Journal of Animal Ecology 2006 **75**, 948–958

A functional response model of a predator population foraging in a patchy habitat

GÖSTA NACHMAN

Department of Population Biology, Institute of Biology, University of Copenhagen, Denmark, Universitetsparken 15, DK 2100 Ø Copenhagen

Summary

1. Functional response models (e.g. Holling's disc equation) that do not take the spatial distributions of prey and predators into account are likely to produce biased estimates of predation rates.

2. To investigate the consequences of ignoring prey distribution and predator aggregation, a general analytical model of a predator population occupying a patchy environment with a single species of prey is developed.

3. The model includes the density and the spatial distribution of the prey population, the aggregative response of the predators and their mutual interference.

4. The model provides explicit solutions to a number of scenarios that can be independently combined: the prey has an even, random or clumped distribution, and the predators show a convex, sigmoid, linear or no aggregative response.

The model is parameterized with data from an acarine predator-prey system consisting of *Phytoseiulus persimis* and *Tetranychus urticae* inhabiting greenhouse cucumbers.
 The model fits empirical data quite well and much better than if prey and predators

were assumed to be evenly distributed among patches, or if the predators were distributed independently of the prey.

7. The analyses show that if the predators do not show an aggregative response it will always be an advantage to the prey to adopt a patchy distribution. On the other hand, if the predators are capable of responding to the distribution of prey, then it will be an advantage to the prey to be evenly distributed when its density is low and switch to a more patchy distribution when its density increases. The effect of mutual interference is negligible unless predator density is very high.

8. The model shows that prey patchiness and predator aggregation in combination can change the functional response at the population level from type II to type III, indicating that these factors may contribute to stabilization of predator–prey dynamics.

Key-words: aggregative response, mutual interference, spatial distribution, stability

Journal of Animal Ecology (2006) **75**, 948–958 doi: 10.1111/j.1365-2656.2006.01114.x

Introduction

The capacity of predators to find, kill and consume prey plays a fundamental role in shaping the trophic interactions of food webs (Begon, Harper & Townsend 1996). The success of an individual predator depends on a combination of prey and predator traits that need to be incorporated in a predation model to understand fully the temporal and spatial dynamics of the species

© 2006 The Author. Journal compilation © 2006 British Ecological Society Correspondence: Department of Population Biology, Institute of Biology, University of Copenhagen, Denmark, Universitetsparken 15, DK 2100 Ø Copenhagen. E-mail: gnachman@bi.ku.dk involved. The most important component in such models is the density of prey that determines the functional response, i.e. the ability of a predator individual to adjust its feeding rate to changes in prey density (Solomon 1949). Phenomenological functional response models like the ones by Holling (1959) and Ivlev (1961) (see Jeschke, Kopp & Tollrian 2002 for a review) predict the predation rate as a function of prey density only. This will be true only if the prey is evenly distributed in space, which limits the general applicability of these models as most prey populations occur in aggregated patterns (Turchin & Kareiva 1989). To improve the precision and realism of functional response models it is thus necessary to include the spatial distributions of Functional response in a patchy environment both prey and predators, especially the ability of the predator to aggregate in patches with abundant prey (Murdoch & Stewart-Oaten 1989; Ives 1992; Ives *et al.* 1999). Furthermore, as many predators tend to concentrate their searching efforts to patches where prey is plentiful, mutual interference between searching predators also needs to be included as this is likely to determine the limit beyond which further aggregation no longer pays-off (Beddington 1975; Hassell & Rogers 1972; Van der Meer & Ens 1997).

As pointed out by Ives *et al.* (1999), a functional response depends on the spatial scale on which it is measured. Thus, the average per capita predation rate of predators occupying a complex environment with a nonhomogeneous distribution of prey is likely to differ from the per capita predation rate of a single predator individual living in a small homogeneous area, even though the mean prey density is the same. Ives *et al.* (1999) coined the former 'the population functional response' and the latter 'the behavioural functional response'. It is usually the behavioural response that is studied experimentally, while it is the population response that is of ecological interest, because it affects the population dynamics of predators and prey.

Recently, Williams & Martinez (2004) suggested a generalized version of Holling's (1959) disc equation, which incorporates an extra parameter (q) that, depending on its value, can change the functional response from being of type II (convex) to type III (sigmoid). The model shows that even small deviations from a type II response in the direction of a type III response can have profound effects on food-chain dynamics. However, the problem is that q has no obvious biological interpretation as it is unclear how it relates to prey distribution and/or predator behaviour. Thus, it seems likely that q is not merely a predator-specific constant but a variable that depends on how the prey is distributed. In order to investigate this in more detail, I present a functional response model that explicitly includes the density and spatial distribution of prey, and the aggregative response and mutual interference of predators. Thus, the contribution of each component to the overall functional response can be studied separately and its potentially stabilizing effect on the predator-prey interaction can be assessed.

In another study (Nachman 2006), empirical data were used to quantify the spatial distributions of twospotted spider mites *Tetranychus urticae* Koch and predatory mites *Phytoseiulus persimilis* Athias-Henriot, and to estimate the per capita predation rate of *P. persimilis* taking the actual distributions of the two species on greenhouse cucumbers into consideration. The results indicate that prey patchiness may be an advantage to the prey at high prey densities but an advantage to the predator at low prey densities, primarily because the specialist predator does not search at random but spends relatively more time in the most profitable patches. Applying the functional response model developed in the present paper to the *Tetranychus–Phytoseiulus* system, allows for a rather general analysis of the ecological and evolutionary consequences of nonhomogeneous spatial distributions of prey and predators.

The empirical background

Spider mites and predatory mites occurring on all leaves from six cucumber plants *Cucumis sativus* L. were counted, amounting to 92 293 spider mites and 24 801 predatory mites distributed over 440 leaves. For each plant consisting of *n* leaves, the instantaneous per capita predation rate \vec{f} was computed as

$$\bar{f}_{obs} = \frac{1}{Y} \sum_{j=1}^{n} \sum_{t} y_{jt} f_{jt} = \frac{1}{Y} \sum_{j=1}^{n} \sum_{t} \sum_{s} \frac{a'_{st} x_{js} y_{jt} / A_{j}}{1 + \left(\sum_{s} a'_{st} h_{st} x_{js} + \eta_{t} (y_{jt} - 1)\right) / A_{j}}$$
eqn 1

where Y denotes the total number of predators on a plant and f_{ii} is the per capita predation rate of a predator individual of stage t staying on leaf j with area A_i . Leaf j is inhabited by x_{is} prey of stage s (s = eggs, juveniles, adults) and y_{it} predators of stage t (t = eggs, juveniles, adults). a'_{st} and h_{st} denote the stage-specific parameters of Holling's (1959) disc equation, i.e. the attack rate and the handling time, respectively, of stage t predators attacking prey of stage s. Finally, η_t is a constant expressing the time a predator of stage t wastes per encounter with conspecifics due to mutual interference (Murdoch 1973; Beddington 1975; Hassell 1978). If stage structure was omitted from eqn 1 (by assuming a fixed stage distribution across leaves), the values of \bar{f} were rather close to those obtained from eqn 1. This indicates that stage structure can be modelled implicitly by using lumped parameters derived by weighting the relative contributions of the different stages to the parameter values (Nachman 2006).

