

Intuition, functional responses and the formulation of predator–prey models when there is a large disparity in the spatial domains of the interacting species

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Summary

1. The disparity of the spatial domains used by predators and prey is a common feature of many terrestrial avian and mammalian predatory interactions, as predators are typically more mobile and have larger home ranges than their prey.
2. Incorporating these realistic behavioural features requires formulating spatial predator–prey models having local prey mortality due to predation and its spatial aggregation, in order to generate a numerical response at timescales longer than the local prey consumption. Coupling the population dynamics occurring at different spatial scales is far from intuitive, and involves making important behavioural and demographic assumptions. Previous spatial predator–prey models resorted to intuition to derive local functional responses from non-spatial equivalents, and often involve unrealistic biological assumptions that restrict their validity.
3. We propose a hierarchical framework for deriving generic models of spatial predator–prey interactions that explicitly considers the behavioural and demographic processes occurring at different spatial and temporal scales.
4. The proposed framework highlights the circumstances wherein static spatial patterns emerge and can be a stabilizing mechanism of consumer–resource interactions.

Key-words: foraging behaviour, population dynamics, predator–prey models, space, spatial patterns

Introduction

Consumer–resource (plant–herbivore, prey–predator and host–parasitoid) interactions are fundamental processes determining changes in abundance and spatial distribution of the interacting populations and the structure of animal communities (Murdoch *et al.* 2003). The bewildering complexity of consumer–resource interactions in natural habitats prompted ecologists to consider simpler systems under controlled conditions (e.g. microcosms) and to use modelling as a means to explore the consequences of these biotic interactions in the natural world. Stemming from the basic predator–prey (Lotka–Volterra) and host–parasitoid (Nicholson–Bailey) models, most modelling approaches start by describing populations as spatially homogeneous and interacting in a well mixed environment, where the interacting species experience and react to spatially constant abundance (Bolker & Pacala 1997; Dieckmann *et al.* 2000).

In the natural world, however, resource and consumer abundances are rarely, if ever, constant over space. This heterogeneity leads to spatial variation in the interaction strength between consumers and resources that can have important consequences for their dynamics and spatial distribution. Using Bolker's (2003) dichotomy, the spatial variation in interaction strength can be due either to habitat spatial variation (patches of higher productivity, refuges) that is extrinsic to the interacting populations, or to the spatial redistribution of individuals of the interacting populations (spatial aggregation to reduce predation risk, or sampling variation in the density of low-mobility predators). That including spatial variation could alter the dynamics of consumer–resource models has been known since the work of Nicholson (1933) and Huffaker (1958), who showed that spatial variation in the distribution and synchrony of the interacting populations could promote persistence of otherwise unstable systems. This ('statistical stabilization') and two other mechanisms (decoupling of immigration from local density and nonlinear spatial averaging) have been suggested to be the main routes to stabilization of resource–consumer

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interactions (see reviews by Murdoch *et al.* 2003; Briggs & Hoopes 2004).

Most spatial predator–prey models assume that predator and prey dynamics occur at commensurate spatial scales (Murdoch *et al.* 2003). However, disparity in the extent of the spatial domains used by each population (hereafter, spatial scale disparity) is a rather common (but by no means universal) situation in most avian and mammalian predator–prey systems, as consumers are typically more mobile and have larger home ranges than their prey (McCann *et al.* 2005; Van de Koppel *et al.* 2005). Predator–prey systems involving spatial scale disparity are typically prone to Turing instabilities (emergence of static spatial patterns from random initial conditions due to the difference in the spatial scales of positive and negative feedbacks) and thus to spatial self-organization (for review see Solé & Bascompte 2006). Spatial scale disparity could therefore play a key role in the emergence of macroscopic spatial patterns observed in real ecosystems (for a recent review see Rietkerk & van de Koppel 2008), and it remains an important issue for theoretical ecologists to clarify the necessary conditions for the emergence of such phenomena. The existing models tackling spatial scale disparity mostly consist of adaptations of those formulated for spatially homogeneous and well mixed environments. While formulating spatial predator–prey models as extensions of non-spatial ones may be justified in some cases, an important exception arises whenever there is spatial scale disparity. In this case, the coupling of the interacting populations is far from intuitive, as it involves making important behavioural and demographic assumptions that clearly depart from the simple extensions of non-spatial models. Here we propose a hierarchical framework to develop models of predator–prey interactions with spatial scale disparity. We start by reviewing two modelling approaches that have dealt with spatial scale disparity as a means to introduce the proposed framework. We then contrast and explain the population dynamic consequences of the resulting models, and discuss them with regard to the generality of the stabilizing role of static spatial patterns in predator–prey interactions.

