

Evolution of foraging strategies on resource gradients

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ABSTRACT

Question: How are competing foragers expected to distribute their lifetime foraging effort on a gradient of resource types that differ in abundance, quality, foraging costs, and associated mortality risks?

Mathematical method: Population dynamics of foragers and resources coupled with adaptive dynamics of foraging strategies based on continuous, function-valued traits.

Key assumptions: We start from generalizing the classical patch-based theory of optimal foraging to continuous resource gradients following the traditional assumptions of constant renewal rates of resources, spatially homogeneous mortality risks, and of foragers that are omniscient, free to move without costs, equal, and not experiencing any saturation of intake. We then relax the restrictive assumptions of the classical model, thus accounting for non-linear functional responses of the foragers, heterogeneous mortality risks and resource qualities, energetically costly foraging, genetic covariances constraining foraging, feedbacks between foraging and resource dynamics, and different types of competition between foragers.

Results: (1) When expressed as instantaneous rates with the same units (time^{-1}), mortality risks (d), foraging costs (c), and resource qualities (q) all influence the evolutionarily stable distribution of foraging effort through the dimensionless expression $(d + c)/q$. (2) Functional responses that imply intake saturation may result in a subset of resources remaining entirely unused. (3) Coupling foraging to resource dynamics results in a rich array of evolutionary outcomes, depending on the type of competition among foragers and the interplay between forager and resource characteristics. (4) Genetic constraints may cause foraging effort to track the resource gradient more coarsely than classical models predict.

Keywords: exploitation competition, frequency-dependent selection, function-valued traits, ideal free distribution, interference competition, optimal foraging, resource dynamics, resource gradient.

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INTRODUCTION

One of the classical problems in evolutionary ecology is to understand the distribution of competing individuals among resource patches. Fretwell and Lucas (1970) coined the term 'ideal free distribution' for a scenario in which foraging individuals distribute themselves among patches such that no individual can improve its resource intake by moving to another patch. 'Free' here refers to the assumption that individuals have the capacity to select any patch without costs of movement, and 'ideal' refers to the assumption that individuals are omniscient and select the patch that provides them with the highest possible payoff. In the wake of this pioneering approach, many researchers have pointed out the overly simplified assumptions of the 'classical' ideal free distribution model, and that relaxing these assumptions usually results in deviations from the predictions of the classical model (see reviews by Kacelnik *et al.*, 1992; Tregenza, 1995). Nevertheless, the simple classical model remains the null model for describing predator distributions among resource patches (Houston and McNamara, 1999).

The aims of this study are twofold. First, we wish to generalize conventional patch-oriented ideal free distribution theory to foraging on resource gradients. Foraging in discrete resource patches is a special case of the more general process of foraging on a range of resource types (e.g. Brew, 1982; Sasaki, 1997; Mitchell, 2000; Richards and Wilson, 2000; Egas *et al.*, 2005). These resource types can often be arranged according to their position along a spatial gradient or according to an intrinsic feature of the resources. When such resource types are continuous, foraging effort can be described as a continuous function of resource type. Resources along such a continuous gradient may differ in their value to the forager, for example, because of differences in their renewal rate and energetic value, or because of differential mortality risks associated with foraging on these resources. The key question then is how foraging effort should evolve to be allocated to exploiting different resources along the gradient, given that total effort is limited and conspecific individuals are competing for the same resources.

The second aim of this study is to show how a unified framework facilitates an understanding of the interplay of various factors affecting the evolution of foraging effort. In particular, such a framework allows an examination of the assumptions about how resource use affects the standing stock of resources. This is an important question, both empirically and theoretically: consumer–resource coupling, despite being ubiquitous, has typically been neglected when studying evolving distributions of foraging efforts. The unified framework we utilize here is the adaptive dynamics approach for analysing the evolution of function-valued traits, as recently developed by Dieckmann *et al.* (2006) and Parvinen *et al.* (2006). The particular strength of this approach lies in the relative ease with which different ecological feedback scenarios that give rise to density- and/or frequency-dependent selection can be investigated. In this framework, obtaining analytical results is possible even for fairly complex models, which greatly facilitates understanding of the relationship between model ingredients and resulting evolutionary outcomes.

We start by introducing a general framework for modelling the evolutionary dynamics of function-valued foraging strategies. Building on the assumptions of classical ideal free distribution theory, we first analyse the simplest possible model of foraging on resource gradients. We subsequently investigate various ecological and genetic factors that may violate the simplifying assumptions of the basic model, and study how relaxing these assumptions influences the evolutionary predictions. In this manner we analyse mortalities,

foraging costs, and resource qualities that differ between resource types. We also analyse finite harvesting capacity and functional responses, resource dynamics that are influenced by harvesting, and finally, genetic constraints that limit the adaptation of foraging strategies.

MODEL AND METHODS

After introducing the foraging dynamics and population dynamics of foragers in the first two sections below, we explain the resultant evolutionary dynamics of foragers in the third section.

Foraging dynamics

We assume that individuals must forage to gain resources that are subsequently used for reproduction. Foragers can utilize different resource types a , and we will often simply refer to these as resources. When resource types a are continuous, they establish a resource gradient. One may envisage this continuum as representing either a spatial gradient (with the resource type a describing the location of the resource) or as a continuous set of resources ranked according to a certain intrinsic feature (with the resource type a describing the considered feature of the resource). Relevant resource features include nutritional value, toxicity, and handling time, as well as catchability, accessibility, and acquisition mortality. The resources are assumed to be dynamically independent from each other, which implies that competitive interactions among foragers are resource-specific. For convenience we scale a such that it lies between 0 and 1.

Foraging behaviour is described by a foraging strategy given by the function $x(a)$. We interpret $x(a)$ as the foraging effort expended on resource a , measured as the proportion of potential total foraging effort devoted to resource a . We impose only minimal constraints on this foraging strategy: it must be non-negative ($x(a) \geq 0$ for all a) and the sum of all proportional foraging efforts must not exceed 100% ($\int x(a) da \leq 1$). An individual's foraging strategy may differ from that prevailing in a population. When this distinction is important, we use a prime to denote the variant foraging strategy, $x'(a)$, while referring to the prevailing, or resident, foraging strategy as $x(a)$.

In the basic model, we assume a so-called 'continuous input' scenario. Thus, each resource a is characterized by a constant renewal rate $r_0(a)$ at which new resource biomass becomes available to foragers. We assume that all foragers have an equal ability to harvest resources that are shared evenly among competing individuals, such that if n foragers harvest resource a with effort $x(a)$, they will experience a prorated potential intake rate

$p(a) = \frac{r_0(a)}{nx(a)}$. The qualifier 'potential' is meant to highlight that this intake can only be

reached when a forager chooses to focus exclusively on that particular resource. We also allow for arbitrary functional responses f that relate the amount of resource available to a forager to the actual amount of resource consumed and assimilated by the forager. Finally, we allow for heterogeneous resource quality, expressed as the energetic value of a resource relative to a baseline value q_0 , with $q(a)$ describing resource-specific deviations from this baseline. The actual intake rate of resource a , $x(a)(q_0 + q(a))f(p(a))$, thus depends on the potential intake rate p , on the resource quality $q_0 + q(a)$, on the functional response f , and on the forager's strategy x . The forager's total intake rate $\int x(a)(q_0 + q(a))f(p(a)) da$ is the sum of all its actual intake rates across the whole resource gradient.

Below we will also consider an extension of this setting to cases with explicit resource dynamics.

Population dynamics

We assume that intake through foraging is measured in units that equal the energetic costs required for producing one offspring. We can then assume that the birth rate of foragers equals their net total intake rate of resources. In calculating the net total intake rate, we have to consider the energetic costs of foraging, which may vary along the gradient. The total foraging cost is $\int c(a)x(a)da$, where $c(a)$ is the cost of foraging on resource a .

The last essential model component is mortality. We decompose the total mortality rate of foragers into a foraging-independent background mortality d_0 and into a component $d(a)$ that depends on foraging on a particular resource a . The total mortality rate thus equals $d_0 + \int x(a)d(a)da$.

Subtracting the mortality rate from the birth rate, we obtain the expected per capita rate of increase in the abundance $n(x)$ of foragers with strategy x as

$$\frac{1}{n(x)} \frac{d}{dt} = \int [x(a)(q_0 + q(a))f\left(\frac{r_0(a)}{n(x)x(a)}\right) - x(a)c(a) - x(a)d(a) - d_0]da. \quad (1)$$

Evolutionary dynamics

To describe the evolution of foraging efforts, we utilize the adaptive dynamics framework for function-valued traits recently introduced by Dieckmann *et al.* (2006). Here we describe the essentials of this approach; for more details, the reader may wish to consult Dieckmann *et al.* (2006) and Parvinen *et al.* (2006).

The basic idea underlying this approach is that evolution proceeds via small mutational changes in the foraging strategy. Mutant strategies that are advantageous in the environment set by the resident foraging strategy result in positive fitness and in an increase of the mutant's frequency. The fitness $r(x', x)$ of a rare mutant strategy x' is its long-term average per capita growth rate in the environment set by the resident strategy x (Metz *et al.*, 1992). Only mutants with positive fitness have a chance of invading the resident population, and do so with some probability, whereas mutants with negative fitness are bound to go extinct.

For the foraging dynamics introduced above, fitness is obtained as

$$r(x', x) = \int [x'(a)(q_0 + q(a))f\left(\frac{r_0(a)}{\hat{n}(x)x(a)}\right) - x'(a)c(a) - x'(a)d(a) - d_0]da, \quad (2)$$

where $\hat{n}(x)$ is the population size of the resident strategy at ecological equilibrium. As the fitness of the resident strategy x must be zero at this ecological equilibrium, the implied $\hat{n}(x)$ is obtained by solving the equation $r(x, x) = 0$.

