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Optimal diet selection, frequency dependence and prey renewal

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Abstract

This paper extends existing models of frequency-dependent diet selection by considering the optimal diet selection of a predator feeding upon prey populations which can be depleted but are also capable of renewal (e.g. immigration, growth, or reproduction). This model and existing models which include prey depletion, predict partial-preference and a generic diet preference for the commonest prey types (apostatic selection). Unlike previous diet selection models, it is found that the optimal diet selection of an individual predator can be to favour the rarest prey type (anti-apostatic selection) when encounter rates are high, even if the individual prey do not differ in their nutritional value. Studies have demonstrated that predators generally show apostatic selection, even when all prey have the same nutritional value. Anti-apostatic selection has also been observed when prey are crowded, and therefore at high density, consistent with the idea of high encounter rates. This anti-apostatic diet selection has previously been proposed as evidence for the use of prey search images by a predator, or variation in individual prey preference. In this paper it is suggested that prey renewal is a further factor, often confounded in experiments, which could favour anti-apostatic selection.

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1. Introduction

Predators are commonly observed to feed upon a variety of prey types (Endler, 1991) and to actively select their prey, since the composition of a predator's diet rarely reflects the relative abundances of the available prey. Even when all prey types have apparently equal nutritional value to a predator (for example different colour morphs of the same species), it is generally found that predators tend to prefer the most common prey types (Allen and Clarke, 1968; Allen, 1972, 1974; Greenwood and Elton, 1979; Allen, 1988; Sherratt and Harvey, 1993; Marini and Weale, 1997; Smithson and MacNair, 1997). This type of frequency-dependent prey selection (known as apostatic selection, or prey switching) is a potentially important mechanism for generating diversity and maintaining polymorphisms between the prey types. The reverse situation, when a predator shows a preference for the rarest prey types (known as anti-apostatic selection, or negative prey switching), reduces prey diversity and would inevitably lead to a monomorphic prey population. Studies have demonstrated that predators do sometimes show a preference for the

rarest prey types when prey are crowded, and therefore at high density (Allen and Anderson, 1984; Greenwood et al., 1984a,b; Allen, 1988; Church et al., 1994). The reasons why predators should adopt the strategy of anti-apostatic prey selection is still uncertain.

Many explanations for frequency-dependent prey selection have been proposed (for reviews see Greenwood, 1984; Allen, 1988; Sherratt and Harvey, 1993). Classical diet selection theory (e.g. MacArthur and Pianka, 1966; Charnov, 1976; Stephens and Krebs, 1986) predicts that prey selection will be non-random if the intrinsic values of the prey types differ (where the intrinsic value is taken to be the net gain to a predator from a prey item divided by the item's handling time). However, frequency-dependent selection is not predicted without further assumptions, such as variation in the relative frequencies of the prey types between foraging patches (Gendron and Staddon, 1983; Endler, 1991) or the intrinsic properties of the prey types being themselves frequency-dependent (Murdoch et al., 1975; Greenwood, 1984). Although predictions from the classical theory have qualitative support from observations, there are also inconsistencies (Stephens and Krebs, 1986). For example, the theory ignores prey depletion and the theory predicts no partial-preference, except when prey selection is predicted to be random

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(partial-preference being when the probability of consuming an encountered prey item is neither zero nor one, but lies somewhere in between). More recent diet selection models have looked at the effect of prey depletion upon a predator's optimal diet selection (Heller, 1980; Hubbard et al., 1982; Brown and Mitchell, 1989; Mitchell, 1990; Visser, 1991a,b) and concluded that partial prey preference can be an optimal diet and that this diet usually exhibits apostatic selection. Similarly, it has been found that if handling time increases within a foraging bout then partial-preference can also be optimal (Hirvonen and Ranta, 1996). Partial-preference has also been shown to result from a predator's limited perception of its prey (Berec and Křivan, 2000).

Models which explain anti-apostatic prey selection are less numerous (Tinbergen, 1960; Chesson, 1984; Engen and Stenseth, 1984; Sherratt and MacDougall, 1995). Anti-apostatic, as well as apostatic selection, can result if prey types are encountered simultaneously (Engen and Stenseth, 1984), or if prey selection varies between individual predators (Chesson, 1984; Sherratt and MacDougall, 1995), or if a visual predator uses a search image to locate its prey (Tinbergen, 1960; Allen, 1989). When prey types are of equal value only the search image or the variation in individual selection rule hypotheses remain workable explanations.

This paper considers a model of optimal diet selection where prey, which can be depleted by a predator's feeding, are continuously being renewed up to some fixed carrying capacity. Such renewal may be due to immigration of prey from neighbouring habitats, re-growth and reproduction of the prey left by the predator or replacement of prey during an experiment. Most experimental investigations of frequency-dependent prey selection have incorporated some form of prey renewal. For example, prey have been replaced either during a predation trial (Jaeger et al., 1982; Tucker and Allen, 1991,1993; Sherratt and MacDougall, 1995; Smithson and MacNair, 1997; Marini and Weale, 1997) or between predation trials (Greenwood et al., 1984a,b; Brown and Mitchell, 1989; Church et al., 1994). In these investigations prey renewal has not been considered as a possible factor affecting a predator's diet selection. Correspondingly, prey renewal has not been included in diet selection models, even though the mechanisms of renewal generally have different consequences from those of prey depletion.

If a predator aims to maximise its intake rate over an extended period of time then both depletion and renewal are important considerations because the future prey density is as important as the present prey density. Whilst depletion tends to give rise to preference for the most common prey type, since the commonest prey can withstand the greatest depletion, prey renewal can

favour selection for the rarest prey, since the rarest prey can, under certain circumstances, show the strongest rate of renewal. Depletion and renewal are, therefore, very different processes. Prey depletion is simply a direct consequence of a predator's feeding behaviour. The rate of depletion, along with the capture rate, would generally be expected to increase with prey density. On the other hand, prey renewal depends upon a prey's population dynamics, and is not directly affected by a predator's behaviour (although prey depletion may have indirect effects on prey renewal). The rate of prey renewal is not expected to be a simple monotonic function of density. Consider a prey population that is at its predation-free carrying capacity, such that the prey renewal exactly balances the predation-independent mortality. If the prey density is reduced below this carrying capacity, by predation say, then the prey renewal may decrease (e.g. because there are fewer prey to reproduce), or increase (e.g. because the reduction in prey density increases the availability of resources) dependent upon the mechanisms regulating the prey's population size. The balance between these opposing factors determines whether the rarest prey types will have the strongest capacity for renewal.