Models

DISPARITIES OF SPATIAL AND TEMPORAL SCALES IN PREDATOR–PREY MODELS

Two key issues in spatial predator–prey modelling are determining the appropriate spatial scale for describing both trophic interactions and individual movements, and the scaling up of behavioural and demographic processes potentially occurring at different spatial scales (Chesson 1998; Melbourne & Chesson 2005).

These two issues lie at the heart of the main assumptions of two important models dealing with predator–prey interactions involving spatial scale disparity. In the first, McLaughlin & Roughgarden (1992) formulated a Lotka–Volterra reaction–diffusion model wherein the dynamics of each population was described at different spatial scales. The predator’s higher mobility allows us to assume its spatial distribution as homogeneous at the timescale of population growth, and to consider its dynamics as resulting from the spatial

summation of local prey consumption (hereafter called ‘local functional response’). In the absence of habitat heterogeneity, the two different spatial scales defined by predator and prey mobility did not change the dynamics from the underlying non-spatial Lotka–Volterra model (McLaughlin & Roughgarden 1992). In contrast, de Roos *et al.* (1998) used Rosenzweig & MacArthur’s (1963) model as their starting point, and assumed the landscape to be composed of k patches. Their model can be written as:

$$\begin{aligned} \frac{dN_i}{dt} &= F(N_i)N_i - G(N_i)P + \text{dispersal} \\ \frac{dP}{dt} &= \frac{1}{k} \sum_{i=1}^k eG(N_i)P - \mu P \Rightarrow \frac{dP}{dt} = e\overline{G(N)}P - \mu P \end{aligned} \quad \text{eqn 1}$$

where N_i is the prey density in patch i , P is the predator density across the landscape, $F(N_i)$ is the local logistic growth rate of prey, $G(N_i)$ is the local, type II functional response, e is the energetic efficiency and μ is the predator per capita mortality rate (as noted by de Roos *et al.* 1998, including moderate prey dispersal does not change their main results). As before, the predator’s numerical response in equation 1b was the spatial average $\overline{G(N)}$ of local, type II functional responses over the predator’s spatial domain. Because $G(N_i)$ is a nonlinear function, the averaging involves Jensen’s inequality (Chesson 1998), and can be shown to be

$$\overline{G(N_i)} \approx G(\bar{N}) + \sigma_N^2 \left. \frac{\partial^2 G(N_i)}{\partial N_i^2} \right|_{\bar{N}}$$

where \bar{N} and σ_N^2 are the mean and variance of prey abundance over space. Because $G(N_i)$ is a convex function,

$$\left. \frac{\partial^2 G(N_i)}{\partial N_i^2} \right|_{\bar{N}}$$

will be negative for all values of \bar{N} . Whenever there is spatial variation in prey density ($\sigma_N^2 \neq 0$), the resulting $\overline{G(N_i)}$ would be smaller compared with the non-spatial version of the same predator–prey model. Equation 1b can thus be rewritten as:

$$\frac{dP}{dt} = \frac{ea\bar{N}}{1+ah\bar{N}}P - \left(\mu + \frac{a^2h}{(1+ah\bar{N})^3}\sigma_N^2 \right)P \quad \text{eqn 2}$$

The reduction of the predator growth rate induced by the spatial variation of prey density is the basis of the spatial scale disparity effect found by de Roos *et al.* (1998) and reported as the ‘nonlinear averaging route to stability’ (Murdoch *et al.* 2003). As shown by de Roos *et al.* (1998), equation 1 has several spatially heterogeneous attractors that coexist with the spatially homogeneous one of the non-spatial version of the same model. Spatially heterogeneous attractors involve the formation of static spatial patterns having permanently depleted patches (where predators would spend as much time as in resource-rich patches due to their invariant searching behaviour) that can stabilize both local and global cyclic dynamics.