The model

Omitting stage distributions from eqn 1, and replacing the observed distributions of X prey ($X = \sum_{j=1}^{n} x_j$) and Y predators ($Y = \sum_{j=1}^{n} y_j$) with probability distributions lead to the generalized functional response model

$$\bar{f} = \frac{1}{\bar{y}} \sum_{x=0}^{\infty} p(x) \sum_{y=0}^{\infty} p(y \mid x) y f(x, y)$$
 eqn 2

where p(x) denotes the probability that a patch is inhabited by exactly $x(x = 0, 1, 2, ..., \infty)$ prey and p(y | x)the conditional probability that patches with x prey are occupied by $y(y = 0, 1, 2, ..., \infty)$ predators. f(x, y) is the instantaneous predation rate of a predator individual staying in a patch occupied by x prey and y predators. f(x, y) depends on the size of a patch (which for simplicity is assumed to be the same for all patches), the number of prey (the behavioural functional response), the number of predators (the aggregative response), and the interaction between predators (mutual interference). The challenge is to find mathematical expressions to

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958

949

substitute p(x), p(y | x) and f(x, y) in eqn 2. These expressions should be simple enough to provide explicit convergent solutions to the infinite summations and at the same time be reasonably realistic.

PREY AND PREDATOR DISTRIBUTIONS

Three different types of prey distribution to substitute p(x) will be considered in the following: (1) a clumped distribution described by the negative binomial distribution (NBD) with clumping parameter k; (2) a random distribution described by the Poisson distribution with parameter \bar{x} (the mean number of prey per patch); and (3) an even distribution where all patches are occupied by the same density of prey. The clumping parameter k can be considered either as a constant or as a function of prey density (Nachman 2006).

The predator distribution has two components: an aggregative response determined by the local density of prey and some amount of spatial variation that cannot be attributed to prey density (Chesson & Murdoch 1986; Hassell & Wilson 1997). The prey density-dependent component expresses the expected value of *y* at a given density of prey, i.e. $E(y | x) = \bar{y}_x$. The prey density-independent component expresses the variance of *y* for a fixed *x* and is described by the conditional probability function p(y | x) with variance $\sigma_{y|x}^2$.

AGGREGATIVE RESPONSE OF THE PREDATOR

The expected number of predators inhabiting a patch with x prey is assumed to increase with x according to the general expression

$$\frac{d\,\bar{y}_x}{dx} = cx^m e^{\mu x} \qquad \text{eqn 3}$$

where m, c and μ are constants (Nachman 2006).

Five main types of aggregative response (see, e.g. Van der Meer & Ens 1997) can be produced by eqn 3 depending on its parameter values: (i) c = 0: the predators do not show any aggregative response; (ii) c > 0, $m = 0, \mu = 0$: the aggregative response increases linearly with prey density; (iii) c > 0, m = 0, $\mu > 0$: the response accelerates with prey density; (iv) c > 0, m = 0, $\mu < 0$, the response increases with decelerating slope and approaches an upper asymptote: (v) $c > 0, m = 1, \mu < 0$: the response is sigmoid. Type (ii), (iv) and (v) correspond to what Gascoigne & Lipcius (2004) classify as type I, II and III aggregative response, respectively. General solutions for \bar{y}_x are found by integration of eqn 3 (Appendix 1). The higher the value of c, the more will the predators tend to aggregate in patches with abundant prey, whereas \bar{y}_x will decrease in patches with few prey. As \bar{y}_x cannot be negative, it sets an upper limit to how large c can be (see Fig. 1).

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958

To obtain explicit solutions to the aggregative response function, it is necessary to specify whether the prey distribution p(x) is clumped, random or even (Appendix 2). Furthermore, as it is most realistic that the aggregative



Fig. 1. The expected number (\bar{y}_{x}) of *P* persimilis on a leaf inhabited by x *T*. urticae for two different combinations of mean prey (\bar{x}) and predator (\bar{y}) density. (a) Full line: $\bar{x} = 400 T$. urticae/leaf and $\bar{y} = 120 P$. persimilis/leaf; (b) broken line: $\bar{x} = 200 T$. urticae/leaf and $\bar{y} = 60 P$. persimilis/leaf. Curves are computed by means of eqn A7 with parameter values given in Table 1, except that c in graph (b) is constrained to 1.298 to prevent \bar{y}_x from becoming negative.

response levels off at high prey densities, only cases in which μ is negative will be considered, encompassing convex (m = 0) and sigmoid aggregative responses (m = 1).

PREY-INDEPENDENT AGGREGATION OF PREDATORS

Three specific distributions of p(y | x) are considered to describe the prey-independent component of predator aggregation: (1) a clumped distribution characterized by ;(2) a random distribution ($\sigma_{y|x}^2 = \bar{y}_x$); and (3) an even distribution ($\sigma_{y|x}^2 = 0$). Applying the NBD to represent the clumped distribution yields $\sigma_{y|x}^2 = \bar{y}_x + \bar{y}_x^2/\kappa$, where κ expresses the tendency of the predators to clump independently of the prey. The random (Poisson) distribution appears as a special case of the NBD as $\kappa \to \infty$.

FUNCTIONAL RESPONSE TO PREY DENSITY

The behavioural functional response of a predator individual staying in a patch with x prey is assumed to be convex (type II). A model that describes such response is given by Ivlev (1961) as

$$f(x) = f_m(1 - e^{-\psi x/A}) \qquad \text{eqn 4}$$

where f_m is the maximal predation rate per individual, ψ a positive constant expressing the efficiency of the predators to find and attack prey and A the patch area. For simplicity, A is assumed to be the same for all patches (and equal to the mean patch area \tilde{A}).

MUTUAL INTERFERENCE BETWEEN PREDATORS

Mutual interference among the y predators in a patch with x prey may tend to reduce the per capita predation rate. This effect is included in eqn 4 as (cf. Royama 1992)

$$f(x, y) = f_m e^{-\varepsilon(y-1)/A} (1 - e^{-\psi x/A})$$

where ε is a positive constant expressing the intensity of mutual interference ($\varepsilon = 0$ implies no mutual interference).

