



A generalized functional response for predators that switch between multiple prey species

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HIGHLIGHTS

- ▶ Mechanistically derived functional response describing prey switching by a predator.
- ▶ Functional response suitable to describe predators feeding on many prey species.
- ▶ The functional response avoids inconsistencies pertinent to other approaches currently in use.
- ▶ Predictions from the functional response are consistent with experimental data

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ABSTRACT

We develop a theory for the food intake of a predator that can switch between multiple prey species. The theory addresses empirical observations of prey switching and is based on the behavioural assumption that a predator tends to continue feeding on prey that are similar to the prey it has consumed last, in terms of, e.g., their morphology, defences, location, habitat choice, or behaviour. From a predator's dietary history and the assumed similarity relationship among prey species, we derive a general closed-form multi-species functional response for describing predators switching between multiple prey species. Our theory includes the Holling type II functional response as a special case and makes consistent predictions when populations of equivalent prey are aggregated or split. An analysis of the derived functional response enables us to highlight the following five main findings. (1) Prey switching leads to an approximate power-law relationship between ratios of prey abundance and prey intake, consistent with experimental data. (2) In agreement with empirical observations, the theory predicts an upper limit of 2 for the exponent of such power laws. (3) Our theory predicts deviations from power-law switching at very low and very high prey-abundance ratios. (4) The theory can predict the diet composition of a predator feeding on multiple prey species from diet observations for predators feeding only on pairs of prey species. (5) Predators foraging on more prey species will show less pronounced prey switching than predators foraging on fewer prey species, thus providing a natural explanation for the known difficulties of observing prey switching in the field.

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1. Introduction

A predator (or a heterotrophic species in general) is said to be switching between prey (or resource) species if the relative rate with which it attacks a prey species is disproportionately large when that prey species is relatively abundant and disproportionately small when that prey is relatively rare (Murdoch, 1969). While we use the term “prey species” throughout this study for

the sake of brevity, it must be borne in mind that such prey switching can just as well involve several types of prey within a species or functional groups comprising several prey species. Prey switching has been documented for a range of predator species (Greenwood and Elton, 1979; Gendron, 1987; Allen, 1988). It is a form of adaptive foraging and leads to frequency-dependent selection. It has been associated with community permanence (Roughgarden and Feldman, 1975; May, 1977; van Leeuwen et al., 2007) and with polymorphism in prey (Allen, 1988; Bond and Kamil, 2006). As such, it is of general importance for the dynamics of food webs. Prey switching has also found wide use as a mechanism to stabilise population dynamics in food-web models

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(Drossel et al., 2001; Kondoh, 2003; Brose et al., 2006; Uchida et al., 2007; Rossberg et al., 2008; see also Valdovinos, 2010; Loeuille, 2010 for a recent review). If predators switch between multiple prey, larger and more complex communities can persist (Drossel et al., 2001; Kondoh, 2003) because individuals of rare species are then less at risk of being predated upon than individuals of abundant species. Against this background, it is of critical importance that multi-species population-dynamical models account for prey switching, in order to avoid over- or underestimating the stability of real ecological communities.

Incorporating good descriptions of prey switching is often difficult, however, as food-web models are intrinsically mathematically complex and computationally costly, even without the inclusion of mechanistically detailed descriptions of prey switching, which would substantially aggravate these burdens. The functional responses used in food-web models to describe prey switching are therefore often simplified in a heuristic manner. Examples of heuristic functional responses used in food-web models are Greenwood and Elton's (1979) power-law model, type III functional responses (Murdoch, 1969; van Baalen et al., 2001; Williams, 2008), or adaptations of "effort"-based models (Drossel, 2001; Drossel et al., 2001; Kondoh, 2003; Uchida et al., 2007). However, heuristic attempts to generalise classical single-prey functional responses to many prey species can easily lead to inconsistencies. For example, if a single prey population were arbitrarily split into two equivalent groups, some heuristically derived models would predict the predator to switch between these two arbitrary subpopulations of the same species. Avoidance of this problem is known as the "common sense" condition on multi-species functional responses (Arditi and Michalski, 1995; Berryman et al., 1995). In an attempt to resolve this inconsistency, similar prey species are sometimes grouped into "prey trophic species" and the whole group is treated as a single prey species with respect to switching (Matsuda and Namba, 1991; Rossberg et al., 2008). While this may offer a practical ad hoc solution, such groupings of prey species are not typically derived from underlying principles.

Power-law models of prey switching emerge as phenomenological models for empirical observations. For a predator switching between two prey species, double-logarithmic graphs relating the ratio of consumed prey to the ratio of available prey generally exhibit near-linear relationships, implying power-laws on linear axes (Greenwood and Elton, 1979; Elliott, 2004, 2006). The exponent of such a power law is used as a measure of the strength of prey switching; a value of 1 implies an absence of prey switching, since the ratio of consumed prey is then proportional to the ratio of available prey. When the exponent is larger than 1, the predator exhibits prey switching. When the exponent is smaller than 1, the predator is said to exhibit negative prey switching because it consumes disproportionately less of the more available prey (Abrams et al., 1993; Weale et al., 2000; Rindorf et al., 2006).

These findings are difficult to translate directly into a multi-species setting, however, as an inconsistency arises when attempting to combine power-law models. Specifically, if one chooses three prey species A , B and C such that the exponents for switching between A/B and between B/C are identical, then it follows that the predator will always switch between A/C with exactly the same exponent. This cannot be true in general because one must expect that switching becomes the stronger the more two prey species differ in terms of traits that are relevant for the predator's prey choice. If such traits for B are intermediate between those of A and C , then switching between A/C must be expected to be stronger than that between A/B and B/C . For plain power-law switching, this is never possible. Uchida et al. (2007) showed that effort-based models can produce power-law

switching by introducing a non-linear trade-off between the foraging efforts put into different prey species. Yet, even with this model it appears difficult to describe foragers that switch between different pairs of prey with different switching exponents.

Here we address and overcome the two aforementioned problems: analytic intractability of mechanistically detailed models of prey switching on the one hand, and mutual inconsistency of simplified models of prey switching based on power laws on the other. Building on earlier work by Oaten and Murdoch (1975) and van Leeuwen et al. (2007), we develop a generalized theory of predators that switch between multiple prey species. An important feature of this functional response is that it tracks the order in which prey are encountered and attacked and, therefore, allows the incorporation of behaviour based on dietary history. It is based on a Holling type II functional response and also includes attack rates and handling time, which allows one to include prey preference. Based on this theory, we derive a closed-form multi-species functional response that incorporates prey switching and is suitable for incorporation in complex food-web models. By deriving this functional response from basic assumptions on individual foraging behaviour, we ensure that conceptual inconsistencies, such as those described above, do not arise. The empirically important case of predators switching between two prey species is analysed in detail. In particular, we determine when prey switching is well approximated by a power law, and when such an approximation fails. For completeness, we also consider predators switching among multiple prey species. Finally, a worked example is presented that shows how our model can be calibrated to experimental data and used to make testable new predictions, by forecasting outcomes of experiments in which predators can choose among more than two prey species.

2. Methods

After introducing our modelling framework in Section 2.1, Section 2.2 highlights our key simplifying assumption, which is that predators do not prefer cycling through a list of prey species in forward order over cycling in reverse order.

2.1. Model description

To construct a functional response that incorporates switching between multiple prey species, we follow Oaten and Murdoch (1975) and van Leeuwen et al. (2007) in modelling a predator's diet such that it incorporates the order in which it encounters and successfully attacks prey. As a simplifying assumption required for analytical tractability, only the last consumed prey is taken into account. Foraging individuals can then be modelled by a Markov process (a fundamental class of stochastic processes in which transitions to future states only depend on the current state, and hence are independent of previous states). Markov processes have often been used to derive functional responses; the most famous such derivation may be that of the Holling type II functional response, or "disk equation" (Holling, 1959; Metz and Diekmann, 1986). Through the feedback of the population dynamics the functional response tends to converge to a Holling type II functional response. Yet, it was shown in van Leeuwen et al. (2007) that this same functional response can also exhibit Holling type III like behaviour, if one prey type is kept constant, as this functional response allows for a form of learning (van Leeuwen and Jansen, 2010).

