Models of interference and their consequences for the spatial distribution of ideal and free predators
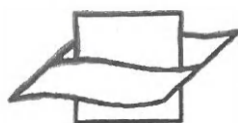
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Summary

1. In order to predict the spatial distribution of 'ideal' and 'free' predators, one needs to know how food intake rate of an individual predator is related to characteristics of the population of the prey as well as the predators themselves.

2. Surprisingly, a systematic theoretical investigation of models for the basic case, where both prey and predators are best characterized by their 'standing stock' density, is lacking. In these models intake rate is supposed to decrease with increasing predator density as a result of interference among predators, instead of immediate consumption of the prey.

3. This paper compares the various ways applied so far of incorporating interference in Holling's functional response model. It is shown that the different models of interference result in qualitatively different predictions for 'ideal' and 'free' predators on: (i) the form of the aggregative response; (ii) the trajectory of the aggregative response as prey is depleted; and (iii) the change in the aggregative response following an influx of predators. This sheds doubt on the general relevance of any one of these models, particularly if the mathematical formulation of interference is phenomenological and merely based on convention, instead of being derived from the underlying mechanism of interactions between predators.

4. Our results underline the need for detailed knowledge about the components of the predation process in order to arrive at predictions for a specific case.

Key-words: aggregative response, functional response, ideal free distribution, numerical response, oystercatcher.

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Introduction

One of the fundamental problems in ecology is to understand the way in which animals distribute themselves over different habitats. The notion that animal distribution might best be understood by recognizing that each animal will behave so as to maximize its fitness was a major breakthrough. Embroidering on the buffer hypothesis of Kluyver & Tinbergen (1953), Fretwell & Lucas (1970) gave concrete form to this idea by simplifying the problem to, what was hoped, its bare essentials. They assumed that animals are 'ideal', which means that each individual animal is able to choose the habitat that maximizes its fitness rewards, and 'free', which means that there are no costs associated with moving between and entering habitats. Additionally, animals were assumed to be all

alike. This set of assumptions is not sufficient to specify how a group of animals will distribute themselves among a set of habitats. One should know how the rewards for each individual depend on the relevant characteristics of the habitat and on the number of animals present in the habitat. Strictly speaking, in order to predict the 'ideal free distribution', when defined as the frequency distribution of habitats in terms of the number of animals each habitat contains, one must also know the frequency distribution of habitats in terms of their characteristics as well as the total number of animals in the system.

Fretwell & Lucas (1970) described the fitness rewards (as well as the dependence of the rewards on competitor density, see later) only in general terms (Oksanen, Oksanen & Fretwell 1992). In contrast, students of the distribution of foraging animals in a patchy environment interpreted the fitness rewards in terms of a short-term goal, most often the rate of food

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intake (Kacelnik, Krebs & Bernstein 1992). As the primary aim of the present article is to compare various models that have been proposed for the distribution of foraging predators, we necessarily follow the assumption that maximizing intake rate will maximize fitness.

Two types of models can be distinguished, depending on whether the maximal rate of food intake is set by the rate at which prey is put into the system or by the standing stock of prey. In the first case, new food is immediately consumed and standing stocks are effectively zero. In these models patches vary in terms of the rate at which food is offered and this input rate has the dimension 'something per unit time'. For this reason these models are generally referred to as 'continuous input' models, but we think that 'immediate consumption' would be a better label, since the alternative 'standing stock' models may also have a continuous input of prey (Lessells 1995). When individuals do not differ, the food intake rate for each individual is assumed to be equal to the input rate divided by the number of foragers in the patch. As a result, 'ideal' and 'free' animals will partition their numbers such that the number in each patch is proportional to the input rate of the patch. This is known as Parker's (1978) 'input matching rule'. The immediate consumption models, especially those dealing with unequal competitors (Sutherland & Parker 1985; Parker & Sutherland 1986), have inspired many experimental tests (Harper 1982; Abrahams 1989; Milinski *et al.* 1995). Yet, examples of immediate consumption that actually apply to the field are extremely rare. They include the study of Parker (1970) on male dung flies, *Scatophaga stercoraria*, competing to 'consume' (mate with) arriving females and the suggestion of Milinski (1979) on stream-dwelling fish competing for prey drifting by. In fact, there can be little doubt that standing stocks are not zero in the vast majority of distributions of foraging animals in the wild, if only because the prey need a nonzero population size to reproduce and survive.

This leads to the second case, where food availability can be characterized by the density of the standing crop in a patch, without time in the dimension (Lessells 1995), and where one needs to know how food intake rate is related to standing crop (prey density) and to the density of foragers. An 'ideal' and 'free' distribution so predicted only applies to a single instant in time. If consumed prey items are not replaced immediately, densities will decrease, and the foragers will redistribute themselves in response to the new prey distribution. Models dealing with this type of distribution are generally referred to as interference models, because it is often assumed that the predators suffer from mutual interference, which in studies on waders is defined as the more or less immediately reversible negative effect on intake rate of high predator densities (Goss-Custard 1980). However, we prefer the term 'standing stock' models to emphasize that

the rate of food intake depends on the standing stock of prey, not on the input rate. In these models interference may or may not occur (Lessells 1995). In the absence of interference, food intake rate can be modelled as a function of prey density only, by means of the Holling's disc equation (Holling 1959). In such cases 'ideal' and 'free' animals will all aggregate in the patch with the highest prey density, where the animals obtain the highest intake rate they can achieve (Royama 1970; Comins & Hassell 1979). Such strong aggregation is, of course, rather unlikely. In many cases the predators will mutually interfere with each other, so that intake rate decreases with increasing predator densities. As a consequence some predators will move to areas with lower prey density since this will increase their intake rate. To model this situation, interference must be incorporated into the disc equation. Two approaches have been taken. The first approach applies simple behavioural models of the predation process assuming a homogeneous environment in each patch (Beddington 1975; Ruxton, Gurney & De Roos 1992); for example, the predator population may be divided into three mutually exclusive states: searching individuals, prey handling individuals, and individuals that are involved in encounters with conspecifics. Given the transition rules between the states, the functional response follows from the steady-state solution of the accompanying differential equations (Ruxton *et al.* 1992). Note that the term functional response is used in a general meaning and gives the intake rate of a single predator per unit foraging time as a function of both prey density and predator density. The second approach uses some empirical relationship between searching rate (Hassell & Varley 1969) or intake rate (Zwarts & Drent 1981; Sutherland & Koene 1982; Ens & Goss-Custard 1984; Goss-Custard & Durell 1987) and predator density to model the effect of interference. These two approaches might be called 'mechanistic' and 'phenomenological', respectively.