This paper examines when prey renewal can have a significant effect upon a predator's optimal diet selection. Both the transient effects of a predator on its prey, and the long-term equilibrium between predation and prey renewal are investigated. It is shown that in both cases partial prey preference can emerge as an optimal diet choice and that frequency-dependent diet selection can be either apostatic or anti-apostatic.

2. A model of diet selection with prey renewal

We consider an optimal diet selection model which looks at a predator's optimal diet choice from n prey types (all symbols used in the model are summarised in Table 1). It is assumed that prey types are not cryptic or concealed, so that the time spent selecting a prey type by a predator is small compared to the time spent gathering and handling a prey item, and the rate of gathering a prey type is proportional to its density. It is also assumed that a predator encounters its prey sequentially, that all predators adopt the same diet selection rule, that a predator's capture rate of the i th prey type, C_i , is a function of both the prey densities and the predator's diet selection, that an optimal diet maximises a predator's average nutrient intake rate over a time period, T , and that a predator's diet selection does not change during this time period. Each prey type has a density N_i , a rate of renewal r_i , a carrying capacity K_i , a nutritional value for each item of prey v_i and a density-dependent population growth rate which can be described by a logistic equation. The dynamics of each

Table 1
The parameters and variables used in this paper

Symbol	Description
<i>Variables</i>	
β_i	the selection index for prey type i (Eq. (3))
p_i	probability of consuming prey type i upon encounter
N_i	density of prey type i
<i>Parameters</i>	
T	duration of one foraging bout
P	number of predators
n	number of prey types
v_i	nutritional value of prey type i
r_i	rate of renewal of prey type i
K_i	carrying capacity for prey type i
\bar{K}	weighted harmonic mean of the carrying capacities
α	overall rate of predation
$P\alpha$	a measure of the strength of predation
γ_i	$= P\alpha/r_i$ the strength of predation relative to prey renewal
γ	the value of γ_i when $r_1 = r_2 = \dots = r_n = r$
$\bar{\gamma}$	harmonic mean of all γ_i 's
<i>Derived variables</i>	
$\hat{\beta}_i$	the optimal value of β_i
\hat{N}_i	equilibrium density of prey type i under optimal prey selection
C_i	a predator's capture rate of prey type i
E_i	a predator's intake rate of prey type i
E	a predator's total intake rate
\bar{E}	a predator's average intake rate over a time T
a_i	a predator's attack rate on prey type i
P_i	the probability that the next prey item attacked by a predator is of type i

Derived variables are quantities which are expressed as functions of the other variables and parameters, and are therefore not independent.

prey type can then be simply described by the equation,

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} \right) - P C_i, \tag{1}$$

where P is the number of predators. The goal is to find the diet selection rule which maximises a predator's rate of nutrient intake

$$E = \sum_{i=1}^n v_i C_i \tag{2}$$

averaged over a finite time interval, T , given that the prey densities obey Eq. (1).

The nutritional value of an individual prey item is usually taken to be its energetic value, but it need not be. In certain situations it may be reasonable to associate the nutritional value to the first limiting nutrient, such as sodium in the case of the moose (Belovsky, 1978). For the rest of this paper the nutrient intake rate is simply referred to as the intake rate of the predator.

2.1. Diet selection index

A predator's diet selection is commonly represented by a diet selection index, β_i . One way to define this index is by,

$$\beta_i = \frac{C_i/N_i}{\sum_{j=1}^n C_j/N_j} \tag{3}$$

Equivalently this selection index can be written in terms of the attack rates, a_i . In general the attack rate is a function of the diet selection index and the prey densities, and is defined by

$$C_i = a_i N_i. \tag{4}$$

Substituting Eq. (4) into Eq. (3), gives a second expression for the diet selection index as $\beta_i = a_i / \sum_{j=1}^n a_j$.

The diet selection index is equivalent to the selection index defined by Manly (1995) and has a value which lies between zero and one. Other measures of preference exist (Chesson, 1978; Pearre, 1982; Gendron, 1987), but they all estimate the same basic theoretical quantity, β_i (Chesson, 1983), which can be viewed as the proportion of the diet consisting of type i given that prey in the environment are present in equal numbers. Since a predator must eat at least one of the available prey types the diet selection indices must obey the constraint,

$$\sum_{i=1}^n \beta_i = 1. \tag{5}$$

For n prey types, random prey selection corresponds to $\beta_i = 1/n$, whilst $\beta_i > 1/n$ and $\beta_i < 1/n$ corresponds to a preference and an avoidance of the i th prey type respectively. Frequency-dependent diet selection can be defined as the case when the selection index is a function of the frequency of at least one prey type.

The diet selection index, β_i , is a relative measure of prey selection, since it quantifies the preference of one prey type over another. An absolute measure of prey selection is the probability of consuming a prey type i upon encounter, p_i . This is an absolute measure because p_i is defined with reference to only prey type i . An absolute measure of selection is likely to influence the prey capture rate when the time spent rejecting prey types is an important part of a predator's total feeding time. For example this would be the case if prey are cryptic, or difficult to detect. On the other hand, if prey are easily identifiable then the time spent selecting a prey type can be negligible compared with the time spent gathering and handling a prey item. In this case it is the relative measure of prey selection which is likely to influence the prey capture rate. In this paper the focus is on the relative measure of prey selection. These ideas will be made quantitative when deriving the form of the capture rate, C_i , in the next section.