In our theory, each predator is assumed to be in one of several states that reflect whether it is searching or handling prey of a

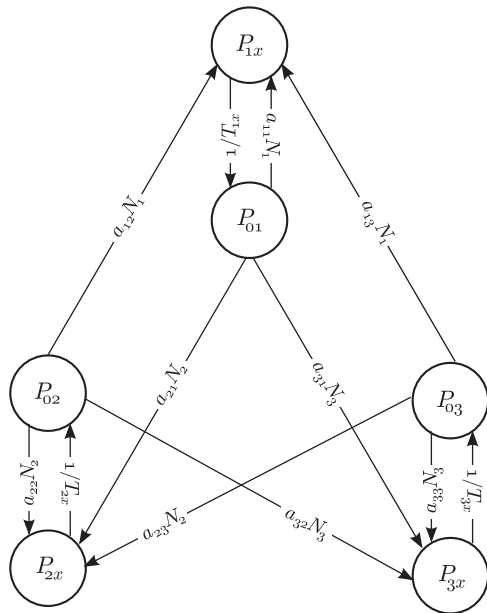


Fig. 1. Diagram depicting the behavioural model underlying the functional response (Eq. (1)). Each node represents different states of the predator and the arrows indicate rates of transition between states. A searching predator (P_{0i}) that previously consumed species i will attack prey j at a rate dependent on its attack rate a_{ij} and the density of prey j (N_j). Similarly, a predator handling prey will become a searching predator at a rate $(1/T_{ij})$ depending on the prey i it is currently handling and the prey j last consumed. To keep the diagram readable we grouped all predators currently handling the same prey together, independent of the previous prey (P_{ix}). In the important special case that handling times depend only on the current prey, the diagram is exact.

certain species (Fig. 1). A predator’s state depends on the previous prey that it has handled. When a searching predator successfully attacks a prey, it enters a new state in which it is handling the captured prey. The rate at which a predator successfully attacks an individual of prey species i is proportional to this prey species’ density N_i and to the predator’s attack rate a_{ij} on individuals of prey species i , given that it has last consumed an individual of prey species j . Thus, the transition rate from a searching state to a state handling prey species i is $a_{ij}N_i$. Prey switching results if predators exhibit some inertia in their choice of prey species, so that in each column of the matrix (a_{ij}) the diagonal elements a_{ii} exceed the other elements. To complete the definition of our Markov model, we assume that a predator currently handling prey species i becomes a searching predator at a rate defined by its handling time T_{ij} , which may (but does not have to) depend on the prey species i it is currently handling and on the prey species j it has handled before.

Our Markov model implies that the durations predators spend continuously in any given state are exponentially distributed, with a mean duration equal to the inverse of the total transition rate for leaving that state. As this contrasts with the usual notion of a handling time, we highlight that this assumption of exponentially distributed durations is not crucial, as long as the mean duration spent in a state equals that described by the Markov model (Acevedo et al., 1996). The resultant class of stochastic processes is known in the mathematical literature as semi-Markovian (Koroliuk and Limnios, 2005).

To derive the functional response of a predator population based on this Markov process, we assume that typical predators consume a large number of prey during their life (which is, parasites excluded, generally the case). Note that this assumption is also made when deriving the Holling type II function response (Metz and Diekmann, 1986). On population-dynamical time scales, the Markov process will then be in what is known as a

stochastic quasi-equilibrium. Once we know this equilibrium state for given states of the prey populations, we can derive the aggregated intakes of a predator and hence its functional response with respect to all these prey populations. Oaten and Murdoch (1975) have proposed a model of multi-prey foraging based on similar ideas, but were unable to derive an explicit expression for the resulting functional response.

2.2. Inversion indifference

It appears that the problem of determining the equilibrium state for multiple prey populations is too complex in its full generality to allow the derivation of an easily evaluated, explicit analytic solution. This complexity can be overcome, however, by assuming that predators will consume three prey species i, j, k with the same probability (or rate) in the order i, j, k, i as they would consume them in the inverse order i, k, j, i , i.e. the predator is indifferent to inversion of the prey order. That is, predators have no preference for cycling through any given list of prey species in forward order as opposed to going through the same list in reverse order. The benefits of making this rather innocuous assumption are remarkable, as the aforementioned Markov model can now be solved analytically; this, in turn, allows the long-sought derivation of a closed-form multi-species functional response. Note that the order of attack is distinct from the order of preference of a predator, i.e. a predator can prefer prey i over prey j and k , while still being indifferent to the order it encounters the prey. As such this assumption does not affect the possibility to account for prey preference in the functional response. In this way our model extends optimal foraging theory, which is largely based on the order of preference, but which does not normally take the temporal order of prey intake explicitly into account (van Leeuwen and Jansen, 2010). See Section 4.4 for further discussion.

As we show in Appendix A, indifference of predators to inverting prey order is mathematically equivalent to the condition that all attack rates can be written in the form $a_{ij} = c_i s_{ij}$, where $s_{ij} = s_{ji} \geq 0$ for all i and j . We call the parameter c_i the predator’s base attack rate on individuals of prey species i and the dimensionless parameter $s_{ij} = s_{ji}$ the similarity between prey i and j with regard to prey switching. While these terms convey helpful intuition, it is of crucial importance for appreciating the generality of our theory that they are not misunderstood. Since the decomposition $a_{ij} = c_i s_{ij}$ immediately follows from the previously described inversion indifference, there is no need for the predators themselves, or for their human observers, to have any explicit understanding of the regard in which the prey species are similar. We just formally call the elements of the matrix (s_{ij}) similarities, since they are positive, symmetric, and a lower similarity s_{ij} between prey species implies proportionately rarer switches of a predator from consuming prey species i to consuming prey species j . In specific applications, these abstract elements may turn out to be correlated with measurable similarities with regard to morphologies, defences, locations, habitat choices, behaviours, or complicated mixtures thereof, but no interpretation of this kind is required for the successful application of our theory. All we need is inversion indifference.

The interpretations of the parameters c_i as base attack rates and of the parameters s_{ij} as switching similarities are most straightforward when $s_{ii} = 1$ for any prey species i . In this case, switching similarity affects relative attack rates equally when switching from prey i to j and vice versa due to the symmetry requirement, since $s_{ij}/s_{ii} = s_{ji}/s_{jj}$. For example, if prey i and j have a similarity of 0.1, then a predator that has attacked prey i is 10 times more likely to attack prey i again than a predator that has attacked prey j is to attack prey i and vice versa. Furthermore, $s_{ij} = 1$ implies that the two prey species i and j are equivalent from

the perspective of the predator and no prey switching takes place. When only prey i is present, c_i is simply the conventional attack rate. To facilitate interpretations of examples, one may thus choose to set all s_{ij} to equal 1. We caution, however, that the convenient choice of $s_{ii}=1$ for all i implies additional constraints on attack rates a_{ij} . The decomposition $a_{ij}=c_i s_{ij}$ enables only one element of s to be chosen freely, e.g., $s_{11}=1$, without loss of generality.

While we have formulated the model above in terms of different prey species i, j, \dots , and will maintain this interpretation below, we reiterate that these indices can just as well represent different morphs, sexes, or life-history stages within one or more prey species, when such distinctions matter for predation, or different functional groups of several prey species, when a predator distinguishes between such groups, but not among the species within each group.

3. Results

In Section 3.1, we first present the closed form of the multi-species functional response implied by our behavioural model and show that it satisfies the “common sense” condition of multi-species functional responses described in the introduction. We then study switching between two prey in Section 3.2 and switching between any number of prey in Section 3.3. To illustrate how theoretical predictions can be interfaced with empirical data, we report in Section 3.4 an attempt to fit the model to empirical data from prey-switching experiments. In the final Section 3.5, we relax the assumption of inversion indifference required for a closed-form analytical solution, and demonstrate numerically the robustness of our key findings.

3.1. Multi-species functional response and its key properties

In Appendix B, we show that the assumption of inversion indifference allows the derivation of the resultant multi-species functional response in a closed analytical form,

$$f_i = \frac{c_i N_i \sum_{k=1}^n s_{ik} c_k N_k}{\sum_{k=1}^n c_k N_k (1 + \sum_{j=1}^n s_{kj} T_{kj} c_j N_j)}, \quad (1)$$

where n is the number of prey species, f_i is the predator’s intake rate of prey species i , N_i is the density of prey species i , c_i is the predator’s base attack rate for prey i , and s_{ij} is the similarity between prey species i and j . To simplify the notation, we introduce the *availabilities* $\tilde{N}_i = c_i N_i$ of prey species, a notational change that can alternatively be interpreted as scaling the densities of prey species with their base attack rates by the predator.