If the functional response equation is known, then one can subsequently derive in what way 'ideal' and 'free' animals will distribute themselves between patches of different prey density at a single moment in time. With this purpose in mind several authors have chosen a single functional response model from one of the two types described above and predicted the relation between prey density and predator density. The additional purpose of these authors varied from: (i) developing a general 'standing stock' model for the aggregative response of 'ideal' and 'free' predators (Sutherland 1983; Moody & Houston 1995), to (ii) using it as a supposedly firm foundation to investigate the inclusion of complexities like differences between individuals (Parker & Sutherland 1986; Sutherland & Parker 1985, 1992), or to (iii) derive and test predictions for a specific well-studied case (Goss-Custard *et al.* 1995a, b). Yet, to our knowledge, no systematic investigation exists of the consequences of choosing a

particular functional response equation for: (i) the predicted distribution pattern; (ii) the change in the distribution pattern as depletion proceeds; and (iii) the change in the distribution pattern following an influx of predators. Without such knowledge it is hard to judge the general validity of the proposed 'standing stock' models, or their derivatives, nor can we judge the reliability of predictions for a specific case. This study therefore compares the various ways of incorporating interference in the functional response model of Holling.

The models

In the equations that follow, uppercase letters usually denote variables, and lowercase letters parameters. Yet, we make an exception to this rule for those variables that refer to prey densities, predator densities and patch areas. In those cases lowercase letters refer to a single patch, and uppercase letters to the entire system; for example, p_i (m^{-2}) is the predator density in patch i, whereas P (m^{-2}) is the overall predator density, that is the total number of predators in the system divided by the total area. For the sake of convenience, prey items are assumed to be of equal size, require equal handling time, and are captured and eaten upon discovery. Unless stated otherwise, predators are always foraging. While foraging, they are either searching, handling, or (in some cases) 'fighting'. We distinguish searching rate A (m^2 s^{-1}), which is the area searched per predator per unit searching time, encounter rate E (s^{-1}), which is the number of prey items encountered per predator per unit searching time, and intake rate W (s^{-1}), which is the number of prey items eaten per predator per unit foraging time, including handling and fighting time.

Generally, the intake rate per unit foraging time per predator in patch i, W_i (s^{-1}) is given by a function of prey density n_i (m^{-2}) and predator density p_i (m^{-2})

$$W_i = f(n_i, p_i). \qquad \text{eqn 1}$$

Usually, the intake rate W increases with increasing prey density n and decreases with increasing predator density. 'Ideal' and 'free' predators will distribute themselves between patches such that none can improve their intake rate by moving to another patch. Providing that individuals are identical, this means that intake rate is equal across patches. Hence for all patches (assuming for the time being that they are all occupied)

$$W_i = f(n_i, p_i) = c. \qquad \text{eqn 2}$$

Below we will for various functions f derive the function g that relates predator density to prey density, the so-called aggregative response:

$$p_i = g(n_i, c) \qquad \text{eqn 3}$$

for all patches. Given the frequency distribution of habitats in terms of surface area d_i and prey density

n_i, the spatial distribution of predators (the 'ideal free distribution') is determined by this aggregative response function. The constant c is determined by the constraint

$$\sum_{i=1}^{I} d_i p_i = DP \qquad \text{eqn 4}$$

where

$$D = \sum_{i=1}^{I} d_i$$

is the total surface area (m^2) of all patches, and DP is the total number of predators in the system. If possible, an explicit equation for c will be given. All model parameters are (unless otherwise stated) assumed to be greater than zero.

THE MECHANISTIC APPROACH

Ruxton *et al.* (1992) made several simple behavioural models of the predation process by using an approach borrowed from chemical reaction kinetics. The predator population is divided into several mutually exclusive states. Given the transition rules between the states, the functional response follows from the steady-state solution of the accompanying differential equations; for example, if a searching and a handling state are distinguished, each transition from handling back to searching is supposed to mean that a prey item is swallowed. Hence the transition rate at the steady-state yields the functional response. It is interesting to note that this simple example leads to Holling's disc equation (Holling 1959), and the intake rate can be written as:

$$W_i = \frac{an_i}{1 + ahn_i} \qquad \text{eqn 5}$$

where a is the constant searching rate (m^2 s^{-1}), and h is the handling time (s). Yet, since interference does not occur (there is no fighting state in which individuals are involved in encounters with conspecifics) and intake rate therefore does not depend on predator density, it is not possible to derive the aggregative response function: all 'ideal' and 'free' animals will aggregate in the patch with the highest prey density. The relation between intake rate and prey density as given in eqn 5 is also known as the type II functional response. Contrarily, a type I functional response refers to the situation where the intake rate is proportional to prey density. This can be regarded as a special case of the type II functional response when the handling time h equals zero.

In the more complex models that Ruxton *et al.* (1992) examined, an encounter between predators could mean that a (searching or handling) predator stops its pursuits and enters the 'fighting' state. They showed that if a searching predator interacts with both searching and handling individuals, the functional

response can be approximated by Beddington's (1975) equation:

$$W_i = \frac{an_i}{1 + ahn_i + qp_i}$$ eqn 6

where q is a parameter which is actually twice the product of the 'rate of predator discovery' ($m^2 s^{-1}$) times the 'loss of searching time per encounter' (s). As these two parameters always occur together, they can be replaced by the compound parameter q (m^2), which may be called the interference area. If a searching predator may also interact with a predator already involved in an aggressive encounter, the same model arises, but with a slightly different interpretation of the parameter q.