The diet selection index, β_i , is not a very sensitive measure of partial-preference (a partial-preference for

prey type i is defined as $0 < p_i < 1$) because it is a relative measure of prey selection. If $\beta_1 = 1$ say, then it follows that the predator only consumes prey type 1, but this does not mean that upon encountering an item of prey type 1 the predator is certain to consume it. So even the extreme case of $\beta_1 = 1$ may correspond to a partial-preference. Nevertheless, a sufficient condition on β_i for the existence of a partial-preference can be found (see appendix for details): when prey encounter is random, a partial-preference on prey type i exists when one other prey type j can be found which obeys the following condition

$$0 < \frac{N_j \beta_i}{N_i \beta_j} < 1. \quad (6)$$

From Eq. (6) it can be deduced that a partial-preference will exist whenever a predator's diet has two or more prey types that have different values of β_i/N_i . For example, if only two prey types are present in the diet, and if $N_i \beta_j / N_j \beta_i > 1$ say, then nothing can be deduced about the partial-preference for prey type j , but this implies that Eq. (6) must be true for prey type i , and a partial-preference for prey type i must exist.

2.2. Prey capture rate

A predator's intake rate of prey type i can be written as

$$E_i = v_i C_i \quad (7)$$

which when summed over all prey types gives the total intake rate of Eq. (2). It remains to specify a form for the capture rate C_i . The model assumes that the time spent by a predator selecting a prey type is small compared to the time spent gathering and handling prey items. This assumption emphasises that prey selection is fundamentally a choice of one prey type over another. Under this assumption the capture rate will be a function of the probability that the next prey item to be attacked is of type i , P_i (i.e. time spent rejecting prey types is ignored). This probability can be related to the absolute measure of prey selection p_i (Chesson, 1978), which for random prey encounter is $P_i = p_i N_i / \sum_{j=1}^n p_j N_j$.

The simplest functional form for the capture rate is a linear, Type I function. With the above assumption, and assuming that the rate of gathering a prey type is proportional to its density, then the linear function for the capture rate of prey type i can be written as

$$C_i \propto P_i N_i. \quad (8)$$

Substituting Eq. (8) into Eq. (3) gives

$$P_i = \beta_i \quad (9)$$

which can be substituted back in to Eq. (8) to give the expression for the capture rate as (e.g. Chesson, 1984)

$$C_i = \alpha \beta_i N_i, \quad (10)$$

where α is an overall rate of predation. From the definition of β_i given by Eq. (3), α must be identical for all prey types, and from Eq. (4) it is seen that $\alpha = \sum_i a_i$. Whilst the overall rate of predation can be thought of as a measure of the predation strength across all prey types from an individual predator, the selection indices can be thought of as being a measure of how this predation varies between prey types. The $n - 1$ independent values of selection indices and the overall rate of predation together form an alternative representation of the n independent values of attack rate. Eq. (9) shows that the relative selection index is the relevant measure of prey selection under the assumption that the time taken to select a prey type is negligible. Under other assumptions an absolute measure of prey selection, such as p_i , may be more relevant, but this is not considered here.

The next simplest form for the capture rate is a Holling Type II function (Holling, 1959) which would allow C_i to describe diminishing returns as the selected prey densities increase. One choice for a Type II function is (e.g. Murdoch and Oaten, 1975; Chesson, 1984)

$$C_i = \frac{\alpha \beta_i N_i}{1 + \sum_{j=1}^n h_j \alpha \beta_j N_j}, \quad (11)$$

where the h_i 's determine the rate at which C_i decreases with increasing prey density, and is equivalent to a handling time. Once again Eq. (3) requires that α is a constant for all prey types, but the h_i 's can vary between prey types. If the absolute prey selection is of interest then similar functions involving p_i in place of β_i can be used (e.g. Brown and Mitchell, 1989; Mitchell, 1990; Křivan, 1996; Křivan and Sikder, 1999; Berec and Křivan, 2000).

Eqs. (10) and (11) both express the capture rate as a function of the selected prey density, so that the predator behaves as though there were $\beta_i N_i$ individuals of type i (Chesson, 1978). This agrees with the intuitive reasoning on which β_i was originally based (Manly, 1972; Chesson, 1978) and implies that if a prey type is not eaten by the predator ($\beta_i = 0$) then its density does not determine the total prey capture rate, whilst if one prey type is twice as likely to be predated upon than all the other prey types, then the density of this prey type is twice as important in determining the predator's capture rate.

For the rest of this paper we concentrate upon the linear function of Eq. (10), because Eq. (11) does not allow simple analytical solutions. The functional form of the total capture rate does affect the numerical results, and the Type II function is briefly used in numerical

simulations to investigate whether the functional form of C_i alters the general conclusions of the model.

Substituting the Type I equation for C_i (Eq. (10) into Eq. (1) gives the final equation for the prey population as,

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \frac{N_i}{K_i} - \gamma_i \beta_i \right], \tag{12}$$

where $\gamma_i = P\alpha/r_i$ is a measure of the strength of predation compared with the strength of prey renewal. The average intake rate of a predator over a period of time T is then given by

$$\begin{aligned} \bar{E} &= \frac{1}{T} \int_{t=0}^T E dt \\ &= \frac{\alpha}{T} \int_{t=0}^T \sum_i v_i \beta_i N_i(\beta_i, t) dt. \end{aligned} \tag{13}$$

The optimal diet selection rule is found by maximising \bar{E} subject to the constraint of Eq. (5).