These two modelling approaches (McLaughlin & Roughgarden 1992; de Roos *et al.* 1998) highlight the importance of the shape of the local functional response for the predicted predator–prey dynamics in cases of spatial scale disparity. Except for a linear functional response, it is not at all obvious that the resulting global functional response would have the same nonlinear shape as Holling’s (1959) functional response derived from time budgets for a single patch. Wrestling with the definition of a local functional response for a predator that forages landscape-wide, de Roos *et al.* (1998: p. 123) appealed to intuition by stating that the local nonlinear functional response

‘... rested on the assumption that the time scale of the feeding behaviour is much shorter than the time scale at which the movement of predators between different patches is taking place. Nonetheless, this latter time scale should be sufficiently short when compared to the time scales of prey growth and predator death, to assume a uniform predation pressure over the entire spatial domain.’

In the next section we propose a framework for building spatial predator–prey models that account explicitly and more rigorously for the behavioural events involved in a local functional response and its aggregation by a predator foraging over a large spatial domain.

FROM INDIVIDUAL BEHAVIOUR TO POPULATION DYNAMICS USING A HIERARCHICAL APPROACH OF BEHAVIOURAL EVENTS

The proposed approach applies singular perturbation theory (Murray 1993; Auger & Poggiale 1996) to integrate local behavioural and foraging processes. The underlying idea is that spatial scale disparity raises three nested timescales, and that successive quasi-steady-state approximations of behavioural processes at each scale will lead to the resulting model. The fastest temporal scale corresponds to the predator’s behavioural events of searching and handling prey (pursuing, capturing and consuming a food item) at a single patch. (While we follow Holling’s 1959 derivation of a local functional response based on time budgets, other physiologically based assumptions leading to the same functional response are considered later; cf. Jeschke *et al.* 2002.) At the intermediate temporal scale, predators can switch patches while searching or handling prey. Finally, the demographic events leading to the renewal of predator and prey populations takes place at the last and slower timescale. Relative to the latter temporal scale t , the proposed nested hierarchy implies a relative scaling of behavioural processes at a time t/ϵ' (where $0 < \epsilon' \ll 1$) and of interpatch movement at t/ϵ ($0 < \epsilon' \ll \epsilon \ll 1$). For the purpose of this paper, a patch is the spatial domain pertinent to prey population dynamics wherein predators exert their local predation pressure, and the system is well mixed so that individual encounters take place at random. The predator’s population dynamics occurs at a much larger spatial scale, including many patches thus defined. While, for the sake of clarity, we present the derivation for a landscape of two patches, it will be generalized to k patches (Appendix S1 in Supplementary material).

The full system serving as the starting point is:

$$\begin{cases} \frac{dN_1}{dt} = F_1(N_1) - aN_1S_1 \\ \frac{dN_2}{dt} = F_2(N_2) - aN_2S_2 \\ \frac{dS_1}{dt} = \frac{1}{\epsilon'} \left[\frac{1}{h} H_1 - aN_1S_1 \right] + \frac{1}{\epsilon} [m_{21}S_2 - m_{12}S_1] + e \frac{1}{h} H_1 - \mu S_1 \\ \frac{dS_2}{dt} = \frac{1}{\epsilon'} \left[\frac{1}{h} H_2 - aN_2S_2 \right] + \frac{1}{\epsilon} [m_{12}S_1 - m_{21}S_2] + e \frac{1}{h} H_2 - \mu S_2 \\ \frac{dH_1}{dt} = \frac{1}{\epsilon'} \left[-\frac{1}{h} H_1 + aN_1S_1 \right] + \frac{1}{\epsilon} [p_{21}H_2 - p_{12}H_1] - \mu H_1 \\ \frac{dH_2}{dt} = \frac{1}{\epsilon'} \left[\frac{1}{h} H_2 + aN_2S_2 \right] + \frac{1}{\epsilon} [p_{12}H_1 - p_{21}H_2] - \mu H_2 \end{cases} \quad \text{eqn 3}$$

where N_i , S_i , H_i are the densities of prey and those of predators searching and handling prey in patch i ; m_{ij} and p_{ij} are the movement

rates from patch i to j of predators that are either searching or handling prey; a is the prey encounter rate; $1/h$ is the switching rate between the handling and searching states; and $F_i(N_i)$ is the logistic growth of prey population in patch $i = 1, 2$ (although any nonlinear function preventing exponential growth would yield equivalent results). The brackets group the equations governing transitions at each temporal scale. Note that the predator production term ($e * 1/h * H_i$) is scaled by $1/h$ because only predators that have caught prey can convert this energy into population growth.

