.

Krivan, V. and Sikder, A. 1999. Optimal foraging and predator–prey dynamics, II. *Theor. Popul. Biol.*, **55**: 111–126.

Lessells, C.M. 1995. Putting resource dynamics into continuous input ideal free distribution models. *Anim. Behav.*, **49**: 487–494.

Levin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.*, **104**: 413–423.

Levin, S.A., Levin, J.E. and Paine, R.T. 1977. Snowy owl predation on short-eared owls. *Condor*, **79**: 395.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Milinski, M. 1994. Long-term memory for food patches and implications for ideal free distributions in sticklebacks. *Ecology*, **75**: 1150–1156.

Moody, A.L. and Houston, A.I. 1995. Interference and the ideal free distribution. *Anim. Behav.*, **49**: 1065–1072.

Moody, A.L., Houston, A.I. and McNamara, J.M. 1996. Ideal free distributions under predation risk. *Behav. Ecol. Sociobiol.*, **38**: 131–143.

Parker, G.A. and Sutherland, W.J. 1986. Ideal free distributions when individuals differ in competitive ability – phenotype-limited ideal free models. *Anim. Behav.*, **34**: 1222–1242.

Ruxton, G.D. and Humphries, S. 1999. Multiple ideal free distributions of unequal competitors. *Evol. Ecol. Res.*, **1**: 635–640.

Ruxton, G.D., Guerney, W.S.C. and de Roos, A.M. 1992. Interference and generation cycles. *Theor. Popul. Biol.*, **42**: 235–253.

Spencer, H.G., Kennedy, M. and Gray, R.D. 1995. Patch choice with competitive asymmetries and perceptual limits – the importance of history. *Anim. Behav.*, **50**: 497–508.

Spencer, H.G., Kennedy, M. and Gray, R.D. 1996. Perceptual constraints on optimal foraging: the effects of variation among foragers. *Evol. Ecol.*, **10**: 331–339.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Sutherland, W.J. and Parker, G.A. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Anim. Behav.*, **44**: 345–355.

Sutherland, W.J., Townsend, C. and Patmore, J. 1988. A test of the ideal free distribution with unequal competitors. *Behav. Ecol. Sociobiol.*, **23**: 51–53.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Tregenza, T. and Thompson, D.J. 1998. Unequal competitor ideal free distribution in fish? *Evol. Ecol.*, **12**: 655–666.

Tregenza, T., Hack, M.A. and Thompson, D.J. 1996. Relative competitive success of unequal competitors changes with overall density. *Oikos*, **77**: 158–162.

Tyler, J.A. and Gilliam, J.F. 1995. Ideal free distributions of stream fish: a model and test with minnows, *Rhinicthys atratulus*. *Ecology*, **76**: 580–592.

Tyler, J.A. and Rose, K.A. 1997. Effects of individual habitat selection in a heterogeneous environment on fish cohort survivorship: a modelling analysis. *J. Anim. Ecol.*, **66**: 122–136.

Utne, A.C.W., Brannas, E. and Magnhagen, C. 1997. Individual responses to predation risk and food density in perch (*Perca fluviatilis* L.). *Can. J. Zool.*, **75**: 2027–2035.

Van Baalen, M. and Sabelis, M.W. 1999. Nonequilibrium population dynamics of 'ideal and free' prey and predators. *Am. Nat.*, **154**: 69–88.

Vandermeer, J. and Ens, B.J. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *J. Anim. Ecol.*, **66**: 846–858.

Ward, J.F., Austin, R.M. and MacDonald, D.W. 2000. A simulation model of foraging behaviour and the effect of predation risk. *J. Anim. Ecol.*, **69**: 16–30.

APPENDIX 1: CONDITIONS FOR TWO PATCHES TO BECOME IDENTICAL WITH FILTER FEEDERS

The total resource collection abilities for resources R and Q are

$$A_T = \int a(s)N(s)\mathrm{d}s$$
$$B_T = \int b(s)N(s)\mathrm{d}s$$

where the integrals are taken over all values of s. Let Ω_i be the sets of sizes of foragers using patch i. The fractions of foraging pressure A_i on resource R and B_i on resource Q in patch i are

$$A_i = \frac{\int_{s \in \Omega_i} a(s)N(s)\mathrm{d}s}{A_T}$$
$$B_i = \frac{\int_{s \in \Omega_i} b(s)N(s)\mathrm{d}s}{B_T}$$

Suppose two patches follow the dynamics in equation (2). We can solve for the equilibrium resource level in terms of A_i, B_i and the other parameters. The conditions that $R_1^* = R_2^*$ and $Q_1^* = Q_2^*$ can be solved for A_1 and B_1, respectively, as

$$A_1 = \tilde{\rho}(1 + \tilde{\delta}_2) - (1 - \tilde{\rho})\tilde{\delta}_1$$
$$B_1 = \tilde{\sigma}(1 + \tilde{\zeta}_2) - (1 - \tilde{\sigma})\tilde{\zeta}_1$$

where

$$\tilde{\rho} = \frac{\rho_1}{\rho_1 + \rho_2} \qquad \tilde{\delta}_i = \frac{\delta_i}{A_T} \qquad \tilde{\sigma} = \frac{\sigma_1}{\sigma_1 + \sigma_2} \qquad \tilde{\zeta}_i = \frac{\zeta_i}{B_T}$$