Setting the intake rate equal for all patches i

$$\frac{an_i}{1 + ahn_i + qp_i} = c$$ eqn 7

leads after some straightforward algebraic manipulation to a linear relationship between predator density p_i and prey density n_i

$$p_i = -\frac{1}{q} + \frac{a(1/c - h)}{q}n_i.$$ eqn 8

For patches with a prey density

$$n_i < \frac{1}{a(1/c - h)}$$

predator densities are set equal to zero, as negative predator densities are nonsense. For the same reason, $1/c$ (which is the average foraging time per prey item consumed and thus includes handling time) must always be larger than the handling time h. This constraint holds for all models that follow.

Now assume that the first $j - 1$ patches (the I patches are ordered in increasing prey density) remain unoccupied by predators. Then the value for the constant c can be derived from noticing that the total number of birds in the system, which is known, equals

$$D^*P^* = \sum_{i=j}^{I} d_i p_i,$$

where

$$D^* = \sum_{i=j}^{I} d_i$$

is the total surface area (m^2) of all occupied patches, and P^* is the overall predator density (m^{-2}) for all occupied patches. Similarly,

$$D^*N^* = \sum_{i=j}^{I} d_i n_i,$$

where N^* is the overall prey density (m^{-2}) for all occupied patches. Then,

$$P^* = \sum_{i=j}^{I} \frac{d_i}{D^*}p_i = \sum_{i=j}^{I} \frac{d_i(a(1/c - h)n_i - 1)}{D^*q},$$ eqn 9

which results in

$$c = \frac{aN^*}{1 + ahN^* + qP^*}.$$ eqn 10

The value of j can be derived from noticing that the birds should not visit those patches for which the intake rate without considering interference is smaller than the intake rate (taking interference into account) would be if only the plots that have a higher prey density are visited. Thus, the patch $j - 1$ (recall that patches are ordered in increasing prey density), for which

$$\frac{an_{j-1}}{1 + ahn_{j-1}} < \frac{aN^*}{1 + ahN^* + qP^*}$$ eqn 11

holds, remains empty of predators. The same is true for all patches with even lower prey densities. This rule has some conceptual similarity to the classical diet rule of Charnov (1976). Below we will refer to this model, in which searching predators interact with both searching and handling conspecifics, as the Beddington model.

Ruxton *et al.* (1992) also showed that if a searching predator only interacts with other searching predators, the functional response approximately looks like:

$$W_i = \frac{an_i}{1 + ahn_i + \dfrac{qp_i}{1 + ahn_i}}.$$ eqn 12

Proceeding as above,

$$p_i = -\frac{1}{q} + \frac{a(1/c - 2h)}{q}n_i + \frac{a^2h(1/c - h)}{q}n_i^2,$$ eqn 13

and

$$c = \frac{aN^* + a^2h\dfrac{\sum_{i=j}^{I} d_i n_i^2}{D^*}}{1 + 2ahN^* + a^2h^2\dfrac{\sum_{i=j}^{I} d_i n_i^2}{D^*} + qP^*}.$$ eqn 14

In spite of its complexity, the occurrence of the term $\sum d_i n_i^2$ in the latter equation tells us that the intake rate c depends on the variance of the prey densities in the suitable patches $i = j, j + 1, \dots, I$. In contrast, the Beddington model predicted an intake rate (eqn 10) that only depends on the overall prey density N^* in the suitable patches. Below we refer to the 'search-interaction-only' model as the Ruxton model. In the trivial case when the handling time is zero, the two models are equivalent.

Hassell & Varley (1969) observed that for predators in a laboratory cage, the logarithmic transformed searching rate showed a linear relationship with a negative slope when plotted against the logarithm of the number of predators in the cage. Then, with a slight modification due to a generalization to predator density instead of predator number, which enables the use of patches (or cages) of different surface area, the effect of competitors can be described in terms of a decrease in the searching rate A by the empirical relationship

$$A_i = a(p_i/r)^{-m},$$ eqn 15

where r is a reference predator density (m^{-2}) needed to avoid violation of dimensional rules, a is the searching rate ($m^2 s^{-1}$) when the predator density is equal to the reference density, and m is a dimensionless interference coefficient. Taking handling time into account yields the functional response

$$W_i = \frac{a(p_i/r)^{-m} n_i}{1 + a(p_i/r)^{-m} h n_i}.$$ eqn 16

The assumption that predators distribute themselves such that the intake rate is equal for each patch gives (Sutherland 1983)

$$p_i = r(a(1/c - h)n_i)^{1/m}.$$ eqn 17

So the relation between predator density and prey density is described by a power function. The constant intake rate c is given by

$$c = \frac{a}{ah + \frac{1}{r}\left(\frac{P^*D^*}{r\sum d_i(n_i/r)^{1/m}}\right)^m}.$$ eqn 18

In 1981, Zwarts & Drent (1981) published a paper in which they presented field data that showed that the intake rate of oystercatchers, *Haematopus ostralegus*, on a mussel bank decreased with increasing density of conspecifics. Their data were used by Sutherland & Koene (1982) who suggested a linear effect of bird density on intake rate when both variables are expressed in logarithms (note that this is in contrast to a linear effect on log searching rate as in the Hassell–Varley model). Hence

$$W_i = f(n_i) \cdot (p_i/r)^{-m},$$ eqn 19

where again r is a reference predator density (m^{-2}) needed to avoid violation of dimensional rules; $f(n_i)$ is the intake rate (s^{-1}) as a function of the prey density when the predator density is equal to the reference density; m ($-$) is the interference parameter. By convention we use the letter m, as in the Hassell–Varley model. The relationship between intake rate and prey density may be represented by Holling's curve. If the reference predator density is chosen such that the

effect of interference is negligible, we may then write (but see below)

$$W_i = \frac{an_i}{1 + ahn_i}(p_i/r)^{-m}.$$ eqn 20

As a result, the aggregative response looks like

$$p_i = r\left(\frac{1}{c}\frac{an_i}{1 + ahn_i}\right)^{1/m}$$ eqn 21

and

$$c = c_0 \left(\frac{P^*D^*}{r\sum d_i\left(\frac{1}{c_0}\frac{an_i}{1 + ahn_i}\right)^{1/m}}\right)^{-m}$$ eqn 22

where the reference intake rate c_0 (s^{-1}) keeps the equation in line with dimensional rules. Note that only in the trivial case when the handling time is zero, the model (and the resulting aggregative response) is equivalent to the Hassell–Varley model with zero handling time.