COMBINING THE VARIOUS PREDATOR RESPONSES

Replacing f(x,y) in eqn 2 with eqn 5 yields

$$\bar{f} = \frac{f_m}{\bar{y}} \sum_{x=0}^{\infty} \left(p(x)(1 - e^{-\psi x/A}) \sum_{y=0}^{\infty} p(y|x) y e^{-\varepsilon(y-1)/A} \right) \text{ eqn 6}$$

According to Appendix 4, eqn 6 reduces to

$$\bar{f} = \frac{f_m}{\bar{y}} \sum_{x=0}^{\infty} \left(p(x)(1 - e^{-\psi x/A}) \bar{y}_x \left(1 + \frac{\bar{y}_x}{\kappa} (1 - e^{-\varepsilon/A}) \right)^{-(\kappa+1)} \right) \text{ eqn 6a}$$

if $p(y \mid x)$ follows a NBD with parameters (\bar{y}_x, κ) , and to

$$\bar{f} = \frac{f_m}{\bar{y}} \sum_{x=0}^{\infty} (p(x)(1 - e^{-\psi x/A})\bar{y}_x e^{-\bar{y}_x(1 - e^{-\psi/A})})$$
 eqn 6b

if p(y | x) follows a Poisson distribution with mean \bar{y}_x . Finally, if the aggregative response has no prey densityindependent component (i.e. $\sigma_{y|x}^2 = 0$), all patches with x prey are expected to be inhabited by \bar{y}_x predators, so $\sum_{y=0}^{\infty} p(y|x)ye^{-\varepsilon(y-1)/A} = \bar{y}_x e^{-\varepsilon(\bar{y}_x-1)/A} \sum_{y=0}^{\infty} p(y|x) \approx \bar{y}_x e^{-\varepsilon \bar{y}_x/A}$ and eqn 6 therefore becomes

$$\bar{f} = \frac{f_m}{\bar{y}} \sum_{x=0}^{\infty} (p(x)(1 - e^{-\psi x/A})\bar{y}_x e^{-\varepsilon \bar{y}_x/A})$$
 eqn 6c

The three special cases of eqn 6 can be solved numerically, because the infinite sums converge as $x \to \infty$. However, approximate analytical solutions are derived by making some simplifying assumptions. The terms $(1 + (\bar{y}_x/\kappa)(1 - e^{-\epsilon/A}))^{-(\kappa+1)}$ in eqn 6a, $e^{-\bar{y}_x(1-e^{-\epsilon/A})}$ in eqn 6b, and $e^{-\epsilon\bar{y}/A}$ in eqn 6c will be equal to 1 when $\varepsilon = 0$ and less than 1 when $\varepsilon > 0$. Hence, these terms represent the inhibiting effect of mutual interference on the predation rate. As long as ε/A is small, all three terms will be close to unity, but decrease with an increase in \bar{y}_{xy} which in turn increases with \bar{y} . Therefore, as an approximation, the overall inhibiting effect of mutual interference is assumed to depend on the overall density of predators (\bar{y}) rather than on \bar{y}_x . Equation 6 can therefore be replaced by

$$\bar{f} = \frac{f_m}{\bar{y}} I \sum_{x=0}^{\infty} (p(x)(1 - e^{-\psi x/A}) \bar{y}_x)$$
 eqn 7

where *I* is a factor accounting for mutual interference $(0 < I \le 1)$, calculated as $I_{\text{clumped}} = (1 + (\bar{y}/\kappa)(1 - e^{-\varepsilon/A}))^{-(\kappa+1)}$, $I_{\text{random}} = e^{-\bar{y}(1 - e^{-\varepsilon/A})}$ and $I_{\text{even}} = e^{-\varepsilon\bar{y}/A}$, depending on whether the predators for a given value of *x* are clumped, randomly or evenly distributed, respectively. It appears that for $\varepsilon > 0$, $I_{\text{clumped}} < I_{\text{random}} < I_{\text{even}}$ and that I_{clumped} declines with decreasing κ . This implies that scatter (prey density-independent variation) in the aggregative response will increase mutual interference and thereby reduce the overall predation rate.

 \bar{y}_x in eqn 7 depends on prey distribution and on the shape of the aggregative response (Appendix 2). If the prey is either clumped or randomly distributed and the predators show a convex aggregative response, substitution of \bar{y}_x in eqn 7 by eqn A6 gives

$$\bar{f} = \frac{f_m}{\bar{y}} I \left[\sum_{x=0}^{\infty} p(x) (1 - e^{-\psi x/A}) \left(\bar{y} - \frac{c}{\mu} Q_0(\mu) + \frac{c}{\mu} e^{\mu x} \right) \right]$$

which leads to

$$\bar{f} = f_m I \left[1 - Q_0 \left(-\frac{\Psi}{A} \right) + \frac{c}{\mu \bar{y}} \left(Q_0(\mu) Q_0 \left(-\frac{\Psi}{A} \right) - Q_0 \left(\mu - \frac{\Psi}{A} \right) \right) \right]$$
eqn 8a

where the functions $Q_0(\cdot)$ and $Q_1(\cdot)$ depend on the density and distribution of the prey (Appendix 5).

If the predators show a sigmoid aggregative response, and the prey is either clumped or randomly distributed, \bar{y}_x is replaced by eqn A7, yielding

$$\begin{split} \vec{f} &= \frac{f_m}{\vec{y}} I \Biggl\{ \sum_{x=0}^{\infty} p(x) (1 - e^{-\psi x/A}) \\ & \left(\vec{y} + \frac{c}{\mu} \Biggl[x e^{\mu x} - (\vec{x} e^{\mu}) \Biggl(1 + \frac{\vec{x}}{k} (1 - e^{\mu}) \Biggr)^{-(k+1)} \\ & - \frac{1}{\mu} \Biggl(e^{\mu x} - \Biggl(1 + \frac{\vec{x}}{k} (1 - e^{\mu}) \Biggr)^{-k} \Biggr) \Biggr] \Biggr) \Biggr] \end{aligned}$$

$$= f_m I \Biggl[1 - Q_0 \Biggl(-\frac{\Psi}{A} \Biggr) + \frac{c}{\mu \vec{y}} \Biggl(Q_1(\mu) Q_0 \Biggl(-\frac{\Psi}{A} \Biggr) - Q_1 \Biggl(\mu - \frac{\Psi}{A} \Biggr) \Biggr) \Biggr]$$

$$+ \frac{c}{\mu^2 \vec{y}} \Biggl(Q_0 \Biggl(\mu - \frac{\Psi}{A} \Biggr) - Q_0(\mu) Q_0 \Biggl(-\frac{\Psi}{A} \Biggr) \Biggr) \Biggr]$$
eqn 8b

If the predators show no aggregative response and prey distribution is either clumped or random, \bar{y}_x will be equal to \bar{y} for all x. Setting c = 0 in eqn 8b yields

$$\bar{f} = f_m I \left(1 - Q_0 \left(-\frac{\Psi}{A} \right) \right)$$
 eqn 8c

Finally, if the prey is evenly distributed, so that prey density is \bar{x}/A in all patches, eqn 7 reduces to

$$\bar{f} = f_m I(1 - e^{-\psi \bar{x}/A}) \qquad \text{eqn 8d}$$

Analyses

PARAMETERIZATION AND VALIDATION OF THE MODEL

The models require three state variables $(\bar{x}, \bar{y}, \text{ and } A)$ and seven parameters $(f_m, \psi, \varepsilon, c, \mu, k, \text{ and } \kappa)$ to compute \bar{f} . Furthermore, as k may be density-dependent it could be replaced by a function of \bar{x} , which would add two extra parameters to the model (Nachman 1984). Table 1 gives the estimated parameter values for the T. *urticae*–P. *persimilis* system if k is density-independent, otherwise see Nachman 2006).