Assuming that inheritance is clonal, that evolution is mutation-limited (such that populations are close to monomorphic most of the time), and that mutations have small effects, the evolution of function-valued traits can be described as a deterministic process captured by a simple differential equation (Dieckmann *et al.*, 2006; see also Dieckmann and Law, 1996). For the special case in which selection operates independently for each resource type, a , and mutation

probability μ and variance σ^2 of the mutation distribution are independent of x and a , the expected rate of evolutionary change in $x(a)$ takes a particularly simple form,

$$\frac{d}{dt} x(a) = \frac{1}{2} \mu \sigma^2 \hat{n}(x) g_x(a), \tag{3}$$

where $g_x(a)$ is the selection gradient for strategy x and resource type a . This selection gradient is the functional derivative of fitness $r(x', x)$ with respect to x' , evaluated at x . This implies that when fitness is of the form $r(x', x) = \int \rho(x', x, a) da$, the selection gradient is

given by $g_x(a) = \left. \frac{\partial}{\partial x'(a)} \rho(x'(a), x(a), a) \right|_{x'(a)=x(a)}$. How the equilibrium population size

$\hat{n}(x)$ and the selection gradient $g_x(a)$ are derived for specific ecological models will be shown for several examples below. While mutation probability μ and variance σ^2 will usually be unknown, this does not hamper further analysis, as these parameters only influence the overall speed of evolution (in analogy with Fisher’s fundamental theorem of natural selection), but do not affect the resultant evolutionary outcomes.

Equation (3) is normally too simplistic for describing the evolution of function-valued traits such as foraging effort. This is because evolutionary change in foraging effort on one resource is typically coupled to evolutionary changes in foraging effort on other resources (Dieckmann *et al.*, 2006): such dependencies can arise from genetic constraints (e.g. when pleiotropy or epistasis occur, changes in one phenotypic component necessarily imply changes in other phenotypic components) and from ecological limitations or trade-offs (e.g. when total foraging effort is limited, increased foraging effort on one resource can only occur at the expense of decreasing foraging effort on other resources). The resultant coupling between mutational changes of foraging effort on resources a and a' is described by the variance–covariance function $\sigma_x^2(a, a')$. Taking this into account, the following differential equation – the canonical equation of adaptive dynamics of function-valued traits (Dieckmann *et al.*, 2006) – describes the expected rate of evolutionary change in $x(a)$:

$$\frac{d}{dt} x(a) = \frac{1}{2} \mu \hat{n}(x) \int \sigma_x^2(a, a') g_x(a') da'. \tag{4}$$

Here the integral averages the selection gradients $g_x(a')$ across all resources a' to obtain the effective selection pressure on foraging effort $x(a)$, with the weights for this averaging being provided by the variance–covariance function $\sigma_x^2(a, a')$. The constraints that this evolutionary dynamics may have to respect (foraging effort is non-negative and total foraging effort is bounded) can now be incorporated by choosing $\sigma_x^2(a, a')$ appropriately (Dieckmann *et al.*, 2006), as will be illustrated by the examples below.

Solving equation (4) yields evolutionary trajectories of function-valued traits such as foraging effort. Of particular importance are strategies $x^*(a)$ for which the expected rate of evolutionary change vanishes, $\frac{d}{dt} x^*(a) = 0$. These correspond to evolutionary singularities, which include evolutionarily stable strategies. There are basically three ways to find the evolutionary singularities of the dynamics described by equation (4):

- setting the left-hand side of equation (4) to zero and solving it analytically,
- using the calculus of variations, or
- integrating equation (4) numerically.

The first option is conceptually straightforward, but analytical calculations often become intractable for all but the simplest examples. The second option, although slightly more demanding technically, has proved powerful (Parvinen *et al.*, 2006) and often works when the first one fails. The last option will always work, but can be computationally intensive and does not yield as much insight as an analytical solution. Our analyses below combine all three of these methods for maximum effect.

RESULTS

The first section below revisits the assumptions and predictions of classical ideal free foraging in the context of a continuous resource gradient. We then move beyond the classical model by considering mortality risks, foraging costs, or resource qualities that vary across the resource gradient; non-linear functional responses; dynamic resources; and finally, complex variance–covariance functions.

'Classical' ideal free foraging

Our starting point is a simple ecological model reflecting the key assumptions of classical ideal free distribution theory: individuals are equal, omniscient, and free to forage wherever they wish; they have an unlimited capacity to harvest and to assimilate resources ($f(p) = p$); there are no costs of movement or foraging ($c(a) = 0$); resource quality is uniform at unity ($q_0 = 1$ and $q(a) = 0$); and also mortality risk is uniform ($d(a) = 0$).

Based on these assumptions, the actual intake rate of individual foragers takes a particularly simple form: $[x(a)r_0(a)]/[n(x)x(a)] = r_0(a)/n(x)$. Curiously, the $x(a)$ here cancel out – this occurs because an increase in foraging effort on a particular resource (as described by the $x(a)$ in the numerator) is exactly compensated by a corresponding decrease in resource availability per forager (as described by the $x(a)$ in the denominator). Actual intake rate appears to depend on the foraging strategy $x(a)$ only through the potential dependence of population size $n(x)$ on x . However, even that dependence does not actually occur, as it turns out that the foraging strategy does not affect the equilibrium population size: $\hat{n} = r_0/d_0$, where $r_0 = \int r_0(a)da$ is the average resource renewal rate across the resource gradient.

The analogue of the classical ideal free foraging model thus allows for a Garden of Eden of lazy foragers: as long as some foraging effort is exerted on all resources, actual per capita intake remains unaffected. In fact, when foraging effort on a particular resource approaches zero, supply rate approaches infinity. The state of almost effortless foraging in this Garden of Eden is nonetheless vulnerable to mutant invasions. Even though birth rate and population size are independent of the foraging strategy adopted by a population as a whole, an individual may gain from adopting a foraging strategy that differs from the prevailing strategy. In particular, a mutant preferentially exploiting resources with above-average potential intake rates (should any such disparity exist) would have an advantage over resident individuals. This realization naturally begs the following question: Is there a foraging strategy that, once adopted by a population, cannot be outperformed by any mutant strategy?

To answer this question, we must consider the dependence of a mutant individual's birth and death rates on mutant and resident strategies. Just as for the residents, the death rate of a mutant is constant and equals d_0 . However, the birth rate of a mutant depends on both mutant and resident foraging strategies, $b(x', x) = \int x'(a)r_0(a)/(\hat{n}x(a))da$. (Note that since

$x'(a)$ and $x(a)$ are now different, they no longer cancel out as the resident strategy $x(a)$ alone did before.) The selection gradient is then given by the following function,

$$g_x(a) = \frac{r_0(a)}{\hat{n}x(a)}. \tag{5}$$

This selection gradient simply equals the supply rate. Both are always positive: increasing foraging effort on a particular resource a thus inevitably results in a fitness gain. Selection therefore favours expending all available foraging effort, which must eventually become a limiting factor. Accordingly, competitive foragers sooner or later will face the constraint $\int x(a)da \leq 1$; in the end, foraging effort on one resource cannot be increased without a corresponding decrease of effort on one or more other resources. The influence of this constraint on the evolutionary dynamics can be taken into account using the variance–covariance function $\sigma_x^2(a, a') = \sigma^2[\delta(a - a') - 1]$, where δ denotes the Dirac delta function (Dieckmann *et al.*, 2006) – any decrease (increase) in foraging effort on resource a will then be exactly compensated by a uniform increase (decrease) in foraging effort on all other resources (this is but the simplest possible choice; another one will be considered below). The evolutionary dynamics of the foraging strategy $x(a)$ can now be captured by the following equation:

$$\frac{d}{dt} x(a) = \frac{1}{2} \mu \hat{n}(x) \sigma^2 \left[\frac{r_0(a)}{x(a)} - \int \frac{r_0(a')}{x(a')} da' \right]. \tag{6}$$

At evolutionary equilibrium, this rate of evolutionary change vanishes. As shown in Appendix 1, the evolutionarily singular foraging strategy satisfying this condition is given by

$$x^*(a) = \frac{r_0(a)}{\int r_0(a') da'}. \tag{7}$$

We thus recover the predictions of the classical ideal free distribution model (Fig. 1). Effort spent foraging on resource a is strictly proportional to the renewal rate $r_0(a)$ of that resource. This is the ‘input matching rule’ of Parker (1978). In addition, the ‘equal intake prediction’ of Fretwell and Lucas (1970) holds: the potential intake rate is uniform across the resource gradient, $p(a) = r_0(a)/(\hat{n}x^*(a)) = d_0$.

As shown in Appendix 2, the fitness of a mutant with foraging strategy x' , when the resident is at the singularity, $x = x^*$, is

$$r(x', x^*) = d_0 \left[\int x'(a) da - 1 \right]. \tag{8}$$

We thus see that the singular strategy is evolutionarily stable against all mutants that waste foraging effort, $\int x'(a) da < 1$, and neutral against all mutants that do expend all foraging effort. No mutant has positive fitness.

Heterogeneous mortality risks

Extending the classical model of ideal free foraging, we first allow mortality to vary across the resource gradient ($d(a) \neq 0$) while keeping the functional response linear ($f(p) = p$). As shown in Appendix 1, the singular strategy is

$$x^*(a) = \frac{r_0(a)}{\hat{n}(x^*)(d_0 + d(a))}, \tag{9}$$

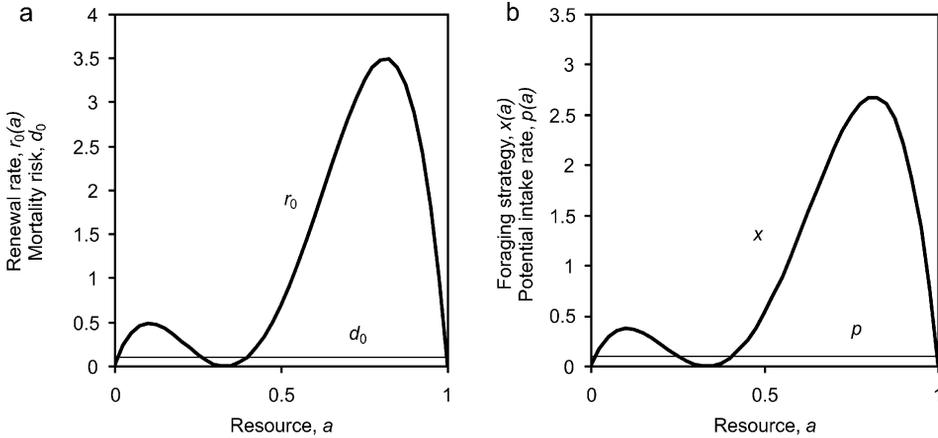


Fig. 1. Application of the classic ideal free foraging model to a resource gradient. (a) Mortality risk (thin line) is independent of resource type a , whereas renewal rate (thick curve), determining resource availability, varies along the gradient, $r_0(a) = 1/100 + 100a(1 - a)(a - 1/3)^2$. (b) The evolutionarily singular foraging strategy (measuring the proportion of total effort spent foraging on a particular resource) tracks the variation in renewal rate exactly. The potential intake rate is uniform along the gradient, and the equilibrium population size of foragers is given by $\hat{n}(x^*) = 13.0$.

where $\hat{n}(x^*) = \int r_0(a)/(d_0 + d(a))da$. Also in this case, the evolutionary singularity involves using all available effort and is neutrally stable against mutants that do the same (Appendix 1). The result shows that more effort is expended on resources that have high renewal rates and imply low mortality risks. Consequently, heterogeneous mortalities lead to a systematic departure from the strict proportionality between effort and renewal rate predicted by the classical model. Also, the potential intake rates at x^* can be computed and take a simple form, $p(a) = r_0(a)/(\hat{n}x^*(a)) = d_0 + d(a)$. This violates the classical prediction of equalized potential intake rates – risky resources provide higher energetic rewards. For this reason, all resources are always used, even if they imply a very high risk of mortality.

