Space race functional responses

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We derive functional responses under the assumption that predators and prey are engaged in a space race in which prey avoid patches with many predators and predators avoid patches with few or no prey. The resulting functional response models have a simple structure and include functions describing how the emigration of prey and predators depend on interspecific densities. As such, they provide a link between dispersal behaviours and community dynamics. The derived functional response is general but is here modelled in accordance with empirically documented emigration responses. We find that the prey emigration response to predators has stabilizing effects similar to that of the DeAngelis–Beddington functional response, and that the predator emigration response to prey has destabilizing effects similar to that of the Holling type II response. A stability criterion describing the net effect of the two emigration responses on a Lotka–Volterra predator–prey system is presented. The winner of the space race (i.e. whether predators or prey are favoured) is determined by the relationship between the slopes of the species’ emigration responses. It is predicted that predators win the space race in poor habitats, where predator and prey densities are low, and that prey are more successful in richer habitats.

1. Introduction

Functional responses are essential components of dynamic food-web models, describing the rates at which prey are consumed by predators. Classical functional responses describe the population-level consumption rates emerging from the behaviours of randomly moving predators foraging in evenly or randomly distributed prey populations [1,2]. These assumptions are rarely fulfilled in natural systems, because predators and prey typically have clumped spatial distributions [3–5] that are spatially correlated as a consequence of density-dependent processes such as birth, death and dispersal, and exogenous features such as physical habitat structures [4]. To better describe predator–prey interactions, it is important to elucidate relationships between spatial geometries of food-webs, underlying processes and corresponding nonlinearities in birth and death rates [6–8].

A common observation among mobile organisms which select habitats in response to the densities of predators, competitors and prey is that prey avoid predator-rich areas, while predators prefer prey-rich areas [9–12]. This conflict of interest leads to a spatial game that has been termed a space race [13]. Space races between predators and prey are dominant drivers of small-scale spatial distributions [14], and have significant effects on predator–prey encounter rates [15]. Although the importance of space races is widely recognized, it remains unclear how they affect functional responses. Studies on how functional responses change in spatial settings have investigated specific non-random spatial distributions of predators or prey (e.g. [16,17]) or the effects of other movement behaviours such as refuge use by prey [18–20], central-place foraging [3,21] or aggregation of predators in areas of high resource density [17,22,23]. Many of these mechanisms produce nonlinearities in consumption rates similar to those of the well-known Holling and DeAngelis–Beddington responses.

In this paper, we investigate the relationship between consumption rates and the densities of predators and prey that are engaged in a space race. This relationship is governed by the ‘within-community’ spatial structure generated by space race processes. The space race considered here is fairly simple in the sense that it
Figure 1. A representation of the link between reaction efficiencies and the outcome of the space race. (a) The space race sign $S$, given by equation (4.1), determines the outcome of the game. The thick line at $S = 0$ divides the plane into a positive region (light shade) where the predator wins, and a negative region (dark shade) where the prey wins. As an example, the open circle marks a point where the predator wins $(N_1, P_1)$, and the closed circle a point where the prey wins $(N_2, P_2)$. The positions of these points along the emigration responses are shown in (b). In the $(N_1, P_1)$ case, the predator wins because it has a higher reaction efficiency (i.e. the predator’s emigration response is steeper). The opposite is true in the second case $(N_2, P_2)$. The emigration responses are $E_P(N) = 1 + e^{-\theta N}$ and $E_N(P) = 1 + 20e^{-\theta P}$, where $\theta = 0.5$.

concerns only movements in response to densities of heterospecifics and does not involve reactions to conspecifics, the prey’s resources or other environmental factors. Our analyses are based on an approximation of the spatial covariance between predators and prey, which was derived in [15]. We show how empirically documented emigration responses give rise to a new nonlinear functional response which we compare with the Holling type II and DeAngelis–Beddington responses. Furthermore, we give analytical conditions under which the stabilizing/destabilizing influences of these classical functional responses coincide with our new functional response. Additionally, we derive a simple criterion which determines the winner of the space race between prey and predator.

