HOW POPULATION DYNAMICS SHAPE THE FUNCTIONAL RESPONSE IN A ONE-PREDATOR–TWO-PREY SYSTEM

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Abstract. The type III functional response has historically been associated with switching predators; when there is a choice of prey the predator favors the more abundant prey type. Although this functional response has been found in experiments where both prey densities are manipulated, in real world studies the type II functional response is more commonly found. In modeling, the type III functional response is often used in systems where the second prey type is, implicitly, assumed to be constant. Here we define a functional response that takes into account both prey densities. This causes the functional response to show both type II and type III behavior, dependent on the interaction between the two prey densities. If we take into account population dynamics, we find a type II functional response in most cases, because predation regulates the relative prey densities. This explains why type III functional responses are found in experiments where both prey densities are manipulated, but type II functional responses occur when the feedback of population dynamics on the functional response is important. Furthermore, the results show that switching can have a stabilizing or destabilizing effect and can even lead to predator extinction.

Key words: alternative food; apostatic selection; dietary history; functional response; Holling; mechanistic; population dynamics; predator–prey; switching; type II; type III.

INTRODUCTION

The way in which predation varies with prey and predator densities is central to our understanding of predator-prey relations. Predation is normally quantified in terms of the functional and numerical responses, which are the effects of predation on, respectively, the prey and predator growth rates. The rate of predation determines the way in which a prey population dynamically responds to predation and, ultimately, the extent to which the prey population is regulated. Therefore, understanding functional and numerical responses is important to practical and applied aspects of predator–prey biology, biological control, and biodiversity.

The dependence of the functional response on prey density was broadly classified by Holling (1959*a, b*). Holling recognized three different forms of functional response: for the Holling type I the per predator predation rate increases linearly with the prey density, implying a constant rate of capture per prey. A Holling type II response is characterized by a predation rate that saturates with prey density; the per prey capture rate decreases with prey density. This occurs, for instance, if predators are limited in the number of prey they can handle per unit of time. The Holling type III functional is a sigmoid function of the prey density. Such a response is found if the predation rate increases with

increasing prey density and results in a per prey capture rate that initially increases, and then decreases, with prey density.

The type II functional response is thought to occur mainly in specialist predators, while a type III functional response is associated with generalist predators (Andersson and Erlinge 1977, Hansson and Henttonen 1985). It is well established how a type II functional response results from predation on a single prey species. The idea underlying the type III functional responses is that a generalist predator could switch to a prey type if it is more abundant than other types, which would result in lower attack rates at low densities of a prey species. To do so, a predator should be able to modify its attack rate on a certain prey type in response to the prey's density. This apparent link between switching and a type III functional response has been confirmed in laboratory experiments (Murdoch and Oaten 1975, Akre and Johnson 1979, Elliott 2004).

In biological models an, at low prey densities, accelerating functional response, like a type III functional response, has mostly been described in a context in which other prey types are, often implicitly, assumed to be constant. A case in point is the often used formulation of a sigmoid response:

$$f(N) = \frac{N^2}{h + N^2}.$$ (1)

This function does indeed show a sigmoid relationship, but does not explicitly account for multiple prey types. This formulation was derived as an analogy with an enzyme that has two binding places (Real 1977).

Although this does indeed result in an accelerating predation rate, it implicitly assumes that other prey types, if present, are constant.

In a recent meta-analysis, Oksanen et al. 2001 observed that the occurrence of type III functional responses for polyphagous predators in field situations is rather infrequent. A possible explanation for this phenomenon is that, although polyphagous predators, in principle, can exhibit a type III functional response, such a response is not seen in natural situations because of the regulatory influence of the predators on the prey population. To investigate this dependence one needs a quantitative description of the dynamics of polyphagous predators and their prey.

The type III functional response has been demonstrated to occur in experiments with a predator preying on two prey species (Holling 1959a, 1965, Murdoch 1969, Akre and Johnson 1979, Elliot 2004). In these studies, the functional response is measured in an environment in which the prey densities are manipulated. Typically, the functional response to a certain prey type is measured under varying densities of this prey while the densities of all other prey types are kept constant or the total prey density is kept constant. Extrapolating these studies to real world population dynamics can be problematic, because they do not include the feedback from the population dynamics on the prey densities.

Predators and their prey are linked through their trophic relation and their numbers will change dependent on each others' density. To describe and predict the population dynamics of a polyphagous predator and its prey, it is therefore essential to have an accurate description of functional and numerical responses. Surprisingly, there appears to have been little theoretical effort to describe the population dynamics of a predator with multiple prey with a type III functional response. Here we will endeavor to describe and analyze the dynamics of a predator with two prey types, based on a functional type III response which depends on the densities of all prey types.

To do so, we will extend the functional response developed by Oaten and Murdock (1975b) and use this to implement functional and numerical responses in a model for a predator and two prey types. This functional response has attack rates which depend on the dietary history of a predator. In this functional response, the predator samples the prey density through the prey items it has previously captured, which provides a plausible mechanistic underpinning for the type III functional response. There is some experimental justification for this as predators' attack rates can increase with increased prey exposure (Tinbergen 1960, Murdoch 1969, Orians 1969, Royama 1970, Bergelson 1985). Oaten and Murdoch (1975b) have used this functional response to model switching in predators. We follow Murdoch's (1969) definition of the term "switching," which refers to a situation where the number of attacks upon a species is disproportionally large when the species is abundant relative to other prey, and disproportionally small when the species is relatively rare.

Switching predators, in the sense of Murdoch (1969), are generally associated with population dynamical stability. However, in the case of polyphagous predators, the issue about stability has two aspects (Oaten and Murdoch 1975a, May 1977). First, a switching predator can regulate the relative abundances of prey and in this way mediate coexistence between different prey types (Murdoch 1969, Roughgarden and Feldman 1975). Second, a predator preying on multiple prey can destabilize the predator–prey interaction and give rise to predator–prey cycles (Steele 1974, Fryxell and Lundberg 1994, Krivan 1996, Abrams 1999, Krivan and Sikder 1999, Van Baalen et al. 2001). To decide which of these two effects is predominant, one needs a description of the predator–prey interaction including functional and numerical responses in which the density of all prey types can be included.

There is an important issue relating to the form of the functional response that, to our knowledge, has not been addressed in detail. A functional response for a polyphagous predator should depend on the densities of all prey types. As a consequence, in order to predict the form of the functional response, one would need to know how prey densities are regulated. One of the factors regulating prey densities is the amount of predation. This means that the form of the functional response depends on feedback between predation and the population dynamics of the predator and prey populations.