Heterogeneous foraging costs

The classical model ignores foraging costs, which is unreasonable. One solution is to assume that intake is measured as net intake, with costs already deducted. However, here we explicitly consider heterogeneous foraging costs ($c(a) \neq 0$). A closer look at equation (2) immediately reveals that resource-specific foraging costs $c(a)$ have exactly the same effect as resource-specific mortality risks $d(a)$. Therefore, all conclusions about heterogeneous mortality risks ($d(a) \neq 0$) described in this study carry over directly to situations with heterogeneous foraging costs ($c(a) \neq 0$). We therefore simplify the presentation of our analysis below by ignoring foraging costs, keeping in mind that whatever is said about mortality risks applies equally to foraging costs.

Heterogeneous resource qualities

Until now, we have assumed that all resources are of similar quality, or, equivalently, that their biomasses are measured in units that correspond to their energetic value. We now relax

this assumption by describing resource quality as $q_0 + q(a)$, i.e. as the sum of a baseline quality value q_0 and of a resource-specific quality component $q(a)$. We can again show (Appendix 1) that the evolutionarily singular foraging strategy involves using all effort and that it is neutrally stable:

$$x^*(a) = \frac{r_0(a)(q_0 + q(a))}{\hat{n}(x^*)(d_0 + d(a))}. \tag{10}$$

Not surprisingly, resources of high quality will thus receive more effort than low-quality resources. This means that changes in resource quality have an effect that is exactly the opposite of the effect of changes in mortality. In fact, for all models presented in this study, resource quality affects the evolutionary singularity as part of the ratio $[q_0 + q(a)]/[d_0 + d(a)]$. Therefore, without any loss of generality, we can keep using the simple model in which resource quality is uniform at unity ($q_0 = 1$ and $q(a) = 0$).

Non-linear functional responses

We now allow for the functional response of foragers to take arbitrary, non-linear forms – as long as it is a monotonically increasing function. Finding evolutionary singularities by solving the canonical equation (4) then turns out not to be possible in general. Yet solutions can be obtained through the calculus of variations (Parvinen *et al.*, 2006).

As shown in Appendix 2, the evolutionary singularity again involves expending all available effort:

$$x^*(a) = \frac{r_0(a)}{\hat{n}(x^*)f^{-1}(d_0 + d(a))}. \tag{11}$$

Here f^{-1} is the inverse of the functional response function f and $\hat{n}(x^*)$ is given by $\hat{n}(x^*) = \int r_0(a) f^{-1}(d_0 + d(a)) da$. The potential intake rates at x^* are now $p(a) = r_0(a)/(n(x^*)x^*(a)) = f^{-1}(d_0 + d(a))$. Thus, a non-linear functional response will always affect the potential intake rate and equilibrium population size at x^* . In contrast, the singular strategy x^* itself will remain unaffected by such a non-linear functional response only when mortality risks are uniform across the resource gradient; recalling the similar roles of mortality risks, foraging costs, and resource qualities, also the latter factors must be uniform for this result to hold. As before, the singularity is only neutrally stable against mutants that expend all foraging effort.

As a concrete example, we now consider a forager with a Holling type-II functional response, which implies the saturation of intake with increasing resource availability. The functional response is described by the function $f(p) = mp/(m + p)$, where m is the maximum intake rate and p is the potential intake rate. The latter measures the availability of resources of type a and in our model is given by $p(a) = r_0(a)/(\hat{n}(x)x(a))$. The inverse of the functional response function is $f^{-1}(p') = mp'/(m - p')$, which yields

$$x^*(a) = \begin{cases} \frac{r_0(a)(m - d_0 - d(a))}{\hat{n}(x^*)m(d_0 + d(a))} & \text{if } d_0 + d(a) < m, \\ 0 & \text{otherwise.} \end{cases} \tag{12}$$

The evolutionarily singular strategy thus implies not using any resources for which the total mortality rate $d_0 + d(a)$ exceeds the maximum intake rate m . This latter finding readily

generalizes to all functional responses that describe intake saturation towards a horizontal asymptote.

Figure 2 shows results for a linear and a Holling type-II functional response and for homogeneous and heterogeneous mortality risks. If mortality risk is uniform, the non-linear functional response has no effect on the evolutionarily singular foraging strategy, even though it affects the resultant potential intake rate, $p(a) = f^{-1}(d_0)$. The evolutionary response to heterogeneous mortality risks is to divert foraging effort away from resources that imply relatively high mortality risk; as a consequence, these thus less utilized resources provide higher potential intake rates, $f^{-1}(d_0) > d_0$. The interaction between functional response and mortality risk means that a lowering of the functional response's saturation level causes high-mortality resources to become even more under-utilized relative to their intrinsic renewal rates r_0 .

Dynamic resources

The models above are all based on the assumption that resources are renewed and become available at a constant rate, independent of how they are harvested by the foragers. This presumes a scenario in which unused resources do not accumulate for later consumption and foragers do not have access to the resource population itself, but only to some form of surplus production. Such assumptions may be appropriate for describing animals feeding on carcasses, easily perishable fruits and seeds, or stream drift.

More typically, however, unused resources accumulate and foragers consume the productive part of a resource, so that consumption influences the standing stock of the resource as well as its renewal rate. Under these circumstances, foragers regulate the dynamics of the resource. Here we ask how such ecological feedback will influence the evolution of foraging strategies. We assume that a logistic growth model describes resource dynamics in the absence of foraging. Each resource is thus characterized by its intrinsic growth rate $g(a)$ and carrying capacity $K(a)$.

The coupling between resource and forager dynamics depends on how foragers compete for resources. First, we may assume that foragers influence each others' resource acquisition directly, through interference, such that the mere presence of other foragers is experienced as reduced resource availability. This kind of resource competition is akin to the scenario studied for non-dynamic resources. Second, we may assume indirect resource competition, so that each forager takes its share of the resource, without directly experiencing the presence of the other foragers. Competitive effects then unfold only indirectly, through changes in resource abundance caused by foraging. Below we consider two alternative ways of coupling resource and forager dynamics, resulting from exploitation competition with and without interference in resource acquisition. These two cases represent extremes of a continuum of intermediate scenarios, in which interference in resource acquisition rises from absent to full as the total foraging effort collectively invested on any resource increases.

Dynamic resources: exploitation competition with interference in resource acquisition

We first examine the evolution of foraging strategies of foragers experiencing interference in resource acquisition because this model readily emerges as an immediate extension of the classic model without resource dynamics. In the fitness function of foragers, we can simply replace the constant renewal rate $r_0(a)$ used in the models above with the product of

