Space race functional responses

Henrik Sjödin^{1,2,*}, Åke Brännström^{2,3} and Göran Englund^{1}

^{1}*Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden*
^{2}*Evolution and Ecology Program, International Institute for Applied Systems Analysis, 2361 Laxenburg, Austria*
^{3}*Department of Mathematics and Mathematical Statistics, Umeå University, 90187 Umeå, Sweden*

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.

Keywords: functional response; dispersal behaviours; space race; community dynamics

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[*] Author for correspondence (sjodin.h@gmail.com)

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, 4, 5] that are spatially correlated as 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 non-linearities in birth and death rates [6, 7, 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, 10, 11, 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 are 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, 19, 20], central-place foraging [3, 21], or aggregation of predators in areas of high resource density [17, 22, 23]. Many of these mechanisms produce non-linearities 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 concerns only movements in response to densities of heterospecifics, and do 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 non-linear functional response which we compare with the Holling type II and DeAngelis-Beddington responses. Furthermore, we give analytical conditions under which the stabilising/destabilising 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.

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 $N = \langle X_{\mathrm{n}} \rangle$ and $P = \langle X_{\mathrm{p}} \rangle$ 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 $E_{\mathrm{p}}\left(X_{\mathrm{n}}\right)$ and $E_{\mathrm{n}}\left(X_{\mathrm{p}}\right)$ 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 timescales. 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, $D(x_{\mathrm{n}}, x_{\mathrm{p}}, t)$, in which all features except the average numbers 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, $G(X_{\mathrm{n}}, X_{\mathrm{p}}) = \alpha_{\mathrm{e}} X_{\mathrm{n}} X_{\mathrm{p}}$, where α_{e} is the corresponding per capita encounter rate. If prey and predators are randomly distributed among patches, the population-level encounter rate would be $\alpha_{\mathrm{e}} N P$. 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.

EMERGENT POPULATION-LEVEL ENCOUNTER RATES

The density-dependent (state-dependent) emigration processes given by $E_{\mathrm{n}}\left(X_{\mathrm{p}}\right)$ and $E_{\mathrm{p}}\left(X_{\mathrm{n}}\right)$ give rise to a population-level encounter rate

$$g(N,P) = \alpha_{\mathrm{e}} NP\left(1 + C(N,P)\right), \tag{1}$$

where $C(N,P) = \mathrm{cov}(X_{\mathrm{n}}, X_{\mathrm{p}})/(NP)$ is a standardised covariance that we refer to as the per capita covariance and which corrects the "well-mixed" encounter rate for density-dependent movements [electronic supplementary material; see also 24, 25, 15]. Dividing equation (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 $D(x_{\mathrm{n}}, x_{\mathrm{p}}, t)$ is achievable. An approximation of the per capita covariance in the form

$$C(N,P) \approx -\frac{E'_{\mathrm{n}}\left(P\right) + E'_{\mathrm{p}}\left(N\right)}{E_{\mathrm{n}}\left(P\right) + E_{\mathrm{p}}\left(N\right)}, \tag{2}$$

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

We adopt this approximation and substitute it into equation (1) to investigate the functional responses that emerge from density-dependent movements.

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].