We first observe that this functional response simplifies to a Holling type II functional response when all switching similarities and handling times are independent of previously consumed prey ($s_{ij}=s_i$ and $T_{ij}=T_i$), since in that case $f_i = \tilde{N}_i s_i \sum_{k=1}^n \tilde{N}_k / (\sum_{k=1}^n \tilde{N}_k + \sum_{k=1}^n \tilde{N}_k s_k T_k \sum_{j=1}^n \tilde{N}_j) = \tilde{N}_i s_i / (1 + \sum_{k=1}^n \tilde{N}_k s_k T_k)$. This is always fulfilled when only one prey species i is present, so our multi-species functional response naturally comprises n single-species functional responses of Holling type II, $f_i = s_{ii} \tilde{N}_i / (1 + T_{ii} s_{ii} \tilde{N}_i)$. This functional response also exhibits type III like behaviour for certain parameter combinations and if one prey type is kept constant (van Leeuwen et al., 2007).

We can furthermore demonstrate that this functional response satisfies the “common sense” condition mentioned in the Introduction. If we assume that of n prey species that are present Species 1 and 2 are equivalent with regard to the modelled predator, we have $s_{i1}=s_{i2}=s_{11}=s_{21}$, $T_{1i}=T_{2i}$, and $T_{i1}=T_{i2}$ for all i . It is easy to see from Eq. (1) that the total intake rate $f_2=f_1+f_2$ of

these two species then depends only on their total availability, and hence remains unchanged, as it should, when the two equivalent species are aggregated into a single species with availability $\tilde{N}_\Sigma = \tilde{N}_1 + \tilde{N}_2$.

3.2. Predators switching between two prey species

We now investigate the simplest and best studied case of prey switching, when only two prey species are involved. Using Eq. (1), we obtain the diet ratio f_1/f_2 as

$$\frac{f_1}{f_2} = \frac{\tilde{N}_1 (s_{11} \tilde{N}_1 + s_{12} \tilde{N}_2)}{\tilde{N}_2 (s_{12} \tilde{N}_1 + s_{22} \tilde{N}_2)}. \quad (2)$$

Experimental data are often interpreted, following Greenwood and Elton (1979), in terms of a power-law relationship between diet ratios and density ratios. The exponents of such power laws are used to measure the strength of prey switching. On scales that are logarithmic in both ratios, the power law simply implies a line with a slope that equals the power-law exponent. In contrast to the related power law for diet partitioning that is found in dietary data at community level (Rossberg et al., 2011), power-law prey switching is generally observed already at the individual level.

As, according to Eq. (2), our model does not predict an exact power-law relationship, we define instead the *equivalent exponent* β as the local slope of the relationship between diet ratio and availability density ratio when both are expressed on logarithmic scales. Unlike a power-law exponent, the equivalent exponent is not constant, but depends on the availability ratio of the prey species.

It follows from Eq. (2) that the equivalent exponent is given by

$$\beta = \frac{d \log(f_1/f_2)}{d \log(\tilde{N}_1/\tilde{N}_2)} = \frac{s_{22} \tilde{N}_2}{s_{22} \tilde{N}_2 + s_{12} \tilde{N}_1} + \frac{s_{11} \tilde{N}_1}{s_{11} \tilde{N}_1 + s_{12} \tilde{N}_2}. \quad (3)$$

While the equivalent exponent β would be constant if switching followed a strict power law, calculating it for two prey species generally requires knowing their availability ratio (or, equivalently, their density ratio and base attack rates). In the two limits $\tilde{N}_1/\tilde{N}_2 \rightarrow \infty$ and $\tilde{N}_1/\tilde{N}_2 \rightarrow 0$, the value of β approaches 1, that is, the effect of prey switching disappears. At $\tilde{N}_1/\tilde{N}_2 = \sqrt{s_{22}/s_{11}}$, the value of the equivalent exponent β reaches a global extremum, i.e. a global maximum for $\beta_{ext} > 1$ and a global minimum for $\beta_{ext} < 1$, and simplifies to

$$\beta_{ext} = 2(1 + s_{12}/\sqrt{s_{11}/s_{22}})^{-1}. \quad (4)$$

Thus, β reaches a maximal value of 2 when $s_{12}=0$ and approaches 0 as $s_{12} \rightarrow \infty$. For the special case of $s_{ij}=1$, this global extremum is reached at $\tilde{N}_1 = \tilde{N}_2$. These results are illustrated in Fig. 2, where we show that a low rate of attacking prey 1 after prey 2 and vice versa, due to low similarity, results in a high equivalent exponent. It follows that, in our model, the equivalent exponent for switching between two prey species can never exceed 2.

To quantify how closely our model resembles a power law, we can estimate the range of availability ratios over which β differs substantially from 1. Specifically, we define the width of the range over which significant prey switching occurs as the distance between the two inflection points of β on a \log_{10} availability-ratio scale (Fig. 3a). Fig. 3b shows this width as a function of the maximum value of β (Eq. (4)). For modest to strong prey switching, β is relatively constant and our model can be approximated by a power law over two orders of magnitude. Since most available experimental data do not cover more than two orders of magnitude in density ratios, it will often be difficult to differentiate between our model and a power law model using currently available data. We can thus conclude that our model,

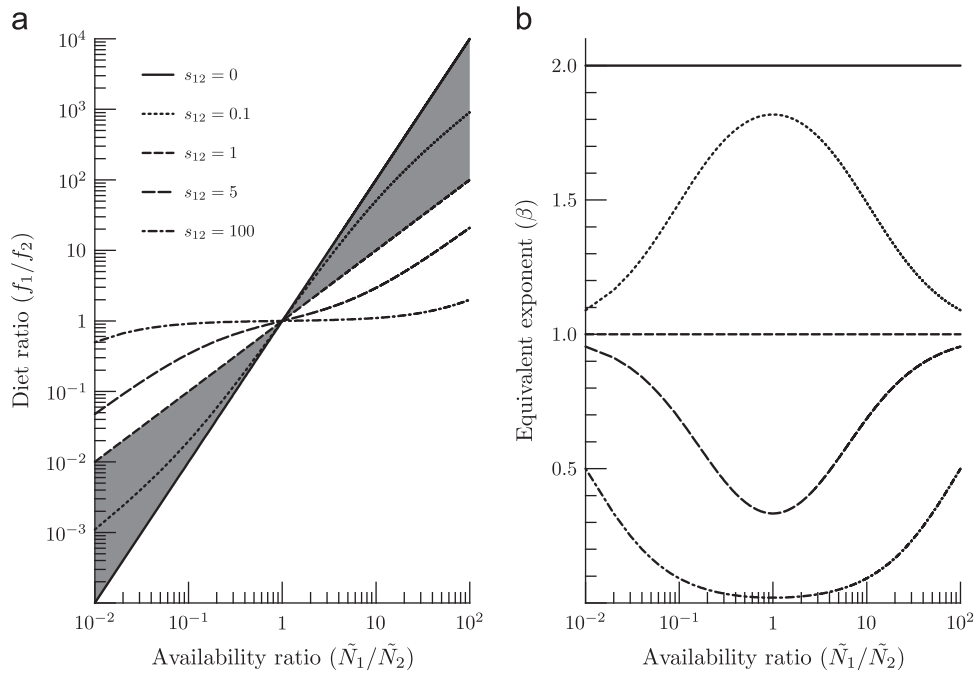


Fig. 2. Switching between two prey species for different switching similarities. (a) Diet ratios depending on availability ratios for different switching similarities s_{12} . The grey area indicates the range of possible relationships resulting from our model for (positive) prey switching. In contrast, an equivalent exponent (local slope) β of less than 1 indicates negative prey switching; this occurs for $s_{12} > \sqrt{s_{11}s_{22}}$ in general and for $s_{12} > 1$ in this figure. (b) Equivalent exponents β depending on availability ratios for the same set of switching similarities as shown in panel (a). Other parameters: $s_{11}=s_{22}=1$.

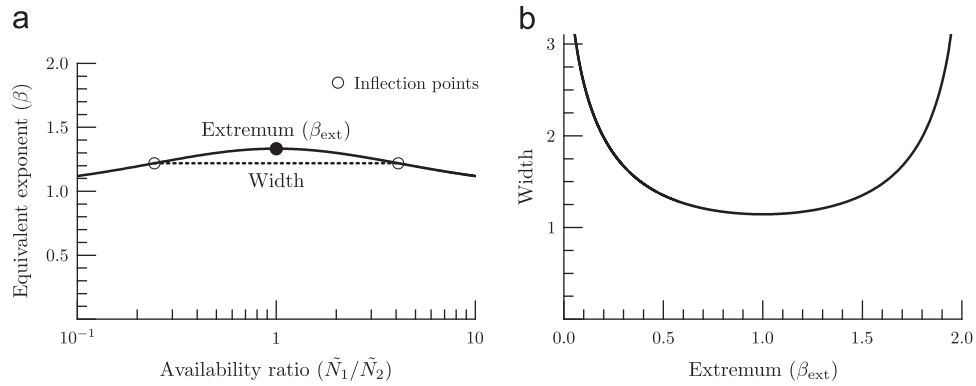


Fig. 3. (a) Illustration of the method for characterizing the range of approximate power-law switching: we consider the dependence of the equivalent exponent β on the availability ratio and measure this range's width by the distance, on a logarithmic scale, between the two inflection points. This width can then be used to indicate the range, in terms of the orders of magnitude it covers, over which our model can be approximated by a power law. (b) Relationship between this width and the extremum β_{ext} of the equivalent exponent β . For prey switching of intermediate strength, the power-law range is most narrow. Other parameters: $s_{11}=s_{22}=1$.

which satisfies the “common sense” condition by consistently describing the effects of extreme abundance ratios, is compatible with all empirical data that does not probe extreme abundance ratios.