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958 **Table 1.** Parameter values of the model. Parameters allowing for density dependence ink are given in Nachman (2006)

Parameter	Parameter description	Value	
f_m	Maximal predation rate	7·787 day-1	
Ψ	Attack efficiency	0.887 cm^2	
ε	Mutual interference coefficient	0.0402 cm ²	
$\begin{bmatrix} c \\ \mu \end{bmatrix}$	Aggregative response of P. persimilis	2.220 - 0.0834	
k	Aggregation index of T. urticae	0.091	
κ	Aggregative response of <i>P. persimilis</i> conditioned on \bar{y}_x	0.450	

The model-predicted predation rates (f_{pred}) were compared with the empirical values (f_{obs}) , which were obtained by means of eqn 1. It should be emphasized that observed and predicted values of f are not completely independent, as data from the same plants were used to calculate the values of f_{obs} and to estimate the model's parameters. However, no attempts were made afterwards to calibrate the parameters to the observed predation rates so as to improve the agreement between f_{obs} and f_{pred} .

STABILITY PROPERTIES OF THE FUNCTIONAL RESPONSE

The functional response of a predator has a stabilizing effect on the dynamics of the prey if the predation risk per prey increases with increasing prey density (Murdoch & Oaten 1975). Convex functional response curves (type II), like Holling's disc equation or Ivlev's predation model, lead to a monotonous decline in the predation risk for a given predator density, and therefore do not posses the potential of being stabilizing, whereas a sigmoid (type III) response may be stabilizing up to a certain prey density. Murdoch (1977) suggests using $\partial f/\partial \bar{x} > f/\bar{x}$ as a criterion to identify the density interval for which the func-

tional response has the capacity to be stabilizing. It should be emphasized that even if this criterion is met, it does not necessarily mean that the predator–prey system will be stable, because other conditions have to be fulfilled as well (see Discussion). However, applying the above criterion to the model can reveal whether incorporation of spatial heterogeneity, mutual interference and predator aggregation change an otherwise type II functional response to a type III.

Results

AGREEMENT BETWEEN MODEL PREDICTIONS AND DATA

The correlation coefficient (*R*) between the observed predation rates (\bar{f}_{obs}) and the model-predicted rates (\bar{f}_{pred}) expresses the qualitative fit of a model to data. *R* was high and almost the same irrespective of whether *k* was assumed to be density-dependent (using the relationship $(1 + \bar{x}/k)^{-k} = e^{-\alpha x^{\beta}}$, where α and β are positive constants (cf. eqn A3 in Nachman 2006) or density-independent provided the prey was clumped and the predators showed an aggregative response. The correlation decreased when the predators were assumed to lack an aggregative response or when the prey was assumed to be evenly distributed (Table 2).

Table 2 also shows how much of the variation in \bar{f}_{obs} that could be explained by the respective models. The best quantitative agreement (88.9%) between \bar{f}_{obs} and \bar{f}_{pred} was achieved by eqn 6 assuming density independence of k, although k was found to vary with prey density (Nachman 2006). However, density dependence of k will only be of importance when prey density is either very low or very high, but not within the range of observed densities (0.002–3.758 *T. urticae* cm⁻²). Equation 8 explained

Table 2. Comparisons between observed (f_{obs}) and predicted predation rates (f_{pred}) . The models are compared with respect to the correlation between f_{obs} and f_{pred} and the percentage variation in f_{obs} explained by means of the model

Greenhouse data					Predicted predation rates $(\vec{f_{pred}})$					
					Prey clumped				Prey even	
					Predator aggregation No predato				r aggregation	
Plant	Average leaf size (cm ²)	$T.$ <i>urt.</i> /leaf (\bar{x})	<i>P. per./</i> leaf (<i>y</i>)	$ar{f}_{obs}$	k density- dependent Eqn 6*	k density-independent				
						Eqn 6†	Eqn 8‡	Eqn 8§	Eqn 8¶	
1	166.8	416.3	73.52	3.932	4.676	4.569	5.006	1.871	6.558	
2	168.3	17.53	7.096	3.318	2.772	2.508	2.574	0.475	0.680	
3	160.6	0.316	4.776	0.096	0.186	0.075	0.078	0.013	0.014	
4	234.6	58.33	99.43	1.471	2.217	2.260	2.547	0.780	1.460	
5	191.1	0.262	2.857	0.014	0.185	0.068	0.070	0.009	0.009	
6	175.5	659.6	187.4	3.362	4.299	3.388	3.832	1.914	6.580	
Correlation between \bar{f}_{abs} and $\bar{f}_{nred}(R)$					0.959	0.949	0.937	0.828	0.771	
% variation in \bar{f}_{obs} explained by \bar{f}_{pred}					84.7	88.9	79.6	1.6	0	

*Predictions based on eqn 6 and parameter values in Table 1, but with a density-dependent prey clumping parameter (k). †Predictions based on eqn 6 but with density-independent k. ‡Predictions based on eqn 8 but with the same assumptions as in the previous column. §Predators are assumed to search independently of prey distribution. ¶Prey is assumed to be evenly distributed.

953 Functional response in a patchy environment



Fig. 2. The predicted per capita predation rate (\overline{f}_{pred}) for different densities of *T. urticae* and *P. persimilis* based on eqn 6 and parameter values given in Table 1.

79.6%, which indicates that the approximations made to derive this equation from eqn 6 were acceptable. The last two columns of Table 2 demonstrate the importance of taking the aggregative response and distribution of prey into consideration when predicting predation rates. Without predator aggregation (i.e. c = 0), the predicted predation rates become consistently lower than \bar{f}_{obs} , which shows the advantage to the predators of being able to adopt nonrandom search. On the other hand, if the prey is assumed to be evenly distributed the predicted predation rates will be lower than \bar{f}_{obs} at low prey densities but higher than \bar{f}_{obs} when prey density is high.

FUNCTIONAL RESPONSE IN RELATION TO DENSITY AND BEHAVIOUR OF PREY AND PREDATORS

The parameters obtained from the *P. persimilis*—*T. urticae* system were used as the standard case to which changes in the model assumptions could be compared. All predictions of \overline{f} were obtained from eqn 6 assuming density independence of *k*.