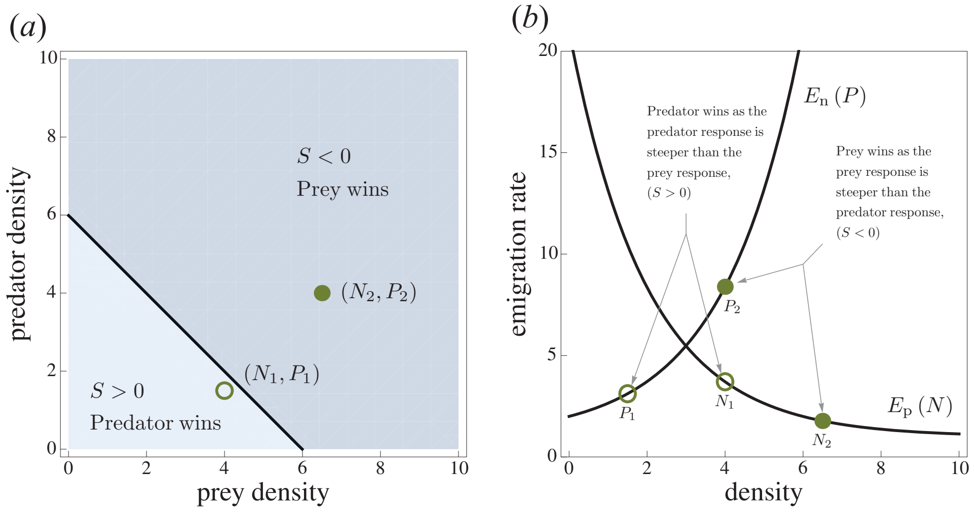

Figure 1: A representation of the link between reaction efficiencies and the outcome of the space race. (*a*) The space race sign S, given by eq. (3), determines the outcome of the game. The thick line at $S = 0$ divides the plane into a positive region (bright) where the predator wins, and a negative region (dark) 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 $E_{\mathrm{n}}(P) = 1 + e^{\theta P}$ and $E_{\mathrm{p}}(N) = 1 + 20e^{-\theta N}$, where $\theta = 0.5$.

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 mean prey density and so the predator becomes the winner of the space race [15].

Consequently, it is the difference between the reaction efficiencies of the prey and the predator that determines which of the two species wins the space race. This can be expressed by the simple formula

$$S = -E_{\mathrm{n}}'(P) - E_{\mathrm{p}}'(N)\,, \tag{3}$$

which is derived from eq. (2). S is thus approximative. However, a numerical analysis of the underpinning master equation [15] indicates that S is in good agreement with the exact relationship even for relatively large values of θ (electronic supplementary material, figure S1).

The interplay of the "space race sign" S and the emigration responses is depicted in figure 1. If S is positive, the predator is the winner and if it is negative the prey is the winner (figure 1a). When $S = 0$, which is indicated by the diagonal line in figure 1a, neither species wins and the spatial correlation between the two species remains zero. This line thus represents the situation described by classical functional response models, which assume density independent and unlimited dispersal. As shown in figure 1b, the space race sign originates from the relationship between the steepness of the two species' emigration responses.

Figure 1 also shows that predators win the space race when both species are rare and that instead prey win when both species are abundant. Stated differently, we can expect positive spatial correlations between predators and prey in poor habitats and negative correlations in rich habitats.

Since the emigration responses have direct effects on the likelihood of encounters between predators and prey, they necessarily affect consumption rates. This link is analyzed in the following section.

SPACE RACE FUNCTIONAL RESPONSES

By defining the attack rate $\alpha = \alpha_{\mathrm{e}}\alpha_{\mathrm{c}}\alpha_{\mathrm{s}}$, where α_{c} is the rate at which a predator tries to capture a prey individual upon encounter and α_{s} 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 (eq. 1) multiplied by $\alpha_{\mathrm{c}}\alpha_{\mathrm{s}}/P$, i.e.,

$$f(N, P) = \alpha N \left(1 + C(N, P)\right). \tag{4}$$

The space race functional response, where $C(N, P)$ is substituted by equation (2), is illustrated in figure 2. The predator emigration rate response $E_{\mathrm{p}}\left(N\right)$ to prey affects the functional response in the prey dimension, whereas the prey emigration rate response $E_{\mathrm{n}}\left(P\right)$ 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, non-linearities emerge.

If we limit the analysis to emigration responses of the types observed in empirical studies, we can identify three non-linear cases: (i) Decelerating predator emigration and density-independent prey emigration produce a non-linear 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 destabilising 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 non-linearity occurs in the predator dimension (figure 2c). The consumption rate decreases with increasing predator density, which tends to stabilise 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 dependently of each other, the functional response is non-linear in both species dimensions (figure 2d). This has either stabilising or destabilising 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 (figures 2b, 2d) corresponds to a decelerating predator emigration response to prey