2. Model description

We consider a predatory species and a prey species which are distributed among and moving between a large number of patches that are equal in all features except for the numbers of predators and prey. To account for the intrinsically random nature of ecological interactions, we assume that the number of individuals in each patch is small and finite. Here and throughout, we write $X_n$ and $X_p$ for the actual numbers of prey and predators in a patch, and $N = \langle X_n \rangle$ and $P = \langle X_p \rangle$ for the corresponding average (expected) numbers. The former are random variables, taking any integer values $x_n$ and $x_p$ respectively, while the latter are customary population densities (i.e. the number of individuals averaged over all patches). The number of individuals in a patch changes over time due to births, deaths and interpatch dispersal.

We assume that individuals in any given patch have information about the number of predators or prey within that patch, and that they use this information to varying degrees when deciding whether to leave or stay. The rate at which a predator (prey) individual leaves a patch is thus a function of the number of prey (predators) in that patch (figure 1). We denote by $E_P(X_n)$ and $E_N(X_p)$ the predator’s and prey’s respective emigration rate functions.

Movements associated with predator avoidance and prey search are daily activities for most mobile organisms. We can therefore assume that dispersal events take place much more often than births and deaths, which enables separation of time scales. That is to say, we can assume that a steady-state distribution of predators and prey is reached in the time period between successive birth or mortality events. Reactive movement thus generates a distribution of individuals among patches, $D(x_n, x_p, t)$, in which all features except the average number of predators and prey depend exclusively on dispersal processes.

We assume that the rate at which predators encounter prey within a patch is governed by the law of mass action, $G(X_n, X_p) = \alpha_e X_n X_p$, where $\alpha_e$ is the corresponding per capita encounter rate. If prey and predators are randomly distributed among patches, then the population-level encounter rate would be $\alpha_e N P$. In the following section, we show how density-dependent movements and the resulting spatial correlations between predator and prey alter the rate of predator–prey encounters and thus the functional response.

3. Emergent population-level encounter rates

The density-dependent (state-dependent) emigration processes given by $E_N(X_n)$ and $E_P(X_p)$ give rise to a population-level encounter rate

$$g(N, P) = \alpha_e N P (1 + C(N, P)),$$

where $C(N, P) = \text{cov}(X_n, X_p)/(NP)$ is a standardized covariance that we refer to as the per capita covariance and which corrects the ‘well-mixed’ encounter rate for density-dependent
movements [15,24,25]. Dividing equation (3.1) by $P$ gives the rate at which individual predators encounter prey, which is conventionally referred to as the ‘encounter rate’.

We can hope to find an exact analytical expression for $C(N, P)$ only in cases where an analytical expression for the distribution $D(x_P, x_p, t)$ is achievable. An approximation of the per capita covariance in the form

$$C(N, P) \approx \frac{E_g(P) + E_p(N)}{E_{a}(P) + E_{p}(N)}$$

(3.2)

was derived in [15], where $E_{a}(P)$ and $E_{p}(N)$ are the contributions to the population-level covariance from the microscopic emigration processes $E_{a}(X_P)$ and $E_{p}(X_p)$, and where prime denotes the derivative with respect to the corresponding dependent variable. This approximation becomes accurate when the degree of density dependence, $\theta$, in $E_{a}(P)$ and $E_{p}(N)$ is weak and the densities are not very small. Technically, the approximation becomes exact as $\theta$ tends to zero provided that $N$ or $P$ do not approach zero [15].

We adopt this approximation and substitute it into equation (3.1) to investigate the functional responses that emerge from density-dependent movements.

4. Emigration responses and their relationship with space races

Empirical data show that predators have decreasing and decelerating emigration responses to prey, whereas prey typically have increasing and accelerating emigration responses to predators (figure 1b; electronic supplementary material, figure S6) [15].