Given all the parameters, we can find the fraction of foraging pressure consistent with equality of the resources in the two patches. We need only find values of A_1 and B_1 that can be achieved simultaneously. A given fraction of foraging pressure on resource R in patch 1 can be achieved in many different ways, which produce different fractions of foraging pressure on resource Q in patch 1

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(unless the collection functions $a(s)$ and $b(s)$ are proportional). Let $F_l(A_1)$ be the smallest and $F_h(A_1)$ be the largest possible value of B_1. Then

$$F_l(A_1) < B_1 < F_h(A_1)$$

gives the condition on the parameters for the existence of an equilibrium where both patches match. If the collection functions $a(s)$ and $b(s)$ are proportional, then $F_l = F_h$ and convergence is impossible unless the parameters are perfectly balanced.

For example, suppose $N(s) = 1$ for $0 \leq s \leq 1$, $a(s) = 1$ and $b(s) = 2s$. Then, $A_T = B_T = 1$. The minimum foraging pressure on resource Q consistent with a given pressure on resource R occurs when the smallest foragers with $0 \leq s \leq A_1$ are in patch 1, implying that $F_l(A_1) = A_1^2$. The highest foraging pressure on resource Q consistent with a given pressure on resource R occurs when the largest foragers with $1 - A_1 \leq s \leq 1$ are in patch 1, implying that $F_h(A_1) = 1 - (1 - A_1)^2$. Therefore, the condition for equalization becomes

$$A_1^2 < B_1 < 1 - (1 - A_1)^2$$

If, furthermore, $\delta_i = \zeta_i = 1$, we can solve for A_1 in terms of $\tilde{\rho}$ and B_1 in terms of $\tilde{\sigma}$. The condition simplifies to

$$\frac{(3\tilde{\rho} - 1)^2 + 1}{3} < \tilde{\sigma} < \frac{2 - (2 - 3\tilde{\rho})^2}{3}$$

Only when the fraction of resource Q renewal in patch 1 lies between these bounds can the two patches become identical (Fig. 4).

Outside the region of resource convergence, either one or both patches are used. Patch 1 is universally rejected if it is inferior to patch 2 for all sizes even when all foragers are active in patch 2. Formally, patch 1 is universally rejected if

$$a(s)\frac{\rho_2}{\delta_2 + A_T} + b(s)\frac{\sigma_2}{\zeta_2 + B_T} > a(s)\frac{\rho_1}{\delta_1} + b(s)\frac{\sigma_1}{\zeta_1}$$

for all s. The condition for universally rejecting patch 2 is similar.

In the example, the absolute levels of ρ and σ matter in addition to the fraction in each patch. With $\rho_2 = \sigma_2 = 1$, we find that patch 1 is universally rejected if

$$\tilde{\rho} < \frac{1}{3} \quad \text{and} \quad \tilde{\sigma} < \frac{3 - 5\tilde{\rho}}{7 - 9\tilde{\rho}}$$

and patch 2 is universally rejected if

$$\tilde{\rho} > \frac{2}{3} \quad \text{and} \quad \tilde{\sigma} > \frac{6 - 7\tilde{\rho}}{8 - 9\tilde{\rho}}$$

These are the curves shown in Fig. 4.

APPENDIX 2: CONDITIONS FOR TWO PATCHES TO BECOME IDENTICAL WITH INTERFERENCE COMPETITION

As in Appendix 1, let Ω_i be the set of sizes of foragers using patch i. We require that $\bar{N}_1 = \bar{N}_2$, or that

$$\int_{s \in \Omega_1} c(s)p_1(s)N(s)\mathrm{d}s = \int_{s \in \Omega_2} c(s)p_2(s)N(s)\mathrm{d}s$$

For the equilibria to be equal, we require that $R_1^* = R_2^*$, where

$$R_i^* = \frac{\rho_i}{\delta_i + \int_{s \in \Omega_i} (a(s)c(s)N_i(s))/(c(s) + N_i)\mathrm{d}s}$$

(from equation 3).

As in Appendix 1, the extreme values of ρ_i and δ_i occur when either the smallest foragers or the largest foragers are in patch 1 ($\Omega_1 = [0, s_c]$ or $\Omega_1 = [s_c, 1]$ for the value of s_c determined by $\bar{N}_1 = \bar{N}_2$).

When $c(s) = 1 + ks$ and $N(s) = 1$ for $0 \leq s \leq 1$, $\bar{N}_i = 1/2 + k/4$, so s_c solves

$$s_c + \frac{ks_c^2}{2} = \frac{1}{2} + \frac{k}{4}$$

Substituting the form for $c(s)$ and this value of s_c into the equation $R_1^* = R_2^*$ gives a complicated (but analytically computable) form for $\tilde{\rho}$. This is the case shown in Fig. 9. As in Appendix 1, a patch is universally rejected if it is inferior even in the absence of foragers.