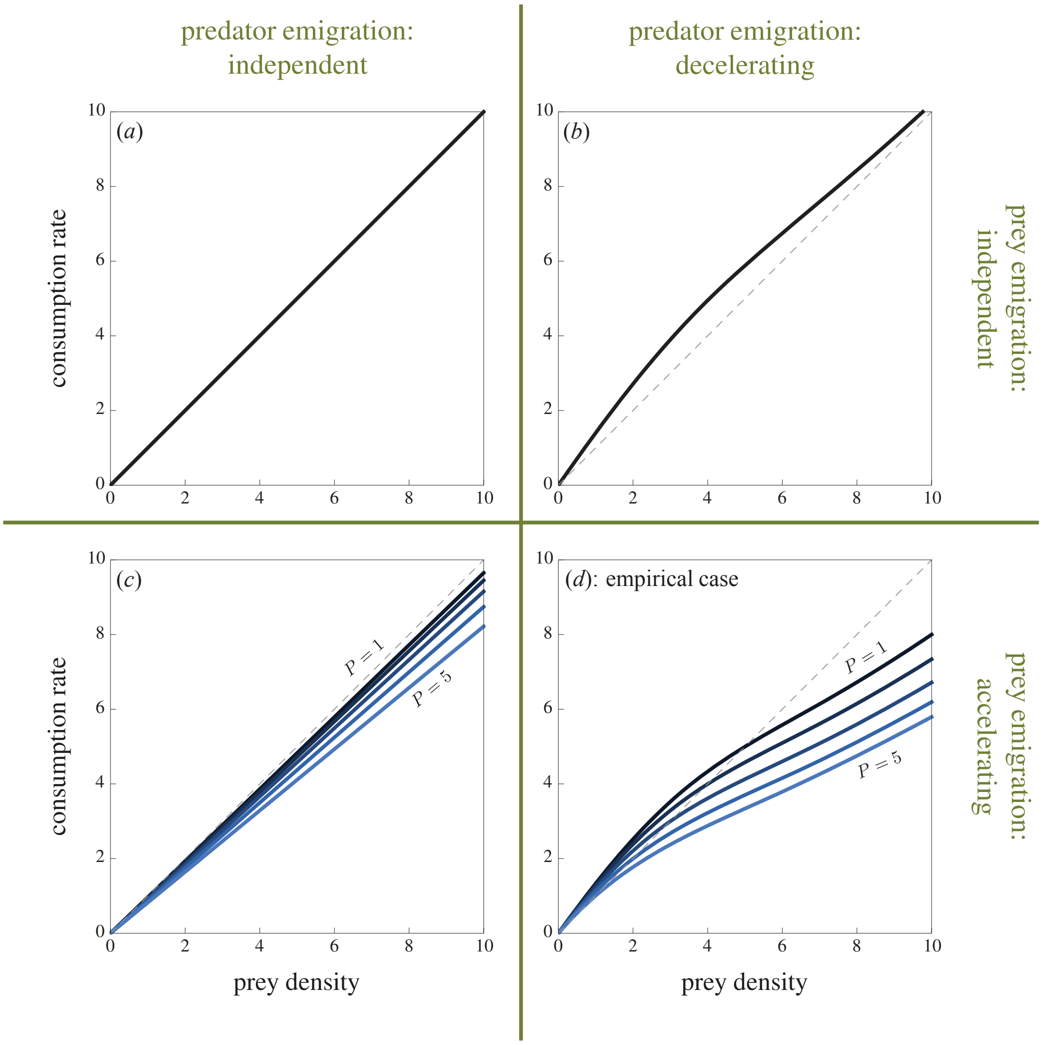

Figure 2: Space race functional responses. Dashed lines indicate the Holling type I functional response. (*a*) The consumption rate when both species move independently of each other. (*b*) The consumption rate when the predator species has a decelerating emigration response to prey. (*c*) The consumption 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 $E_{\mathrm{n}}\left(P\right) = 1 + e^{\theta P}$ and $E_{\mathrm{p}}\left(N\right) = 1 + 20e^{-\theta N}$, 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).

(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.

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 or not, 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) is for a given fixed point (N^*, P^*) influenced only by the properties of the per capita covariance and the conversion efficiency η. The fixed point is a stable attractor if

$$\delta = 1 + C(N^*, P^*) + N^* \frac{\partial C(N, P^*)}{\partial N}\Big|_{N=N^*} + P^* \frac{\partial C(N^*, P)}{\partial P}\Big|_{P=P^*}$$

and

$$\tau = \frac{\partial C(N, P^*)}{\partial N}\Big|_{N=N^*} - \eta \frac{\partial C(N^*, P)}{\partial P}\Big|_{P=P^*}$$

are both greater than zero. When applying the approximation of the per capita covariance (equation 2), $\delta > 0$ is always true, which means that stability hinges only on the sign of τ. If then $\tau < 0$, the fixed point, typically at low equilibrium densities, constitute an unstable equilibrium producing unstable dynamics which tend to attract to limit cycles around the fixed point at an average distance that depend on the shape of $C(N, P)$ [electronic supplementary material, figure S3-S5; 15].