At the fastest behavioural timescale (scaled with ϵ'), the number of predators per patch (defined as $C_i = S_i + H_i$) is assumed to remain constant because it is driven by the slower process of predator interpatch movement (scaled with ϵ). It is then possible to reduce the behavioural subsystem of equation 3 by making a first quasi-steady-state approximation (setting the terms between brackets corresponding to ϵ' equal to zero) to obtain

$$S_i = \frac{1}{1 + ahN_i} C_i$$

and

$$H_i = \frac{ahN_i}{1 + ahN_i} C_i.$$

Using the state variables C_1 and C_2 , equation 3 is rewritten as:

$$\begin{cases} \frac{dN_1}{dt} = F_1(N_1) - \frac{aN_1}{1 + ahN_1} C_1 \\ \frac{dN_2}{dt} = F_2(N_2) - \frac{aN_2}{1 + ahN_2} C_2 \\ \frac{dC_1}{dt} = \frac{1}{\epsilon} \left[\frac{m_{21} + p_{21}ahN_2}{1 + ahN_2} C_2 - \frac{m_{12} + p_{12}ahN_1}{1 + ahN_1} C_1 \right] + e \frac{aN_1}{1 + ahN_1} C_1 - \mu C_1 \\ \frac{dC_2}{dt} = \frac{1}{\epsilon} \left[\frac{m_{12} + p_{12}ahN_1}{1 + ahN_1} C_1 - \frac{m_{21} + p_{21}ahN_2}{1 + ahN_2} C_2 \right] + e \frac{aN_2}{1 + ahN_2} C_2 - \mu C_2 \end{cases} \quad \text{eqn 4}$$

Defining $\tilde{a}_i = (m_{ij} + p_{ij}ahN_j)/(1 + ahN_i)$, the latter can be interpreted as an emergent function governing predator movement rates between patches. Finally, assuming that global predator density, P , defined as $C_1 + C_2$, is constant at the interpatch movement timescale (scaled with ϵ), a second quasi-steady-state approximation ($dC_i/dt = 0$) yields:

$$\begin{cases} \frac{dN_1}{dt} = F_1(N_1) - \frac{aN_1(m_{21} + p_{21}ahN_2)}{(m_{21} + p_{21}ahN_2)(1 + ahN_1) + (m_{12} + p_{12}ahN_1)(1 + ahN_2)} P \\ \frac{dN_2}{dt} = F_2(N_2) - \frac{aN_2(m_{12} + p_{12}ahN_1)}{(m_{21} + p_{21}ahN_2)(1 + ahN_1) + (m_{12} + p_{12}ahN_1)(1 + ahN_2)} P \\ \frac{dP}{dt} = e \left[\frac{aN_1(m_{21} + p_{21}ahN_2) + aN_2(m_{12} + p_{12}ahN_1)}{(m_{21} + p_{21}ahN_2)(1 + ahN_1) + (m_{12} + p_{12}ahN_1)(1 + ahN_2)} \right] P - \mu P \end{cases} \quad \text{eqn 5}$$

Although we made two quasi-steady-state approximations to obtain equation 5, singular perturbation theory (cf. Auger & Poggiale 1995) assures us that equation 5 has the same dynamics as equation 3 provided ϵ and ϵ' remain small ($0 < \epsilon' \ll \epsilon \ll 1$). Several features can be discerned from this general spatial foraging model (equation 5). If we assume $m_{ij} = p_{ij}$ (predators searching and handling prey switch patches at the same rate) and define predator’s patch preference

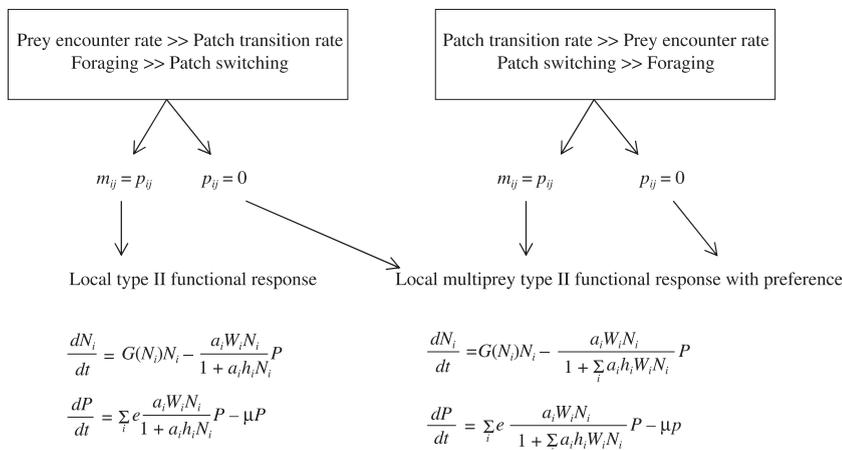


Fig. 1. Summary of the assumptions leading from the spatial foraging model (equation 5) to two limiting models depending on the relative values of prey encounter rate and patch transition rate, and on whether individuals searching and handling, or only searching, prey can switch patches. m_{ij} and p_{ij} are the movement rates from patch i to j of predators that are either searching or handling. For remaining parameters see text.