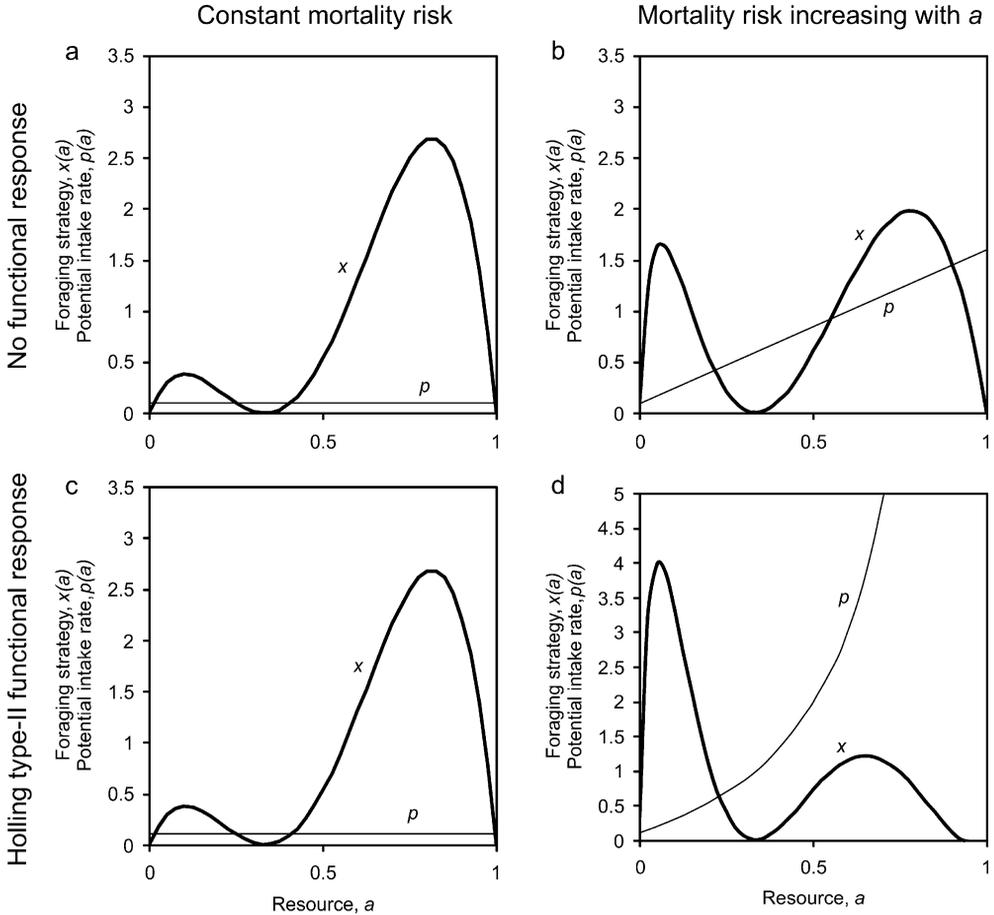


Fig. 2. The influence on evolutionarily singular foraging strategies of non-linearity in functional responses and of heterogeneity in mortality risks. The top row shows results for a linear functional response, while the bottom row refers to a Holling type-II functional response with an asymptotic maximum intake rate of $m = 1$. The left-hand column shows results for uniform mortality risk ($d = 0.1$), while the right-hand column refers to mortality risk that increases linearly with resource type a ($d = 0.1 + 1.5a$). An increase in the heterogeneity of mortality risks diverts effort away from risky resources. However, as risky resources are used less intensively, they provide higher potential intake rates. If mortality risk is uniform, a non-linearity in functional responses has no effect on foraging strategy, and only a small effect on potential intake (which is the same for all resources). If mortality risk is not uniform, functional responses can have strong effects on resource use. Because a non-linear functional response causes the actual intake rate of foragers to saturate, they cannot take full advantage of resources that are risky in terms of mortality, but which provide high potential intake rate. Risky resources thus become even more under-utilized, up to a point where, beyond a certain level of mortality, they are not used at all. Note that changes and heterogeneities in mortality risks are equivalent to those in foraging costs and the inverse quality of resources. Renewal rates are chosen as in Fig. 1. The equilibrium population size of foragers varies from $\hat{n}(x^*) = 13.0$ in (a) to $\hat{n}(x^*) = 0.5$ in (d).

resource biomass $B(a)$ and a harvest rate h that describes the maximum per capita rate at which resource biomass can be exploited, $r(x', x) = \int [x'(a)f\left(\frac{hB(a)}{n(x)x(a)}\right) - x'(a)d(a) - d_0] da$.

Exploitation competition occurs because foragers remove resources, which happens at a per capita rate that is proportional to foraging effort $x(a)$ on that resource, the functional response f , and a parameter z converting forager intake rate into the corresponding removal rate of resource biomass, with the potential intake rate of foragers given by their per capita share of the harvestable resource biomass, $hB(a)/(n(x)x(a))$. The dynamics of each resource type a , for a given foraging strategy x and forager population size $n(x)$, is now described by the following equation:

$$\frac{d}{dt} B(a) = g(a) \left(1 - \frac{B(a)}{K(a)} \right) B(a) - zn(x)x(a)f\left(\frac{hB(a)}{n(x)x(a)}\right). \tag{13}$$

Note that when the functional response is linear, $f(p) = p$, the resource dynamics become decoupled from the evolutionary dynamics of foraging strategies, as the product $n(x)x(a)$ then cancels out in the second term above.

While equations describing equilibrium population sizes of the foragers and resources become formidable for non-linear functional responses, the calculus of variations approach still yields analytical results. Details of the derivation are given in Appendix 2. To simplify the presentation, we first give the result for the equilibrium distribution of resource biomass at the evolutionarily singular foraging strategy:

$$\hat{B}(x^*, a) = \begin{cases} K(a) \left[1 - \frac{hz(d(a) + d_0)}{g(a)f^{-1}(d(a) + d_0)} \right] & \text{if } g(a)f^{-1}(d(a) + d_0) > hz(d(a) + d_0), \\ 0 & \text{otherwise.} \end{cases} \tag{14}$$

The evolutionarily singular foraging strategy then takes the following simple form:

$$x^*(a) = \begin{cases} \frac{h\hat{B}(x^*, a)}{\hat{n}(x^*)f^{-1}(d(a) + d_0)} & \text{if } g(a)f^{-1}(d(a) + d_0) > hz(d(a) + d_0), \\ 0 & \text{otherwise.} \end{cases} \tag{15}$$

This equation is similar to equation (11) obtained for non-dynamic resources. Again, the singularity involves using all available effort and is of the degenerate type in the sense that it is evolutionarily stable against all mutants wasting foraging effort, $\int x'(a)da < 1$, but only neutrally stable against all mutants expending all their foraging effort. The equilibrium population size of the forager, $\hat{n}(x^*) = h \int \hat{B}(x^*, a) / f^{-1}(d(a) + d_0) da$, depends on the equilibrium distribution of resource biomass, as well as on mortality risks along the resource gradient and on the functional response. Mortality diverts foraging effort away from resources with high risk (Fig. 3). The potential intake rate at x^* is again given by $p(a) = f^{-1}(d(a) + d_0)$. Thus, if mortality risk is uniform along the resource gradient, the evolutionarily singular foraging effort is proportional to the equilibrium distribution of resource biomass, $x^*(a) \propto \hat{B}(x^*, a)$, so that input matching holds. Resources that have high carrying capacity and high intrinsic growth rate tend to have high equilibrium biomass and will thus be foraged more intensively than resources with low carrying capacity and low intrinsic growth rate. Resources with low growth rate may be driven to extinction.

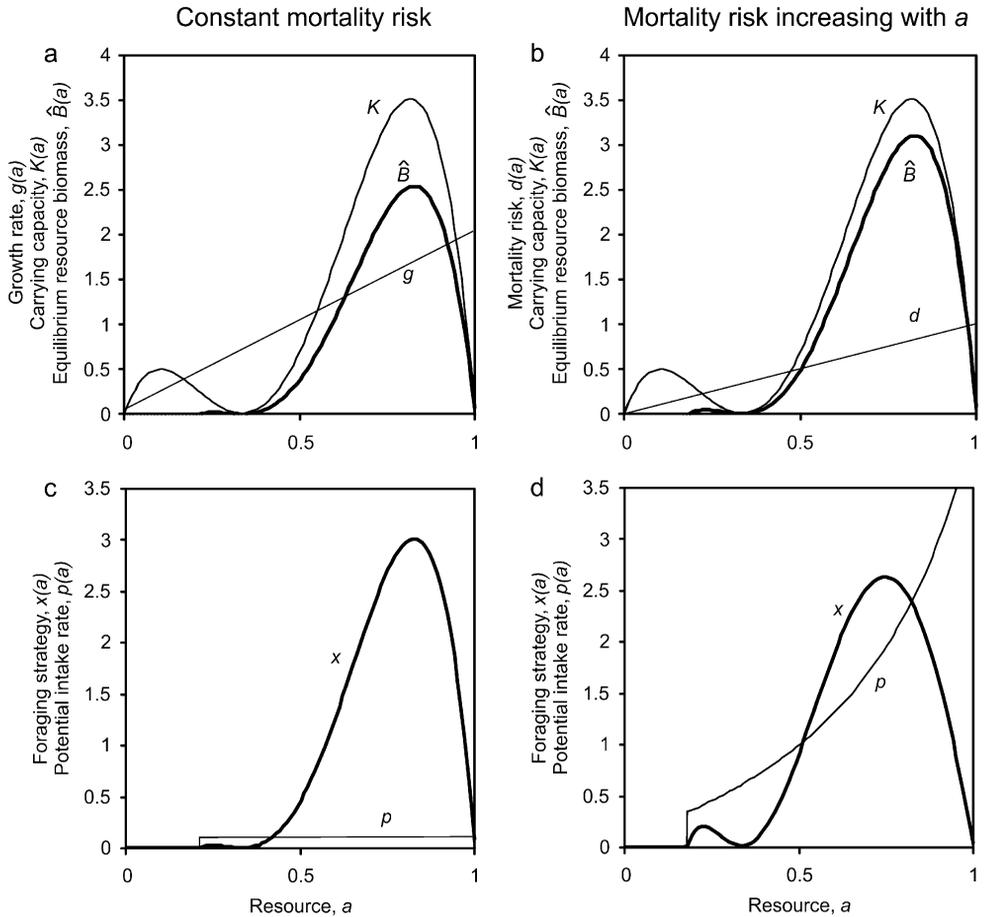


Fig. 3. Evolutionarily singular strategies for foraging on dynamic resources when foragers interfere with each other during resource acquisition. The top row shows how growth rates (g : thin straight lines), carrying capacities (K : thin curves), and evolutionary equilibrium abundances (\hat{B} : thick curves) vary across resources. The bottom row shows the resultant potential intake rates (p : thin curves) and evolutionarily singular foraging strategies (x : thick curves). Similar to Fig. 2, the left-hand column shows results for uniform mortality risk ($d = 0.1$), while the right-hand column refers to mortality risk that increases linearly with a ($d = 0.1 + a$). Resource dynamics are determined by resource-specific carrying capacities $K(a)$ and intrinsic growth rates $g(a)$ and by the removal of resource biomass through foraging. At equilibrium, resource abundances are closer to carrying capacities for those resources that imply high mortality risks for foragers, as can be seen from panels (a) and (b). Resources that have low growth rates may be extinct at equilibrium. If mortality risks are uniform, all non-extinct resources provide the same potential intake rate, as shown in panel (c). If mortality risks are not uniform, effort is diverted away from high-risk resources, which then offer higher potential intake rates, as shown in panel (d). The equilibrium population size of foragers is $\hat{n}(x^*) = 7.9$ for uniform and $\hat{n}(x^*) = 0.54$ for non-uniform mortality risks. Carrying capacities K follow the same curve as r_0 in Fig. 1. The functional response is of Holling type-II with an asymptotic maximum intake rate of $m = 1$. The maximum harvest rate of foragers is $h = 1$, the conversion ratio is $z = 0.5$, and the intrinsic growth rate of resources a is $g(a) = 0.05 + 2a$.