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 destabilising density dependence comparable to that described by the Holling type II functional response, although the underlying mechanism is different. In contrast, the prey's accelerating emigration response leads to stabilising density dependence, as the prey density experienced by the predators decreases with increasing predator density. This mechanism is analogous to the one proposed by [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 per 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 $\frac{\partial \hat{f}}{\partial N} < 0$ and $\frac{\partial \hat{f}}{\partial P} < 0$. Since $\hat{f}(N,P) = \alpha(1 + C(N,P))$, we can reduce the problem to an examination of how $C(N,P)$ changes with the two species' densities. This reveals that if

$$C(N,P) < -\frac{E''_{\mathrm{p}}(N)}{E'_{\mathrm{p}}(N)} \tag{5}$$

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

$$C(N,P) > -\frac{E''_{\mathrm{n}}(P)}{E'_{\mathrm{n}}(P)} \tag{6}$$

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.

DISCUSSION

In a predator-prey system where the two species are engaged in a space race, the functional response is a non-linear 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 destabilising density dependence in the prey dimension and, in most cases, a stabilising density dependence in the predator dimension.

In equivalence with the Holling type II functional response, the destabilising effect in the space race functional response occurs because the prey per 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 destabilising density dependence is instead a consequence of the decelerating emigration response of predators, $E_{\mathrm{p}}(N)$. The predation efficiency decreases with increasing prey density because the predators put less effort into finding the best foraging patches when prey is abundant. In 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 stabilising effects in the space race functional response are caused by reduced predation efficiencies at high predator densities - i.e., predator growth exhibit a negative dependence of predator density. However, the mechanism in the space race functional response is different from that proposed by [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 reduce 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, also the equilbrium densities of predators will 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 tend 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 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 [see e.g., 26, 13, 14]. 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 likely be valuable contributions to our understanding of the mechanism controlling persistence of food webs in ecological systems.

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Electronic supplementary material to "Space race functional responses"

Henrik Sjödin[1,2,*], **Åke Brännström**[2,3] **and Göran Englund**[1]

[1]*Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden*
[2]*Evolution and Ecology Program, International Institute for Applied Systems Analysis, 2361 Laxenburg, Austria*
[3]*Department of Mathematics and Mathematical Statistics, Umeå University, 90187 Umeå, Sweden*

1 POPULATION-LEVEL ENCOUNTER RATES

The population-level encounter rate $g(N, P)$ is determined by taking the average over all local encounter rates. This is obtained as usual by summing over the products of the states of the process and the probabilities D that each state will occur. Hence,

$$\begin{aligned} g(N,P) &= \langle G(X_\mathrm{n}, X_\mathrm{p}) \rangle \\ &= \sum_{x_\mathrm{n}=0}^{\infty} \sum_{x_\mathrm{p}=0}^{\infty} D(x_\mathrm{n}, x_\mathrm{p}, t) G(x_\mathrm{n}, x_\mathrm{p}) \\ &= \alpha_\mathrm{e} \langle X_\mathrm{n} X_\mathrm{p} \rangle , \end{aligned} \tag{1}$$

and since $\mathrm{cov}(X_\mathrm{n}, X_\mathrm{p}) = \langle X_\mathrm{n} X_\mathrm{p} \rangle - NP$ by definition, we find that

$$g(N,P) = \alpha_\mathrm{e} \mathrm{cov}(X_\mathrm{n}, X_\mathrm{p}) + \alpha_\mathrm{e} NP, \tag{2}$$

which simplifies to

$$g(N,P) = \alpha_\mathrm{e} NP \left(1 + \frac{\mathrm{cov}(X_\mathrm{n}, X_\mathrm{p})}{NP} \right), \tag{3}$$

where $\mathrm{cov}(X_\mathrm{n}, X_\mathrm{p})/NP$ is the per capita covariance $C(N, P)$. Finally, we therefore write

$$g(N,P) = \alpha_\mathrm{e} NP \left(1 + C(N,P) \right). \tag{4}$$

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[*] Author for correspondence (sjodin.h@gmail.com)