Figure 2 shows that the functional response of P. persimilis is predicted to increase when mean prey density (\bar{x}) increases and/or when mean predator density (\bar{v}) decreases. The upper plateau is reached more steeply when predator density is low than when it is high. Figure 3 shows that prey clumping increases the predation rate at low prey densities and decreases it at high prey densities as compared with a random distribution of prey. The result for an even prey distribution is almost identical to that of a random prey distribution and is therefore not shown. Higher predator density reduces the per capita predation rate, in particular when the prey is aggregated, because of the intense mutual interference experienced by the predators when crowding in the same patches as the prey. A change in prey distribution from random to aggregated also changes the functional response from type II to type III (Fig. 4), indicating that prey patchiness per se may be able to stabilize the predator-prey dynamics as long as the mean prey density does not

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958



Fig. 3. The effect of prey distribution and predator density on the functional response predicted by means of eqn 6 and parameter values given in Table 1.



Fig. 4. The instantaneous risk of predation calculated from Fig. 2, assuming a mean predator density of one individual per cm².

exceed c.0.02 prey cm⁻². Nonrandom search for a patchily distributed prey (k = 0.091) leads to higher predation rates than random search, in particular at low predator densities (Fig. 5).

Discussion

EFFECTS OF PREY PATCHINESS AND PREDATOR AGGREGATION ON THE FUNCTIONAL RESPONSE

Traditionally, predator–prey (or parasitoid–host) theory has presumed that populations are homogeneously distributed in space (e.g. Vandermeer & Goldberg 2003). However, in the real world this will hardly ever be true, which means that the performance of the predators will depend on how the prey is distributed and how the predators respond to this distribution. Ignoring these spatial effects may seriously bias the estimated predation rates at the population level (Ives *et al.* 1999) and may lead to erroneous conclusions concerning the ability of the predators to regulate the density of their prey (Hochberg & Holt 1999) or exaggerate the risk of prey extinction due to a predator-mediated Allee effect (Gascoigne & Lipcius 2004). Thus, analyses of host–parasitoid models have



Fig. 5. The effect of predator aggregation and density on the functional response predicted by means of eqn 6 and parameter values given in Table 1.

shown that nonrandom distribution of parasitism (either in time or space) can stabilize the interactions between hosts and parasitoids with discrete generations (Hassell *et al.* 1991). It seems likely that this also applies to predator– prey systems with overlapping generations, but because such systems are not as straightforward to analyse mathematically as host–parasitoid systems where the $CV^2 >$ l criterion can be used (Hassell *et al.* 1991; Taylor 1993), the analyses of predator–prey interactions have often been limited to whether the functional response is potentially stabilizing or not (Murdoch 1977; Murdoch & Stewart-Oaten 1989). A full analysis of predator–prey stability based on Kolmogorov's theorem would require additional information about the relationship between prey density and the numerical response of the predators (May 1974).

The present model shows that prey patchiness can markedly reduce the feeding rate of a predator individual unless it is able to compensate by adopting a nonrandom searching behaviour. Such behaviour will lead to a positive aggregative response where the majority of predators will cluster in the most profitable prey patches. If the degree of prey aggregation is high, the predators may actually be able to achieve a higher predation rate than they would obtain if the prey had been evenly distributed, but only as long as prey density is low. At high prey densities, a relatively large part of the predator population will waste time by searching patches with prey densities below average, whereas the remaining part spends time in patches with high prey density. Owing to satiation of the predators staying in the most profitable patches, the arithmetic mean of the predation rates averaged over all patches will thus be lower than if all predators had been exposed to the mean prey density \bar{x} . The fact that prey aggregation benefits the predators at low densities may also have implications for biological control, because it slows down the growth rate of the prey and helps the predators to survive during periods of prey scarcity (Murdoch & Briggs 1996). However, when the model was applied to the P. persimilis-T. urticae system, the type III response was only regulatory up to a prey density of about 0.02 spider mites per cm² (corresponding to about 200-400 individuals on a cucumber plant),

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958 so it seems unlikely that such a weak type III response can prevent outbreaks of spider mites. In an experimental set-up, Ryoo (1996) did not find evidence for a type III response when he varied the distribution of *T. urticae* eggs in an arena, but the area of his system (2500 cm²) was much smaller than that of a cucumber plant. Besides, it may not be possible to distinguish between a type II response and a weak type III response when experimental data are analysed statistically (Juliano 1993).

EVOLUTIONARY PERSPECTIVES

From an evolutionary point of view, a prey species may switch from a random distribution to a more clumped distribution in order to reduce the predation pressure, but this strategy will only work as long as the predators search at random. Once the predators have responded by evolving searching behaviours that improve their foraging success, the prey should be selected to reduce predation pressure by being evenly distributed at low density and being more patchily distributed at high densities. Prey aggregation may lead to the so-called 'dilution effect', where the risk of predation to individual prey declines with the number of surrounding conspecifics because of relatively fewer predators per prey and/or because the individual predator becomes satiated (Turchin & Kareiva 1989). In fact, many prey species tend to become more aggregated as the mean density increases [see Taylor (1984) for a review]. This also applies to T. urticae (Nachman 1981). Hence, prey patchiness and predator aggregation might be seen as the outcome of a coevolutionary arms race (Janzen 1980; Abrams 2000; Lima 2002), although other factors than avoidance of predation may also contribute to prey aggregation, e.g. the quality and distribution of the prey's food, females laying eggs in clusters, and offspring tending to stay close to their natal site (Turchin & Kareiva 1989; Begon et al. 1996).

ADVANCES AND LIMITATIONS OF THE PRESENT MODEL

The present model represents progress relative to other analytical functional response models (e.g. Murdoch & Oaten 1975; Hassell et al. 1991; Ives et al. 1999; Williams & Martinez 2004) because it integrates prey patchiness, predator aggregation and mutual interference between predators into a single analytical model, which can be solved either numerically (eqn 6) or explicitly (eqn 8), depending on the validity of the approximations. The model is general in the sense: (1) that it allows for variation in mean densities of both prey and predators; (2) it includes the most common (type II) functional response type at the patch level; (3) it allows for different types of prey distribution (even, random and clumped); (4) it allows for different types of prey density-dependent aggregative responses (none, linear, hyperbolic, sigmoid); and (5) it allows the predators to exhibit mutual interference. Furthermore, the model's parameters can be estimated experimentally and interpreted in a biologically meaningful

955 Functional response in a patchy environment

way. Finally, the model can be used to make specific predictions that can be compared against empirical data as demonstrated for the *T. urticae–P. persimilis* system.

The model also has limitations:

- 1. It focuses on only one prey and one predator species.
- It ignores variation among individuals within species.
 Patches are assumed to be identical except for variation in number of prey and predators.

 The functional response, the aggregative response and mutual interference are modelled as empirically based (phenomenological) mathematical relationships that do not necessarily incorporate the underlying biological mechanisms in a realistic way (van der Meer & Ens 1997).
 The model is computational complex and contains many parameters that have to be estimated from separate experiments. If predation could be observed directly, an alternative way of estimating the parameters might be to fit the complete model to the observed predation rates, but the large number of parameters makes it unlikely that this will yield values that are biologically meaningful (see, e.g. Jost & Arditi 2001).