3.3. Predators switching between multiple prey species

Most data on prey switching come from laboratory experiments. This is partially because data acquisition in the field is difficult and laborious, but perhaps also due to the nature of prey switching itself. To understand how hard it can be to detect prey switching in the field, we can express the diet ratio f_1/f_2 of two prey species as a function of the availabilities of all n prey species,

$$\frac{f_1}{f_2} = \frac{\tilde{N}_1(s_{11}\tilde{N}_1 + s_{12}\tilde{N}_2 + \sum_{k=3}^n s_{1k}\tilde{N}_k)}{\tilde{N}_2(s_{12}\tilde{N}_1 + s_{22}\tilde{N}_2 + \sum_{k=3}^n s_{2k}\tilde{N}_k)} \tag{5}$$

From this expression it becomes clear that, when the sums over the remaining species $k=3, \dots, n$ contribute substantially to the expressions in the parentheses, prey switching is bound to become less pronounced compared to situations in which only two prey are present. As a general rule, prey switching is less pronounced when the predator consumes many different prey species and when no single prey species accounts for a large share of the predator’s diet. Fig. 4 illustrates this point for three species by varying the availability of the third species. The degree of prey switching depends on the similarities between the two focal species and the third species. If the third species is not overly abundant and very dissimilar from Species 1 and 2 (Fig. 4a), a predator that forages for Species 1 or 2 will continue doing so for a while, so the influence of Species 3 on the predator’s rate of switching between Species 1 and 2 is comparatively weak. When the third species is intermediate in its character, so that it is rather similar to both Species 1 and 2, even though Species 1 and

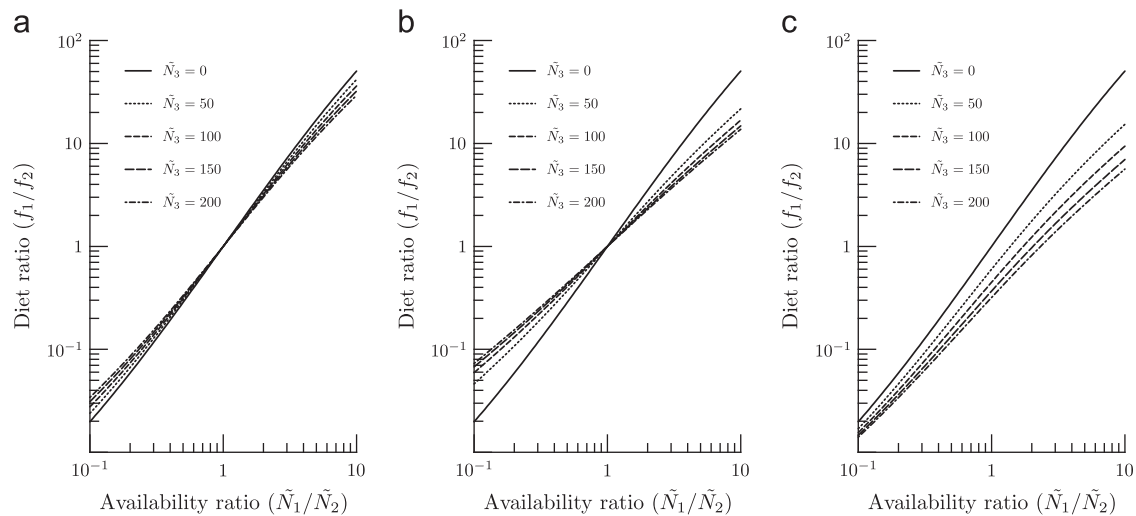


Fig. 4. Switching between two prey species when a third prey species is present at varying availabilities. In all cases, switching between the first two prey species becomes less pronounced at higher availabilities of the third prey species. (a) Switching between the first two species when the third species is very dissimilar from either of them ($s_{13}=0.1$ and $s_{23}=0.1$). (b) Switching between the first two species when the third species is similar to both of them ($s_{13}=0.9$ and $s_{23}=0.9$). (c) Switching between the first two species when the third species is dissimilar from the first species, but similar to the second species ($s_{13}=0.1$ and $s_{23}=0.9$). In this last case, the effect of the third species is more pronounced at high availability ratios \tilde{N}_1/\tilde{N}_2 than at low availability ratios. Other parameters: $\tilde{N}_1 + \tilde{N}_2 = 100$, $s_{12}=0.1$ and $s_{ii}=1$ for $i=1,2,3$.

2 are dissimilar from each other, then the effect of the third species is particularly evident (Fig. 4b). The reason is that Species 3, when abundant, mediates transitions between the two focal species. Finally, a much lower similarity between Species 1 and 3 than between Species 2 and 3 will cause prey switching between Species 1 and 2 to be much more pronounced at lower availability ratios \tilde{N}_1/\tilde{N}_2 (Fig. 4c). This can be understood from Eq. (5), too, since a comparatively large value of \tilde{N}_2 is required to dominate the contribution of the third species in the denominator, while a smaller value of \tilde{N}_1 is sufficient to dominate its contribution in the numerator.

3.4. Calibration to empirical data

To clarify how our results can be fitted to experimental data and how the predictions can be interpreted, we fit it to data on diet ratios and density ratios from a laboratory experiment by Elliott (2006) on prey switching by the fifth instar of the sand fly *Rhyacophila dorsalis* between large *Chironomus* sp. larvae (Type 1) and small *Chironomus* larvae (Type 2) and between large *Chironomus* larvae (Type 1) and *Baetis rhodani* larvae (Type 3). The raw data from these experiments are not available any more, but Prof. J. Malcolm Elliott has kindly provided the summary statistics on the data, such that at each ratio we know the mean number of prey attacked for both species and the associated standard deviations. These experimental results are not rich enough to test if our model provides a better fit than other models. Therefore, the calibration of our model to empirical data presented below serves as a proof of concept and as a demonstration of possible results, the achievable accuracy, and the implied predictions. Details of the model-fitting procedure are provided in Appendix C.

To estimate all parameters in Eq. (1), absolute-intake data are required. Relative intakes are already fully determined by the values of the parameter combinations $\tilde{s}_{ij} = s_{ij}/\sqrt{s_{ii}s_{jj}}$ and $\tilde{c}_i = c_i\sqrt{s_{ii}}/c_1\sqrt{s_{11}}$ for all i and j , and hence only these can be estimated from relative intake data. The value of \tilde{s}_{ij} can be interpreted as a normalized switching similarity (with $\tilde{s}_{ii} = 1$ being implied for all species or, in the present case, types i), while the value of \tilde{c}_i scales the predator's base attack rate for type i . For example, a predator foraging on two equally abundant prey types consumes these at equal rates if and only if their scaled

Table 1

Parameter values for prey switching by the fifth instar of the sand fly *Rhyacophila dorsalis* between large and small *Chironomus* larvae and between large *Chironomus* larvae and *Baetis* larvae. The table shows the maximum-likelihood estimates for four parameters of our model, as well as their 5th and 95th percentiles as described in Appendix C.

Parameter	Maximum-likelihood estimate	5th percentile	95th percentile
\tilde{c}_1	n.a. (set to 1)	n.a	n.a
\tilde{c}_2	0.785	0.776	0.835
\tilde{c}_3	1.326	1.294	1.394
\tilde{s}_{12}	0.154	0.096	0.164
\tilde{s}_{13}	0.010	0	0.043

base attack rates \tilde{c}_1 and \tilde{c}_2 are equal. The scaled parameters therefore allow meaningful ecological interpretations, without fully specifying the functional response. Furthermore, since the number of scaled parameters is lower than that of original parameters, higher estimation accuracies can be achieved.

Table 1 reports the parameter values estimated by maximum-likelihood methods. Fig. 5 shows the original empirical data alongside with new model predictions for the estimated parameter values. Our estimates show that the predator is predisposed to attacking large *Chironomus* larvae over small *Chironomus* larvae and *Baetis* larvae over large *Chironomus* larvae. Furthermore, large and small *Chironomus* larvae have a higher normalized switching similarity for this predator than large *Chironomus* larvae and *Baetis* larvae. The latter finding could be related to the fact that the first pair of prey types are just different size classes of the same species, while in the second pair the two prey types belong to different species.