$W_i = m_{ij}/(m_{ij} + m_{ji})$ in terms of their relative movement between patches, equation 5 becomes:

$$\begin{cases} \frac{dN_1}{dt} = F_1(N_1) - \frac{W_1 a N_1}{(1 + ahN_1)} P \\ \frac{dN_2}{dt} = F_2(N_2) - \frac{W_2 a N_2}{(1 + ahN_2)} P \end{cases} \quad \text{eqn 6}$$

$$\frac{dP}{dt} = e \left[\frac{W_1 a N_1}{(1 + ahN_1)} + \frac{W_2 a N_2}{(1 + ahN_2)} \right] P - \mu P$$

By setting $W_i = W_j = 1/k = 0.5$ (predators show no patch preference), we obtain the predator-prey model with local aggregated functional responses used by de Roos *et al.* (1998). We can now identify precisely the underlying assumptions necessary to use a local type II functional response as used by de Roos *et al.* (1998): both predators searching and handling prey must switch patches at the same rate. By contrast, if we assume that predators handling prey cannot switch patches ($p_{ij} = 0$ in equation 5) and keep the W_j notation, we obtain:

$$\begin{aligned} \frac{dN_1}{dt} &= F_1(N_1) - \frac{W_1 a N_1}{(1 + W_1 ahN_1 + W_2 ahN_2)} P \\ \frac{dN_2}{dt} &= F_2(N_2) - \frac{W_2 a N_2}{(1 + W_2 ahN_1 + W_2 ahN_2)} P \\ \frac{dP}{dt} &= e \left[\frac{W_1 a N_1 + W_2 a N_2}{(1 + W_1 ahN_1 + W_2 ahN_2)} \right] P - \mu P \end{aligned} \quad \text{eqn 7}$$

The functional response in equation 7 is identical to the multi-species one with exclusive foraging and prey preference (Murdoch 1973; Gurney & Nisbet 1998), except that the different prey are replaced by a single prey species in different patches in a coarsely grained landscape.

The scaling parameters ϵ and ϵ' can also indicate the prey encounter and patch transition rates. By inverting the hierarchy of the temporal scales considered (setting the rate of movement between patches to be faster than that of prey encounter; see Appendix S2 in Supplementary material), we obtain equation 7 regardless of the values of p_{ij} . The spatial foraging model (equation 3) can be generalized to a landscape composed of k patches (Appendix S1), and the structure of the resulting model depends on the relative rates of prey encounter and patch transition, and on whether individuals searching and handling, or only searching, prey can switch patches (Fig. 1).

DOES IT MATTER?

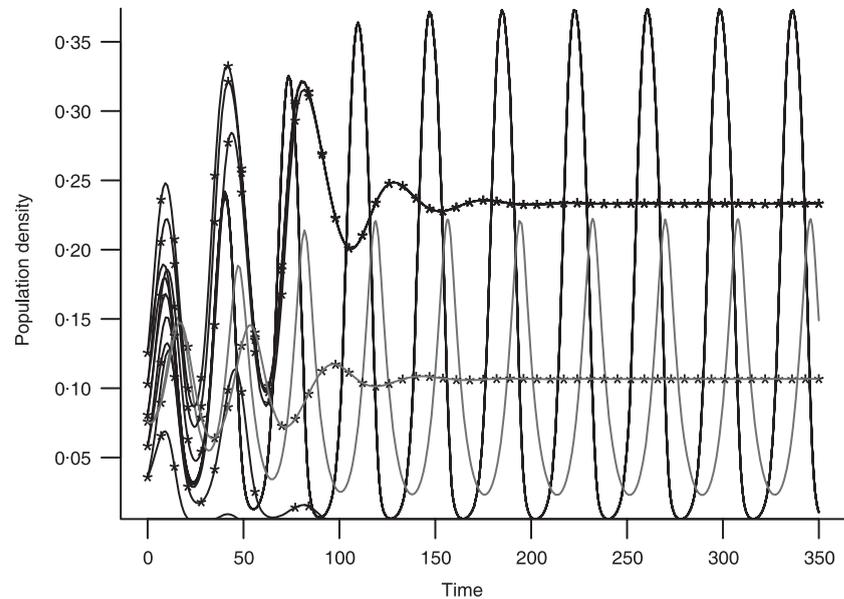
Different functional responses can be obtained depending on the relative rates of local prey encounter and of transition between patches, and on whether individuals searching and handling (equation 6) or only searching (equation 7) prey can switch patches. In comparing the spatio-temporal dynamics of equations 6 and 7, we will assume that all patches are equally attractive ($W_i = 1/k$) regardless of local prey density (as done by de Roos *et al.* 1998). Rather than repeating the detailed stability analyses of equations 6 and 7 carried out by Křivan (1996) and de Roos *et al.* (1998), we focus instead on examining the conditions under which spatial scale disparity could contribute to stabilizing predator-prey dynamics. It is important to stress that the parameters (particularly those of the functional response) of equations 6 and 7 and of their non-spatial analogue (Rosenzweig & MacArthur 1963 have the same biological meaning, thus the dynamics can be compared directly among the three models.