As an alternative, Ens & Goss-Custard (1984) applied a linear model between untransformed intake rate and log-transformed bird density, leading to

$$W_i = \frac{an_i}{1 + ahn_i}(1 - m\log(p_i/r)),$$ eqn 23

where again the parameter m ($-$) determines the strength of the interference. Predator densities above $r\exp(1/m)$ are not feasible, as they will result in negative intake rates. The model results in

$$p_i = r\exp\left(\frac{1 - ch}{m} - \frac{c}{am}\frac{1}{n_i}\right).$$ eqn 24

No explicit equation for c could be found.

Another alternative was considered by Goss-Custard & Durell (1987). They assumed a linear relationship between untransformed intake rate and untransformed predator density. Proceeding as above, this results in

$$W_i = \frac{an_i}{1 + ahn_i}(1 - qp_i),$$ eqn 25

where q (m^2) determines the strength of the interference. Predator densities above $1/q$ are not feasible. Then,

$$p_i = \left(\frac{1 - ch}{q}\right) - \frac{c}{aq}\frac{1}{n_i}$$ eqn 26

and

$$c = \frac{1 - qP^*}{h + \frac{1}{aD^*}\sum_{i=1}^{i}\frac{d_i}{n_i}}.$$ eqn 27

In the remainder of this paper the latter three phenomenological models, which are based on empirical relationships between intake rate and predator

density, will be named the 'Doublelog', the 'Semilog' and the 'Untransformed' model, respectively.

DIFFERENCES IN THE AGGREGATIVE RESPONSE

A comparison of the six aggregative response functions, which resulted from the six alternative ways to model interference, immediately points to some differences. Three models (Beddington, Ruxton, and Untransformed) have a threshold prey density n_{min} greater than zero, below which predators are absent (i.e. $g(n) > 0$ only if $n > n_{min}$). The threshold density is the same for all three models and is not related to the interference coefficients (Table 1). The other three models do not have a threshold density. A maximum predator density p_{max}, which is approached when prey density becomes large (i.e. $p_{max} = \lim g(n)$ when $n \to \infty$), is only found for the three models that were based on an empirical relationship between intake rate and predator density (Table 1). In all three cases the size of p_{max} depends on the interference coefficient; the higher the interference coefficient, the lower the maximum predator density.

A further look at the first and second derivatives of the aggregative response functions (for $p > 0$ and $n > 0$) allows a more detailed examination of the characteristics of the functions and shows to what extent these characteristics depend on the parameter values that can be chosen; for example, if the first derivative is always positive for all possible sets of parameter values, then predator density always increases with increasing prey density. If the second derivative is positive, the rate of increase goes up with

increasing prey density. If the second derivative is negative, the rate of increase goes down. We mentioned above (although without proof) that for all models intake rate W increases with increasing prey density ($\partial f(n, p)/\partial n > 0$) and decreases with increasing predator density ($\partial f(n, p)/\partial p < 0$) for all $p > 0$ and $n > 0$. Then the first derivative of the aggregative response function is positive ($dg(n)/dn > 0$) for all $p > 0$ and $n > 0$, which follows from the so-called implicit function proposition

$$\frac{dg(n)}{dn} = -\frac{\partial f(n, p)/\partial n}{\partial f(n, p)/\partial p}. \qquad \text{eqn 28}$$

So, in the present context, emphasis should be put on examination of the second derivative.

For the Ruxton model, for example, the first derivative is

$$\frac{dg(n)}{dn} = \frac{a(1/c - 2h)}{q} + \frac{2a^2 h(1/c - h)}{q}n, \qquad \text{eqn 29}$$

and the second derivative is

$$\frac{d^2 g(n)}{dn^2} = \frac{2a^2 h(1/c - h)}{q}. \qquad \text{eqn 30}$$

The first derivative is greater than zero if

$$n > -\frac{a(1/c - 2h)}{2a^2 h(1/c - h)} = \frac{1}{a(1/c - h)} - \frac{1}{h}. \qquad \text{eqn 31}$$

As the handling time h cannot be smaller than zero, the first derivative is indeed positive for all prey densities above the threshold density $1/(a(1/c - h))$. Since $1/c > h$ the second derivative is also always greater than zero (recall that we assumed that all parameters,

Table 1. A characterization of the interference models. The last column shows whether the second derivative of the aggregative response function is positive, zero or negative for all prey densities greater than zero (provided that the searching rate, handling time and interference coefficient are greater than zero). The sign (x) function gives the sign of x, thus if $x > 0$ then sign (x) should be read as $+$

Model	Effect on	Threshold prey density	Maximum predator density	Second derivative
Beddington	Searching and handling	$\dfrac{1}{a(1/c - h)}$		0
Ruxton	Searching	$\dfrac{1}{a(1/c - h)}$		$+$
Hassell–Varley	Searching rate			$\text{sign}\left(\dfrac{1}{m} - 1\right)$
Doublelog	Intake rate		$r\left(\dfrac{1}{ch}\right)^{1/m}$	$-$
Semilog	Intake rate		$r\exp\left(\dfrac{1-ch}{m}\right)$	$-$
Untransformed	Intake rate	$\dfrac{1}{a(1/c - h)}$	$\dfrac{1-ch}{q}$	$-$

including searching rate a, handling time h, and interference coefficient q, are greater than zero). Thus the rate at which predator density increases goes up with increasing prey density.