Since the original data did not include an experiment in which the predator switches between small *Chironomus* larvae and *Baetis* larvae, no estimate is available for \tilde{s}_{23} . We consider the two extremes in which (1) there is no perceived difference between the two species ($\tilde{s}_{23} = 1$) or (2) the difference is so great that the predator will not attack Species 2 directly after attacking Species 3 and vice versa ($\tilde{s}_{23} = 0$). Using these values, we study a hypothetical three-type experiment in which the densities of small *Chironomus* larvae (N_2) and *Baetis* larvae (N_3) are kept equal ($N_2 = N_3$). We then vary the combined density $N_2 + N_3$ relative to

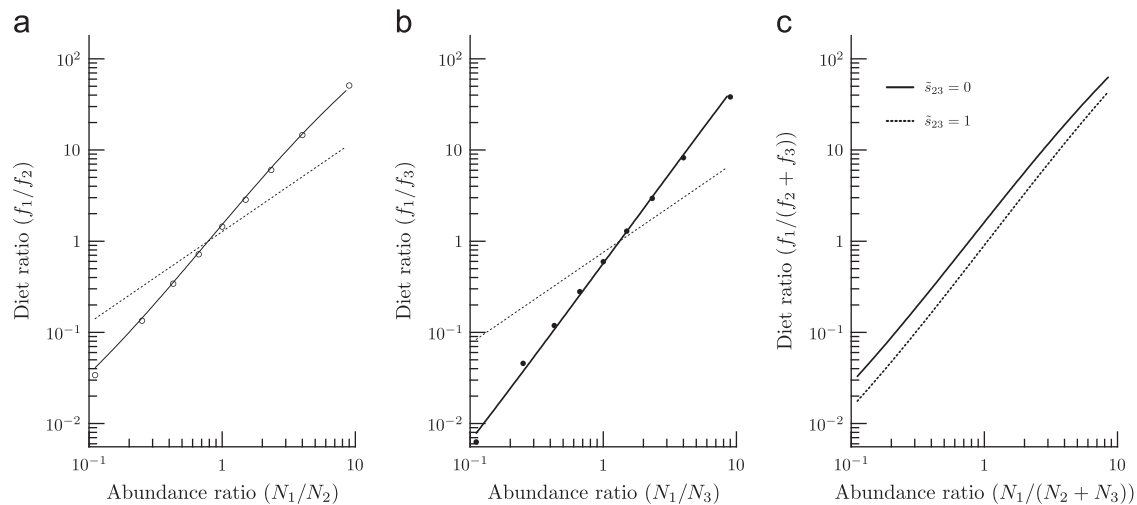


Fig. 5. Switching of the fifth instar of the sand fly *Rhyacophila dorsalis* between (a) large and small *Chironomus* sp. larvae and (b) large *Chironomus* larvae and *Baetis* larvae. The thin dashed lines correspond to the absence of prey switching. The points show the average ratio of prey attacked at each abundance ratio. (c) Predicted outcome of a hypothetical experiment in which all three prey types are present simultaneously.

the density of large *Chironomus* larvae (N_1), while the total prey density ($N_1 + N_2 + N_3$) is kept constant. As shown in Fig. 5c, the equivalent exponent for the hypothetical three-species experiment is intermediate between the two experiments with only two prey species, for both extremes of \bar{s}_{23} .

3.5. Relaxation of inversion indifference

The functional response in Eq. (1) is derived under the assumption of indifference of predators to prey-order inversion or, equivalently, the assumption that switching similarities are symmetric ($s_{ij} = s_{ji}$). This assumption allows the analytic solution of the Markov model described in Methods. In the general case ($s_{ij} \neq s_{ji}$), the Markov model can instead be solved numerically to obtain the predator's functional response. In this section, we relax the simplifying assumption of inversion indifference and numerically study the robustness of the main features of our derived functional response. As the elements s_{ij} no longer allow a natural interpretation as similarities (since $s_{ij} \neq s_{ji}$), we refer to them as acceptance rates below.

For our numerical explorations, the acceptance rates s_{ij} are drawn from a uniform distribution between 0 and 1, and we set $s_{ii} = 1$ for all i . In the general case this can be done without loss of generality, since setting $a_{ij} = c_i s_{ij}$, without the symmetry requirement, introduces free parameters. Prey availabilities (\tilde{N}_i) for $i > 2$ are first drawn from a uniform distribution between 0 and 100. The value of \tilde{N}_1 is chosen such as to obtain a given availability ratio $\tilde{N}_1 / \sum_{i=2}^n \tilde{N}_i$. The diet ratio $f_1 / \sum_{i=2}^n f_i$, that is, the intake of the first species divided by the intakes of all other species (Rossberg et al., 2011), is then computed as a function of the availability ratio $\tilde{N}_1 / \sum_{i=2}^n \tilde{N}_i$. For easier visual comparison, the resultant relationships between those two ratios are shifted up or down along the logarithmic diet-ratio axis such that they pass a diet ratio of 1 at an availability ratio of 1. For communities with two, three, and 10 prey species, these relationships are estimated for 50,000 random parameter combinations each.

The top row of Fig. 6 shows the outcome of our numerical analyses, with the shading indicating the local density of the resultant relationships. For each parameter combination, the equivalent exponent is calculated by numerically differentiating the diet ratio at the availability ratio 1, with the resultant distributions of exponents shown in the bottom row of Fig. 6. These numerical results are similar to the analytical predications

derived from the analytically tractable model. In particular, most equivalent exponents lie between 1 (no switching) and 2, the upper limit for the simplified model. The maximum exponent also decreases with the number of involved species: for ten species, the highest exponent found is smaller than 1.55, underscoring once again that the number of species involved influences the strength of prey switching (Fig. 6c).

4. Discussion

We have developed a generic functional response of a predator switching between multiple prey species. This functional response was derived from an underlying simple model of foraging behaviour. Prey switching emerges when the predator's probability of attacking a prey species depends on its dietary history; otherwise, we recover the standard Holling type II functional response. We have shown that this mechanism leads to power-law switching over approximately two orders of magnitude, conforming to empirical observations. As the functional response is derived from an underlying behavioural model, it fulfils two natural requirements that proved difficult to combine in previous formulations. First, our functional response satisfies the "common sense" condition that population dynamics should be invariant if prey populations with identical properties are aggregated or split. Second, our functional response allows the strength of prey switching to differ among pairs of prey species, thus satisfying a key requirement for matching empirical observations.

4.1. Model assumptions

The analytical results presented here are based on the assumption of indifference of predators to prey-order inversion, which implies similarity symmetry (Appendix A). This assumption seems ecologically plausible, but it need not hold under all circumstances. The general Markov model underlying our results does not depend on this assumption, and thus can be analysed independently of it. The assumption of inversion indifference is required, however, to obtain a closed-form analytic solution for the multi-species function response. In Section 3.5, we analysed the general case numerically and showed that even when relaxing our simplifying assumption, our qualitative results largely hold.