The multi-patch (or multi-prey) model with exclusive foraging (equation 7) can have a spatio-temporal dynamics very different from that of equation 6 (Fig. 2) for the same parameter values and initial conditions: the latter shows a stable dynamics with static spatial patterns, the former a spatially homogeneous limit cycle (Fig. 2). The dynamics of an average patch of the multi-patch model with exclusive foraging (equation 7) is identical to that of the Rosenzweig & MacArthur (1963) model for the same parameter values, regardless of the initial prey and predator abundances and their spatial distributions. This equivalence is because the local functional response $G(N_i)$ in equation 7 averaged over k patches $\bar{G}(\bar{N}_i)$ equals $\bar{G}(\bar{N})$ and thus the nonlinear averaging effect inherent in de Roos *et al.*'s (1998) model (see equation 2) cannot operate. Therefore the dynamics of equation 7 can be studied in its spatially averaged form:

$$\begin{aligned} \frac{d\bar{N}}{dt} &= r\bar{N} \left(1 - \frac{\bar{N}}{K} \right) - \frac{r}{K} \sigma_N^2 - \frac{a\bar{N}}{1 + ah\bar{N}} \bar{P} \\ \frac{d\bar{P}}{dt} &= e \frac{a\bar{N}}{1 + ah\bar{N}} \bar{P} - \mu \bar{P} \end{aligned} \quad \text{eqn 8}$$

Equation 8 is exact (it does not result from an approximation as is the case for equation 2), and is identical to the Rosenzweig & MacArthur (1963) model except for the spatial variance of prey abundance that stems from the quadratic term of the prey's logistic growth function. In the absence of strong asymmetrical prey dispersal between patches and/or strong exogenous heterogeneity (differences in local prey

Fig. 2. Comparison of the predator–prey dynamics predicted by the models of equation 6 (in the case of a spatially heterogeneous attractor) and equation 7 for a one-dimensional linear landscape of five identical patches with reflecting boundary condition, and for the same parameter values and initial conditions. Grey curves, prey densities of each patch for equation 7 (plain line) and equation 6 (plain line with cross). Black curves, predator densities per patch for equation 7 (plain line) and equation 6 (plain line with cross). Values for parameters and initial conditions are identical to those used by de Roos *et al.* (1998) ($a = 6$; $h = 1$; $\mu = 0.175$; $e = 0.5$; $r = 0.5$; $K = 0.5$).



growth rates or in the accessibility of prey, etc.), there should be no reason for σ_N^2 to be different from zero. This is why the disparity of spatial scales between predators and prey in equation 7 does not induce any departure from the dynamics predicted by the Rosenzweig & MacArthur (1963) model. Therefore the disparity of spatial scales would only have a stabilizing effect (equation 6) through the nonlinear averaging of local, type II functional responses that weakens the trophic coupling and decreases the predator's growth rate (equation 2).