3. Results

3.1. Equilibrium dynamics

If a predator persists on a prey patch for an extended period of time (usually a time greater than $1/(r_i\gamma_i)$), or if the predator continually revisits a prey patch with the same diet selection rule, then the evolution of the prey populations on this patch will be dominated by the equilibrium solution of Eq. (12), which describes a balance between prey renewal and prey depletion. Assuming that all prey regenerate at the same rate (i.e. $r_i = r$ and $\gamma_i = \gamma$) then the optimal diet selection rule at equilibrium can be calculated as,

$$\hat{\beta}_i = \frac{1}{2\gamma} + \left(\frac{1}{n} - \frac{1}{2\gamma} \right) \frac{\tilde{K}}{v_i K_i}, \tag{14}$$

where

$$\tilde{K} = n \left(\sum_{i=1}^n \frac{1}{v_i K_i} \right)^{-1} \tag{15}$$

is the harmonic mean of the carrying capacities weighted by the nutritional values for the prey. Details of this calculation, and the general case where regeneration rates vary between prey types are given in the appendix. The equilibrium prey density corresponding to the diet selection rule of Eq. (14) is then,

$$\hat{N}_i = \frac{v_i K_i}{2} + (1 - \gamma) \frac{\tilde{K}}{2}. \tag{16}$$

The optimal diet selection is strongly determined by the strength of predation relative to the rate of renewal, γ . Random prey selection occurs when either

$$v_i K_i = \tilde{K} \tag{17}$$

or

$$\gamma = \frac{n}{2}. \tag{18}$$

Considering just two prey types where prey encounter is random (i.e. the probability of encountering a prey type is proportional to its frequency in the environment), and ordering the selection indices such that $\hat{\beta}_1 > \hat{\beta}_2$, then both prey types will be eaten by a predator if $\hat{\beta}_2 > 0$. From Eq. (14), this inequality can be written as

$$\frac{v_2 K_2}{\tilde{K}} > \gamma - 1. \tag{19}$$

Eq. (19) implies that a predator will have a generalist diet provided that γ does not greatly exceed one. Since $\gamma = P\alpha/r$, this implies that the *per capita* rate of depletion, $P\alpha$, must not greatly exceed the rate of prey renewal, r for a generalist diet to be optimal.

The above conditions for the presence of both prey types in a predator’s diet also strongly implies, from Eq. (6), that a partial-preference will exist for at least one prey type, provided selection is not random. The precise regions of parameter space where partial-preference occurs can be found by substituting Eqs. (14) and (16) in the condition for partial-preference, Eq. (6).

The frequency dependence of the diet selection is also determined by γ . If we start by assuming that all prey types have equal nutritional value, then when $\gamma < 1$, the optimal diet selection is to prefer the most common prey type (i.e. if $\hat{N}_1 > \hat{N}_2$ then $\hat{\beta}_1 > 0.5 > \hat{\beta}_2$). So when predation is relatively weak compared to renewal (i.e. $\gamma < 1$) the optimal diet selection is apostatic. Conversely, when $\gamma > 1$, a predator can have a significant impact upon the prey abundance, and the optimal diet selection is to prefer the rarest prey, and prey selection is anti-apostatic (i.e. if $\hat{N}_1 > \hat{N}_2$ then $\hat{\beta}_1 < 0.5 < \hat{\beta}_2$).

Differences in the nutritional values of the prey types will have an effect upon the optimal diet selection rule. If the nutritional value of the first prey type, v_1 , increases relative to the other prey types then Eq. (14) predicts that prey type 1 will be increasingly predated upon (increasing selection index, $\hat{\beta}_1$) whenever $\gamma < 1$. Conversely, if $\gamma > 1$ then as v_1 increases the selection index, $\hat{\beta}_1$, is predicted to decrease. In this second case, where $\gamma > 1$, predation has an important effect upon the prey equilibrium. If the response to increasing v_1 were to increase selection for prey 1, then this increase in predation would reduce the prey density to such an extent that the overall intake rate would decrease. Instead it is optimal to lessen the predation pressure on the nutritious prey type and allow their density to increase. The extension of these arguments to more than two prey types is given in the appendix.

3.2. Transient dynamics

If a predator frequently changes its diet selection rule, or if a predator commonly moves from patch to patch, then it is unlikely that the prey types within a patch will ever reach an equilibrium density. A predator's average capture rate will be predominantly determined by the transient behaviour of the prey population, as opposed to the equilibrium behaviour. This raises the question of whether the effects of prey renewal seen in the equilibrium results of the previous section will also be seen in the non-equilibrium case?

Maximising the average intake rate, Eq. (13), for the non-equilibrium system, Eq. (12), does not give simple analytical solutions, and so we resort to computer simulation of the model with two prey types. It is shown in the appendix that a predator's diet selection behaviour is dependent upon three prey-specific variables, αv_i the specific intake rate for a predator, the carrying capacity K_i and the initial prey density $N_i(0)$, and two prey independent variables, the potential prey renewal during a foraging bout, rT and the strength of predation relative to the rate of prey renewal γ . In the following runs, all carrying capacities were set at $K_i = 20$, the overall strength of predation was set to $\alpha = 1$, and all prey types had the same nutritional value with $v_i = 1$. Since the prey densities are no longer constant through time the classification of diet selection into apostatic and anti-apostatic uses the initial prey densities, as is often done in experimental studies. Using initial densities will tend to bias the diet classification towards apostatic and against anti-apostatic selection.

The optimal diet selection of the transient model has two general classes of behaviour which are separated by a critical threshold prey density (Fig. 1). For initial densities greater than the critical threshold, N_{th} , the average intake rate has one maximum, which gives rise to apostatic selection. Below this threshold density there are two local maxima; one which gives rise to apostatic selection and the other to anti-apostatic selection. Which of these two local maxima is the global maximum depends upon the other parameters. Generally, for initial densities just below the threshold, the optimal diet selection is apostatic, whilst if one prey type starts off as being sufficiently rare then anti-apostatic selection becomes optimal (Fig. 2).