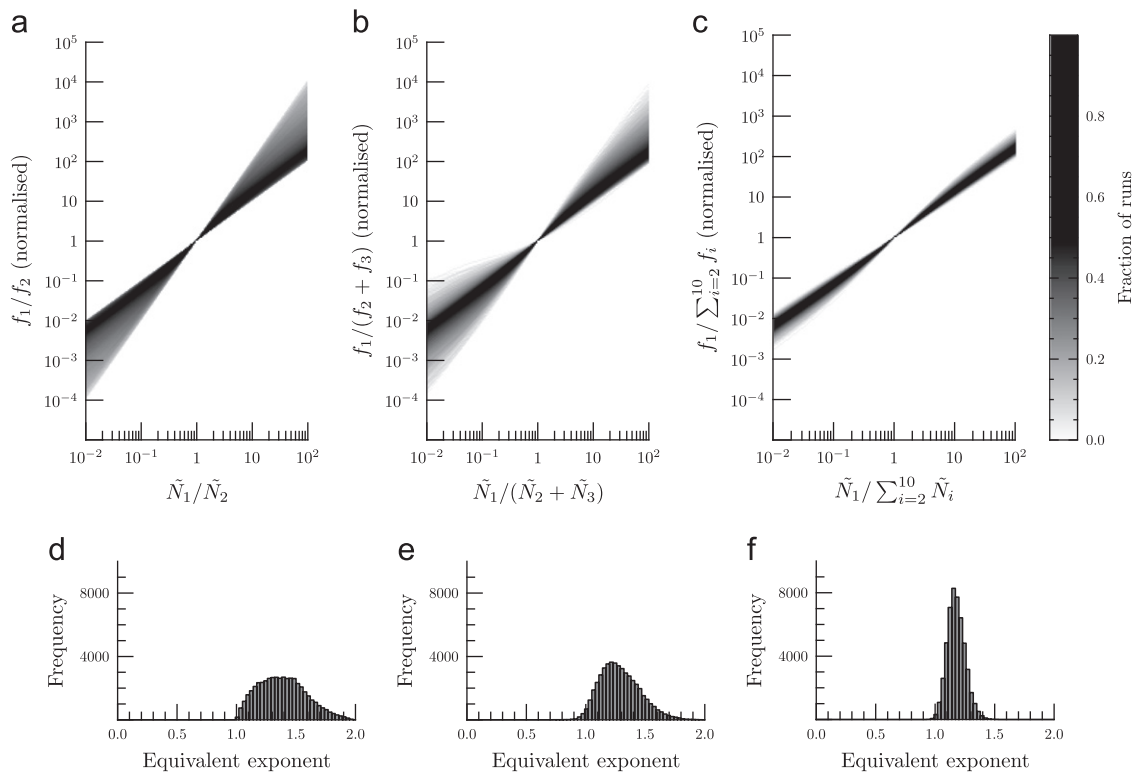


Fig. 6. Switching between multiple prey species without the simplifying assumption of inversion indifference. The (a,d) left, (b,e) middle, and (c,f) right columns show results for communities with two, three, and 10 prey species, respectively. Model parameters and prey availabilities were randomly chosen as explained in the text. (a–c) Using grayscale, the top row shows the density of the resultant dependences of diet ratios on availability ratios. All dependences are normalized so as to pass through the point (1,1). (d–f) The bottom row shows the corresponding distributions of equivalent exponents at $\tilde{N}_1/\sum_{i=2}^n \tilde{N}_i = 1$.

This suggests that the closed-form multi-species functional response derived here is a good model even in the presence of deviations from perfect inversion indifference.

Our model is based on the assumption that a predator's foraging behaviour is only influenced by the last prey attacked and not by any preceding prey. This is a simplification of the effect of dietary history on foraging because, while the last prey attacked often has the strongest influence (Belisle and Cresswell, 1997; Melcer and Chiszar, 1989), previous prey will also influence behaviour (Belisle and Cresswell, 1997). In principle, longer-lasting impacts of dietary history can be taken into account by extending the present theory, but such extensions are likely to considerably complicate the resulting functional response, leading to higher computational burdens in community models. A related simplifying assumption of our model is that the influence of the last prey consumed does not diminish with time. It might be possible to include such limited “memory” in the Markov model by adding a state that represents a foraging predator unaffected by previous history. Understanding the feasibility and implications of such model extensions are promising topics for future research.

4.2. Computational constraints

Real ecological communities can consist of thousands of different species. Modelling population dynamics and evolution of such communities is computationally challenging, so it is useful to estimate how much computation time rises as the number n of modelled species increases. For example, for Lotka–Volterra dynamics of the form $dN_i/dt = r_i(1 + \sum_{j=1}^n f_{ij})N_i$ with $f_{ij} = \alpha_{ji}N_j$ for $ij = 1, \dots, n$, the most time-consuming computational task is to determine the sums over j . In general, the number of operations this requires in each time step increases as n^2 with

community size. If (α_{ji}) is a sparse matrix containing on average only $Z \ll n$ non-zero elements in each row or column, then sparse-matrix algorithms can be used, and the computation time per time step increases only as nZ . The question of how the mean number of non-zero elements of (α_{ji}) , which is closely related to the link density denoted by Z in food-web theory, depends on community size has long been discussed in the literature (Justus, 2008). Recent analyses suggest that Z remains relatively small and bounded as community size increases (Rossberg et al., 2011).

Using our derived functional response, Eq. (1), in numerical analyses of food-web models requires evaluation of the sum $\sum_{i=1}^n f_{ij}$ for each predator (we have suppressed the index j so far, focusing our preceding discussions on a single predator). This sum determines the total rate of food intake by predator j , and a similar expression determines the total predation mortality experienced by each prey species. Since the denominator of our functional response in Eq. (1) does not depend on i , this amounts to evaluating at most three double sums over n species for each of n species in a community (for non-predators only one such sum is required). Without sparse-matrix algorithms, the computation time for each time step therefore increases as n^3 with community size, potentially rendering numerical analyses infeasible. But if, for each predator j , the vector c_{ij} of its base attack rates is sparse, that is, if each consumer attacks on average only a small number $Z \ll n$ of prey, then all three double sums can be evaluated in a computation time that grows as Z^2 . Computation time per time step then increases as nZ^2 , imposing more moderate computational constraints. For $Z \ll n$, we can thus be optimistic that numerical analyses remain computationally feasible even when the scaling of computation time changes from nZ for Lotka–Volterra dynamics to nZ^2 for the multi-species functional response we have derived in this study.

4.3. Transitivity of equivalent exponents or the A–B–C problem

Let us shortly come back to the problem, highlighted in the introduction, that for some multi-species functional responses the switching exponent or, by extension, the equivalent switching exponents are necessarily equal for all three pairings of three resource species *A*, *B*, and *C* when they are equal for *A*–*B* and *B*–*C*. In Appendix D we show that this artifact persists for any kind of functional response where the prey intake ratio of two species, say *B* and *C*, is independent of the abundances of other species, such as *A*. The functional response derived here is more flexible. Appendix D argues that, in agreement with ecological intuition, the equivalent switching exponent tends to be larger for *A*–*C* than for the pairings *A*–*B* and *B*–*C* when *A* and *C* are ecologically less similar to each other than they are to *B* (specifically, when $\tilde{s}_{AB} = \tilde{s}_{BC} > \tilde{s}_{AC}$).

4.4. Implications for community dynamics

Our model predicts that equivalent exponents approach 1 at very high and very low relative abundances, so there is only an intermediate range of abundance ratios over which prey switching can be observed. This model prediction can be tested empirically and may have implications for the maintenance of biodiversity. Equivalent exponents larger than 1 imply that per-capita predation pressures on a species steadily decrease as its relative abundance declines and vanishes for very rare species. Based on this traditional expectation, rare species involved in prey switching would experience reduced predation mortality, which could help them to avoid extinction. In contrast, our results imply a finite lower limit on the per-capita predation pressures on a rare species; this limit depends on the abundances of other prey species and is readily computed from Eq. (1). Our results thus imply that, in contrast to the traditional theory, prey switching hardly protects rare species once they have fallen below a certain relative abundance.

4.5. Prey quality and optimal foraging

For predators, prey quality can be an important factor influencing prey choice. The assumption that prey quality is the main factor determining prey choice is pursued in optimal-foraging theory (Emlen, 1966; Charnov, 1976). Under the additional assumption of a trade-off in attack rates, this leads to prey switching (Abrams and Matsuda, 2004; Rueffler et al., 2004). Dynamic implications for this assumption in simple two-resource one-consumer models were studied extensively by (Abrams and Matsuda, 2003, 2004; Rueffler et al., 2004; Matsuda, 1985). A generalisation of these trade-offs to many prey species leads to effort-based functional responses (Drossel, 2001; Kondoh, 2003; Uchida et al., 2007). The strength of prey switching then depends on a trade-off in attack rates; however, our knowledge of the exact nature of these trade-offs is still limited (Palaima, 2007).

Our approach assumes that dietary history affects switching. One potential underlying mechanism is the trade-off resulting from the limited total attention a predator can give to prey (Dukas and Kamil, 2001; Dukas, 2002; Bond, 2007), which leads to the formation of search images (Tinbergen, 1960; Dawkins, 1971; Pietrewicz and Kamil, 1979; Melcer and Chiszar, 1989; Reid and Shettleworth, 1992; Bond and Kamil, 1999; Jackson and Li, 2004; van Leeuwen and Jansen, 2010). To some degree, the effects of prey quality can implicitly be incorporated in our model by multiplicative factors contributing to the base attack rates and/or switching rates. Through such extensions, our model can be used to study optimal foraging while relaxing the, often implicit, assumption that predators have perfect knowledge of prey

densities (Belisle and Cresswell, 1997). Instead predators obtain knowledge about prey densities through their foraging activity (Belisle and Cresswell, 1997; van Leeuwen et al., 2007; van Leeuwen and Jansen, 2010).