6. The number of patches and their distribution in space are not modelled explicitly. In principle, the model presumes that any patch in the habitat is equally likely to be found by a predator, allowing the predators to redistribute in response to a changing prey distribution. This may be a reasonable assumption for a mobile predator inhabiting a small system, such as P. persimilis and T. urticae occupying a single cucumber plant, although the large scatter about the aggregative response indicates that redistribution is far from being perfect. At a spatial scale larger than a single plant, the predators are likely to show even less coupling with their prey, making the prey density-dependent component of the aggregative response less clear (i.e. c decreases) while the prey density-independent component becomes more pronounced (i.e. 1/k increases).

7. Transit time for individuals moving from one patch to another is not included. If transit time is long, it will delay the redistribution of individuals and thereby contribute to the scatter in the aggregative response. Transit time may also reduce the overall foraging efficiency (Ryoo 1996).

APPLICATIONS OF THE MODEL

Incorporating spatial effects into population models tends to render such models analytically intractable, unless several simplifying assumptions are being made. Therefore, alternative approaches, such as simulation of population-based (e.g. Nachman 2001) and individualbased (e.g. Casas 1990; Bancroft & Margolies 1999) models, are usually preferred in order not to sacrifice realism. However, instead of regarding analytical models as alternatives to simulation models, they may rather be considered as supplements serving two purposes: (1) they are better to provide theoretical insight into the factors that affect population dynamics, and (2) they can serve as submodels in simulation models to save computing time. The model presented here may fulfil both purposes: On one hand, it can be used to analyse the importance of incorporating spatial heterogeneity in population models and to analyse the costs and benefits of being patchily distributed. On the other hand, the model may be included as a submodel in a metapopulation model of predator-prey dynamics to predict the current predation rate (i.e. the predation rate from time t to time $t + \Delta t$ where Δt has to be so short that prey distribution can be regarded as constant) of the predators occupying a patch (e.g. a plant), which in itself consists of patches (e.g. leaves). For instance, in the T. urticae-P. persimilis system at least three different spatial scales can be identified: leaves, plants and an entire field (or a greenhouse). Plants within a field can be modelled in a metapopulation context (Nachman 2001), but computing time would increase dramatically if the within-plant dynamics should be modelled explicitly. Instead, the present model may be used as a short-cut by modelling within-plant processes implicitly.

Acknowledgements

The author thanks Professor Koos Boomsma, Institute of Biology, University of Copenhagen, for his many constructive comments to improve the manuscript.

References

- Abrams, P.A. (2000) The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics*, **31**, 79–105.
- Bancroft, J.S. & Margolies, D.C. (1999) An individual-based model of an acarine tritrophic system: lima bean, *Phaseolus lunatus* L., twospotted spider mite, *Tetranychus urtieae* (Acari: Tetranychidae), and *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Ecological Modelling*, **123**, 161–181.
- Beddington, J.R. (1975) Mutual interference between parasites or predators, and its effect on searching efficiency. *Journal of Animal Ecology*, 44, 331–340.
- Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, Populations, Communities*, 3rd edn. Blackwell Scientific Publications, Oxford.
- Casas, J. (1990) Multidimensional host distribution and nonrandom parasitism: a case study and a stochastic model. *Ecology*, **71**, 1893–1903.
- Chesson, P.L. & Murdoch, W.W. (1986) Aggregation of risk: relationships among host-parasitoid models. *American Naturalist*, **127**, 696–715.
- Gascoigne, J.C. & Lipcius, R.N. (2004) Allee effects driven by predation. *Journal of Applied Ecology*, **41**, 801–810.
- Hassell, M.P. (1978) Arthropod Predator-prey Systems. Monographs in Population Biology, 13. Princeton University Press, Princeton, NJ.
- Hassell, M.P. & Rogers, D.J. (1972) Insect parasite responses in the development of population models. *Journal of Animal Ecology*, 41, 661–672.
- Hassell, M.P. & Wilson, H.B. (1997) The dynamics of spatially distributed host-parasitoid systems. *Spatial Ecology* (eds D. Tilman & P. Kareiva), pp. 75–110. Princeton University Press, Princeton, NJ.
- Hassell, M.P., May, R.M., Pacala, S.W. & Chesson, P.L. (1991) The persistence of host–parasitoid associations in patchy environments. I. A general criterion. *American Naturalist*, **138**, 568–583.

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, **75**, 948–958

- Hochberg, M.E. & Holt, R.D. (1999) The uniformity and density of pest exploitation as guides to success in biological control. Theoretical Approaches to Biology Control (eds B.A. Hawkins & H.V. Cornell), pp. 71-88. Cambridge University Press, Cambridge.
- Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. Canadian Entomologist, 91, 385-398.
- Ives, A.R. (1992) Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. American Naturalist, 140, 912–937.
- Ives, A.R., Schooler, S.S., Jagar, V.J., Knuteson, S.E., Grbic, M. & Settle, W.H. (1999) Variability and parasitoid foraging efficiency: a case study of pea aphids and Aphidius ervi. American Naturalist, 154, 652-673.
- Ivlev, V.S. (1961) Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, CT.
- Janzen, D.H. (1980) When is it coevolution? Evolution, 34, 611-612.
- Jeschke, J.J., Kopp, M. & Tollrian, R. (2002) Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs, 72, 95-112.
- Jost, C. & Arditi, R. (2001) From pattern to process: identifying predator-prey models from time series data. Population Ecology, 43, 229-243.
- Juliano, S.A. (1993) Nonlinear curve fitting: predation and functional response curves. Design and Analysis of Ecological Experiments (eds S.M. Scheiner & J. Gurevitch), pp. 159-182. Chapman & Hall, New York.
- Lima, S.L. (2002) Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution, 17, 70-75.
- May, R.M. (1974) Stability and Complexity in Model Ecosystems. Monographs in Population Biology, 2nd edn. Princeton University Press, Princeton, NJ.
- Murdoch, W.W. (1973) The functional response of predators. Journal of Applied Ecology, 14, 335-341.
- Murdoch, W.W. (1977) Stabilizing effects of spatial heterogeneity in predator-prey systems. Theoretical Population Biology, 11, 252-273.
- Murdoch, W.W. & Briggs, C.J. (1996) Theory for biological control: recent developments. Ecology, 77, 2001-2013.
- Murdoch, W.W. & Oaten, A. (1975) Predation and population stability. Advances in Ecological Research, 9, 1-125.
- Murdoch, W.W. & Stewart-Oaten, A. (1989) Aggregation by parasitoids and predators: effects on equilibrium and stability. American Naturalist, 134, 288-310.