Dynamic resources: exploitation competition without interference in resource acquisition

We now consider the case of pure exploitation competition. Each forager then harvests at rate $f(hB)$, distributed over different resources according to the foraging strategy $x(a)$. Forager fitness is as above, but with the interference effect removed, $r(x', x) = \int [x'(a)f(hB(a)) - x'(a)d(a) - d_0]da$. Analogously, the resource dynamics are now given by

$$\frac{d}{dt} B(a) = g(a) \left(1 - \frac{B(a)}{K(a)} \right) B(a) - zn(x)x(a)f(hB(a)). \tag{16}$$

The derivation of results is provided in Appendix 2. At the evolutionarily singular foraging strategy, the equilibrium distribution of resource biomass is

$$\hat{B}(x^*, a) = \begin{cases} f^{-1}(d(a) + d_0)/h & \text{if } f^{-1}(d(a) + d_0)/h < K(a), \\ K(a) & \text{otherwise.} \end{cases} \tag{17}$$

The evolutionarily singular foraging strategy is

$$x^*(a) = \begin{cases} g(a)\hat{B}(x^*, a) \frac{1 - \hat{B}(x^*, a)/K(a)}{z\hat{n}(x^*)f(h\hat{B}(x^*, a))} & \text{if } f^{-1}(d(a) + d_0)/h < K(a), \\ 0 & \text{otherwise,} \end{cases} \tag{18}$$

where $\hat{n}(x^*) = \frac{1}{z} \int g(a)\hat{B}(x^*, a)[1 - \hat{B}(x^*, a)/K(a)]/f(h\hat{B}(x^*, a))da$. Equation (18) is complex and the results are best interpreted graphically. However, the potential intake rate is simple, $p(a) = h\hat{B}(x^*, a) = \min[hK(a), f^{-1}(d(a) + d_0)]$. It can also be shown that the singularity again involves using all available effort and that it is of the degenerate type.

Results for pure exploitation competition are shown in Fig. 4. The singular foraging strategy involves driving the resources to ‘optimal’ levels that are determined by the corresponding mortality risks (and/or, through direct extension, by foraging costs and resource qualities); if the corresponding carrying capacity is lower than this hypothetical optimal level, then the resource is not used at all. If there are such unused resources, then the input matching rule breaks down even when mortality risks are uniform across the resource gradient. Note that the potential intake rates exactly track the pattern of resource biomass, because there are no direct interactions between foragers. Not surprisingly, increasing mortality risks lower forager population size, and may thus cause more resources to remain unexploited. The foraging effort is then redistributed to those resources that provide high potential intake rates, which are the high-risk resources.

Note that the results for pure exploitation competition are qualitatively different from those based on the inclusion of interference in resource acquisition. First, the equilibrium biomasses of unused resources are positive and given by $K(a)$ for pure exploitation competition, whereas they are zero when interference in resource acquisition is included. Thus, certain resources are intrinsically unattractive in the former case, whereas in the latter case resources become unattractive by being driven to extinction through foraging. This difference seems to occur because, in the presence of interference competition, there are two negative feedback mechanisms between foraging effort and potential intake rate: if exploitation is reduced, a resource can increase in abundance and there will also be less

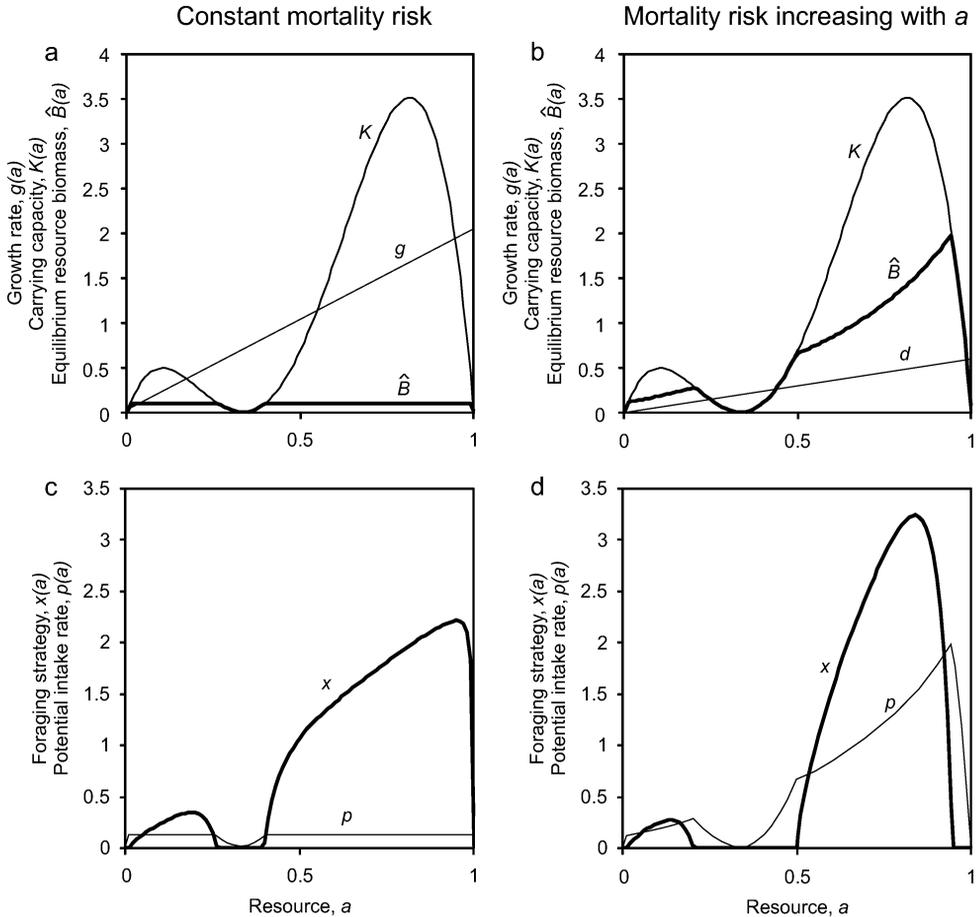


Fig. 4. Evolutionarily singular strategies for foraging on dynamic resources when foragers do not interfere with each other during resource acquisition. The top row shows how growth rates (g : thin straight lines), carrying capacities (K : thin curves), and evolutionary equilibrium abundances (B : thick curves) vary across resources. Similar to Figs. 2 and 3, the left-hand column shows results for uniform mortality risk ($d=0.1$), while the right-hand column refers to mortality risk that increases linearly with a ($d=0.1+0.6a$). Resource dynamics are determined by resource-specific carrying capacities $K(a)$ and intrinsic growth rates $g(a)$ and by the removal of resource biomass through foraging. Resource abundance at equilibrium is determined by the mortality risks of foraging, as shown in panels (a) and (b) – if mortality risks are uniform (a), then all utilized resources equilibrate at the same level. If the carrying capacity of a resource is lower than that level, then that resource is not used. Thus, there may be resources that would provide intake if harvested, and yet it does not pay for foragers to include them in their diet (c). If mortality risks are not uniform, some unused resources may even provide a higher potential intake rate than some resources that are used (d). The equilibrium population size of foragers is $\hat{n}(x^*)=4.6$ for uniform and $\hat{n}(x^*)=3.8$ for non-uniform mortality risks. Carrying capacities K follow the same curve as r_0 in Fig. 1. The functional response is of Holling type-II with an asymptotic maximum intake rate of $m=1$. The maximum harvest rate of foragers is $h=1$, the conversion ratio is $z=0.1$, and the intrinsic growth rate of resources a is $g(a)=0.05+2a$.

interference in resource acquisition. The advantage of reduced interference is then strong enough to render beneficial the foraging of scarce resources. Second, whether a resource is used depends on its carrying capacity but not on its intrinsic growth rate for pure exploitation competition, whereas the converse dependence applies when interference in resource acquisition is included. This is because in the presence of such interference competition, resources become unused through extinction. Close to the extinction threshold, a resource's carrying capacity has no effect and only its intrinsic growth rate matters. In contrast, unused resources under pure exploitation competition remain at their carrying capacity. Third, the equilibrium level of used resources is independent of all resource parameters for pure exploitation competition, whereas it depends on carrying capacity and intrinsic growth rate when interference in resource acquisition is included.

Complex variance–covariance functions

Until now, we have considered foraging strategies that can take any shape provided efforts are non-negative and the global constraint $\int x(a)da \leq 1$ is respected. In reality, however, genetic constraints may prevent attaining such perfect adaptations: mutations that change foraging strategy on a particular resource type are likely to affect foraging on similar resource types as well. Such local correlations are described by variance–covariance functions of the form shown in Fig. 5a (Dieckmann *et al.*, 2006). The singular strategies $x^*(a)$ have now to be sought numerically. To make comparisons straightforward, we again resort to the ecological assumptions of the classic model.

For the relatively smooth and slowly changing resource distribution used in the previous examples, local correlations in mutational effects have little effect on the evolutionary singularity (compare Fig. 5b with Fig. 1b). In contrast, if the resource distribution is ragged, the variance–covariance function can drastically affect the evolutionary singularity, which then only superficially tracks resource availability (Fig. 5c). Consequently, potential intake rate is not uniform but varies among resources by a factor as large as about 4. Even when the resource distribution varies smoothly, genetic constraints must thus be expected to prevent foraging strategies from tracking fine-grained variation in resource distribution (Fig. 5d).

Models with complex variance–covariance functions may have more than one singularity. In particular, the foraging strategy that exactly tracks the resource distribution is always a singularity in the classic setting in which mortality risks, foraging costs, and resource qualities are uniform. However, this singularity is not convergence stable, so that any small perturbation will trigger evolution towards another, convergence-stable singularity, leading to evolutionary outcomes as shown in Figs. 5(c, d).

DISCUSSION

In this study, we have generalized patch-based foraging models to continuous resource gradients. Using a unifying perspective offered by function-valued adaptive dynamics, we have analysed the impacts on evolutionarily singular foraging strategies of non-linear functional responses, heterogeneous mortality risks, foraging costs, and resource qualities, genetic covariances constraining foraging, and feedbacks between foraging and resource dynamics through exploitation competition and interference competition.