To investigate the importance of the functional form of the prey capture rate, a Holling Type II function was used, given by Eq. (11). Two simulations were performed, one where $h_1 = h_2 = h$ with h varying between 0 and 0.1 (Fig. 3(a)) and one where $h_2 = h_1/2$ with h_1 varying between 0 and 0.1 (Fig. 3(b)). The linear case of Eq. (10) corresponds to $h = h_1 = h_2 = 0$, whilst positive h_i corresponds to a capture rate with diminishing returns. The Holling Type II function not only incorporates diminishing returns, but also provides a

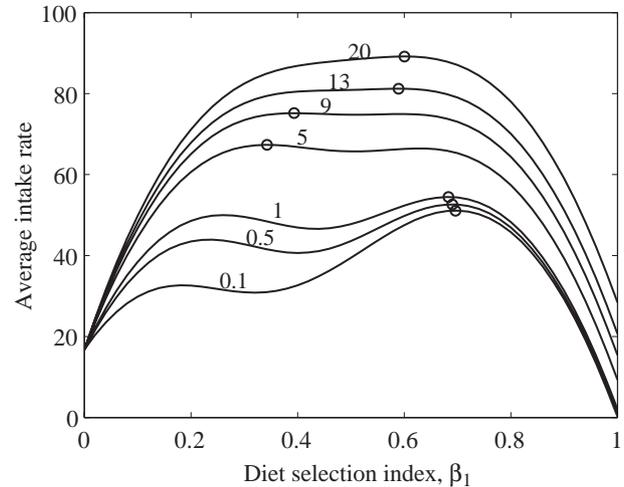


Fig. 1. The average intake rate, Eq. (13), from two prey types, as a function of the diet selection index for prey type 1 (β_1), and the initial density of prey type 1 ($N_1(0) = 0.1, 0.5, 1, 5, 9, 13, 20$ shown above each line). Both prey type have the same nutritional value, $v_1 = v_2 = 1$. Each global maximum is marked with a circle. Above a threshold prey density the average intake rate has one local maximum, whilst below this threshold prey density the average intake rate has two local maxima. Other parameters are $N_2(0) = 10$, $K_1 = K_2 = 20$, $\gamma = 1.9$, and $rT = 10$. The qualitative behaviour of the model is robust to changes in parameter values.

direct coupling between the dynamics of the different prey types. Increasing h_i has a quantitative effect upon the model. As h_i increases, the total prey capture rate decreases making predation weaker. This is reflected in Fig. 3, where the initial anti-apostatic selection of the linear model becomes weaker as h_i increases until apostatic selection becomes the optimal diet selection strategy. However, the qualitative behaviour of the model is not affected, and all the behaviours found when C_i was a linear function, could also be reproduced with the appropriate parametrisation of a Holling Type II function.

If the initial densities of the two prey types are equal then the model starts in a symmetric state with no difference between prey types. Above the critical density threshold, N_{th} , the single maximum in the nutrient intake rate corresponds to random prey selection and $\beta_1 = 0.5$. In this case the frequency of each prey type in the environment will remain unaffected by the predation at 0.5, and the initial symmetry will be preserved. Below the threshold density the initial symmetry is broken by the optimal diet selection rule, which is to favour one prey type over the other, even though the initial densities were equal. In this case the frequency of the preferred prey in the environment will decrease below its initial density of 0.5 (Fig. 4). As the strength of predation, γ , or the potential prey renewal during a foraging bout, rT , increase the threshold density, N_{th} , also increases.

The optimal diet selection when considering the transient prey population dynamics is similar to the

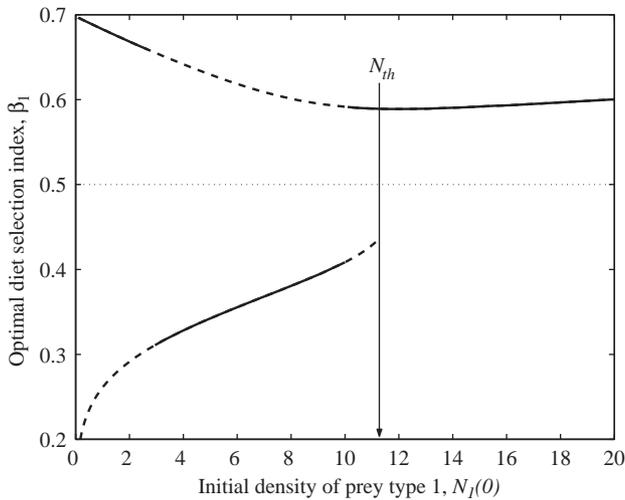
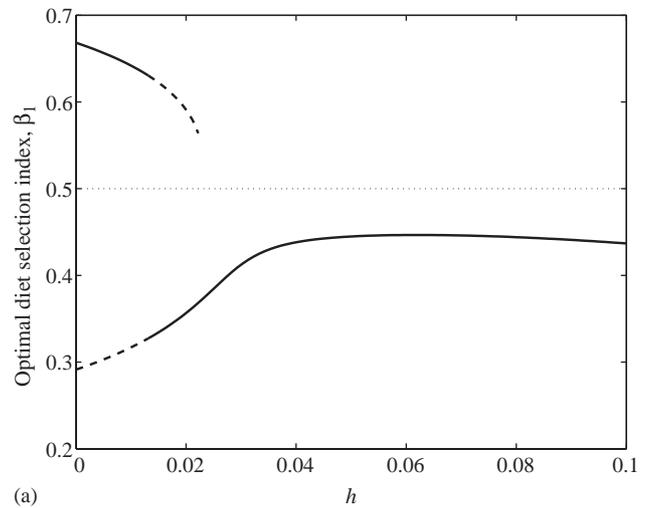


Fig. 2. The optimal diet selection for prey type 1 ($\hat{\beta}_1$) as a function of initial density of prey type 1 ($N_1(0)$) when prey capture rate is a linear function of density as in Eq. (10). Random prey selection is shown as a light dotted line, whilst local optima are shown as a dashed line, and the global optimum by a solid line. Anti-apostatic selection is optimal for small initial densities. Above a threshold prey density (N_{th}) the average intake rate has one maximum, whilst below this threshold prey density the average intake rate has two local maxima. Other parameters are $N_2(0) = 10$, $K_1 = K_2 = 20$, $v_1 = v_2 = 1$, $\gamma = 1.9$, and $rT = 10$.