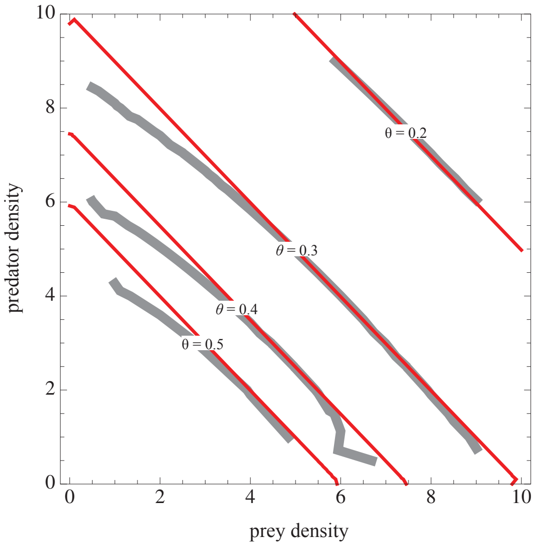

Figure S1: The analytical relationship $S = -E'_{\mathrm{n}}(P) - E'_{\mathrm{p}}(N)$ (thin) is a good estimate of the border between $S > 0$ and $S < 0$, except when mean densities of prey are low. This is verified by comparison with results from a numerical analysis of a master equation (thick). Prey emigration are given by θ in $E_{\mathrm{n}}(P) = 1 + e^{\theta P}$ and predator emigration by $E_{\mathrm{p}}(N) = 1 + 20e^{-\theta N}$.

2 ROBUSTNESS

2.1 *Numerical analysis of the space race sign*

The border between negative and positive space race signs, which determines whether predator or prey wins the space race, is well estimated by the analytical relationship $S = -E'_{\mathrm{n}}(P) - E'_{\mathrm{p}}(N)$. This is verified by comparison with results from a numerical analysis of a master equation (figure S1).

2.2 *Robustness of analytical responses*

The functional responses graphically represented in the main text are, even for large θ, in qualitative agreement with the exact functional responses obtained from numerical analysis of the corresponding master equation (figure S2).

2.3 *Dynamics of eight cases of the predator-prey system with a space-race functional response*

Here we present a stability analysis of the specific system $\dot{N} = rN - \alpha NP(1 + C(N,P))$; $\dot{P} = \alpha\eta NP(1 + C(N,P)) - mP$, with $r = 1.5, \alpha = 0.57, \eta = 1.0, m = 2.0$, where $C(N,P) = -\frac{E'_{\mathrm{n}}(P)+E'_{\mathrm{p}}(N)}{E_{\mathrm{n}}(P)+E_{\mathrm{p}}(N)}$, $E_{\mathrm{n}}(P) = 1 + e^{\theta_{\mathrm{n}} P}$ and $E_{\mathrm{p}}(N) = 1 + 20e^{-\theta_{\mathrm{p}} N}$, with $\theta_{\mathrm{n}} = 0.3$ and for a number

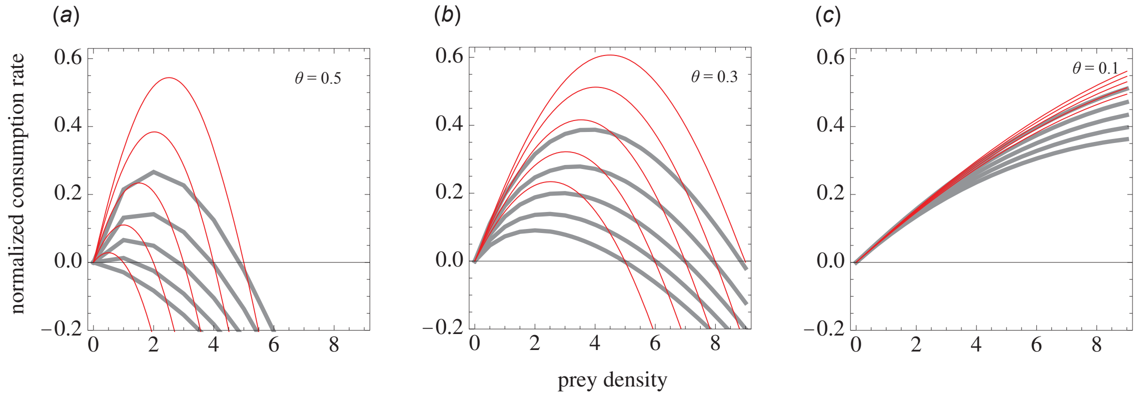

Figure S2: Normalised functional responses ($f(N,P) - \alpha N$; where then the Holling type I response equals zero) corresponding to the functional responses $f(N,P)$ in figure 2d in the main text, show that the exact space race functional responses (thick) (obtained by numerical analysis of a corresponding master equation) is in qualitative agreement with the corresponding analytical responses (thin) even for high degrees ($\theta \in [0.1, 0.5]$) of density dependence in emigration rates.