A similar analysis can be performed for the other five models. Obviously, the second derivative of the linear aggregative response function of Beddington is always zero. The second derivatives of the three models that were based on empirical relationships between intake rate and predator density (Doublelog, Semilog and Untransformed) are always smaller than zero and approach zero when prey density becomes large. To give one example, the second derivative for the Untransformed model is

$$\frac{d^2g(n)}{dn^2} = -\frac{2c}{aq}\frac{1}{n^3},\qquad \text{eqn 32}$$

which indeed is negative for all prey densities greater than zero and approaches zero when prey density becomes large. The only model where the second derivative can be either positive, zero or negative is the Hassell–Varley model. The second derivative is

$$\frac{d^2g(n)}{dn^2} = \left(\frac{1}{m} - 1\right)\frac{1}{m}$$

$$\times r(a(1/c - h))^2(a(1/c - h)n)^{(1/m)-2}.\quad \text{eqn 33}$$

It follows that the second derivative is positive when the interference coefficient $0 < m < 1$, is zero when $m = 1$, and is negative for $m > 1$. Thus, apart from the Hassell–Varley model, the general characteristics of the models are not sensitive to the exact parameter values that are chosen (Table 1). Below, the models will be compared in a more graphical way by using a few numerical examples.

FIRST EXAMPLE: OYSTERCATCHERS FEEDING ON BIVALVES

In western Europe, oystercatchers, *Haematopus ostralegus* L., move in autumn from the breeding grounds to their winter quarters along the marine shores. Having arrived on the mudflats, the birds mainly feed on a few bivalve species like mussel, *Mytilus edulis* L., and cockle, *Cerastoderma edule* (L.). Densities of these prey species can vary considerably among the various mudflats. In the numerical example that follows, the birds forage on prey items of 0·25 g ash-free dry mass (AFDM). These prey items require a handling time h of 50 s. The constant (interference free) searching rate a equals 7 cm² s⁻¹ (Hulscher 1976). The values for the interference parameters for the various functions that relate intake rate to prey density and predator density (the reference predator density r, the dimensionless interference coefficients m, or the interference areas q,

Table 2. Parameter values used in the numerical example. B, Beddington; D, Doublelog; H, Hassell–Varley; R, Ruxton; S, Semilog; U, Untransformed

Parameter	Dimension	Value	Models
a	m² s⁻¹	0·0007	BDHRSU
h	s	50·0000	BDHRSU
q	m²	1000·0000	B
q	m²	1000·0000	R
q	m²	20·0000	U
m	–	0·2700	D
m	–	0·4000	H
m	–	0·1300	S
r	m⁻²	0·0001	DHS

listed in Table 2) were chosen in such way that the fits more or less resembled published (Ens & Goss-Custard 1984) and unpublished data (Table 2). The way the parameters are chosen may look rather crude, but one must realize that our approach is not meant to model a specific situation very precisely, but to facilitate a comparison of the various theoretical models. The results should therefore not be over-interpreted.

For two different prey densities intake rate is plotted against log predator density (Fig. 1). A few things are noteworthy. According to the Untransformed model,
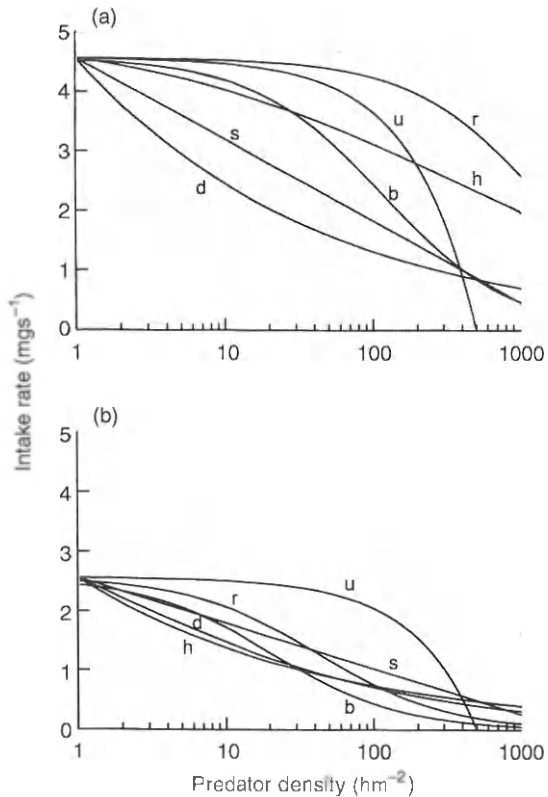

Fig. 1. The various functional response models. Intake rate (mg s⁻¹) is plotted vs. log predator density (h m⁻²) for (a) high prey density (300 prey items of 0·25 g each m⁻²) and (b) low prey density (30 prey items of 0·25 g each m⁻²). First example: b, Beddington; d, Doublelog; h, Hassell–Varley; r, Ruxton; s, Semilog; u, Untransformed.

intake rate changes very little at low predator densities, but it rather quickly decreases to zero at intermediate predator densities. At high prey densities the Ruxton functional response predicts a similar pattern, although the decrease in intake rate, which also starts at intermediate predator densities, is much slower. At low prey density the resemblance between the Untransformed and Ruxton predictions becomes less striking, and the Ruxton curve tends to the Beddington curve. In contrast, at high prey densities the Ruxton model predicts much higher intake rates than the Beddington model. Intuitively, this makes sense. At low prey densities the birds are mainly searching, in which state they are vulnerable to interference, according to both models. At high prey densities the birds are mainly handling prey. In the handling state the birds are insensitive to interference, but only according to the Ruxton model. In the Beddington model searching birds may interfere with handling birds as well. The same reasoning explains that at low prey densities the Doublelog and Hassell–Varley curves are very similar (birds are mainly searching), but that at high prey densities the effect of interference is much more pronounced in the Doublelog model (in which interference affects intake rate, and not just searching rate). Yet, the differences between the various functional responses are relatively small when compared to the noisy field data that are available (Zwarts & Drent 1981; Ens & Goss-Custard 1984; Goss-Custard & Durell 1987). The consequences, in terms of the aggregative response, however, are much more serious (Fig. 2). Two models in particular (Hassell–Varley and Ruxton) predict that the birds strongly aggregate in the most suitable patch. The proportion of predators in the best patches is higher than the proportion of prey in the same patches. Remember that only these two models assume that handling individuals are not susceptible to interference. On the contrary, the three models that were based on the empirical relationship between intake rate and predator density (Doublelog, Semilog and Untransformed) predict a limited predator density in the best patches. This has been called undermatching. Beddington's model takes an intermediate position.