In this article, we analyse the population dynamics of a one-predator–two-prey system with a functional response that depends on the densities of both prey. This functional response can lead to switching, but can also give rise to a type II functional response. We demonstrate how, and under what conditions, the two forms of stability, mentioned previously, occur and in doing so we hope to unify and clarify some of the issues relating to functional responses and stability. Our most important result is that the population dynamics generally give rise to a functional response of the type II form, despite the fact that this same functional response shows the sigmoid curve associated with a type III predator prey system if the density of one prey is kept constant.

THEORY AND RESULTS

We use a functional response that is similar to the one derived by Oaten and Murdoch (1975b). Our derivation is slightly different and extends Oaten and Murdoch's as it also models the effect of dietary history on handling times.

Fig. 1 gives an outline of the method used. The six circles represent the six states of the predator. We discriminate between predators that have previously successfully attacked different prey. The two prey types

are referred to as 1 and 2. Therefore, we have two states currently searching, one has successfully attacked prey 1 (P_{01}) the other prey 2 (P_{02}). Similarly, we have two states currently handling prey 1 (P_{12} and P_{11}) and two states handling prey 2 (P_{21} and P_{22}). Predators in the states P_{12} and P_{21} are predators that changed prey type. The rate of change from state to state is dependent on the prey densities (N_1 and N_2), attack rates, and handling times. The attack rates are represented by a_{ij} where i is the prey species most recently attacked, while j represents the species captured before that. The same notation is used for the handling times (T_{ij}). This results in the functional response shown in Eq. 2 (at the bottom of the page), where i and j are 1 or 2 and $i \neq j$. Appendix A gives the details of the derivation.

Functional response

We will start by investigating the properties of the functional response given by Eq. 2. First we note that this functional response takes the type II form if one of the prey densities is zero:

$$f_1(N_1, 0) = \frac{a_{11}N_1}{1 + a_{11}T_{11}N_1}.$$

If we set $a_{ii} = a_{ij}$; $T_{ii} = T_{ij}$, the predator cannot gather information about past prey taken. The resulting functional response is

$$f_1(N_1, N_2) = \frac{a_{11}N_1}{1 + a_{11}T_{11}N_1 + a_{22}T_{22}N_2} \quad (3)$$

which is a type II response to two prey types. In contrast, it is not possible to relate our functional response (Eq. 2) to the often-used form of the type III functional response (Eq. 1). This is because, in Eq. 2, the denominator will always have both N_i and N_i^2. Therefore we will never see a denominator with only a constant (h) and the square of the species density (N^2). Note that the derivation by Real (1977) assumes that a predator has to encounter the same prey type twice in succession before it attacks. This scenario is not possible in our model.

The difference between a type II and a type III functional response is that the type III functional response is a S-shaped curve (Holling 1959a), which is convex at prey density zero, while type II is a concave function. This definition allows us to check if our functional response (Eq. 2) conforms to a type II or a type III response.

We explore three cases for the functional response here and see if they result in a type II or a type III response (Fig. 2). First, if the relative density of both prey species is constant, $N_2 = cN_1$, the functional response is always a concave function and we do not
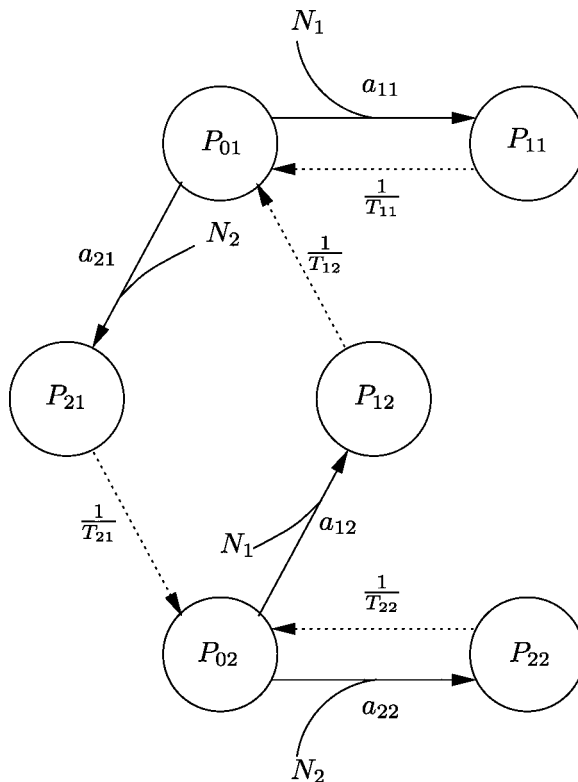

FIG. 1. A graphical explanation of the method used to derive a functional response. The circles represent a predator ($P..$) in different states of searching and handling two prey species. Solid arrows represent the transitions between different states (e.g., $P_{01} \rightarrow P_{11}$) that are dependent on attack rate ($a..$) and population sizes ($N.$). Dotted arrows represent the transitions between different states that are dependent on handling time ($T..$).

have a sigmoid functional response. This is not surprising, because as the relative density of the two prey is stable the predator will not change its relative attack rates on the prey and we will not see switching, resulting in a type II functional response. Secondly, if the density of the second prey species is constant, $N_2 = c$, the functional response is a convex function of the density of prey 1 if

$$a_{12}[1 + a_{21}c(T_{12} + T_{21})] - a_{11}(1 + a_{22}cT_{22}) < 0.$$

Now both a type II and a type III functional response are possible. Finally, in a system where both prey species are in competition over limited resources the total prey density (k) will be determined by the available resources and, therefore, more or less constant ($N_1 + N_2 = k$). In this case, the functional response is a convex function of the density of prey 1 and, hence, act as a type III curve