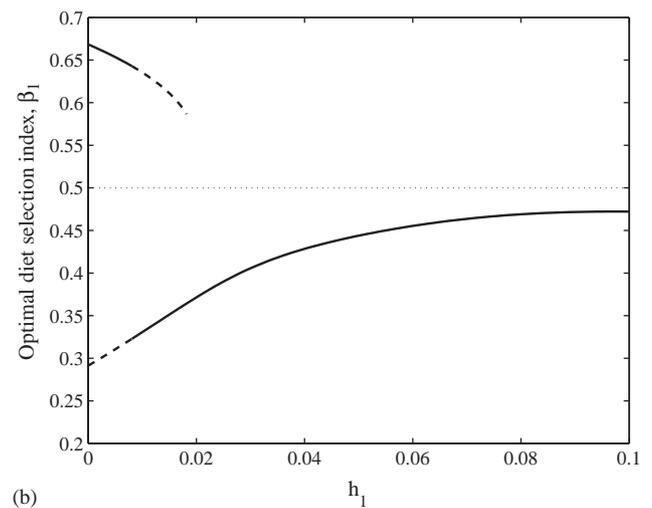
equilibrium case, in that it shows partial-preference and a strong effect of predation strength upon the optimal diet. When the strength of predation is weak (i.e. when γ is small) diet selection tends to be apostatic, whilst increasing the strength of predation increases the likelihood of anti-apostatic selection. However, the transient model differs from the equilibrium model in a number of aspects. Firstly, optimal diet selection can be non-random even when the carrying capacities of all prey are equal, because the optimal behaviour now depends upon the initial prey densities. Secondly, even when the initial prey densities are equal, optimal diet selection may still favour one of the prey types thus breaking the symmetry of the initial model configuration. Thirdly, the rate of prey renewal, in addition to the strength of predation affects the optimal diet selection. Finally, the behaviour of the transient model is more sensitive to the functional forms used in Eq. (12).

4. Discussion

In keeping with earlier models that include prey depletion (Heller, 1980; Hubbard et al., 1982; Brown and Mitchell, 1989; Mitchell, 1990; Visser, 1991a,b), the prey renewal diet selection model predicts that partial-preferences are likely to exist when a predator's diet contains more than one prey type. For two prey types this will be the case when the strength of predation ($P\alpha$) does not greatly exceed the rate of prey renewal (r).



(a)



(b)

Fig. 3. The effect of a Holling Type II functional response, given by Eq. (11), upon the optimal diet selection ($\hat{\beta}_1$) for an initial prey density $N_1(0) = 2$, $N_2(0) = 10$. (a) The case where $h_1 = h_2 = h$ (b) The case where $h_2 = h_1/2$, which is an example of a general case with no special symmetry. In both (a) and (b) the same qualitative behaviour is seen, showing that the behaviour of the model is not dependent upon the simple choice of functions in the analysis. Random prey selection is shown as a light dotted line, whilst local optima are shown as a dashed line, and the global optimum by a solid line. Anti-apostatic selection is optimal for small initial densities. Above a threshold prey density (N_{th}) the average intake rate has one maximum, whilst below this threshold prey density the average intake rate has two local maxima. Other parameters are $N_2(0) = 10$, $K_1 = K_2 = 20$, $\alpha v_i = 1$, $\gamma = 1.9$, and $rT = 10$.

Depletion is important in determining the optimal diet selection because it affects the future prey encounter rate and, therefore, the future prey capture rate. In addition to depletion, prey renewal is also important in determining the optimal diet selection, because the value of a prey type lies not only in its immediate nutritional rewards, but also in its future benefit to a predator, due to its renewal. The relevance of future rewards to the optimal strategy depends upon the time-scale on which

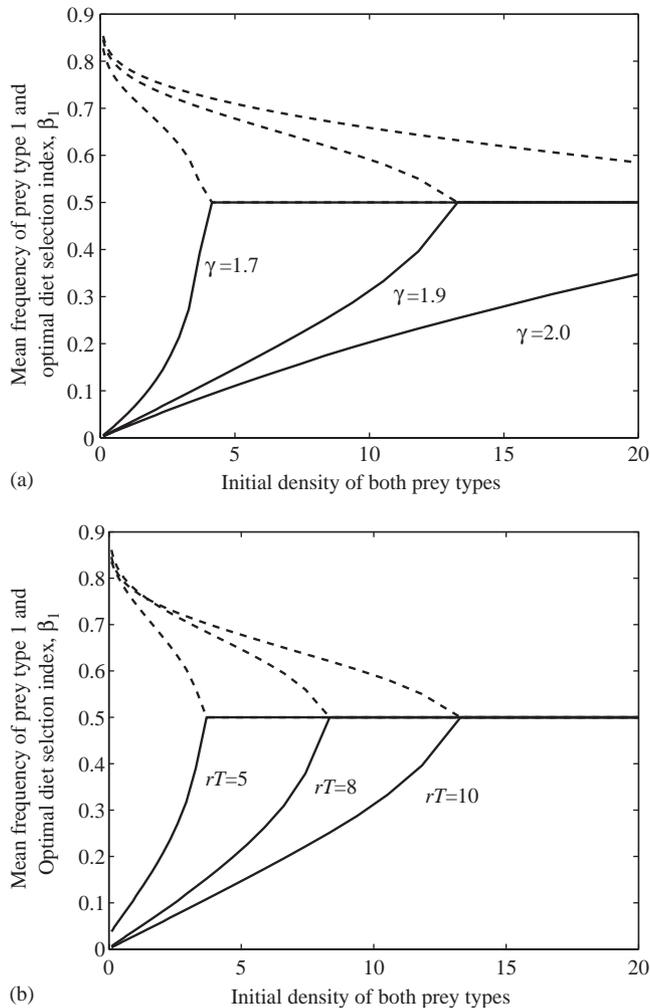


Fig. 4. The mean frequency of prey type 1 over one foraging bout (solid line) and the corresponding optimal diet selection index (dashed line) as a function of the initial prey densities. (a) Different lines show $\gamma = 1.7, 1.9, 2.0$. (b) Different lines show $rT = 5, 8, 10$. Both prey types have the same initial density ($N_1(0) = N_2(0)$). Only one of the two possible solutions is shown, where prey type 1 is the preferred prey ($\beta_1 > 0.5$). If not otherwise stated parameter values are $\alpha v_i = 1$, $\gamma = 1.9$, $rT = 10$, and $K_1 = K_2 = 20$.

the predator is foraging. If a foraging bout is long (i.e. large rT) then future rewards are important. For short foraging bouts (i.e. rT close to zero) both depletion and renewal are unimportant to the predator's intake rate and the model reduces to the classical model. The results from the model show that prey renewal can either accentuate, or oppose the effects caused by prey depletion.