SECOND EXAMPLE: PREY DEPLETION

The aggregative responses that we calculated only apply to a single moment in time. However, due to predation, prey will be depleted. If there is no concurrent prey renewal, as is the case for waders that feed on benthic invertebrates in winter, this means that the standing stocks of prey in the occupied patches continually decline. Under the ideal free assumption, this may lead to a redistribution of the predators. We are not able to provide analytical solutions for this process of redistribution under depletion, but a look at the shape of the aggregative response points to some generalizations. First, for those aggregative responses that are characterized by a threshold density, it is clear that this threshold prey density will shift downwards as depletion proceeds, poorer and poorer patches will be occupied. Second, for those models (Hassell–Varley, Ruxton) where predators strongly aggregate in the best patches, these patches will be severely depleted and the predators will subsequently spread out to patches of lower quality; patches will quickly become more similar in the course of the winter. In contrast, if there is a maximum predator density, as in the models that were based on the empirical relationship between intake rate and predator density, it could be that a good patch is effectively underused relative to a poor patch so that depletion in terms of the fraction of prey removed will be more intense in the poor patch. Our second example examines these suggestions by numerical simulations. We will extend the previous example of foraging oystercatchers further by showing the effect of prey depletion in the course of the winter on changes in the aggregative response of the oystercatcher. In our approach, each day (the winters starts at 1 September and ends at day 215, 31 March) the birds are redistributed over all patches according to the various aggregative response functions. In order to survive, the birds have to balance their energy budget. This requirement implies that they have to gather a more or less fixed amount of food each day. Extra food intake will not increase their fitness, as they cannot direct it into growth or reproduction. Thus, the predator–prey system is of a relatively simple structure. Prey decreases at a rate determined by the number of predators in the system times the fixed rate of food intake per predator. Predators either survive or die. They die when their intake rate falls consistently below their energy requirements. Yet in the numerical example presented here this did not occur. Each day prey density n_i in each patch decreases by the bird density p_i times the required intake rate c_0 (s^{-1}) times the day length (s). Model runs are performed for oystercatchers feeding on bivalves of 0.25 g AFDM. The required intake rate c_0
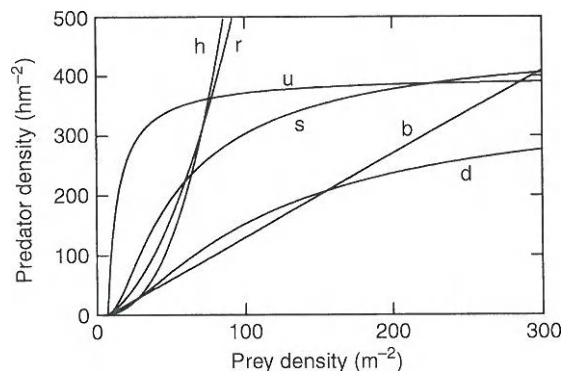

Fig. 2. The aggregative response functions, relating the density of predators at which each predator can obtain an intake rate of $4 \cdot 10^{-3}$ s^{-1}, one prey item per 250 s, to prey density. First example; b, Beddington; d, Doublelog; h, Hassell–Varley; r, Ruxton; s, Semilog; u, Untransformed.

is based on a power of 8·8 W, which is the estimate for a winter day with a temperature of about 5 °C (Kersten & Piersma 1987). These energy needs correspond to a digestion efficiency of 0·8 ($-$) times energy content of 22000 ($J g^{-1}$) times a daily averaged AFDM intake rate of 0·0005 ($g s^{-1}$). This implies a daily food intake of 0·0005 ($g s^{-1}$) times 86400 (s) is 43·2 g day^{-1} or 173 day^{-1}. If a day contains 12 h foraging time, the required intake rate while foraging is 0·001 g s^{-1} or 0·004 s^{-1}, that is one prey every 250 s. The initial prey densities, and the patch areas are given in Table 3. These figures resemble the situation on the Roggenplaat, a tidal flat in the Oosterschelde, SW Netherlands, and were based on data gathered in 1989 by Meire *et al.* (1994). The number of birds that use the area is set to 15 000 (Lambeck, Sandee & De Wolf 1989).

The predicted spatial distribution at the start of the winter season shows major differences between the various models. As was shown earlier, according to the Hassell–Varley model predators would strongly aggregate in the most suitable patches. On the contrary, for the Doublelog model, for example, the highest predicted density is substantially lower. A more interesting result is the qualitative behaviour of the changes in the aggregative response. According to the Hassell–Varley model patches tend to become more similar in the course of the winter, both in terms of prey density and predator density. The Doublelog model predicts the opposite. Predator densities in the most suitable patches increase, whereas predator densities in the least suitable patches decrease in the course of time (Fig. 3). The Beddington model takes an intermediate position. The Ruxton model gives a similar picture to the Hassell–Varley model, whereas the Semilog and Untransformed models resemble the Doublelog model.

At this point we would like to mention one apparent contradiction in the example (which is, however, of minor importance in the present context). Our 'ideal' and 'free' birds aim to maximize their intake rate. On the other hand, we assume that they just need a fixed amount of food per day. This implies that if the intake rate that can be achieved is higher than the required amount of food per day divided by the available foraging time per day, the birds have spare time. If we assume that each bird contributes to the interference during this extra spare time, or that all birds take their spare time at the same moment, there are no conceptual problems.

THIRD EXAMPLE: AN INFLUX OF PREDATORS

The last example considers the build-up of oyster-catcher numbers in a wintering area at the start of the winter season. Goss-Custard and coworkers (1995a, b) considered a situation of that kind on the mussel beds of the Exe. They constructed a model in which they took account of various complicating phenomena, such as the presence of multiple prey of various sizes, and differences in prey opening techniques, in interference-free intake rates and in the susceptibility to interference among individual oystercatchers. We just mimicked this system by translating the average interference-free intake rate for hammering oystercatchers for each mussel bed as presented by Goss-Custard *et al.* (1995, Table 1) into an 'effective' density of bivalves of 0·25 g AFDM by using the inverse of Holling's type II functional response (with the same parameters as in the previous examples). Stated otherwise, for each 'effective' density Holling's type II functional response reveals exactly the accompanying interference-free intake rate (Table 4). Subsequently, we used the various models for interference to predict the distribution over the mussel beds with increasing predator density, ignoring any (minor) changes in prey density. Our approach is highly simplified, but illustrates the essential differences between the various models. Beddington's model shows the greatest changes in relative densities with increasing predator numbers (Fig. 4). The model of Hassell & Varley does not show any change in relative distribution when predator numbers increase. The Semilog model takes an intermediate position.