$$f_i(N_1, N_2) = \frac{a_{ij}N_i(a_{ii}N_i + a_{ji}N_j)}{a_{12}N_1 + a_{11}a_{12}T_{11}N_1^2 + a_{12}a_{21}N_1N_2(T_{12} + T_{21}) + a_{22}a_{21}T_{22}N_2^2 + a_{21}N_2} \quad (2)$$
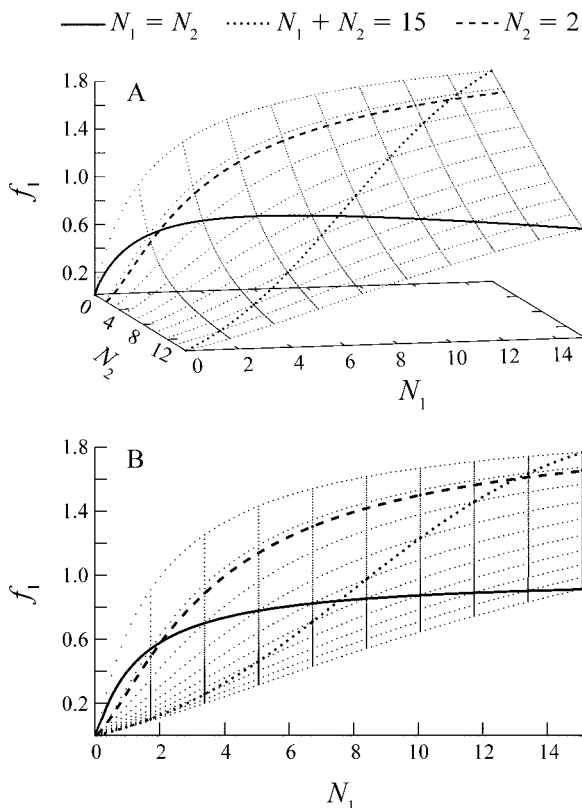
FIG. 2. Functional response (f_1) for population size N_1 with different values of N_2. Parameter values: attack rates, $a_{11} = a_{22} = 1$; $a_{12} = a_{21} = 0.4$; handling times, $T_{11} = T_{12} = T_{22} = T_{21} = 0.5$. (A) The number of prey type 1 captured vs. both prey densities. The lines represent different scenarios for the interaction between both prey densities. The dotted mesh defines all the possible solutions for the functional response. (B) The same lines, but ignoring the second prey densities, which is how functional responses are often measured.

if the following inequality holds:

$$a_{12}[1 + a_{21}k(T_{12} + T_{21})] - a_{11}(1 + a_{22}kT_{22})$$
$$- a_{22}a_{21}kT_{22} < 0.$$

In conclusion, the functional response (Eq. 2) can show both type II and type III behavior. If prey density is assumed to be constant we will often see a type III functional response. If, in contrast, the density of one prey species is proportional to that of the other prey, a type II response will result. Studies of functional responses under laboratory conditions that find type III curves often keep the second prey density constant (Holling 1959a, 1965) or keep the total prey density constant (Murdoch 1969, Akre and Johnson 1979, Elliott 2004), which explains the type III functional responses found.

This shows that the shape of the functional response depends on how both prey densities change over time. In experiments, these densities are known and manipulated, but, in real world situations, the change of densities over time depends on the interaction between both prey

densities and the predator density. Using a population dynamical model it is possible to model the change of these densities, based on their interactions. This will allow us to make predictions about which form the functional response is likely to take.

Predator-mediated coexistence

To study the effect of predation, we incorporate this new functional response into a simple one-predator–two-prey model:

$$\frac{dN_1}{dt} = N_1 g_1(N_1, N_2) - P f_1(N_1, N_2)$$

$$\frac{dN_2}{dt} = N_2 g_2(N_1, N_2) - P f_2(N_1, N_2)$$

$$\frac{dP}{dt} = P[c_1 f_1(N_1, N_2) + c_2 f_2(N_1, N_2)] - mP \quad (4)$$

where c_i is the conversion factor of captured prey species i into predators, the predator has a constant mortality rate of m and $g_i(N_1, N_2)$ is the growth function of prey type i, which depends on both prey densities.

Switching, in the sense of Murdoch (1969), is a nonlinear dependence between the relative prey abundance and representation of prey in the diet, such that a prey is over represented in the diet when it is relatively abundant, i.e., relative to the other prey densities, and under represented when it is relatively rare (see Fig. 3A). We can quantify this as follows: the functional response (Eq. 2) gives us the relationship between the number of prey and the number of successful attacks and can, therefore, be used to describe switching. Let η be the proportion of prey 1,

$$\eta = \frac{N_1}{N_1 + N_2} \quad (5)$$

and let ϕ be the proportion of successful attacks on prey 1,

$$\phi = \frac{f_1(N_1, N_2)}{f_1(N_1, N_2) + f_2(N_1, N_2)}. \quad (6)$$

Substituting Eqs. 2 and 5 in Eq. 6 results in

$$\phi(\eta) = \frac{a_{12}\eta[a_{11}\eta + a_{21}(1 - \eta)]}{a_{12}a_{11}\eta^2 + 2a_{21}a_{12}\eta(1 - \eta) + a_{21}a_{22}(1 - \eta)^2}.$$

The predator is not switching if the proportion of prey 1 successfully attacked is always equal to the proportion of prey 1 ($\eta = \phi(\eta)$ for all η). This is mostly not the case here. To find out when there is switching, we first need to know at which η the proportion of prey attacked is equal to the proportion of prey available by solving the equation $\eta = \phi(\eta)$, which gives us three solutions: $\eta = 0$, $\eta = 1$, and