General results from the prey renewal model show that if the strength of predation ($P\alpha$) is measured relative to the rate of prey renewal (r) then the most common prey type will be preferred when predation is weak, whilst the rarest prey will be preferred when predation is strong relative to the rate of prey renewal. Anti-apostatic selection is generally observed when prey are crowded, in which case high capture rates and strong

predation may be expected, although the data are not ideally suited for testing the model. The threshold between apostatic and anti-apostatic selection depends upon a number of factors, such as the initial prey densities, the time spent foraging, and the carrying capacities for each prey type. For frequency-dependent diet preferences to exist, the model requires only that different prey types occur at different densities in the environment, and is therefore applicable to nutritionally identical prey types. If prey types differ in their nutritional value then the optimal selection indices can be skewed, either exaggerating or diminishing a preference depending upon the value of γ . The model further predicts that apostatic selection will decrease in strength as the strength of predation increases (i.e. as γ increases, in agreement with the model of Hubbard et al., 1982) eventually giving way to anti-apostatic selection at high predation rates. Apostatic selection is also predicted to increase in strength as the number of prey types is increased, in agreement with observational evidence (Allen, 1988). These results are robust to the exact form of the functional response of the predator. These results show that non-random diet preferences can be optimal when all else is equal, because a preference for one prey type may stimulate prey renewal, and increase future prey capture rates.

The frequency-dependent diet selection strategies presented above are somewhat analogous to the idea of a predator managing its resource, and assume that the availability of prey is largely predictable in the near future. When more than one predator is in competition for the available prey on a patch then foraging becomes a game in which the strategy of your competitors must be considered when searching for an optimal diet selection rule (Visser, 1991b; Mitchell, 1990). In this situation a strategy which maximises intake rate over an extended period of time is less likely to be optimal because the future availability of the prey resource is now uncertain. Instead, strategies which are more short term in their outlook are likely to be favoured. The lack of evidence for herbivores managing their resources is consistent with this short-term strategy (Gordon and Lindsay, 1990). The model presented here does not consider this kind of competition and is only of general interest for solitary predators. The present model also assumes that prey types are independent in the absence of a predator. If prey share a common resource niche then their carrying capacities will not be independent, and the present model would require extension.

Dynamic predator-prey models which include diet selection have shown that allowing the number of predators to change in response to the number of prey consumed produces a range of complex behaviours (Křivan, 1996; Abrams, 1999; Křivan and Sikder, 1999). Even basic concepts, such as a generalist and specialist predator, may be too simplistic to describe the diet

selection of these models (Křivan, 1996). The model presented in this paper does not allow dynamic variation in the number of predators. For a sufficiently short-time scale the effect of predator dynamics will be small. However, to study the effects of prey renewal upon long-term diet selection a dynamic model will have to be developed.

Finally, the model considered here assumes that the time spent by a predator rejecting prey types is not an important contribution to the overall foraging time. In some circumstances, such as when prey are cryptic, this assumption will not be valid and the model should be recast in terms of an absolute measure of prey selection.

It remains to be seen whether prey renewal is an important mechanism in nature which affects a predator’s diet selection. As with prey depletion, it has the potential to strongly affect the optimal diet choice and to predict counter-intuitive frequency-dependent diet selection. Rare prey may be favoured, despite their reduced encounter rate because of the future benefits from prey renewal.

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Appendix A. Diet selection at equilibrium

If a predator spends a sufficient length of time feeding in a patch then the prey populations will reach an equilibrium abundance under the predation load, assuming a constant number of predators. As the time spent feeding increases the effect of transient prey dynamics upon the predator’s diet selection will decrease and the equilibrium behaviour will dominate. In this section a predator’s optimal diet selection assuming an equilibrium prey population, Eq. (14), will be calculated.

The prey populations described by Eq. (12) have an equilibrium solution at zero and at

$$\hat{N}_i = (1 - \hat{\beta}_i \gamma_i) K_i, \tag{A.1}$$

where $\gamma_i = P\alpha/r_i$ is the strength of predation relative to the strength of prey renewal. The zero solution corresponds to zero intake rate, whilst the equilibrium of Eq. (A.1) gives a positive nutrient intake rate, provided the equilibrium exists (i.e. $\hat{N}_i > 0$). Putting the non-zero solution into Eq. (2), and assuming that all n prey types are in the predator’s diet, gives the total intake rate as

$$\hat{E} = \alpha \sum_{i=1}^n v_i \beta_i (1 - \beta_i \gamma_i) K_i. \tag{A.2}$$