The slope of the emigration rate function determines an individual’s ability to respond to differences in the local densities of the species it reacts to. The steepness of the response functions can thus be interpreted as a measure of how strongly prey react to differences in predator densities, and how strongly predators react to variation in prey densities. We refer to this as the species’ reaction efficiency. If the prey has a higher reaction efficiency than the predator, the covariance will be negative and the average predator individual will experience fewer prey than expected based on the overall mean density of prey. In this sense, the prey wins the space race. If it is the other way around, the average predator will encounter more prey individuals than would be expected based on the overall mean density of prey. In this sense, the prey wins the space race. If it is the other way around, the average predator will encounter more prey individuals than would be expected based on the overall mean density of prey. In this sense, the prey wins the space race. (ii) If instead the prey has an accelerating response towards linearity at higher prey densities. This type of density-independent prey emigration produce a nonlinear case. (i) Decelerating predator emigration and density-independent prey emigration produce a nonlinear prey-dependent functional response (figure 2b). The consumption rate is initially decelerating but converges back towards linearity at higher prey densities. This type of density dependence has destabilizing effects (e.g. [5,15]). Also, the consumption rate is higher than expected if movements are random, which reflects that the predator is winning the space race. (ii) If instead the prey has an accelerating response and predator emigration is density independent, the result is a predator-dependent type of functional response where the nonlinearity occurs in the predator dimension (figure 2c). The consumption rate decreases with increasing predator density, which tends to stabilize predator-prey dynamics (e.g. [5,15]). Also, the consumption rate is lower than predicted if movements are random, which reflects that the prey is winning the space race. (iii) When there is a predator-prey space race where both species move independently on each other, the functional response is nonlinear in both species dimensions (figure 2d). This has either stabilizing or destabilizing effects on predator-prey dynamics depending on which of the two dynamical effects is strongest (i.e. mainly on the magnitudes of reaction efficiencies and the changes in reaction efficiencies with densities).

5. Space race functional responses

By defining the attack rate $a = a_c a_w a_t$, where $a_c$ is the rate at which a predator tries to capture a prey individual upon encounter and $a_w$ is the rate at which it succeeds and consumes the prey, we find that the space race functional response is equal to the encounter rate (equation (3.1)) multiplied by $a_c a_w / P$:

$$f(N, P) = aN(1 + C(N, P))$$

(5.1)

The space race functional response, where $C(N, P)$ is substituted by equation (3.2), is illustrated in figure 2. The predator emigration rate response $E_p(N)$ to prey affects the functional response in the prey dimension, whereas the prey emigration rate response $E_p(N)$ affects the functional response in the predator dimension (figure 2).

Given density-independent emigration responses, we recover the typical linear Holling type I functional response (figure 2a). However, if either of the species emigrates in response to the other, nonlinearities emerge.

If we limit the analysis to emigration responses of the types observed in empirical studies, we can identify three nonlinear cases. (i) Decelerating predator emigration and density-independent prey emigration produce a nonlinear prey-dependent functional response (figure 2b). The consumption rate is initially decelerating but converges back towards linearity at higher prey densities. This type of density dependence has destabilizing effects (e.g. [5,15]). Also, the consumption rate is higher than expected if movements are random, which reflects that the predator is winning the space race. (ii) If instead the prey has an accelerating response and predator emigration is density independent, the result is a predator-dependent type of functional response where the nonlinearity occurs in the predator dimension (figure 2c). The consumption rate decreases with increasing predator density, which tends to stabilize predator-prey dynamics (e.g. [5,15]). Also, the consumption rate is lower than predicted if movements are random, which reflects that the prey is winning the space race. (iii) When there is a predator-prey space race where both species move independently on each other, the functional response is nonlinear in both species dimensions (figure 2d). This has either stabilizing or destabilizing effects on predator-prey dynamics depending on which of the two dynamical effects is strongest (i.e. mainly on the magnitudes of reaction efficiencies and the changes in reaction efficiencies with densities).
The convergence towards a linear consumption rate at high prey densities (figure 2b,d) corresponds to a decelerating predator emigration response to prey (figure 1b). As prey become more abundant, the predators’ reaction efficiency approaches zero and their dispersal behaviour becomes increasingly random, resulting in a negative and nearly constant per capita covariance in the prey dimension. Decelerating predator emigration responses to prey are observed in experiments. This is probably because predators gain little in these experiments when most sites hold more prey than they can handle.