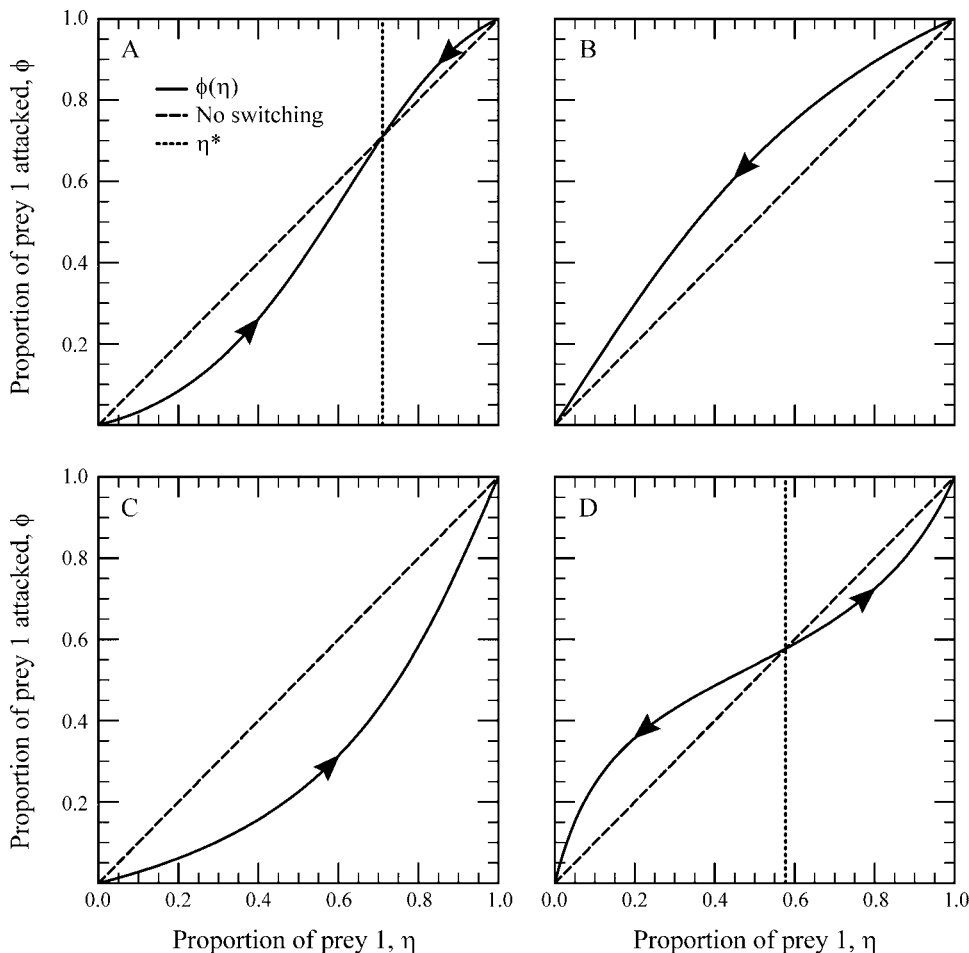$$\eta^* = \frac{\beta_2}{\beta_2 + \beta_1}$$

FIG. 3. The proportion of prey 1 attacked vs. the proportion of prey 1 in the total population. The arrows indicate the state the system will converge to, depending on the value of β_i ($a_{ij}[a_{ii} - a_{ji}]$). (A) β_1 and β_2 are positive (attack rates, $a_{11} = 2$; $a_{12} = 0.6$; $a_{22} = 2.4$; $a_{21} = 0.9$); (B) β_2 is negative ($a_{11} = 2$; $a_{12} = 0.9$; $a_{22} = 0.6$; $a_{21} = 0.9$); (C) β_1 is negative ($a_{11} = 0.9$; $a_{12} = 0.6$; $a_{22} = 2.4$; $a_{21} = 2$); and (D) β_1 and β_2 are negative ($a_{11} = 0.9$; $a_{12} = 2.4$; $a_{22} = 0.6$; $a_{21} = 2$). The dashed line ($\phi = \eta$) is the line where no switching occurs. At η^*, the prey switches from being underrepresented to being overrepresented in the predator's diet if $\phi'(\eta^*) > 1$.

with $\beta_i = a_{ij}(a_{ii} - a_{ji})$. At η^*, the prey switches from being underrepresented to being overrepresented in the predator's diet if $\phi'(\eta^*) > 1$. As long as β_1 and β_2 are both positive, this condition is fulfilled and we do have prey switching.

Prey switching regulates the relative abundance of prey and if there is no direct competition between the two prey types, then predation will be the only factor that determines the balance between the two prey. This amounts to setting $g_1(N_1,N_2) = g_2(N_1,N_2)$ in Eq. 4. In Appendix B, we show that, in this case, if both β_1 and β_2 are positive and for any positive nonzero initial condition, the prey will coexist and the proportion of prey 1 will always converge to η^*. This is independent of the precise form of the prey's and predator's growth functions.

Fig. 3 gives a graphical representation of these results. We have prey switching and the proportion of prey will converge to η^* where the switching line crosses the no-

switching (dashed) line (Fig. 3A), if β_1 and β_2 are both positive. If β_2 is negative, species 1 will always be easier to capture than species 2, resulting in a system where species 1 is driven to extinction and only species 2 exists (Fig. 3B). Similarly, in Fig. 3C, species 2 will be driven to extinction. When β_1 and β_2 are both negative, the proportion of attacks increases less than linearly at η^* and we get the opposite of switching, where predation actually drives the less abundant prey to extinction (Fig. 3D).

Population dynamics

Even if the relative prey abundances equilibrate to η^*, the actual densities may still show sustained oscillations when the predator–prey equilibrium is unstable. To explore these dynamics, we observe that, if $\eta = \eta^*$, the dynamics are restricted to a two-dimensional plane in the three-dimensional state space on which $N_1/N_2 = \beta_2/\beta_1$. We will refer to this plane as the coexistence plane. In Appendix B, we show by means of a Lyapunov

function that the system will always converge to this plane if $\beta_i > 0$ and both growth functions are the same.

If we denote the total prey density as $S = N_1 + N_2$, the functional response on the coexistence plane is given by

$$f(S) = \frac{bS}{1 + bdS} \qquad (7)$$

with b and d being compound parameters (for more details on the derivation see Appendix C). This is an important result and in line with our earlier result that if the proportion of the prey types is constant we will never find a convex (type III) functional response (*Theory and Results: Functional response*). It proves that, irrespective of initial conditions and irrespective of the resulting dynamics, predation regulates the proportions of prey and results in a type II functional response. Simply replacing the functional response with the type II functional response (Eq. 3) will give different results, because without dietary history there will be no switching by the predator (Fig. 3B or C) and, as a result, the type II system will lead to prey exclusion due to apparent competition (see Appendix B and Holt [1977]).

We can use this functional response (Eq. 7) and rewrite the one-predator–two-prey system (Eq. 4) on the coexistence plane to a one-predator–one-prey system:

$$\frac{dS}{dt} = Sg(S) - Pf(S)$$

$$\frac{dP}{dt} = Pcf(S) - mP$$

with $c = \eta^* c_1 + (1 - \eta^*)c_2$. If we choose

$$g(N_1, N_2) = r\left(1 - \frac{N_1 + N_2}{K}\right)$$

resulting in $g(S) = r(1 - S/K)$, the model on the coexistence plane reduces to the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963). Such a system shows three types of behavior dependent on the parameter values: (1) the predator can die out, (2) the system will converge to a stable equilibrium, and (3) the system will follow a limit cycle.

We will discuss the dynamics of the one-predator–two-prey system (Eq. 4) in detail for the case $a_{ii} = a$; $a_{ij} = a_s$; $T_{ii} = T$; $T_{ij} = T_s$ using a bifurcation analysis (Appendix C). For this parameter combination, both prey species are essentially the same and we can concentrate on the effects of the attack rates and handling times on systems stability.