It is difficult to differentiate between the two models using currently available data because qualitatively the predictions made by the two models are similar. For example, studies classified as qualitatively consistent with the optimal-foraging theory in Sih and Christensen, (2001) are also qualitatively consistent with our model, since the two criteria used in that study are also satisfied by our model. Firstly, the condition that predators select for higher quality prey is satisfied in our model under the assumption that the preferences \tilde{c}_j for prey species *j* are positively related to their quality. Secondly, in both models an increase in higher quality prey results in a disproportionately increase of this prey in the predator's diet. Therefore, it will be difficult to differentiate between data supporting our model and optimal foraging, without setting up experiments that specifically tests for different predictions made by the two models.

4.6. Comparison with empirical observations

Greenwood and Elton (1979) and Elliott (2004, 2006) analysed a combined total of 24 experiments using Greenwood and Elton (1979) heuristic model of prey switching. The switching exponents they estimated for those experiments cover the range between 0.4 and 2.0. This range is consistent with the predictions of our model, in particular with the finding that the equivalent exponent will always be smaller than 2 (Section 3.2). This upper limit essentially persists when the simplifying assumption of inversion indifference is relaxed (Section 3.5). The fact that our model accurately predicts this upper bound sets it apart from other approaches to prey switching.

The upper bound on prey-switching exponents is only one of several predictions enabled by our theory. It should thus be possible to corroborate our theory empirically. This would require modifying existing experimental designs to extend the range of prey-abundance ratios to about three orders of magnitude or more. Alternatively or in addition, experimenters could also systematically confront predators with different combinations of two, three, or more prey species. It is then straightforward to compare Eq. (1) or (5) to such data, and thus to assess which of our theory's multiple testable predictions are borne out.

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Ministry of Science and Research, and the Vienna Science and Technology Fund. E.v.L. and A.G.R. conceived the study and formulated the model. E.v.L., Å.B. and A.G.R. performed the analyses. E.v.L. led the writing, all authors contributed to the interpretation of results and the writing of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2013.02.003>.

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APPENDIX A. EQUIVALENCE OF INVERSION INDIFFERENCE WITH SIMILARITY SYMMETRY

Here we explain why inversion indifference implies similarity symmetry, and vice versa. We first prove the following theorem. For any integer $n \geq 1$, and any $n \times n$ matrix (a_{ij}) with a_{ij} real and positive for all $1 \leq i, j \leq n$, the following two conditions are equivalent:

- (I) $a_{ij}a_{jk}a_{ki} = a_{ik}a_{kj}a_{ji}$ for all $1 \leq i, j, k \leq n$.
- (II) There are positive real numbers s_{ij} and c_i such that $s_{ij} = s_{ji}$ and $a_{ij} = c_i s_{ij}$ for all $1 \leq i, j \leq n$.

Proof: To see that (II) implies (I), we can just insert $a_{ij} = c_i s_{ij}$ into the equation in (I) and use $s_{ij} = s_{ji}$ from (II). To see that (I) implies (II), we construct an appropriate set of numbers s_{ij} and c_i , and demonstrate that $s_{ij} = s_{ji}$. First, we set $c_i = a_{i1}a_{i1} / a_{1i}$ for all i . From $a_{ij} = c_i s_{ij}$ and $c_i > 0$, we then obtain $s_{ij} = a_{ij} / c_i = (a_{ij}a_{1i}) / (a_{1i}a_{1i})$. The fact that $s_{ij} = s_{ji}$ is best verified by demonstrating that $s_{ij} / s_{ji} = 1$, $s_{ij} / s_{ji} = [(a_{ij}a_{1i}) / (a_{1i}a_{1i})] / [(a_{ji}a_{1j}) / (a_{1j}a_{1j})] = (a_{ij}a_{1i}a_{1j}) / (a_{1i}a_{1j}a_{ji}) = 1$, where we have used (I) in the last step. \square

While (II) has the obvious ecological interpretation that the similarities s_{ij} between species are symmetric, (I) needs more explanation. The probability that a predator that just consumed species j next consumes species i is

$$P_{i|j} = \frac{a_{ij}N_i}{\sum_{k=1}^n a_{kj}N_k}. \quad (\text{A.1})$$

Consequently, the probability that a predator, after having consumed i , will then consume, in this order, j , k , and again i , is

$$P_{i|k|j|i} = P_{i|k}P_{k|j}P_{j|i}, \quad (\text{A.2})$$

while the probability for consumption in the reverse order is

$$P_{i|j|k|i} = P_{i|j}P_{j|k}P_{k|i}. \quad (\text{A.3})$$

By inserting eq. (A.1) into eqs. (A.2) and (A.3), we see that these two probabilities are equal, $P_{i|k|j|i} = P_{i|j|k|i}$, if, and generally only if, (I) holds. (I) can therefore be interpreted as meaning that the probability of having cyclic sequences of three prey does not depend on the orientation of the cycle. Since (I) implies (II), and since from (II) equalities as in (I) but with longer prey cycles are easily derived, this interpretation immediately extends to longer cycles of prey consumption.

The theorem above technically excludes cases in which $a_{ij} = 0$ for some prey species i or j . While such cases could be included with some technical overhead, this effort would not seem to yield additional ecological insights, as ecological situations in which some attack rates vanish are well approximated by setting those rates to very small positive values.

APPENDIX B. DERIVATION OF THE FUNCTIONAL RESPONSE TO MULTIPLE PREY SPECIES

Here we present a formal derivation of the general functional response in eq. (1) from our Markov model accounting for dietary history.

In our model, a predator is either foraging or handling prey, with n species of prey to choose from. We denote by P_{0i} for $1 \leq i \leq n$ the probability that, at a given time, a specific predator individual is alive, foraging, and its previous prey was of species i . Likewise, we denote by P_{ij} for $1 \leq i, j \leq n$ the probability that the predator is currently handling prey species i and its previous prey was of species j . Handling is here meant to include all activities other than foraging, specifically the times spent resting or reproducing. Just as Van Leeuwen et al. (1), we set up the equations determining the Markov process as

$$\frac{dP_{0i}}{dt} = \sum_{j=1}^n \left\{ -a_{ji} N_j P_{0i} + \frac{1}{T_{ij}} P_{ij} \right\} + (\text{birth} - \text{death}), \quad (\text{B.1})$$

$$\frac{dP_{ij}}{dt} = -\frac{1}{T_{ij}} P_{ij} + a_{ij} N_i P_{0j} + (\text{birth} - \text{death}), \quad (\text{B.2})$$

where a_{ij} denotes the predator's attack rate on prey species i if its previous prey was species j , T_{ij} denotes the handling time for species i if the previous prey species was j , and N_i denotes the density of prey species i .

When birth and death are slow processes compared to prey capture and handling, so that a predator will handle many prey during its lifetime, the corresponding contributions above will be small and can thus be ignored. On population-dynamical timescales, the Markov process will therefore be in a quasi-equilibrium, so the time derivatives on the left-hand sides above can be set to 0 and we are left with a homogeneous system of linear equations for P_{0i} and P_{ij} with $1 \leq i, j \leq n$. We can then solve eq. (B.2) for P_{ij} / T_{ij} and substitute the result into eq. (B.1),

$$0 = \sum_{j=1}^n \left\{ -a_{ji} N_j P_{0i} + a_{ij} N_i P_{0j} \right\}. \quad (\text{B.3})$$

In general, this system of n linear equations has to be solved numerically. Before making use of our simplifying assumption to obtain a closed-form solution, we first show how the general solution of eq. (B.3) determines the predator's functional response.