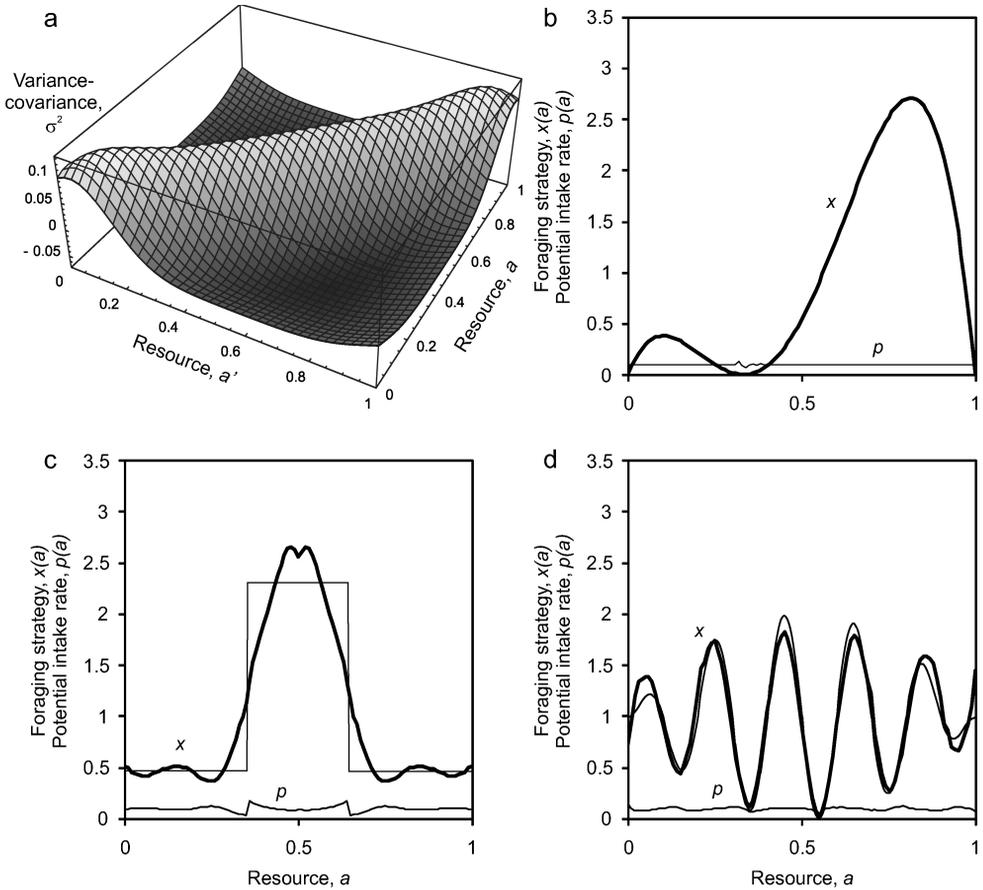


Fig. 5. The effects of complex variance–covariance functions on evolutionarily singular foraging strategies. (a) The variance–covariance function constraining the evolution of foraging strategy is chosen such that evolutionary changes in foraging effort on one resource are positively correlated with evolutionary changes in foraging effort on nearby resources, and negatively correlated with changes further away; for the derivation of the particular function shown, see Dieckmann *et al.* (2006). (b) For a smooth resource distribution, such covariances have no visually discernible effect on the singular foraging strategy (thick curve; cf. with Fig. 1b). The thin curve shows the potential intake rate p (computational inaccuracies cause some unevenness in the numerical results when foraging effort is very low). However, for a highly variable resource distribution, the effects imposed by the variance–covariance function can be large. In (c), the step function (thin curve) shows the singular foraging strategy in the absence of genetic constraints. In the presence of genetic constraints, this singular foraging strategy is not convergence stable. The convergence-stable singular foraging strategy, in contrast, only roughly tracks the variability in resource abundance. (d) Similar results are obtained when the resource distribution is smooth but rugged: unconstrained (thin curve) and constrained (thick curve) singular foraging strategies differ, with this difference increasing as the resource distribution becomes more fine-grained. In panels (c) and (d), genetic constraints result in the violation of the ‘equal intake rule’, so that the potential intake rate p varies along the gradient (thin curves at the bottom, with values multiplied by 5 for improved visibility).

We have applied three complementary methods (Dieckmann *et al.*, 2006; Parvinen *et al.*, 2006) for finding evolutionarily singular foraging strategies. Solving the canonical equation of adaptive dynamics, either analytically or numerically, is perhaps the most intuitive method. Unfortunately, an analytical approach of this sort is often impossible as equations easily get intractable. The numerical approach, in contrast, will always work, although it is usually difficult to gain as many general insights into a model's behaviour as when based on analytical solutions; computational challenges might also occur. Both methods of solving the canonical equation allow characterization of evolutionary transients and evolutionary singularities. The third alternative is to use the calculus of variations. As we have seen in this study, this method can provide analytical results even when solving the canonical equation analytically proves impossible. The calculus of variations also allows characterizing the second-order conditions that characterize the evolutionary stability of singularities (Parvinen *et al.*, 2006). The disadvantage of this method is that it can tell us nothing about evolutionary transients, nor does it help to evaluate whether a particular singularity is evolutionarily attractive in terms of convergence stability.

Function-valued traits naturally arise in many situations in which adaptations depend on continuous variables describing an individual's environment or state. Examples include age- and size-dependent traits such as energy allocation strategies, and reaction norms in response to environmental variables like temperature (see Kingsolver *et al.*, 2001, for a review). Outside biology, problems of optimal control and search have also called for function-valued solutions (Pontryagin *et al.*, 1962; Stone, 1975). Modelling the evolution of function-valued traits has until recently relied on quantitative genetics or optimality models (e.g. Stearns and Koella, 1986; Gomulkiewicz and Kirkpatrick, 1992; Beder and Gomulkiewicz, 1998). In practice, a limitation of these approaches is that they over-simplify or ignore ecological feedback. While such a simplification is often acceptable in experimental settings, which have motivated much of the earlier work, understanding long-term evolution in natural systems requires accounting for ecological feedback. This feedback is easily accounted for in the adaptive dynamics approach, which is hence ideally suited for studying the evolution of foraging strategies under frequency-dependent ecological interactions. Other models based on this framework include evolutionary models of phenotypic plasticity (Ernande and Dieckmann, 2004), maturation reaction norms (Ernande *et al.*, 2004), metabolic investment strategies (Dieckmann *et al.*, 2006; Parvinen *et al.*, 2006), and flowering phenology (Dieckmann *et al.*, 2006).

Not unexpectedly, predictions of classical patch models (reviewed by Kacelnik *et al.*, 1992) are recovered for resource gradients, as long as the simplifying assumptions underlying those models are maintained: at evolutionary equilibrium, resource intake is uniform across the gradient, and the distribution of foraging effort is proportional to resource availability. However, allowing for greater realism by relaxing these simplifying assumptions results in systematic deviations from the classical predictions.

In the simplest possible setting, patches have just two attributes, resource abundance and number of foragers. We have considered three additional attributes: mortality risks, foraging costs, and resource qualities. The effects of mortality risks and foraging costs are to divert foraging effort away from risky and costly resources, while high resource qualities have the opposite effect. Interestingly, when measured in a common currency – that is, in terms of fitness implications – these resource attributes affect the distribution of foraging effort in a similar way: mortality risks (d), foraging costs (c), and resource quality (q) always appear as one dimensionless compound variable $(d + c)/q$. This happens in our model because these factors all affect the fitness benefits of foraging directly. If there were

feedbacks – for example, through density-dependent mortality risks or through the deterioration of resource quality caused by inducible defences – this simple relationship would break down. We have found that whenever the ratio $(d+c)/q$ varies along the resource gradient, the classical prediction of equal intake breaks down. However, when costs and benefits are measured properly, in terms of overall fitness benefits, these fitness benefits are uniform along the resource gradient at evolutionary equilibrium. Interestingly, Fretwell and Lucas (1970) had formulated their theory in terms of fitness, whereas the bulk of the later literature has adopted resource intake as a surrogate measure of fitness.

While the importance of functional responses in predator–prey interactions has generally been acknowledged (e.g. Abrams, 1982; Kacelnik *et al.*, 1992), only a few models based on ideal free distribution theory have incorporated non-linear functional responses (e.g. Sutherland, 1983; Bernstein *et al.*, 1988, 1991; Krivan, 1997, 2003). In particular, we are not aware of any systematic analysis of the consequences of non-linear functional responses. An important caveat is to realize that if equal potential intake rates are assumed, then non-linear functional responses will not alter the predictions of forager distribution – as the functional response then amounts to no more than a uniform transformation that does not alter the relative benefits of different resources. More generally, however, the assumption of equal intake will not hold, so that functional responses become crucially important for predicting foraging strategies. In particular, based on any saturating functional response, such as one of Holling type II, foragers cannot take full advantage of resources that provide high potential intake rates. This tends to amplify any differences that exist in intake rates for other reasons. For example, if some resources are more risky to forage on, they will be exposed to less foraging effort than their renewal rate would suggest, and thus provide above-average intake rates. This violation of the input matching rule is known as ‘undermatching’ (Baum, 1974) and is commonly observed in empirical tests of ideal free distribution theory (Kennedy and Gray, 1993; Giannico and Healey, 1999), as well as in models allowing for predation (McNamara and Houston, 1990; Moody *et al.*, 1996). In summary, while functional responses are not sufficient to explain undermatching, they can significantly amplify it.

In this study, we have analysed two non-trivial settings for coupling the dynamics of foragers and their resources that go beyond the existing literature. The first is based on pure exploitation competition: foragers are only affected by each other through their collective effect on the available amounts of resources. The second, more general, setting includes interference in resource acquisition (as in the classic model) in addition to exploitation competition. These alternative couplings result in qualitatively different predictions. Under pure exploitation competition, some resources may not be used at all and thus remain at their carrying capacity. If the ratio $(d+c)/q$ is uniform across the gradient, all exploited resources will have the same equilibrium biomass, irrespective of their intrinsic growth rate or carrying capacity. When interference in resource acquisition is included, the equilibrium resource biomasses roughly track variations in carrying capacities, but some resources may be exploited to extinction. The distribution of foraging effort follows the equilibrium resource biomasses in a way that is similar to the classic model, but now those biomasses are determined jointly by foragers and resources. In contrast, under pure exploitation competition, one should expect to observe no more than a weak correlation between resource availability and foraging effort.