Fig. 4A shows a summary of the dynamical behavior if only one prey species is present. We see that if the attack rate is very low, the predator goes extinct; if it is very high, we find a limit cycle; and, in between, a stable equilibrium. It can also be seen that, if the attack rate on a repeatedly encountered prey is higher than on alternative prey types ($a > a_s$), a second prey type can invade and coexist with the prey type already present.

Fig. 4B summarizes the dynamics for two prey species. This shows that there is a large parameter region, shown in dark gray, where the single prey system will exhibit a limit cycle, while the system with both prey has a stable equilibrium. This indicates that the availability of multiple prey has a stabilising effect on the system. There is also a small parameter space shown in light grey where the single prey system has a stable equilibrium with all three species present, while switching leads to the extinction of the predator. This is due to the fact that the predator will be changing from one prey type to the other a lot, which results in a lower mean attack rate for the predator and eventually predator extinction.

Fig. 4C summarizes the results for the handling time for a single prey species. When the handling times are low, the system will converge to a stable equilibrium. For larger handling times, it will result in a limit cycle. If the handling times increase further, it will go back to a stable equilibrium, and when the handling times get too long the predator will die out. Whether or not a second prey species can invade and coexist depends on the attack rates, but not on the handling times.

In Fig. 4D, the gray areas indicate the effects of the availability of multiple prey on stability. The most interesting part of the graph is where $T_s > T$, because one would expect handling time to increase due to a change in prey type and we will not show the results for $T < T_s$. In contrast to the results for the attack rate, the results for handling time indicate that switching mainly causes extinction. The light gray area in the figure shows a large area where the predator is not able to maintain itself when switching. This is because the constant changing from one prey type to the other leads to a bigger mean handling time. The dark gray areas show the effects of switching between prey types on stability. Area 1 is the parameter region where switching stabilizes the population dynamics. Area 2 is the region where switching actually destabilizes the dynamics.

Competing prey species

The above results are all based on the assumption that the growth functions for both prey are the same. These results are still valid when the growth functions are not the same. To demonstrate this, we will discuss some results for different growth functions. We assume that the growth functions take the form of the Lotka-Volterra competition model:

$$g_i(N_i, N_j) = r_i\left(1 - \frac{N_i + \alpha_{ij}N_j}{K}\right)$$

with r_i the growth rate of species i, K the carrying capacity, and α_{ij} the competition coefficient that describes the strength of the effect of species j on species i. If only the growth rates (r_i) differ, our coexistence plane still exists and a complete description similar to the one given in the previous section is possible (see Appendix B).
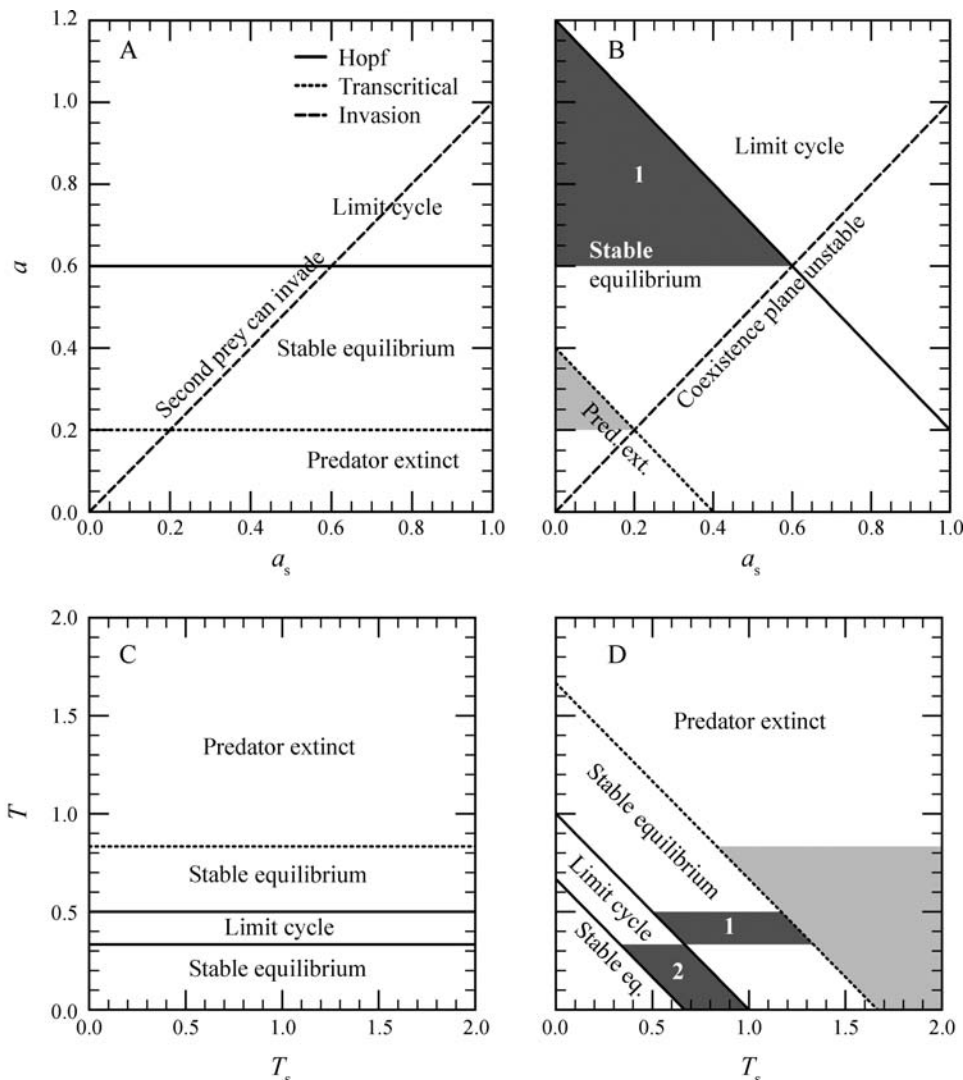
FIG. 4. Bifurcation diagrams showing the effect of attack rates (a) and handling times (T) on system stability, with the following parameter values: predator mortality rate, $m = 0.5$; conversion of prey into predator, $c = 0.5$; growth rate, $r = 1.5$; carrying capacity, $K = 10$. The effect of the attack rates is shown when (A) one of the prey species is extinct and (B) one prey species is on the coexistence plane (handling time $T = T_s = 0.5$). (C) and (D) show similar results, but for the handling times (attack rate $a = a_s = 0.6$). The dark gray area 1 is the parameter region where switching of prey type by the predator stabilizes the population dynamics. Area 2 is where switching destabilizes the dynamics. The light gray area is where switching causes predator extinction.