According our definitions above, the probability P that a predator is alive at all, rather than dead or as yet unborn, is given by the sum of all P_{0k} and P_{kj} ,

$$P = \sum_{k=1}^n \left\{ P_{0k} + \sum_{j=1}^n P_{kj} \right\}, \quad (\text{B.4})$$

which gives, using eq. (B.2),

$$P = \sum_{k=1}^n \left\{ P_{0k} + \sum_{j=1}^n a_{kj} N_k P_{0j} T_{kj} \right\}. \quad (\text{B.5})$$

The mean consumption rate of prey species i by a given living predator is the rate at which the predator (successfully) attacks i . If the predator had previously attacked species k , this rate equals $N_i a_{ik}$. Taking the expectation over all prey species k , using the probabilities P_{0k} , and dividing by P to condition on the predator being alive, this yields the mean consumption rate $f_i = (\sum_{k=1}^n N_i a_{ik} P_{0k}) / P$. Making use of eq. (B.5), we thus obtain the

general functional response

$$f_i = \frac{N_i \sum_{k=1}^n a_{ik} P_{0k}}{\sum_{k=1}^n \left(P_{0k} + \sum_{j=1}^n a_{kj} N_k P_{0j} T_{kj} \right)}. \quad (\text{B.6})$$

To eliminate the probabilities P_{0k} and P_{0j} from eq. (B.6), we now solve eq. (B.3) by employing the additional assumption that $a_{ij} = c_i s_{ij}$ with $s_{ij} = s_{ji}$ for all $1 \leq i, j \leq n$. Considering $P_{0k} = \kappa c_k N_k$ as an ansatz for all k , with some unknown normalization constant κ , we see that each individual term $-a_{ji} N_j P_{0i} + a_{ij} N_i P_{0j}$ in the sum over j in eq. (B.3) then evaluates to $-c_j s_{ji} N_j \kappa c_i N_i + c_i s_{ij} N_i \kappa c_j N_j = 0$. Except in special cases, the solution of the linear system in eq. (B.3) is unique up to normalization, so $P_{0k} = \kappa c_k N_k$ must be this unique solution. (The special cases are not of interest here, since they involve matrices a that are reducible: these occur, for example, when a predator that has foraged on one subset of prey species can never forage on another subset of prey species, because those two subsets live on different islands.) Inserting the expressions for a_{ij} and P_{0k} into eq. (B.6), we obtain our main result,

$$f_i = \frac{c_i N_i \sum_{k=1}^n s_{ik} c_k N_k}{\sum_{k=1}^n c_k N_k \left(1 + \sum_{j=1}^n s_{kj} T_{kj} c_j N_j \right)}, \quad (\text{B.7})$$

as shown in eq. (1).

APPENDIX C. DATA ANALYSIS

To illustrate the estimation of parameters of our model, we used data analyzed by Elliott (2) on prey switching by the fifth instar of the sand fly *Rhyacophila dorsalis*. The data derives from two experiments, in which *Rhyacophila* could predate on large and small *Chironomus* sp. larvae, and on large *Chironomus* larvae and *Baetis rhodani* larvae, respectively. Both experiments investigated nine different prey-abundance ratios, with predators being offered in each case a total of 200 prey individuals. Each ratio was replicated 10 times. Since the raw data from these experiments is not available, our results are based on the means and standard deviations of the numbers of prey attacked for each prey-abundance ratio.

For estimating the parameters, we set $\tilde{c}_1 = 1$ without loss of generality. To obtain the maximum-likelihood estimates of the model parameters shown in Table 1, intake ratios and abundance ratios were calculated based on the assumption that logarithmic mean diet ratios had identically and normally distributed measurement errors. The model parameters were then determined using the fitting methods provided by Bolker's maximum-likelihood package for R (3).

Confidence intervals for the parameters were established as follows. First, we calculated the standard errors of the means by dividing the known sample standard deviations by the square root of the number of observations ($\sqrt{10}$). We generated 5,000 randomized data sets by drawing each data point from a normal distribution with a mean equal to the empirical mean and a standard deviation equal to the empirical standard error. The model was fitted to

the randomized data and confidence intervals for each model parameter were obtained as the range between the 5th and 95th percentiles of the 5,000 resultant maximum-likelihood estimates.

APPENDIX D. TRANSITIVITY OF EQUIVALENT EXPONENTS

Here we analyze the problem, highlighted in the introduction, that for some multi-species functional responses the switching exponent and, by extension, the equivalent switching exponent are necessarily equal for all three pairing between resource species A , B , and C if they are equal for switching between A and B and between B and C . The following general formulation helps understanding under which circumstances this phenomenon will arise, and when it will not. Denote the logarithms of the abundances of three prey species A , B , and C of a consumer by $v_i = \log N_i$ ($i = A, B, C$). Let $r_1(v_A, v_B, v_C)$ be the ratio of prey A taken by the predator relative to B , and $r_2(v_A, v_B, v_C)$ the intake ratio of B to C , and define $\rho_i(v_A, v_B, v_C) = \log r_i(v_A, v_B, v_C)$ (with $i = 1, 2$).

In this general setting, the values of equivalent exponents depend on the degree to which a change in the abundance ratio of two prey species is due to changes in the abundance of one species or the other. These dependences are quantified by the parameters $q_1 = d \log(N_A/N_B) / d \log N_A = d(v_A - v_B) / dv_A = 1 - dv_B / dv_A$, $q_2 = d(v_B - v_C) / dv_B$, and $q_3 = d(v_A - v_C) / dv_A$. Values of $q_i < 1$ ($i=1,2,3$) correspond to the less intuitive situations where the denominator of the abundance ratio increases at the same time as the numerator increases, and vice versa. A balanced change in the abundances, e.g., of N_A and N_B , such that $N_A N_B$ remains fixed, corresponds to $q_1 = 2$.

The equivalent exponents for the three pairings $A - B$ (β_1), $B - C$ (β_2), and $A - C$ (β_3) then evaluate to

$$\begin{aligned}\beta_1 &= \frac{d\rho_1}{d(v_A - v_B)} = \frac{1}{q_1} \frac{d\rho_1}{dv_A} = \frac{1}{q_1} \frac{\partial \rho_1}{\partial v_A} + \frac{1 - q_1}{q_1} \frac{\partial \rho_1}{\partial v_B}, \\ \beta_2 &= \frac{d\rho_2}{d(v_B - v_C)} = \frac{1}{q_2} \frac{d\rho_2}{dv_B} = \frac{1}{q_2} \frac{\partial \rho_2}{\partial v_B} + \frac{1 - q_2}{q_2} \frac{\partial \rho_2}{\partial v_C}, \\ \beta_3 &= \frac{d(\rho_1 + \rho_2)}{d(v_A - v_C)} = \frac{1}{q_3} \frac{\partial \rho_1}{\partial v_A} + \frac{1 - q_3}{q_3} \frac{\partial \rho_1}{\partial v_C} + \frac{1}{q_3} \frac{\partial \rho_2}{\partial v_A} + \frac{1 - q_3}{q_3} \frac{\partial \rho_2}{\partial v_C}.\end{aligned}\tag{D.1}$$

We now consider the special case of equally abundant A and C and symmetry in their ecological roles relative to B , so that $\partial \rho_2 / \partial v_C = -\partial \rho_1 / \partial v_A$ and $\partial \rho_1 / \partial v_C = -\partial \rho_2 / \partial v_A$. Further, let intake ratios depend only on relative but not on absolute abundances, as most theories would predict, so that $\partial \rho_i / \partial v_A + \partial \rho_i / \partial v_B + \partial \rho_i / \partial v_C = 0$ for $i = 1, 2$. The expressions for the equivalent exponents then simplify to

$$\begin{aligned}\beta_1 &= \frac{\partial \rho_1}{\partial v_A} + \frac{1 - q_1}{q_1} \frac{\partial \rho_2}{\partial v_A}, \\ \beta_2 &= \frac{\partial \rho_1}{\partial v_A} - \frac{1}{q_2} \frac{\partial \rho_2}{\partial v_A}, \\ \beta_3 &= \frac{\partial \rho_1}{\partial v_A} + \frac{\partial \rho_2}{\partial v_A}.\end{aligned}\tag{D.2}$$

In the special case $q_1 = 1/2$, $q_2 = -1$ all three equivalent exponents are equal. But in

general this is the case only for functional responses satisfying $\partial\rho_2/\partial v_A = 0$, that is, when the intake ratio of B and C is independent of the abundance of A . This is the case, for example, for power-law switching. For the functional response derived here and under the assumed symmetry between A and C ,

$$\frac{\partial\rho_2}{\partial v_A} = \frac{\tilde{s}_{AB}(\tilde{s}_{AB}h+1)-\tilde{s}_{AC}(h+\tilde{s}_{AC})}{(2\tilde{s}_{AB}+h)(\tilde{s}_{AC}+\tilde{s}_{AB}h+1)}, \quad (\text{D.3})$$

abbreviating $h = \tilde{c}_B N_B / (\tilde{c}_A N_A)$ and using the tilde notation as in Sec. 3.4. With equal availabilities of all prey, i.e., $h = 1$, this becomes

$$\frac{\partial\rho_2}{\partial v_A} = \frac{\tilde{s}_{AB}-\tilde{s}_{AC}}{2\tilde{s}_{AB}+1}. \quad (\text{D.4})$$

That is, in this highly symmetric case the three equivalent exponents become all equal only by setting $\tilde{s}_{AB} = \tilde{s}_{AC}$, thus making all three prey species ecologically equivalent. If, on the other hand, both A and C are ecologically more similar to B than they are to each other, one can expect $\tilde{s}_{AB} > \tilde{s}_{AC}$. Then $\partial\rho_2/\partial v_A > 0$, and, as long as $q_1, q_2 > 1$, the equivalent exponent β_3 for the pair A - C becomes larger than those for A - B and B - C , as expected.

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