To find the diet selection rule, β_i , which maximises \hat{E} , subject to the constraint $\sum_i \beta_i = 1$, we maximise the function

$$L = \hat{E} + \lambda \left(1 - \sum_{i=1}^n \beta_i \right), \tag{A.3}$$

where λ is a Lagrange multiplier. L has a maximum when

$$2\gamma_i \beta_i = 1 - \frac{\lambda}{\alpha v_i K_i} \tag{A.4}$$

which can be substituted back into the constraint $\sum_i \beta_i = 1$ to find the value λ as

$$\lambda = \alpha \tilde{K} \left(1 - \frac{2\tilde{\gamma}}{n} \right), \tag{A.5}$$

where

$$\tilde{\gamma} = n \left(\sum_i \frac{1}{\gamma_i} \right)^{-1} \tag{A.6}$$

is the harmonic mean of the γ ’s and

$$\tilde{K} = \frac{n}{\tilde{\gamma}} \left(\sum_i \frac{1}{v_i \gamma_i K_i} \right)^{-1} \tag{A.7}$$

is a weighted harmonic mean carrying capacity, which simplifies to Eq. (15) when the rate of renewal is the same for all prey types. Substituting Eq. (A.5) into Eq. (A.4) gives the optimal diet selection rule of

$$\hat{\beta}_i = \frac{1}{2\gamma_i} \left[1 + \left(\frac{2\tilde{\gamma}}{n} - 1 \right) \frac{\tilde{K}}{v_i K_i} \right] \tag{A.8}$$

which simplifies to Eq. (14) when $\gamma_i = \gamma$.

The selection rule of Eq. (14) is optimal provided that all prey types are included in the diet. This requires that no prey population becomes extinct ($N_i > 0$) and that $0 < \beta_i < 1$ for all prey types. Using Eq. (14), and ordering the prey types such that $\hat{\beta}_1 > \hat{\beta}_2 > \dots > \hat{\beta}_n$, these conditions can be written as

$$\frac{v_n K_n}{\tilde{K}} < \frac{2\tilde{\gamma}}{n} - 1 \tag{A.9a}$$

so that $\hat{\beta}_n > 0$,

$$\frac{v_1 K_1}{\tilde{K}} (2\gamma_1 - 1) > \frac{2\tilde{\gamma}}{n} - 1 \tag{A.9b}$$

so that $\hat{\beta}_1 < 1$, and

$$\frac{v_i K_i}{\tilde{K}} > \frac{2\tilde{\gamma}}{n} - 1 \tag{A.9c}$$

so that $\hat{N}_i > 0$ for all the prey types.

The selective effect of a predator’s diet choice (i.e. apostatic, anti-apostatic or random) is given by the predator’s prey preference relative to the prey abun-

dances. This is quantifiable by ranking the prey in order of their diet selection index β_i , where the prey type with the largest β_i is the most preferred prey, and the prey type with the smallest β_i is the least preferred. Concentrating upon a pair of prey types (labelled by the indices i and j) then the diet choice will give rise to apostatic selection if the preferred prey is also the most abundant (i.e. $\beta_i > \beta_j$ and $N_i > N_j$). Anti-apostatic selection will occur in the reverse situation when the preferred prey is also the least abundant. Using Eq. (14), the difference between two selection indices is given by

$$\hat{\beta}_i - \hat{\beta}_j = \tilde{K} \left(\frac{1}{n} - \frac{1}{2\gamma} \right) \frac{K_j - K_i}{K_i K_j} \quad (\text{A.10})$$

and substituting in the equilibrium abundances for each prey type,

$$\hat{\beta}_i - \hat{\beta}_j = 2\tilde{K} \left(\frac{1}{n} - \frac{1}{2\gamma} \right) \frac{\hat{N}_j - \hat{N}_i}{K_i K_j}. \quad (\text{A.11})$$

Since all carrying capacities are positive, from Eq. (A.11) it can be seen that apostatic selection occurs between prey type i and j when $\gamma < n/2$, which corresponds to the case when predation is weak compared to renewal. Conversely anti-apostatic selection occurs when $\gamma > n/2$, which is when predation is strong compared to renewal.

Appendix B. Diet selection away from equilibrium

If the prey populations are not in equilibrium, then the predator's optimal diet selection will depend upon the initial prey densities as well as the other parameters. Solving Eq. (12) gives the prey population densities after the predator with diet selection rule β_i has been feeding for a time T as

$$N_i(T) = \hat{N}_i \left(1 + \frac{\hat{N}_i - N_i(0)}{N_i(0)} e^{-rT \frac{\hat{N}_i}{K_i}} \right)^{-1}, \quad (\text{B.1})$$

where $N_i(0)$ is the initial prey density and $\hat{N}_i = (1 - \gamma\beta_i)K_i$ is the non-zero equilibrium prey density. Substituting this result into Eq. (13) and integrating gives the average nutrient intake rate as

$$\bar{E} = \sum_i \alpha v_i \beta_i \left\{ \hat{N}_i + \frac{K_i}{rT} \ln \left[\frac{N_i(0)}{\hat{N}_i} \right] + \left(1 - \frac{N_i(0)}{\hat{N}_i} \right) e^{-rT \frac{\hat{N}_i}{K_i}} \right\}. \quad (\text{B.2})$$

The first term of Eq. (B.2) corresponds to the average intake rate when the prey population is in equilibrium (i.e. Eq. (A.2)), whilst the second term quantifies the effect of the transient prey dynamics upon \bar{E} . From Eq. (B.2) it can be seen that the average intake rate is a function of three composite parameters for each prey type; $\alpha v_i \beta_i \hat{N}_i$, $rT \hat{N}_i / K_i$ and $N_i(0) / \hat{N}_i$. Calculation of this

optimal solution is done through computer simulation, and the results are presented in the main text.

Appendix C. A condition for partial-preference

A partial-preference for prey type i occurs when $0 < p_i < 1$, where p_i is an absolute measure of prey selection (Table 1). Assuming a Type I function for C_i (Eq. (10)), and random prey encounter, then Eq. (9) can be used to relate the relative measure of prey selection, β_i , to the absolute measure of prey selection, p_i . A result by Chesson (1978) proves that

$$P_i = \frac{p_i N_i}{\sum_j p_j N_j}. \quad (\text{C.1})$$

Using Eq. (9) and taking the ratio of two different prey types gives

$$p_j \frac{N_j \beta_i}{N_i \beta_j} = p_i. \quad (\text{C.2})$$

Since $0 \leq p_j \leq 1$, a sufficient condition for a partial-preference of prey type i is that a second prey type j exists for which the inequality of Eq. (6) is true.

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