We will study the case in which prey species 2 will out compete species 1 when the predator is not present, this is achieved by setting $\alpha_{12} > 1$, $\alpha_{21} < 1$. Fig. 5A shows that, in this case, the predator regulates the proportion of the prey and "pushes" this proportion to η^*. This is counteracted by the effect of direct competition between prey. The resulting dynamics depend on the interplay between these two forces. The dynamics can either go to a stable equilibrium or a limit cycle.

When the prey densities fluctuate it is possible to plot the prey density against the number of prey successfully attacked over a range of densities (Fig. 5B). This allows us to determine the shape of the functional response in a fluctuating system. The functional response under competition is not S shaped and therefore seems not to conform to a type III functional response; it is closer to a type II functional response. This indicates that, as long as predation is an important factor in the population dynamics of the prey, field data will reveal a type II functional response, even though the predators are switching.

To gain insight in the combined effect of direct and indirect competition we constructed a bifurcation diagram under competition (Fig. 5C) and compare this to Fig. 4B. We can see that the area where predation stabilizes the interaction is preserved, showing that this is a robust phenomenon. Second, the area in which switching caused predator extinction has disappeared.
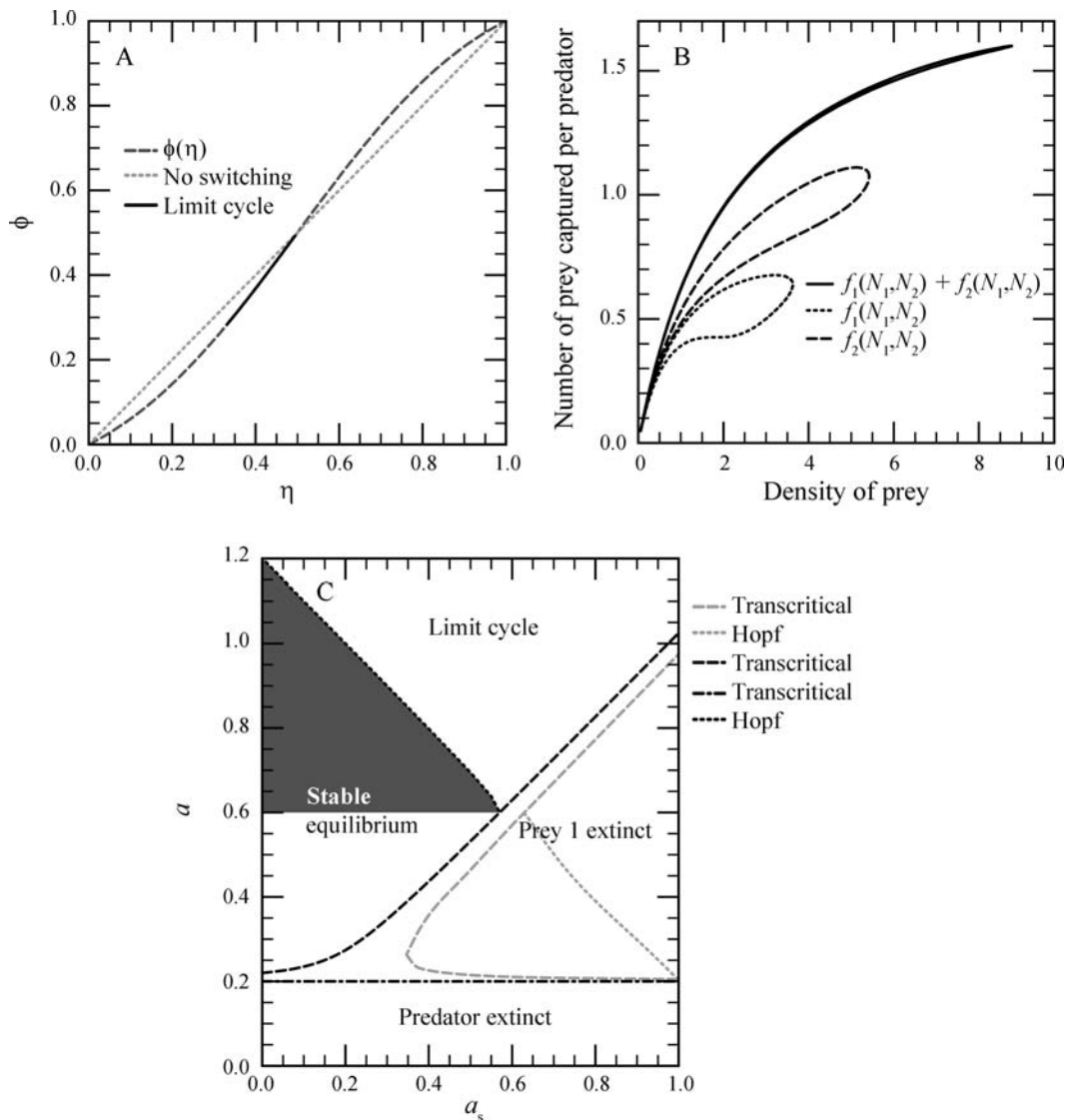
FIG. 5.   Results of the model with competition included. (A) The switching behavior of the model, with ϕ being the proportion of prey 1 attacked. This shows the result if the system shows a limit cycle (predator mortality rate, $m = 0.5$; conversion of prey into predator, $c = 0.5$; attack rate, $a = 1.2$; $a_s = 0.6$; handling times, $T_{11} = T_{12} = T_{22} = T_{21} = 0.5$; carrying capacity, $K = 10$; growth rate of species 1, $r_1 = 1.5$; competition coefficients, $\alpha_{12} = 1.1$, $\alpha_{21} = 0.9$). (B) The resulting functional response for the limit cycle. (C) Bifurcation diagram showing the effect of attack rates on system stability on the coexistence plane. The black lines are the biologically relevant bifurcations. They divide the parameter space in areas where the predator goes extinct, prey species 1 goes extinct, and a stable equilibrium or a limit cycle exists. The dark gray area shows where switching stabilizes predator–prey relations.