- Nachman, G. (1981) A mathematical model of the functional relationship between density and spatial distribution of a population. Journal of Animal Ecology, 50, 453-460.
- Nachman, G. (1984) Estimates of mean population density and spatial distribution of Tetranychus urticae and Phytoseiulus persimilis based upon the proportion of empty sampling units. Journal of Applied Ecology, 21, 903-913.
- Nachman, G. (2001) Predator-prey interactions in a nonequilibrium context: the metapopulation approach to modelling 'hide-and-seek' dynamics in a spatially explicit tri-trophic system. Oikos, 94, 72-88.
- Nachman, G. (2006) The effect of prey patchiness, predator aggregation, and mutual interference on the functional response of Phytoseiulus persimilis feeding on Tetranychus urticae (Acari: Phytoseiidae, Tetranychidae). Experimental and Applied Acarology, 38, 87-111.
- Royama, T. (1992) Analytical Population Dynamics. Chapman & Hall, London.
- Ryoo, M.I. (1996) Influence of the spatial distribution pattern of prey among patches and spatial coincidence on the functional and numerical response of Phytoseiulus persimilis (Acarina, Phytoseiidae). Journal of Applied Entomology, 120, 187-192.
- Solomon, M.E. (1949) The natural control of animal populations. Journal of Animal Ecology, 18, 1-35.
- Taylor, L.R. (1984) Assessing and interpreting the spatial distributions of insect populations. Annual Review of Entomology, 29, 321-357.
- Taylor, A.D. (1993) Heterogeneity in host-parasitoid interactions: 'Aggregation of risk' and the 'CV² > 1 rule'. Trends in Ecology and Evolution, 8, 400-405.
- Turchin, P. & Kareiva, P. (1989) Aggregation in Aphis varians: an effective strategy for reducing predation risk. Ecology, 70, 1008-1016.
- Van der Meer, J. & Ens, B.J. (1997) Models of interference and their consequences for the spatial distribution of ideal and free predators. Journal of Animal Ecology, 66, 846-858.
- Vandermeer, J.H. & Goldberg, D.E. (2003) Population Ecology - First Principles. Princeton University Press, Princeton, NJ.
- Williams, R.J. & Martinez, N.D. (2004) Stabilization of chaotic and non-permanent food-web dynamics. European Physical Journal of B, 38, 297–303.

Received 30 August 2005; accepted 28 February 2006

Appendix 1. The aggregative response

Integration of eqn 3 and constraining the solution so that $\sum_{x=0}^{\infty} p(x)\bar{y}_x = \bar{y}$ and $\bar{y}_x \ge 0$ for $x \ge 0$ yield the following solutions:

1 No response (i.e. c = 0):

$$\bar{y}_x = \bar{y}$$

2 Linear (i.e. $c > 0, m = 0, \mu = 0$):

$$\bar{y}_x = \bar{y} + c(x - \bar{x}) \left(c \le \frac{\bar{y}}{\bar{x}} \right)$$
eqn A2

3 Accelerating (i.e. $c > 0, m = 1, \mu = 0$):

© 2006 The Author. Journal compilation © 2006 British Ecological Society, Journal of Animal Ecology, 75, 948-958

 $\bar{y}_{x} = \bar{y} + \frac{c}{2} \left[x^{2} - \sum_{x=0}^{\infty} p(x) x^{2} \right] = \bar{y} + \frac{c}{2} \left[x^{2} - (\sigma^{2} + \bar{x}^{2}) \right] \left(c \le \frac{2\bar{y}}{\sigma^{2} + \bar{x}^{2}} \right)$ eqn A3

where δ^2 is the sportial variance of the prey population. 4 Convex (i.e. $c > 0, m = 0, \mu < 0$):

eqn A1

957 Functional response in a patch environment

$$ny \qquad \bar{y}_{x} = \bar{y} + \frac{c}{\mu} \left(e^{\mu x} - \sum_{x=0}^{\infty} p(x) e^{\mu x} \right) \left(c \le \frac{\mu \bar{y}}{\sum_{x=0}^{\infty} p(x) e^{\mu x} - 1} \right)$$
eqn A4

5 Sigmoid (i.e. $c > 0, m = 1, \mu < 0$):

$$\bar{y}_{x} = \bar{y} + \frac{c}{\mu} \left(xe^{\mu x} - \sum_{x=0}^{\infty} p(x)xe^{\mu x} - \frac{1}{\mu} \left(e^{\mu x} - \sum_{x=0}^{\infty} p(x)e^{\mu x} \right) \right) \left| c \le \frac{\mu^{2}\bar{y}}{1 + \mu \sum_{j=1}^{n} p(x)xe^{\mu x} - \sum_{x=0}^{\infty} p(x)e^{\mu x}} \right|$$
eqn A5

1

)

Appendix 2. The aggregative response for specific prey distributions

PREY DISTRIBUTION IS CLUMPED

Replacing p(x) in eqns A4 and A5 with the individual terms of the NBD (see Appendix 3) yields

$$m = 0: \quad \bar{y}_x = \bar{y} + \frac{c}{\mu} \left[e^{\mu x} - \left(1 + \frac{\bar{x}}{k} (1 - e^{\mu}) \right)^{-k} \right] \left[c \le \frac{\mu \bar{y}}{\left(1 + \frac{\bar{x}}{k} (1 - e^{\mu}) \right)^{-k} - 1} \right]$$
eqn A6

$$m = 1: \ \bar{y}_{x} = \bar{y} + \frac{c}{\mu} \left[xe^{\mu x} - (\bar{x}e^{\mu}) \left(1 + \frac{\bar{x}}{k} (1 - e^{\mu}) \right)^{-(k+1)} - \frac{1}{\mu} \left(e^{\mu x} - \left(1 + \frac{\bar{x}}{k} (1 - e^{\mu}) \right)^{-k} \right) \right]$$

$$eqn A7$$

$$eqn A7$$

PREY DISTRIBUTION IS RANDOM

Replacing p(x) with the individual terms of the Poisson distribution (Appendix 3) yields:

$$m = 0; \ \bar{y}_{x} = \bar{y} + \frac{c}{\mu} \bigg[e^{\mu x} - e^{-\bar{x}(1-e^{\mu})} \bigg] \bigg(c \le \frac{\mu \bar{y}}{e^{-\bar{x}(1-e^{\mu})} - 1} \bigg)$$
eqn A8

$$m = 1: \ \bar{y}_x = \bar{y} + \frac{c}{\mu} \bigg[x e^{\mu x} - \bar{x} e^{\mu - \bar{x}(1 - e^{\mu})} - \frac{1}{\mu} (e^{\mu x} - e^{-\bar{x}(1 - e^{\mu})}) \bigg] \bigg[c \le \frac{\mu^2 \bar{y}}{1 + \mu \bar{x} e^{\mu - \bar{x}(1 - e^{\mu})} - e^{-\bar{x}(1 - e^{\mu})}} \bigg]$$
eqn A9

PREY DISTRIBUTION IS EVEN

,

As x is equal to \bar{x} in all patches, the expected number of predators per patch is given by eqn A1.