6. Predator–prey dynamics with a space race functional response

Whether the dynamics of a predator–prey system with a space race functional response is stable will in general depend also on other processes such as prey growth and predator mortality. However, for a multi-patch system where the dynamics within each patch are described by the Lotka–Volterra predator–prey equation, the stability of the global dynamics (including all patches) for a given fixed point \((N^*, P^*)\) is influenced only by the properties of the per capita covariance and the conversion efficiency \(\eta\). The fixed point is a stable attractor if both

\[
\delta = 1 + C(N^*, P^*) + N^* \frac{\partial C(N, P^*)}{\partial N} \big|_{N=N^*} + P^* \frac{\partial C(N^*, P)}{\partial P} \big|_{P=P^*}
\]

and

\[
\tau = \frac{\partial C(N^*, P^*)}{\partial N} \big|_{N=N^*} - \eta \frac{\partial C(N^*, P)}{\partial P} \big|_{P=P^*}
\]

are greater than zero. When applying the approximation of the per capita covariance (equation (3.2)), \(\delta > 0\) is always true, which means that stability hinges only on the sign of \(\tau\). If then \(\tau < 0\), the fixed point, typically at low equilibrium densities, constitutes an unstable equilibrium producing unstable

Figure 2. Space race functional responses. Dashed lines indicate the Holling type I functional response. (a) The consumption rate when both species move independently of each other. (b) The consumption rate when the predator species has a decelerating emigration response to prey. (c) The consumption rate when the prey species has an accelerating emigration response to predators. (d) The consumption rate when the prey species has an accelerating emigration response to predators and the predator species has a decelerating emigration response to prey; these are the emigration responses typically observed in nature. The attack rate is set to \(\alpha = 1\) and the emigration responses of prey and predators are \(E_n(P) = 1 + e^{\theta P}\) and \(E_p(N) = 1 + 20e^{-\theta N}\), respectively, where \(\theta = 0.5\). The functional responses are in qualitative agreement with the exact functional responses obtained from numerical analysis (electronic supplementary material, figure S2).
dynamics that tend to attract to limit cycles around the fixed point at an average distance that depends on the shape of \( C(N, P) \) (electronic supplementary material, figures S3–S5) [15].

7. Relationships with classical functional responses

The density dependencies produced by the exponential movement responses are qualitatively equivalent to those in Holling’s type II and DeAngelis–Beddington’s functional responses. The predators’ decelerating emigration response to prey causes predation efficiency to decrease as prey density increases. This creates a positive and destabilizing density dependence comparable to that described by the Holling type II functional response, although the underlying mechanism is different. By contrast, the prey’s accelerating emigration response leads to stabilizing density dependence, as the prey density experienced by the predators decreases with increasing predator density. This mechanism is analogous to the one proposed by Geritz & Gyllenberg [20] as a mechanistic underpinning for the DeAngelis–Beddington functional response.

To investigate the generality of these findings, we identify the conditions under which the space race functional response produces the same types of density dependencies as Holling’s and DeAngelis–Beddington’s responses. This occurs if the expected capita population-level attack rate, or predation efficiency, \( \hat{f}(N, P) = f(N, P)/N \) decreases in parallel with the densities of the two species such that \( \partial \hat{f} / \partial N < 0 \) and \( \partial \hat{f} / \partial P < 0 \). Since \( f(N, P) = \alpha(1 + C(N, P)) \), we can reduce the problem to an examination of how \( C(N, P) \) changes with the two species’ densities. This reveals that if

\[
C(N, P) < -\frac{E_p^R(N)}{E_p^T(N)} \tag{7.1}
\]

is true for positive values of \( N \) and \( P \), the predators’ emigration behaviour produces a density dependence equivalent to that in the Holling type II functional response, and if

\[
C(N, P) > -\frac{E_p^R(P)}{E_p^T(P)} \tag{7.2}
\]

is true for positive values of \( N \) and \( P \), then the prey emigration behaviour produces a density dependence equivalent to that in the predator-dependent processes of the DeAngelis–Beddington functional response.