This is because at low predator densities the effect of competition will be stronger than the effect of switching. This causes prey species 1 to go extinct before the predator goes extinct and brings the system back to a one-predator–one-prey system. Predator extinction does occur if the prey types coexist in the absence of the predator (if α_{12}, $\alpha_{21} < 1$).

Although the details differ from the case discussed in the previous section, this demonstrates that the previous analysis gives a good insight in the case where competition is not neutral. Therefore, most of our findings when ignoring competition are applicable when competition is included. We still found a type II like functional response and, although details of the bifurcation diagram change, the biologically significant bifurcations remain the same. One interesting and important difference is that with direct competition, switching need not cause the predator to go extinct more often than without switching.

DISCUSSION

Polyphagous predators can respond to the density of their prey by adjusting their predation rate. For this reason, the functional response can depend on the

densities of all their prey species. This dependency can lead to a sigmoid functional response (Holling type III functional response) and prey switching (a disproportionately high predator attack rate when the prey species is abundant and a disproportionately low attack rate when the species is scarce [Murdoch 1969]). We investigated the consequences of this feedback on the population dynamics of a one-predator–two-prey system. We assumed that the predator's attack rates depend on information about the prey densities in its environment. This information can be obtained through prey the predator has taken previously. The change in attack rates can be under active control of the predator (e.g., learning behavior or conditional behavior) or be passive. The latter situation arises, for instance, if prey are assorted in patches, which causes the attack rate of repeatedly encountered prey to be higher than that of alternating prey types.

We found that the population dynamics shape the form of the functional response and typically would lead to decelerating (type II) functional responses, despite the fact that the predator, in principle, could have a type III functional response. Our model also sheds light on when we would expect type III and when we would expect type II responses in field data. Importantly, it demonstrates that the form of the functional response depends on the population dynamics. Therefore, even if it has been observed that a predator under certain (experimental) circumstances has a type III functional response, it may well be that under natural circumstances such a response is never observed.

Functional response

Our results suggest ecological conditions under which different functional responses may arise. Type II responses are more likely in communities where population dynamics is driven by predation and so may actually be the norm. Type III responses arise when the density of one prey species is constant, while that of another prey species changes. Seasonal changes in the abundance of one prey, e.g., migrations, might well drive such responses (Erlinge et al. 1983). We can also expect type III responses where alternative prey is super-abundant (effectively constant). However, it may well be difficult to resolve the form of the functional response in real world studies when predation is not the main influence on predator and prey densities (Stephens et al. 2001, Schenk et al. 2003).

The functional response used here has a large number of parameters (though note that it can be simplified if handling time is unimportant). Despite this, it has significant advantages over standard functional response models, providing in a single equation a mechanistic description of both type II and III responses. In particular, it directly models switching which is known to be widely important (Fullick and Greenwood 1979, Bond 1983, Cooper 1984, Bergelson 1985, McClintock and Lawrence 1985, Elliott 2006). Crucially, it also

accounts for the density of both prey species, which standard type III descriptions do not (Real 1977). Models based on the standard form often do not describe the dynamics of the alternative prey (Steele and Henderson 1981) and this can potentially give rise to spurious results.

Our functional response accounts for the dietary history of the predator in terms of only one prey successfully attacked. This is reasonable given experimental evidence that some predators are able to form a search image after a single encounter with prey (Melcer and Chiszar 1989, Jackson and Li 2004). However, there clearly are predators which do use a longer attack history; we did not include this in our model in order to keep the system tractable and to give insight into the functional response of a multiple prey system. Preliminary results did indicate a longer dietary history will not qualitatively change our conclusions.

Population dynamics

We showed that a predator can mediate the coexistence of two prey species when attack rates on both prey are roughly equal and its attack rate following a change of prey species is lower than when staying on the same prey. Intuitively, this seems likely to occur often in nature, especially for predators where learning plays an important role in the development of foraging strategy or predators following an ideal free distribution (Fretwell and Lucas 1970, Van Baalen and Sabelis 1999). Conversely, if the attack rates on a prey species are always higher than the attack rates on the other species, the predator will drive the preferred prey to extinction. This effect is known as apparent competition (Holt 1977, Holt and Lawton 1994) and encapsulates, for example, the impact of a generalist alien predator driving preferred, but evolutionarily ill-defended, prey to extinction.

The speed with which the population dynamics converge to coexistence is important, because in nature there are many factors aside from predation pressure governing the precise prey densities (e.g., prey competition or nutrient limitation). We have shown (see Appendix B) that this speed is defined by the predation pressure and the strength of switching. As long as these two play a major role within a predator prey system our analysis holds. In systems where predation is low and/or the predator does not switch, other factors will define the population dynamics.

Data suggests that generalist systems are more stable than specialist systems (Andersson and Erlinge 1977, Erlinge et al. 1983, Hanski et al. 1991, Turchin and Hanski 1997), even though both often show a type II functional response (Oksanen et al. 2001). Our results support this finding in that switching in generalists often results in more stable population dynamics while at the same time a plot of the number of prey captured against the density of that one prey type will reveal a type II functional response. In this case, just concentrating on

the functional response of a predator to one of its prey types leads to a confusing picture, because the population dynamics force the system into a type II functional response, not withstanding that the predator is switching.

Our work confirms that switching often stabilizes the population dynamics of a one-predator–two-prey system (Murdoch 1977), leading to fewer limit cycles. Conversely, many previous studies (Fryxell and Lundberg 1994, Krivan 1996, Abrams 1999, Krivan and Sikder 1999, Van Baalen et al. 2001) suggested that switching is destabilising for certain parameter values. However these were based on a "hard switch," a sudden change in predator behavior following a change in prey density. Although a hard switch is predicted by an evolutionary argument, it does presume that sensing and switching are cost free (Jansen and Stumpf 2005, Kussell and Leibler 2005). This gathering of information constrains the predator and can make its behavior suboptimal. The functional response we derived assumes that predators gain information from previous prey encountered. This provides a mechanistically underpinned description of prey switching, allowing a simple but relatively complete analysis, which clarifies and unifies many previous findings about the dynamics of a predator and multiple prey.

Our model suggests that if a predator often switches between prey species its hunting efficiency will be low. This can potentially cause extinction of the predator. This perhaps counterintuitive finding also has the implication that under stable conditions evolution should tend to select for specialist over generalist predators, since the former switch less often. This is indeed the evolutionary pattern seen across taxonomic groups, where specialist predators have evolved to outnumber generalists (Vermeij 1994). Contrary, we would expect generalism to evolve under unstable conditions where it is important to be able to utilize different food sources.