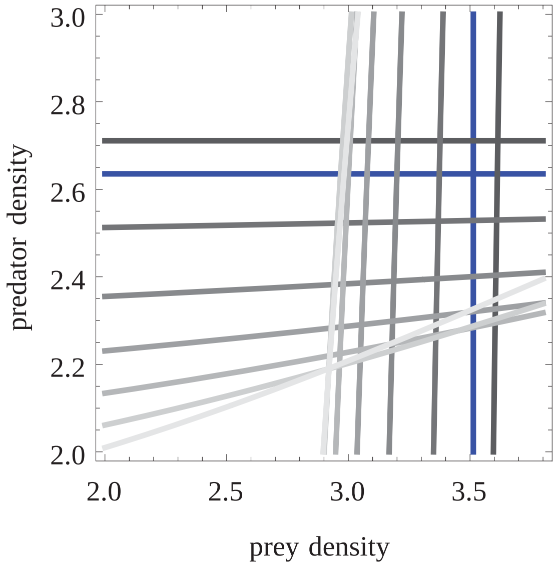

Figure S3: Predator-prey isoclines of the system: $\dot{N} = rN - \alpha NP(1+C(N,P))$; $\dot{P} = \alpha\eta NP(1+C(N,P)) - mP$, plotted with $\theta_{\mathrm{n}} = 0.3$ and for a range of values $(0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6)$ of θ_{p}, where the different values θ_{p} are graphically represented by shades of gray from dark to bright with increasing values of θ_{p}. The blue isoclines correspond to $\theta_{\mathrm{n}} = 0.0, \theta_{\mathrm{p}} = 0.0$ representing the standard Lotka-Volterra isoclines. The fixed points for each respective case are given by the intersection of the two isolines. Prey emigration are given by $E_{\mathrm{n}}(P) = 1 + e^{\theta_{\mathrm{n}} P}$ and predator emigration by $E_{\mathrm{p}}(N) = 1 + 20e^{-\theta_{\mathrm{p}} N}$

of cases $\theta_\mathrm{p} = \{0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6\}$. The system is predicted (given that θ_n and θ_p are suffixciently small) to be stable if the species densities are within the basin of attraction of a fixed point (N^*, P^*) that satisfy

$$E''_\mathrm{p}(N) - \eta E''_\mathrm{n}(P) - C(N,P)(\eta E'_\mathrm{n}(P) - E'_\mathrm{p}(N)) < 0, \tag{5}$$

as was derived in [1].