Discussion

Our contribution emphasized that predictions on habitat distribution of 'ideal' and 'free' predators strongly depend on the assumptions that are made on the effects of interference on intake rate. This notion points almost automatically to a pair of recommendations that can be made.

First, it implies that when 'an' ideal free distribution is involved, one should be explicit about the functional response that was assumed. That is, it should be clear in what precise way intake rate is assumed to be related to both prey density and predator density. This has not always properly been done; for example, Sutherland & Koene (1982) aimed to estimate the interference coefficient *m* of the Hassell–Varley model, but

Table 3. Area and initial prey density for each of the six patches. Second example

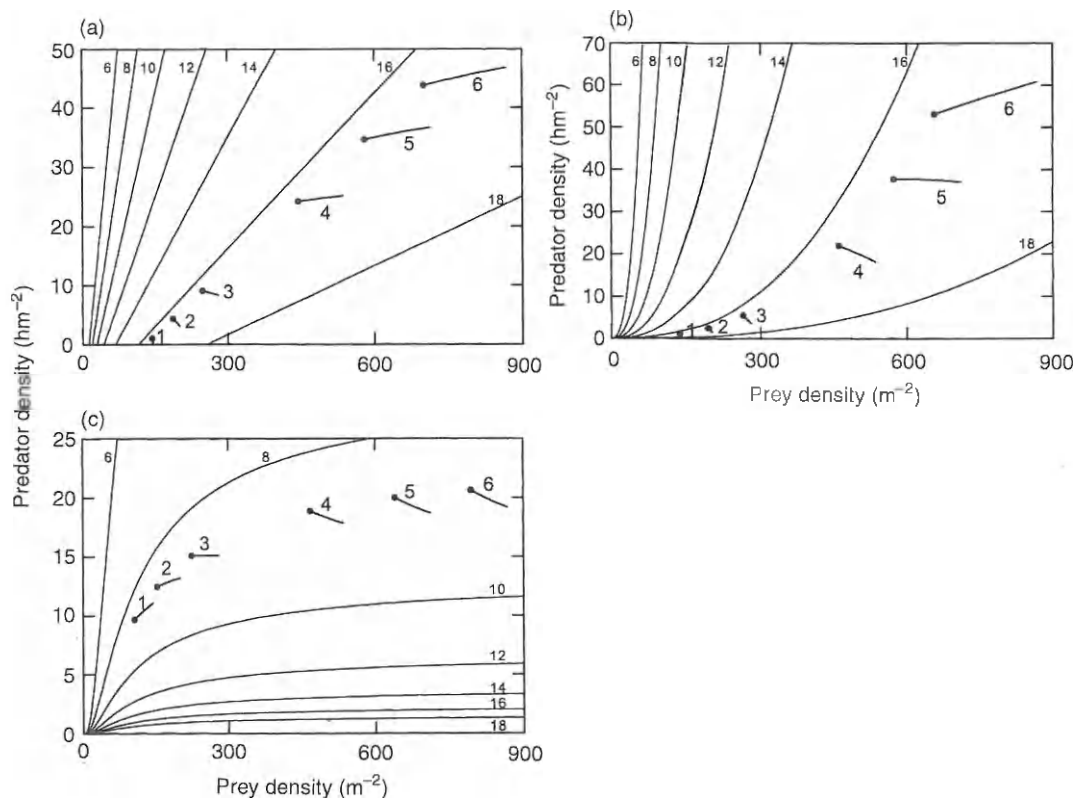| Patch	1	2	3	4	5	6
Area (10^6 m^2)	1·51	6·05	3·85	0·96	1·78	2·34
Prey density (m^{-2})	144·00	200·00	280·00	536·00	712·00	868·00

Fig. 3. Phase diagrams in which each line shows the changes in predator density (m^{-2}) and prey density (m^{-2}) in each patch during the winter season. The dot indicates the end of the trajectory. Aggregative responses for various intake rates c (ranging from $6 \cdot 10^{-3}$ to $18 \cdot 10^{-3} s^{-1}$) are also shown (cf. Fig. 2). Starting values of prey densities and patch surface areas are given in Table 3. (a) Beddington; (b) Hassell–Varley; (c) Doublelog. Second example.

Table 4. Surface area (McGrorty & Goss-Custard 1991), interference-free intake rate and 'effective' prey density for each of the five groups of mussel beds. Third example

Mussel beds	1, 13, 14, 22	27, 31	3, 20	4, 26	25, 30
Area $(10^4 m^2)$	13·0	9·0	13·8	12·6	15·5
Interference-free intake rate (mg 5 min^{-1})	346·0	620·0	655·0	696·0	794·0
Prey density (m^{-2})	9·0	20·0	22·0	25·0	32·0

they did not use data on searching rate but data on intake rate. Using intake rate would in the first place refer to the Doublelog model. In a later paper Sutherland & Parker (1985) stated that the discrepancy between both models (Hassell–Varley and Doublelog) is usually likely to be small. Yet, the present study showed that the consequences, in terms of differences in the aggregative response, are rather dramatic.