In recent years, the major focus of functional response theory has been optimal foraging. Optimal foraging theory assumes that evolution leads to predators that will forage in such a way that they will gain the highest amount of energy possible over time. Obviously, there are practical limits to what a predator can do. Most studies take a type II functional response as the basis for their optimal foraging models and, therefore, implicitly assume that there is, apart from physical limits on attack rates and handling times, nothing preventing the predator from gaining as much energy as possible. Here we build a third constraint into the functional response, namely that predators can only gather information about the prey densities by capturing prey. Apart from this having consequences on the population dynamics this is also likely to have evolutionary ramifications, which we hope to address in future work.

<div align="center">Literature Cited</div>

Abrams, P. A. 1999. The adaptive dynamics of consumer choice. American Naturalist 153:83–97.

Akre, B. G., and D. M. Johnson. 1979. Switching and sigmoid functional-response curves by damselfly naiads with alternative prey available. Journal of Animal Ecology 48:703–720.

Andersson, M., and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 29:591–597.

Bergelson, J. M. 1985. A mechanistic interpretation of prey selection by *Anax junius* larvae (Odonata: Aeschnidae). Ecology 66:1699–1705.

Bond, A. B. 1983. Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. Journal of Experimental Psychology: Animal Behavior Processes 9:292–306.

Cooper, J. M. 1984. Apostatic selection on prey that match the background. Biological Journal of the Linnean Society 23:221–228.

Elliott, J. M. 2004. Prey switching in four species of carnivorous stoneflies. Freshwater Biology 49:709–720.

Elliott, J. M. 2006. Prey switching in *Rhyacophila dorsalis* (Trichoptera) alters with larval instar. Freshwater Biology 51:913–924.

Erlinge, S., G. Gransson, and L. Hansson. 1983. Predation as regulating factor on small rodent populations in southernmost Sweden. Oikos 40:36–52.

Fretwell, S., and H. J. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fryxell, J. M., and P. Lundberg. 1994. Diet choice and predator–prey dynamics. Evolutionary Ecology 8:407–421.

Fullick, T. G., and J. J. D. Greenwood. 1979. Frequency dependent food selection in relation to two models. American Naturalist 113:762–765.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60:353–367.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67:394–402.

Holling, C. S. 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385–398.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 45:1–60.

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R., and J. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495–520.

Jackson, R. R., and D. Q. Li. 2004. One-encounter search-image formation by araneophagic spiders. Animal Cognition 7:247–254.

Jansen, V. A. A., and M. P. H. Stumpf. 2005. Making sense of evolution in an uncertain world. Science 309:2005–2007.

Krivan, V. 1996. Optimal foraging and predator–prey dynamics. Theoretical Population Biology 3:265–290.

Krivan, V., and A. Sikder. 1999. Optimal foraging and predator–prey dynamics. II. Theoretical Population Biology 2:111–126.

Kussell, E., and S. Leibler. 2005. Phenotypic diversity, population growth, and information in fluctuating environments. Science 309:2075–2078.

May, R. M. 1977. Predators that switch. Nature 269:103–104.

McClintock, J. B., and J. M. Lawrence. 1985. Characteristics of foraging in the soft-bottom benthic starfish *Luidia clathrata*

(Echninodermata: Asteroidea): prey selectivity, switching behavior, functional responses and movement patterns. Oecologia 66:291–298.

Melcer, T., and D. Chiszar. 1989. Striking prey creates a specific chemical search image in rattlesnakes. Animal Behaviour 37: 477–486.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335–354.

Murdoch, W. W. 1977. Stabilizing effects of spatial heterogeneity in predator–prey systems. Theoretical Population Biology 11:252–273.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1–131.

Oaten, A., and W. W. Murdoch. 1975a. Functional response and stability in predator–prey systems. American Naturalist 109:289–298.

Oaten, A., and W. W. Murdoch. 1975b. Switching, functional response and stability in predator–prey systems. American Naturalist 109:299–318.

Oksanen, T., L. Oksanen, M. Schneider, and M. Aunapuu. 2001. Regulation, cycles and stability in northern carnivore–herbivore systems: back to first principles. Oikos 94:101–117.

Orians, G. H. 1969. Age and hunting success in the brown pelican (Pelecanus occidentalis). Animal Behaviour 1:216–219.

Real, L. A. 1977. The kinetics of functional response. American Naturalist 111:289–300.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator–prey interactions. American Naturalist 97:209–223.

Roughgarden, J., and M. Feldman. 1975. Species packing and predation pressure. Ecology 56:489–492.

Royama, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (Parus major l.). Journal of Animal Ecology 39:619–668.

Schenk, D., L. F. Bersier, and S. Bacher. 2005. An experimental test of the nature of predation: neither prey- nor ratio-dependent. Journal of Animal Ecology 74:86–91.

Steele, J. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, Massachusetts, USA.

Steele, J. H., and E. W. Henderson. 1981. A simple plankton model. American Naturalist 117:676–691.

Stephens, P. A., R. P. Freckleton, A. R. Watkinson, and W. J. Sutherland. 2003. Predicting the response of farmland bird populations to changing food supplies. Journal of Applied Ecology 40:970–983.

Tinbergen, L. 1960. The natural control of insects in pine woods. 1. Factors influencing the intensity of predation by song birds. Archives de Neerlandais Zoologie 13:265–343.

Turchin, P., and I. Hanski. 1997. An empirically based model for latitudinal gradient in vole population dynamics. American Naturalist 149:842–874.

Van Baalen, M., V. Krivan, P. C. J. Van Rijn, and M. W. Sabelis. 2001. Alternative food, switching predators, and the persistence of predator–prey systems. American Naturalist 5: 512–524.

Van Baalen, M., and M. W. Sabelis. 1999. Nonequilibrium population dynamics of "ideal and free" prey and predators. American Naturalist 154:69–88.

Vermeij, G. 1994. The evolutionary interaction among species: selection, escalation and coevolution. Annual Review of Ecology and Systematics 25:219–236.

APPENDIX A

A derivation of the functional response (*Ecological Archives* E088-094-A1).

APPENDIX B

A discussion of predator-mediated coexistence (*Ecological Archives* E088-094-A2).

APPENDIX C

A discussion of bifurcations in the population dynamics (*Ecological Archives* E088-094-A3).