The classical models assume very specific and unusual resource dynamics. In these so-called continuous input models, resources become available continuously and are immediately consumed or otherwise disappear. The dynamics of resources and foragers are

thus essentially decoupled, because foragers are not having any influence on resource dynamics. Since resources are fully characterized by their renewal rates, which are assumed to be constant in time, all changes in foraging conditions are caused by the foragers themselves. Such continuous input systems are probably uncommon in nature (Kacelnik *et al.*, 1992; Tregenza, 1994). Nevertheless, attempts to include more realistic resource dynamics and coupling them to forager dynamics are surprisingly rare. Lessells (1995) considered a model in which the harvestable biomass produced by resources at a constant rate could accumulate in patches. While this is more realistic than the classical assumption, as resources here need not be consumed immediately, the model still remains rather special because resource populations are not influenced by foragers. Also, equal intake in Lessells's model was taken as an assumption rather than obtained as an evolutionary outcome. Realistic resource dynamics seem to have been studied for the first time by Frischknecht (1996), although this model focused on comparing pre-defined rules for the switching of foragers between resource patches. Adler *et al.* (2001) studied the consequences of variable forager body size on foraging strategies in a model that also included resource dynamics. Their focus, however, was on analysing the interactions between differently sized foragers, rather than on connecting resource dynamics to forager dynamics. Krivan (2003) presented a patch model that is similar to our model with resource dynamics and pure exploitation competition among foragers, but without including forager dynamics. Krivan's results are broadly in agreement with ours in that the distribution of foraging effort is proportional to the intrinsic growth rates of resources. He also predicts that some resources may not be used at all and thus stay at their carrying capacity. In another study, Krivan (1997) presented a two-patch model in which both the predator and the prey were dynamic, coupled through a linear functional response. This study's focus, however, was on how adaptive foraging behaviour affected predator-prey dynamics. Our study thus appears to be the first to systematically compare evolution of foraging strategies under both trivial and more realistic coupling between resource dynamics and forager dynamics.

It is typically expected that the selection gradient at evolutionary equilibrium becomes uniform, and remains positive, across the whole resource gradient. This expectation can be seen as the appropriate generalization of the input matching rule, with fitness benefits being matched instead of resource intake. Our results show, however, that the selection gradient does not become uniform when genetic constraints prevent foragers from accurately tracking variability in resource availability. This is realistic, as perfect adaptation is usually very costly and often impossible (Egas *et al.*, 2005). Some relevant costs can indeed be captured as genetic constraints due to antagonistic side-effects of feasible mutations that would improve foraging effort on a particular resource. Moreover, genetic constraints of the more sophisticated type presented in Fig. 5a can probably even approximate the effect of certain other types of costs for which distances along the gradient matter. Prominent examples in this category are movement costs (Bernstein *et al.*, 1991). Also, imperfect information (Bernstein *et al.*, 1988) could result in a smoothing of actual foraging strategies relative to the 'perfect' one akin to our results shown in Fig. 5.

Several factors were not considered in our study. The first is density dependence in the death rates of foragers. For example, per capita death rate may increase when many individuals utilize the same resource (Moody *et al.*, 1996). Second, resource abundance may show temporal variability owing to environmental fluctuations. While our framework is deterministic, some progress in understanding the consequences of such variability could probably be made without resorting to numerical methods, by describing variability along

the lines developed, for example, by Earn and Johnstone (1997) and Hakoyama (2003). Third, individual differences between foragers have been shown to have important effects on their distribution across patches (e.g. Parker and Sutherland, 1986; Grand and Dill, 1999; Adler *et al.*, 2001), but the approach we have developed here is not suited to highly polymorphic forager populations. Fourth, we have assumed that the coupling of foraging across different resources occurs only through total effort constraints and genetic constraints. In addition to movement costs, information limitations, and non-localized competition (Bernstein *et al.*, 1988, 1991; Sasaki, 1997), other mechanisms may couple foraging efforts on adjacent or similar resources. For example, it is conceivable that saturation effects represented by functional responses jointly apply to groups of resources.

Most earlier work on the distribution of foragers in heterogeneous environments has been based on models assuming just two patches. This often suffices to capture some general effects of spatial structure, so that a higher number of patches would only seem to make analyses more difficult. One might therefore think that moving up from two patches to a gradient with an infinite number of resources would be unwieldy and intractable. This, however, turns out not to be the case. Aided by recently developed tools for analysing the evolutionary dynamics of function-valued traits (Dieckmann *et al.*, 2006; Parvinen *et al.*, 2006), we could obtain analytical results even for models that include generic functional responses and resource dynamics fully coupled with forager dynamics.

Our results highlight several issues that impinge on empirical studies of consumer–resource interactions. First, the ecological interactions involved in foraging have a profound impact on observable relationships between foraging effort, potential and actual intake rates, and resource biomass. For example, different resource types may stay unused depending on whether or not foragers experience interference competition. Second, when mortality risks (d), foraging costs (c), and resource qualities (q) are measured in a common currency, in terms of their fitness implications, they affect the distribution of foraging effort only jointly, appearing as a single dimensionless compound variable $(d + c)/q$. Third, heterogeneity in any of these three resource attributes suffices to invalidate the input-matching rule and the equal-intake prediction. When mortality risks, foraging costs, and/or resource qualities are heterogeneous, experimental and observational studies cannot be designed or interpreted without accounting for such heterogeneity.

ACKNOWLEDGEMENTS

We thank Marc Mangel and Shuichi Matsumura for helpful comments on the manuscript. M.H. and U.D. acknowledge financial support by the Marie Curie Research Training Networks ModLife (Modern Life-History Theory and its Application to the Management of Natural Resources) and FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks) funded through the European Community's Fifth and Sixth Framework Programmes. M.H. acknowledges financial support by the Norwegian Research Council and by the Bergen Research Foundation. U.D. acknowledges financial support by the Austrian Science Fund; by the Austrian Federal Ministry of Education, Science, and Cultural Affairs; and by the Vienna Science and Technology Fund.

REFERENCES

- Abrams, P.A. 1982. Functional responses of optimal foragers. *Am. Nat.*, **120**: 382–390.
Adler, F.R., Richards, S.A. and de Roos, A.M. 2001. Patterns of patch rejection in size-structured populations: beyond the ideal free distribution and size segregation. *Evol. Ecol. Res.*, **3**: 805–827.

- Baum, W.M. 1974. On two types of deviation from the matching law: bias and undermatching. *J. Exp. Anal. Behav.*, **22**: 231–242.
- Beder, J.H. and Gomulkiewicz, R. 1998. Computing the selection gradient and evolutionary response of an infinite-dimensional trait. *J. Math. Biol.*, **36**: 299–319.
- Bernstein, C., Kacelnik, A. and Krebs, J.R. 1988. Individual decisions and the distribution of predators in a patchy environment. *J. Anim. Ecol.*, **57**: 1007–1026.
- Bernstein, C., Kacelnik, A. and Krebs, J.R. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *J. Anim. Ecol.*, **60**: 205–225.
- Brew, J.S. 1982. Niche shift and the minimisation of competition. *Theor. Pop. Biol.*, **22**: 367–381.
- Clark, C.W. and Mangel, M. 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford: Oxford University Press.
- Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.
- Dieckmann, U., Heino, M. and Parvinen, K. 2006. The adaptive dynamics of function-valued traits. *J. Theor. Biol.*, **241**: 370–389.
- Earn, D.J.D. and Johnston, R.A. 1997. A systematic error in tests of ideal free theory. *Proc. R. Soc. Lond. B*, **264**: 1671–1675.
- Egas, M., Sabelis, M.W. and Dieckmann, U. 2005. Evolution of specialization and ecological character displacement of herbivores along a gradient of plant quality. *Evolution*, **59**: 507–520.
- Ernande, B. and Dieckmann, U. 2004. The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. *J. Evol. Biol.*, **17**: 613–628.
- Ernande, B., Dieckmann, U. and Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. Lond. B*, **271**: 415–423.
- Fretwell, S.D. and Lucas, H.J. 1970. On territorial behavior and other factors influencing habitat selection. *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.
- 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.
- Gomulkiewicz, R. and Kirkpatrick, M. 1992. Quantitative genetics and the evolution of reaction norms. *Evolution*, **46**: 390–411.
- Grand, T.C. and Dill, L.M. 1999. Predation risk, unequal competitors and the ideal free distribution. *Evol. Ecol. Res.*, **1**: 389–409.
- Hakoyama, H. 2003. The ideal free distribution when the resource is variable. *Behav. Ecol.*, **14**: 109–115.
- Houston, A.I. and McNamara, J.M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- 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.
- Kingsolver, J.G., Gomulkiewicz, R. and Carter, P.A. 2001. Variation, selection and evolution of function-valued traits. *Genetica*, **112/113**: 87–104.
- Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. *Am. Nat.*, **149**: 164–178.
- Krivan, V. 2003. Ideal free distributions when resources undergo population dynamics. *Theor. Pop. Biol.*, **64**: 25–38.