Aside from the mathematical justification, we think it is easy to understand why equation 7 does not show spatio-temporal dynamics similar to that of equation 6. The stabilization in equation 6 is induced by a decrease in the overall prey capture rates that results from individual predators spending as much time in depleted as in resource-rich patches (de Roos *et al.* 1998). However, when the patch-switching timescale is slower than the foraging behaviour one (equation with $\epsilon' \ll \epsilon$), assuming that predators handling prey did not redistribute between patches ($p_{ij} = 0$) makes the predator departure rate proportional to $1/(1 + ahN)_i$ (see equation 4 and γ_i). Whenever predators tend to leave patches depleted of prey, this behaviour would hinder the formation of spatial patterns and their associated role in stabilizing the predator–prey dynamics.

Discussion

Modelling predator–prey interactions when there is disparity in the spatial scales between consumers and resources requires making specific assumptions about the spatial extent and rates of movement of the interacting species, and how local foraging relates to predator numerical response and its demographic renewal at larger spatial and temporal scales. We have proposed a framework that allows us to solve these issues rigorously by explicitly integrating the behavioural and demographic processes occurring at different spatial and temporal scales. Our analyses and findings lead us to highlight three main issues in spatial predator–prey models.

THE MECHANISTIC BASIS OF THE STABILIZING ROLE OF SPACE IN PREDATOR–PREY MODELS WITH SPATIAL SCALE DISPARITY

de Roos *et al.* (1998) promoted the idea that highly mobile predators with a saturating local functional response would stabilize predator–prey dynamics through the appearance of static spatial patterns (de Roos *et al.* 1998; Murdoch *et al.* 2003; Briggs & Hoopes 2004; Van de Koppel *et al.* 2005; Hosseini 2006). Nevertheless, we have shown that the local, nonlinear functional response used by de Roos *et al.*'s (1998) model holds under the biologically restrictive assumptions that predators searching and handling prey must switch patches at the same rate, and that prey encounter rate is higher than patch transition rate. In our view, these findings should call into question the generality that the formation of static spatial patterns is a general mechanism leading to the stabilization of spatial predator–prey interactions. The framework used here can help us to examine the circumstances for the emergence of static spatial patterns and their role in stabilizing predator–prey dynamics.

The local type II (equation 6) and multi-patch (equation 7) functional responses can describe the foraging events involved in predator–prey interactions involving spatial scale disparity. For instance, predators having a central-place foraging strategy and consuming relatively large-sized prey would be constrained to handle and subdue them at their capture site in order to bring them to the breeding site (Orians & Pearson 1979). Their foraging dynamics would be best described by a multi-patch functional response (equation 7). If central-place foragers catch a prey and bring it directly to their breeding site, they tend to return to the site of the last prey capture as long as prey is available there (following a return function inversely related to local prey abundance; see equation 4 and γ_i); their foraging dynamics would also be best

described by the multi-patch functional response (equation 7). Effectively, everything happens as if predators could not change patches when handling prey (including travelling and feeding young, in this case). On the other hand, if predators that are handling prey can switch patches using the same criteria as those that are searching prey, their dynamics would be best described by the local type II functional response model (equation 6). Note that the latter conclusion changes whenever the rate of interpatch movements is faster than that of behavioural transitions (Appendix S2).

The derivations of the local functional responses based on the time-budget considerations (Holling 1959) can be generalized to other mechanisms leading to saturation, such as constraints on ingestion capacity (Jeschke *et al.* 2002; Whelan & Brown 2005). Herbivores (both grazers and browsers) are constrained either by the rate at which food resources can be cropped, or by the rate at which food can be processed (Spalinger & Hobbs 1992), the latter being a function of both plant spacing and herbivore mobility (Hobbs *et al.* 2003; Fortin 2006). Plant–herbivore interactions may correspond to either predation model, depending on whether herbivores are mobile and not limited by the digestion time or capacity (equation 6), or are limited by the digestion capacity or transit time and have to have restricted mobility while digesting (equation 7).

INTUITIVE REASONING FROM FORAGING THEORY AND SPATIAL PREDATION MODELS

de Roos *et al.* (1998) appealed to intuition to obtain a local type II functional response for predators that forage and subdue prey in a patch, and subsequently move on to other patches. Our results show that this is not necessarily the case, as the same scenario can lead to the multi-patch functional response (equation 7). Viewing ϵ and ϵ' , used in this paper as scaling parameters that order the relative magnitudes of the rates of prey encounter and of transition between patches, makes it possible to review the link between models of the optimal foraging theory (Stephens & Krebs 1986) and of predator–prey interactions. Whenever prey encounter frequency was greater than the transition rates between patches (due to limited predator mobility relative to patch size, interpatch distances or prey abundance), predator foraging would intuitively correspond to a local type II functional response (equation 8). This first case corresponds to the ‘patch model’ in optimal foraging theory, which addresses the question of the optimal length of stay in a patch (Stephens & Krebs 1986). However, if the transition rates between patches were higher than prey encounter frequencies, predator foraging would intuitively correspond to the multi-patch functional response (equation 7). This second case corresponds to the ‘prey model’ in optimal foraging theory, which addresses the question of the optimal diet composition (Stephens & Krebs 1986) that, in our context, can be interpreted as the optimal habitat use. We have shown that these intuitive ideas (recalled and used for instance by van Baalen *et al.* 2001) can be misleading, as whenever predators handling prey do not switch patches,