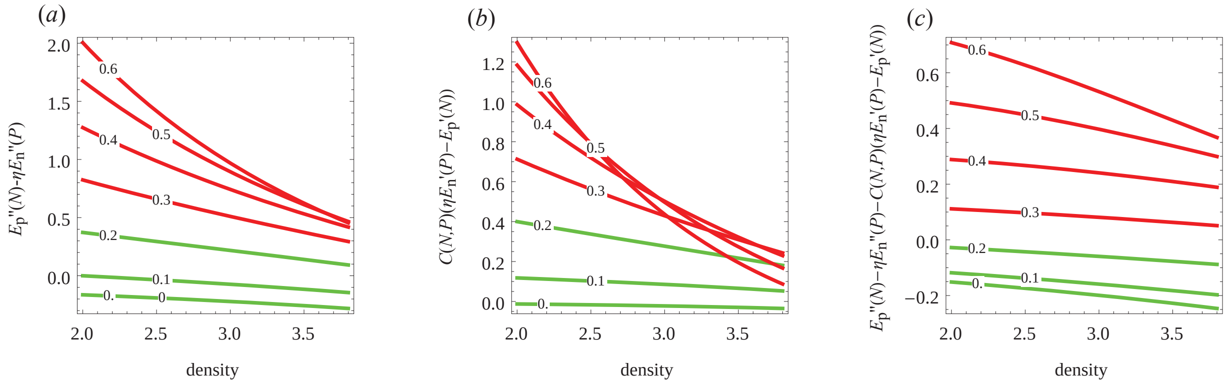

Figure S4: The contribution to stability of emigration responses: (*a*) shows the contribution of the curvature of emigration responses, (*b*) shows the effects of the slopes of emigration responses times the per capita covariance, for different values of θ_p. Figure (*c*) shows the combined effect. The system is going from being stable (green) at low θ_p relative to θ_n to being unstable (red) as θ_p increases. When θ_p exceeds some limit between 0.2 and 0.3, the stability criterion (equation 5) is no longer met and the system becomes unstable.

As figure S3 shows, the fixed points at the intersection of each couple of isoclines depending on the parametrization of θ_n and θ_p lies in the density range 2.0 to 3.6. Figure S4 illustrates in this range how the two principal terms of equation (5) relate to each other. When the destabilising decelerating curvature of the predator response ($E''_\mathrm{p}(N)$) becomes large relative to the stabilising accelerating curvature of the prey response, such that $E''_\mathrm{p}(N) - \eta E''_\mathrm{n}(P)$ (figure S4a) outgrows the stabilizing positive covariance term $C(N,P)(\eta E'_\mathrm{n}(P) - E'_\mathrm{p}(N))$ (figure S4b) the criterion is not satisfied and the system becomes unstable (figure S4c). Only when θ_p is less than 0.3 the system is stable. This applies over the whole range (2.0 to 3.6) of considered equilibrium densities.

The phase-plane dynamics of the considered cases of θ_n and θ_p are depicted in figure S5. Figure S5a shows the case where θ_n and θ_p are zero; constituting a standard Lotka-Volterra system with neutral cycles. The stable fixed points (within green regions in figure S5 b-d) constitute attractors at which the system is stable. In the neighborhood of unstable fixed points (within red regions in figure S5 e-h) the system is attracted by limit cycles around the fixed points, where the magnitude of the oscillations in the limit cycles increases with θ_p. Unstable dynamics are