In general, these criteria are fulfilled if the accelerating prey response and the decelerating predator response are represented by exponential functions or power functions. The only exception is when the prey emigration response follows a power function. In this case, there is a parameter space for which low predator densities produce the same type of density dependence as in DeAngelis–Beddington’s response but higher prey densities generate a reversed density dependence.

8. Discussion

In a predator–prey system where the two species are engaged in a space race, the functional response is a nonlinear function of both prey and predator densities and is conventionally described as being predator dependent. The shape of the two-dimensional functional response reflects the emigration responses of predators and prey to heterospecific densities. The emigration responses can in theory take many different shapes and thus produce different types of density dependencies. However, empirical data suggest that prey emigration responses to predators are increasing and accelerating functions, whereas predator emigration responses to prey are decreasing and decelerating functions. These responses create a destabilizing density dependence in the prey dimension and, in most cases, a stabilizing density dependence in the predator dimension.

In equivalence with the Holling type II functional response, the destabilizing effect in the space race functional response occurs because the prey capita growth rate is an increasing function of prey density (i.e. it exhibits a positive density dependence). In Holling’s type II model, this positive density dependence is due to the time required to handle and digest prey, which leads to saturation and thus a decreased predation efficiency at high prey densities. In the space race functional response, this type of destabilizing density dependence is instead a consequence of the decelerating emigration response of predators, \( E_p(N) \). The predation efficiency decreases with increasing prey density, because the predators put less effort into finding the best foraging patches when prey is abundant. By contrast, when prey is scarce predators do differentiate between patches and therefore become more efficient in locating prey.

In equivalence with the DeAngelis–Beddington functional response, the stabilizing effects in the space race functional response are caused by reduced predation efficiencies at high predator densities (i.e. predator growth exhibits a negative dependence on predator density). However, the mechanism in the space race functional response is different from that proposed by Geritz & Gyllenberg [20] for the DeAngelis–Beddington response, in the sense that predators do not induce increased refuge use by prey but instead prey escape from predator-rich areas. While these mechanisms are somewhat different, they can both be described as examples of predator interference.

An intriguing result of our analysis is that the covariance between predator and prey densities is expected to decrease with increasing densities of both species. Stated differently, we should expect low spatial overlap between predators and prey in rich habitats and high overlap in poor habitats; a prediction that should be testable in laboratory and field experiments. This finding has important implications for the stability and persistence of predator–prey systems. If some external factor reduces the equilibrium densities of predators and prey, the space race will cause increased predation rate, thereby further reducing prey equilibrium densities. For some models, like the Lotka–Volterra predator–prey model, the equilibrium densities of predators will also be reduced. This suggests that the space race increases extinction risk in poor habitats due to demographic and environmental stochasticity. Perhaps more important is the finding that a Lotka–Volterra system with space race functional response tends to show limit cycles when equilibrium densities are low. This means that predator–prey systems in poor habitats, where equilibrium densities are low, at times will reach very low densities and consequently have greatly increased risk of stochastic extinctions. An implication of this result is that models based on local-scale functional responses, which neglect the influence of density-dependent movements, might underestimate the risk of extinction for populations of conservation concern.
Density-dependent dispersal appears to be common among systems of mobile organisms; empirical data suggest that prey typically have accelerating emigration responses to predator density, whereas predators show decelerating responses (without significant convex regions) to prey. The two types of density dependence produced by these responses typically have opposing effects on stability (electronic supplementary material) [15]. It is therefore impossible to precisely predict how space races affect stability based on this information alone. To make robust predictions, we will need more specific information on the relationship between the emigration responses of both species in coupled predator–prey systems; to the best of our knowledge, such data are not currently available.

Future studies may extend the basic space race considered here to include additional emigration cues and spatial heterogeneity in physical variables that influence predation risk and food intake (e.g. [13,14,26]). It would also be valuable to know how the strengths of the density dependencies produced by space races relate to those generated by other mechanisms, such as handling time and refuge use. Such studies will probably be valuable contributions to our understanding of the mechanism controlling persistence of food webs in ecological systems.

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