- Lessells, C.M. 1995. Putting resource dynamics into continuous input ideal free distribution models. *Anim. Behav.*, **49**: 487–494.
- McNamara, J. and Houston, A.I. 1990. State-dependent ideal free distributions. *Evol. Ecol.*, **4**: 298–311.
- Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202.
- Mitchell, W.A. 2000. Limits to species richness in a continuum of habitat heterogeneity: an ESS approach. *Evol. Ecol. Res.*, **2**: 293–316.
- Moody, A.L., Houston, A.I. and McNamara, J.M. 1996. Ideal free distributions under predation risk. *Behav. Ecol. Sociobiol.*, **38**: 131–143.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**: 1–13.
- Parker, G.A. 1978. Searching for mates. In *Behavioural Ecology*. (J.R. Krebs and N.B. Davies, eds.), pp. 214–244. Oxford: Blackwell Scientific.
- 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.
- Parvinen, K., Dieckmann, U. and Heino, M. 2006. Function-valued adaptive dynamics and the calculus of variations. *J. Math. Biol.*, **52**: 1–26.
- Pontryagin, L.S., Boltyanskii, V.G., Gamkrelidze, R.V. and Mishchenko, E.F. 1962. *Mathematical Theory of Optimal Processes*. New York: Wiley.
- Richards, S.A. and Wilson, W.G. 2000. Adaptive feeding across environmental gradients and its effect on population dynamics. *Theor. Pop. Biol.*, **57**: 377–390.
- Sasaki, A. 1997. Clumped distribution by neighborhood competition. *J. Theor. Biol.*, **186**: 415–430.
- Stearns, S.C. and Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: prediction of reaction norms for age and size at maturity. *Evolution*, **40**: 893–913.
- Stone, L.D. 1975. *Theory of Optimal Search*. New York: Academic Press.
- Sutherland, W.J. 1983. Aggregation and the ‘ideal free’ distribution. *J. Anim. Ecol.*, **52**: 821–828.
- Tregenza, T. 1994. Common misconceptions in applying the ideal free distribution. *Anim. Behav.*, **47**: 485–487.
- Tregenza, T. 1995. Building on the ideal free distribution. *Adv. Ecol. Res.*, **26**: 253–302.

APPENDIX 1: USING THE CANONICAL EQUATION FOR FINDING EVOLUTIONARILY SINGULAR FORAGING STRATEGIES

The selection gradient is obtained by taking the functional derivative of the fitness function in equation (2) with respect to the mutant strategy x' ,

$$g_x(a) = \frac{\partial}{\partial \varepsilon} r(x + \varepsilon \delta_a, x) \Big|_{\varepsilon=0}, \quad (19)$$

where δ_a refers to the Dirac delta function peaked at a (Dieckmann *et al.*, 2006). When evaluating this expression, the epsilon derivative is to be taken before the integral over a is collapsed with the help of δ_a . For an evolutionary singularity x^* , $\frac{d}{dt} x^*(a) = 0$ must hold for all a .

‘Classical’ ideal free foraging

The selection gradient and the corresponding canonical equation for the classical model are given by equations (5) and (6), respectively. The right-hand side of equation (6) equals zero

if $\frac{r_0(a)}{x^*(a)} = \int \frac{r_0(a')}{x^*(a')} da'$. The evolutionarily singular foraging strategy is obtained from this equation by exploiting the fact that the integral on its right-hand side is a single number that is independent of a . Denoting this number by C , we get $x^*(a) = r_0(a)/C$. Because we have shown before that the evolutionarily singular foraging strategy implies using all foraging effort, it has to satisfy the constraint $\int x^*(a)da = 1$. We can thus solve for the unknown parameter C , yielding $C = \int r_0(a)da$, and thereby recover equation (7).

Heterogeneous mortality risks and foraging costs

When death rates are not uniform ($d(a) > 0$ for some or all a), the selection gradient is $g_x(a) = \frac{r_0(a)}{\hat{n}(x)x(a)} - d(a)$. By inserting this expression into the canonical equation (4) and assuming the simple variance-covariance function $\sigma_x^2(a, a') = \sigma^2[\delta(a - a') - 1]$ (Dieckmann *et al.*, 2006), we see that the singularity x^* must now satisfy $\frac{r_0(a)}{x^*(a)} - d(a) = \int \left[\frac{r_0(a')}{x^*(a')} - d(a') \right] da'$.

Again, the right-hand side of this equation is a constant that we denote by C . We thus get an expression for the singularity that contains one unknown parameter, $x^*(a) = r_0(a)/[\hat{n}(x^*)(d(a) + C)]$. Using the equality $r(x^*, x^*) = 0$, we can show that $C = d_0/\int x^*(a)da$. Since the selection gradient in this model can be negative, we cannot immediately see whether the singularity involves using all effort. However, if $\int x'(a)da < 1$, then the fitness $r(x', x)$ of mutants x' with $\int x'(a)da = 1$ is always positive. The evolutionary singularity must thus imply using all effort, so that $C = d_0$ and equation (9) is recovered. We also see that when $\int x^*(a)da = 1$, the fitness $r(x', x^*)$ is zero for all mutants x' that do not waste effort and negative for all mutants that do so; x^* is thus neutrally evolutionarily stable.

When foraging costs are not uniform ($c(a) > 0$), the analysis proceeds in exactly the same way as described above for mortality risks.

Heterogeneous resource qualities

The analysis proceeds in very much the same way when heterogeneous resource qualities are considered. The selection gradient is $g_x(a) = \frac{r_0(a)(q(a) + q_0)}{\hat{n}(x)x(a)} - d(a)$, and the same line of argument as described above can be used to show that the singularity is of the form $x^*(a) = r_0(a)(q(a) + q_0)/[\hat{n}(x^*)(d(a) + C)]$. Again, one finds that the singularity implies using all effort, so that $C = d_0$ and equation (10) is recovered.

APPENDIX 2: USING THE CALCULUS OF VARIATIONS FOR FINDING EVOLUTIONARILY SINGULAR FORAGING STRATEGIES

The calculus of variations is a mathematical optimization technique that has recently been adopted to determine evolutionary singularities of function-valued traits (Parvinen *et al.*, 2006). This is based on noting that evolutionarily singular strategies are local fitness extrema,

$\frac{\partial}{\partial x'} r(x', x^*) \Big|_{x'=x^*} = 0$, that also correspond to ecological equilibria, $r(x^*, x^*) = 0$. For the

problems analysed here, local and global inequality constraints of the form $x(a) \geq 0$ and $\int x(a)da \leq 1$ apply, and we therefore follow the corresponding line of analysis given in Section 2.3.2 of Parvinen *et al.* (2006). We must thus solve so-called Euler-Lagrange

equations $\frac{\partial}{\partial x'} L \Big|_{x'=x^*} = 0$, where L is the problem's Lagrange function. For our problems,

this means solving equations of the form $\frac{\partial}{\partial x'} \rho \Big|_{x'=x^*} = \lambda$, where ρ is the integrand of the fitness function in equation (2) and λ is known as a Lagrange multiplier.

Non-linear functional responses

The fitness function is given by equation (2). Initially, we have local and global inequality constraints $x(a) \geq 0$ and $\int x(a)da \leq 1$. However, as we shall see below, for a singular strategy x^* the latter constraint is satisfied with equality $\int x^*(a)da = 1$. The Euler-Lagrange equation is then

$$f\left(\frac{r_0(a)}{\hat{n}(x^*)x^*(a)}\right) - d(a) = \lambda. \tag{20}$$

Since the function f is continuous and monotonically increasing, a unique inverse function f^{-1} exists. We can thus rearrange the equation above to yield $f\left(\frac{r_0(a)}{\hat{n}(x^*)x^*(a)}\right) = \lambda + d(a)$ and then apply the inverse function on both sides. Solving for $x^*(a)$ yields

$$x^*(a) = \frac{r_0(a)}{\hat{n}(x^*)f^{-1}(\lambda + d(a))}. \tag{21}$$

The value of the parameter $\lambda \geq 0$ is specified by the equality $\int x^*(a) da = 1$, if it holds. Otherwise, $\lambda = 0$ and the inequality $\int x^*(a) da < 1$ holds instead.

Now the condition $r(x^*, x^*) = 0$ implies

$$r(x^*, x^*) = \int x^*(a)[f(f^{-1}(\lambda + d(a))) - d(a)] da - d_0 = \lambda \int x^*(a)da - d_0 = 0. \tag{22}$$

If we had $\lambda = 0$, $r(x^*, x^*) = -d_0 \neq 0$ would follow. As this is impossible, we must have $\lambda > 0$, so that the equality $\int x^*(a) da = 1$ holds. Therefore, we can infer from equation (22) that $\lambda = d_0$. From equation (21), we then obtain the evolutionarily singular foraging strategy as

$$x^*(a) = \frac{r_0(a)}{\hat{n}(x^*)f^{-1}(d_0 + d(a))}, \tag{23}$$

thus recovering equation (11). As we now know that $\int x^*(a)da = 1$, we can exploit that condition to solve for the equilibrium population size $\hat{n}(x^*)$ using equation (23).

The fitness $r(x', x^*)$ of a mutant x' when the resident is at the singularity x^* is found by noting that the potential intake rate in that case is simply given by $p(a) = f^{-1}(d_0 + d(a))$. This is the argument of the function f in equation (2) and thus allows simplification of that equation so as to yield equation (8).

Dynamic resources: exploitation competition with interference in resource acquisition

The starting point for this analysis is very similar to the derivation above, with the main difference being that the constant renewal rates $r_0(a)$ are replaced with the dynamic resource biomasses $B_x(a)$. The Euler-Lagrange equation is thus given by

$$f\left(\frac{h\hat{B}(x^*, a)}{\hat{n}(x^*)x^*(a)}\right) - d(a) = \lambda. \tag{24}$$

This leads to an equation for the singularity similar to equation (21), except that this time the result contains three unknowns, $\hat{n}(x^*)$, λ , and $\hat{B}(x^*, a)$:

$$x^*(a) = \frac{h\hat{B}(x^*, a)}{\hat{n}(x^*)f^{-1}(\lambda + d(a))}. \tag{25}$$

To determine these unknowns, we first solve for the equilibrium resource biomasses by setting $\frac{d}{dt}\hat{B}(x^*, a) = 0$. The term in equation (13) corresponding to the removal of resource biomass by foragers can be greatly simplified by taking advantage of equation (25) twice, yielding equation (14). This result can now be inserted into equation (25). The rest of the analysis, to obtain λ and $\hat{n}(x^*)$, proceeds as for the previous example.

Dynamic resources: exploitation competition without interference in resource acquisition

The Euler-Lagrange equation is given by

$$f(\hat{B}(x^*, a)) - d(a) = \lambda. \tag{26}$$

Solving this equation for $\hat{B}(x^*, a)$, we recover equation (17). Inserting the result into $r(x^*, x^*) = 0$ and solving for λ yields $\lambda = d_0$. The result that $\lambda \neq 0$ means that the singularity implies no wasting of effort, $\int x^*(a)da = 1$. The singularity can be found by setting $\frac{d}{dt}\hat{B}(x^*, a) = 0$ and solving for x^* , yielding equation (18).