Appendix 3

Derivation of
$$\sum_{x=0}^{\infty} p(x)e^{ax} = (1 + (\bar{x}/k)(1 - e^{a}))^{-k}$$
 and $\sum_{x=0}^{\infty} p(x)xe^{ax} = \bar{x}e^{a}(1 + (\bar{x}/k)(1 - e^{a}))^{-(k+1)}$

Defining $p = k/(\bar{x} + k)$ and $q = 1 - p = \bar{x}/(\bar{x} + k)$ means that the individual terms of the NBD can be written as $p(x) = [\Gamma(x + k)/x!\Gamma k]p^kq^x$. This means that

$$\sum_{x=0}^{\infty} p(x)e^{ax} = \sum_{x=0}^{\infty} \frac{\Gamma(x+k)}{x!\Gamma k} p^{k} q^{x} e^{ax} = \left(\frac{p}{p'}\right)^{k} \sum_{x=0}^{\infty} \frac{\Gamma(x+k)}{x!\Gamma k} (p')^{k} (q')^{x}$$
eqn A10

where $q' = qe^a$ and p' = 1 - q'. Provided q' < 1, which requires that $a < \ln(1 + k/\bar{x})$, the right-hand sum in eqn A10 will converge to unity, yielding

$$\sum_{x=0}^{\infty} p(x)e^{ax} = \left(\frac{p}{p'}\right)^k = \left(1 + \frac{\bar{x}}{k}(1 - e^a)\right)^{-k}$$
eqn A11

© 2006 The Author. Journal compilation © 2006 British Ecological Society, *Journal of Animal Ecology*, **75**, 948–958 As $(1 + 1/u)^u = e$ for $u \to \infty$, we may define $1/u = \bar{x}/k(1 - e^a)$ yielding $-k = -\bar{x}(1 - e^a)u$. Hence, if p(x) is distributed according to the Poisson distribution (corresponding to $k \to \infty$) we get

$$\sum_{x=0}^{\infty} p(x)e^{ax} = \left(1 + \frac{\bar{x}}{k}(1 - e^{a})\right)^{-k} = \left(1 + \frac{1}{u}\right)^{-\bar{x}(1 - e^{a})u} = e^{-\bar{x}(1 - e^{a})}$$
eqn A12

To solve $\sum_{x=0}^{\infty} p(x)xe^{ax}$, apply eqn A10 to write $\sum_{x=0}^{\infty} p(x)xe^{ax} = (p/p')^k \sum_{x=0}^{\infty} [\Gamma(x+k)]/(x!\Gamma k)(p')^k (q')^x x$, but as $\bar{x} = \sum_{x=0}^{\infty} p(x)x = kq/p$, $\sum_{x=0}^{\infty} [\Gamma(x+k)]/(x\Gamma k)(p')^k (q')^x x$ can be replaced by kq'/p' (provided q' < 1), which leads to

$$\sum_{x=0}^{\infty} p(x)xe^{ax} = \left(\frac{p}{p'}\right)^k \left(\frac{kq'}{p'}\right) = \bar{x}e^{a} \left(1 + \frac{\bar{x}}{k}(1 - e^a)\right)^{-(k+1)}$$
eqn A13

For p(x) being distributed according to the Poisson distribution, eqn A13 reduces to

$$\sum_{x=0}^{\infty} p(x)xe^{ax} = \bar{x}e^{a} \left(1 + \frac{\bar{x}}{k}(1 - e^{a})\right)^{-(k+1)} = \bar{x}e^{a - \bar{x}(1 - e^{a})}$$
eqn A14

Appendix 4

Derivation of $\sum_{x=0}^{\infty} p(y|x) y e^{-\varepsilon(y-1)/A} = \bar{y}_x [1 + (\bar{y}_x/\kappa)(1 - e^{-\varepsilon/A})]^{-(\kappa+1)}$ if $p(y \mid x)$ is a NBD with parameters \bar{y}_x and κ .

In line with Appendix 3, we define $p = \kappa/(\bar{y}_x + \kappa)$, $q = 1 - p = \bar{y}_x/(\bar{y}_x + \kappa)$, $q' = (\bar{y}_x e^{-\epsilon/A})/(\bar{y}_x + \kappa)$, and p' = 1 - q'. $\sum_{x=0}^{\infty} p(y \mid x)ye^{-\epsilon(y-1)/A}$ can therefore be written as

$$\sum_{y=0}^{\infty} p(y \mid x) y e^{-\varepsilon(y-1)/A} = e^{\varepsilon/A} \left(\frac{p}{p'}\right)^{\kappa} \sum_{y=0}^{\infty} \frac{\Gamma(\kappa+y)}{y! \Gamma \kappa} (p')^{\kappa} (q')^{y} y$$
$$= e^{\varepsilon/A} \left(\frac{p}{p'}\right)^{\kappa} \frac{\kappa q'}{p'} = e^{\varepsilon/A} \left(1 + \frac{\bar{y}_{x}}{\kappa} (1 - e^{-\varepsilon/A})\right)^{-\kappa} \left(1 + \frac{\bar{y}_{x}}{\kappa} (1 - e^{-\varepsilon/A})\right)^{-1} \bar{y}_{x} e^{-\varepsilon/A} \qquad \text{eqn A15}$$
$$= \bar{y}_{x} \left(1 + \frac{\bar{y}_{x}}{\kappa} (1 - e^{-\varepsilon/A})\right)^{-(\kappa+1)}$$

If the predators are randomly distributed for a given \bar{y}_x (i.e. $\kappa \to \infty$), eqn A15 reduces to

$$\sum_{y=0}^{\infty} p(y \mid x) y e^{-\varepsilon(y-1)/A} = \bar{y}_x e^{-\bar{y}_x(1-e^{-\varepsilon/A})}$$
eqn A16

Appendix 5. The Q-function

The Q-function is defined (see also Appendix 3) as

$$Q_b(a) = \sum_{x=0}^{\infty} p(x) x^b e^{ax} = (\bar{x}e^a)^b \left(1 + \frac{\bar{x}}{k} (1 - e^a) \right)^{-(k+b)} \quad (a < \ln(1 + k/\bar{x}); b = 0 \text{ or } 1)$$
eqn A17

which gives

$$Q_0(a) = \left(1 + \frac{\bar{x}}{k}(1 - e^a)\right)^{-k}$$
eqn A18

$$Q_{1}(a) = \bar{x}e^{a} \left(1 + \frac{\bar{x}}{k}(1 - e^{a})\right)^{-(k+1)}$$
eqn A19

for b = 0 and b = 1, respectively, if p(x) follows the NBD with parameters \bar{x} and k, and

$$Q_b(a) = \sum_{x=0}^{\infty} p(x) x^b e^{ax} = (\bar{x}e^a)^b e^{-\bar{x}(1-e^a)} \quad (-\infty < a < \infty; b = 0 \text{ or } 1)$$
eqn A20

which becomes

© 2006 The Author. Journal compilation © 2006 British

Ecological Society, Journal of Animal Ecology, **75**,

948-958

$$Q_0(a) = e^{-\bar{x}(1-e^a)}$$
eqn A21

$$Q_1(a) = \bar{x}e^{a - \bar{x}(1 - e^a)}$$
eqn A22

if p(x) follows the Poisson distribution with parameter \bar{x} .