their foraging is always characterized by the multi-patch functional response (equation 7) regardless of the relative magnitudes of prey encounter and patch transition rates.

GENERALITY AND ROBUSTNESS OF THE RESULTS

We have focused in this paper on the population dynamics consequences of spatial scale disparity in an otherwise well mixed and spatially homogeneous habitat. The current framework and modelling results (cf. de Roos *et al.* 1998) should be viewed as reference to assess the (de)stabilizing influence of other aspects of foraging behaviour and of realistic sources of exogenous spatial heterogeneity. Concerning the latter, local differences in prey growth or in prey susceptibility to predation [expressed as the parameters of local prey growth, $F(N_i)$ and attack rates, a_i in equations 6 and 7] would enhance the occurrence of static spatial patterns in the model of equation 6 and hence of the nonlinear averaging effects (de Roos *et al.* 1998). Our preliminary simulations suggest that exogenous spatial heterogeneity has hardly any effect on the dynamics predicted by equation 7 (data not shown). Regarding endogenous heterogeneity, strong density-dependent prey dispersal could generate spatial variation ($\sigma_N^2 > 0$ in equations 2 and 8) in prey abundance. In the case of equation 7, strong density-dependent prey dispersal would only affect the logistic growth of the prey but, in the case of equation 6 it would enhance the nonlinear averaging effects discussed in equation 2.

The stabilizing effect found for equation 6 and in de Roos *et al.* (1998) was essentially due to predators’ patch-residence times being independent of local prey abundance. While the latter may seem a non-adaptive or unrealistic consequence of model assumptions, it may be feasible for cryptic prey and/or structurally complex habitats where prey detection is uncertain. If predators can adapt their foraging behaviour by moving to patches with prey only, and/or by leaving early prey-depleted patches (as in equation 4), this would prevent patch depletion, which in turn should decrease the tendency of static spatial patterns to stabilize the global dynamics. Note that the directed movement in equation 4 (γ_i) is an emergent property resulting from the behavioural events (predators handling prey do shift patches, but those searching prey can choose patches randomly) embodied in the functional response at the population dynamics timescale. Although more recent work (Křivan & Eisner 2003; Abrams & Matsuda 2004) on adaptive foraging strategies involving dynamic and adjustable preferences may have a substantial effect, the general implications of dynamic foraging strategies for predator–prey dynamics remain to be understood.

As indicated by Turing (1952), a nonlinear interaction and a difference in spatial scale of prey and predator behaviour gave rise to the spatial patterns. As the characteristic scale of population distribution patterns is much larger than the size of its constituents (interacting individuals), there is no need to include a detailed description of individual units. This has resulted in the belief that predator–prey dynamics with spatial scale disparity was particularly prone to pattern formations (cf. Solé & Bascompte 2006). Relying on the expected generality

of the phenomena, the existing predator–prey models tackling this issue consist mostly of adaptations of those formulated for spatially homogeneous and well mixed environments. An immediate consequence of this use of intuition is that their validity is presented without recourse to rigorous, deductive reasoning that allows examination of the underlying assumptions and understanding of their implications. The hierarchical framework used in this paper allows us to consider the behavioural processes that, when integrated in a functional response formulated on a population dynamics timescale, allow coupling of the dynamics of predator and prey populations despite the spatial scale disparity. Our results show the dramatic influence that individual behaviour may have on population dynamics (Fig. 2). We thus hope that this paper serves as an invitation to experimental and field biologists to investigate carefully how the tendency to switch patches relates to foraging success, and to theoreticians to integrate behavioural events at the population dynamics timescale, as the basis for formulating more rigorous, robust and realistic models of consumer–resource dynamics.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Generalization of equations 7 and 8 to the k patches case

Appendix S2. Consequences of inverting the relative rates of behavioral transitions and patch switching

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.1419.x>

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