Another example concerns the prerequisites of the 'habitat matching' rule. In the 'immediate consumption' situation the intake rate per predator per unit foraging time is given by $W_i = Q_i p_i^{-1}$, where Q_i is the total food input in patch i per unit time and p_i is the number of predators in the patch. This leads to the 'input matching' rule $p_i = Q_i/c$. As pointed out by Tregenza (1994), who aimed to clarify some misconceptions in applying the ideal free distribution, several authors confused the 'immediate consumption' situation with the situation when resources

are best described in terms of a 'standing stock' density. They mistakenly assumed that in the latter case the ideal free theory predicts a 'habitat matching' rule, $p_i \propto n_i$ (Kennedy & Gray 1993). Tregenza (1994) stated that the 'habitat matching' rule is not generally valid, since the interference coefficient m of the model $Y = Xp^{-m}$ is not necessarily equal to one in the 'standing stock' situation. He defined Y as the individual's payoff, X as the total input, and p as the number of predators in the patch. Tregenza did not mention, however, that in a 'standing stock' situation the 'habitat matching' rule also requires the additional assumption that the individual's payoff Y should be measured in terms of encounter rate (instead of the more obvious intake rate) and that the total input actually means the interference-free encounter rate, an_i in our terminology.

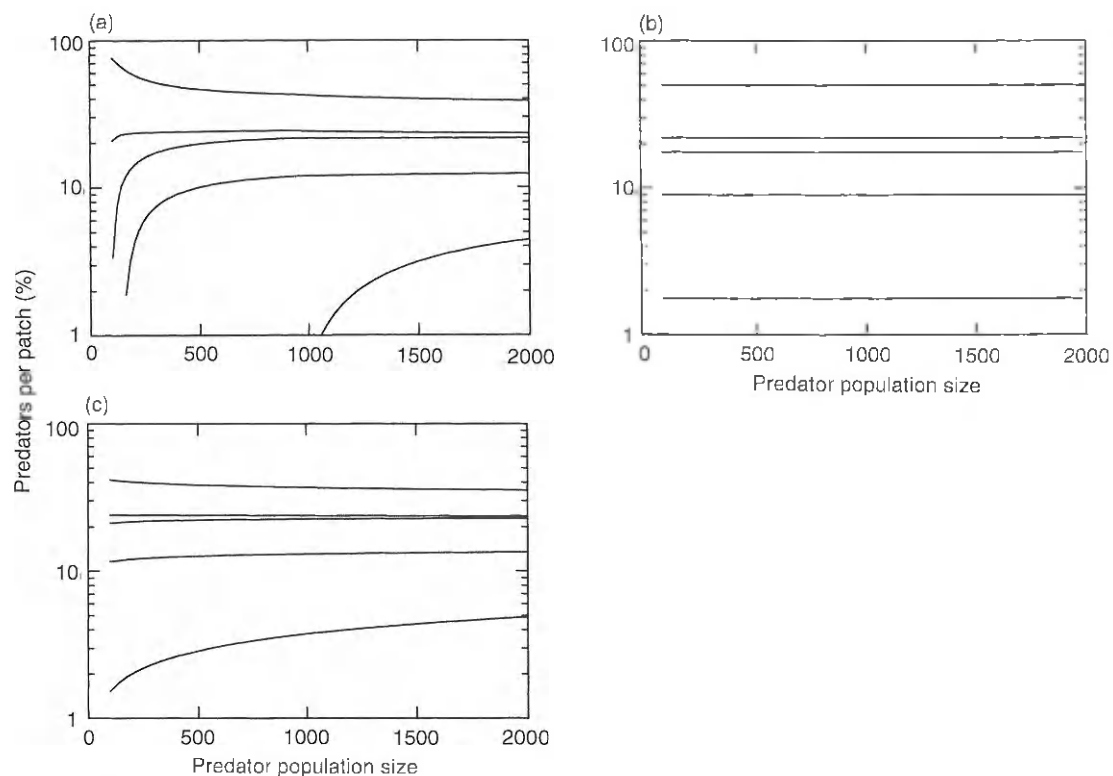Second, the choice of a functional response model, which appeared to be of vital importance when pre-

Fig. 4. Changes in predator distribution over five groups of mussel beds when the number of birds grow (at the start of the season) from zero to 2000. Prey densities and bed surface areas are given in Table 4. The beds are arranged (from above to below) in order of decreasing prey density. (a) Beddington; (b) Hassell–Varley; (c) Semilog. Third example.

dictions about the spatial distribution of ideal and free predators are needed, should be based on detailed knowledge of all components of the predation process and on theoretical appeal; for example, our results suggest that it might be of importance whether or not the model takes into account that handling individuals may suffer from interference (recall that the models which assumed that only searching individuals interact, the Ruxton and the Hassell–Varley model, were the only models that predicted that proportionally more predators aggregate in high-density patches). Our impression is that until now the choice has often been based on convention; for example, Kacelnik *et al.* (1992), in their review of the ideal free distribution, simply state that realistic assumptions about the interference between competitors lead to the Hassell–Varley functional response. They lightheartedly avoid defining the meaning of 'realistic'. Yet, ample empirical evidence exists that for many species log searching rate decreases in a nonlinear way with log predator density (Free, Beddington & Lawton 1977). Besides this lack of empirical support, the model has severe theoretical shortcomings. In fact, it assumes that for predator densities close to zero, searching rate A goes to infinity, which does not seem to be realistic (Free *et al.* 1977). The Doublelog and Semilog models suffer from the same limitation.

Since the choice of a functional response (including the effects of interference) so strongly influences the

predicted aggregative response, conclusions based on a particular choice are unlikely to be generally true. The widely used Hassell–Varley model is both theoretically deficient and lacks empirical support. The status of the other phenomenological models is equally wanting. Although the theoretical appeal of the mechanistic models of interference is higher, they are not fully consistent in the context of ideal free theory, where it is assumed that predators maximize their fitness rewards. In the mechanistic models, the animals behave like aimless billiard balls, and the question why animals should interfere where the result is only a loss of feeding time, is not answered. Development of a model of interference that is consistent with the assumption of rate maximization in the choice of a feeding site stands out as a clear theoretical challenge.

So far, empirical studies of interference in waders and other birds have primarily relied on statistical techniques to control for the many confounding variables in the field (Zwarts & Drent 1981; Ens & Goss-Custard 1984; Goss-Custard, Clarke & Durell 1984). While we are happy to accept the qualitative evidence for interference, we think this approach is inadequate to uncover the underlying processes and the quantitative details. In our view, experimental manipulations of prey density, predator density and tide length in a seminatural environment as pioneered by Swennen, Leopold & De Bruijn (1989) are called for.

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