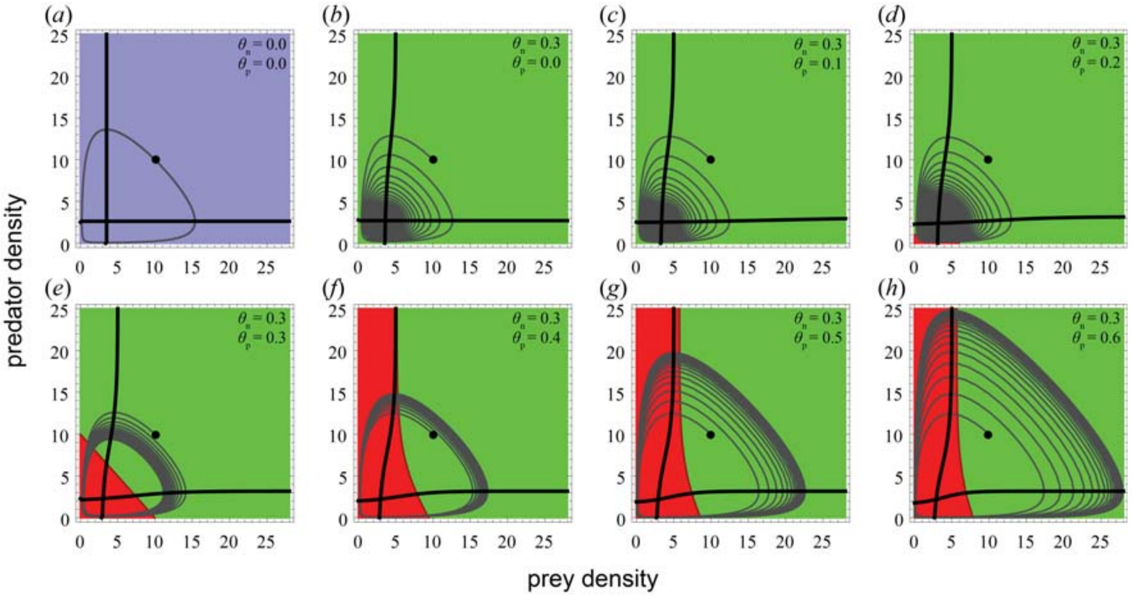

Figure S5: The dynamics in the phase plane, with initial conditions $N = P = 10$ (black points), together with isoclines (black lines; identical to isoclines in figure S3). The intersection points of the isoclines mark the fixed points corresponding to different values of θ_n and θ_p. The green regions illustrate where the criterion (equation 5) is true, the red regions where it is false and the blue region where the left-hand-side of equation 5 equals zero. (*a*) As $\theta_\mathrm{n} = \theta_\mathrm{p} = 0$ the covariance is zero and we have a Lotka-Volterra system with neutral cycles; (*b*)-(*h*) as $\theta_\mathrm{n} + \theta_\mathrm{p} \neq 0$ the covariance is dependent on densities and in (*b*)-(*d*) the system is attracted by stable fixed points, and in (*e*)-(*h*) the fixed points are repellors and the system is attracted to limit cycles around the fixed points.

predicted generally at low equilibrium densities (especially low prey densities) adding to the risk of stochastic extinctions at small population sizes.

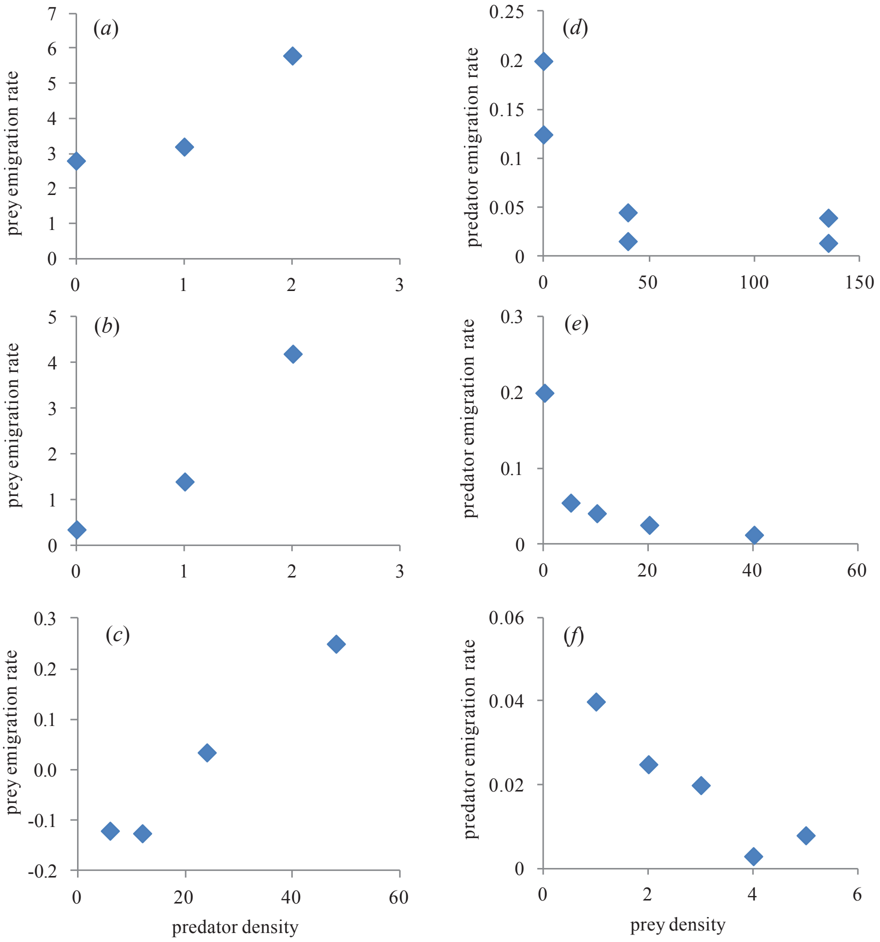

Figure S6: Examples of prey emigration responses to predator densities (*a*)-(*c*) and predator emigration responses to prey density (*d*)-(*f*). Data are taken from (*a*) [2], Baetis; (*b*) [2], Paraleptophlebia; (*c*) [3]; (*d*) [4]; (*e*) [5]; (*f*) [6], small Baetis. Negative values for emigration rate in (*c*) occur because [3] reported residuals from a regression of emigration rate on the amount of plant injury.

3 EMPIRICAL EMIGRATION RATES

Figure S6 shows examples of empirical emigration responses of predators and prey.

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