The adaptation of generalist predators’ diet in a multi-prey context: insights from new functional responses

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February 29, 2016

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1890/15-0427.1
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Abstract

The ability for a generalist consumer to adapt its foraging strategy (the multi-species functional response, MSFR) is a milestone in ecology as it contributes to the structure of food webs. The trophic interaction between a generalist predator, as the red fox or the barn owl, and its prey community, mainly composed of small-mammals, has been empirically and theoretically widely studied. However, the extent to which these predators adapt their diet according to both multi-annual changes in multiple prey species availability (frequency dependence) and the variation of the total prey density (density dependence) is unexplored. We provide a new general model of MSFR disentangling changes in prey preference according to variation of prey frequency (switching) and of total prey density (we propose the new concept of “rank switching”). We apply these models to two large data sets of red fox and barn owl foraging. We show that both frequency-dependent and density-dependent switching are critical properties of these two systems, suggesting that barn owl and red fox have an accurate image of the prey community in terms of frequency and absolute density. Moreover, we show that negative switching, which can lead to prey instability, is a strong property of the two systems.

Keywords predation ; prey community ; preference ; switching ; rank switching ; Vulpes vulpes ; Tyto alba.

Introduction

Many terrestrial species display cyclic dynamics from primary producer to a large range of consumers (Schmidt and Ostfeld, 2008) including small mammals (Lambin et al., 2006;
Krebs, 2013). An increasing interest is how generalist predators adapt their foraging strategies to the variations of prey community (Kondoh, 2003; Loeuille, 2010). Descriptions of the occurrence and strength of predator-prey interactions have led to important insights into how to characterize the organization and dynamics of food webs (May, 1974; Pascual and Dunne, 2005). Since the seminal work of Holling (1959), it is well established that the functional response, defined as the rate per consumer of ingestion of a prey according to its availability, is nonlinear whenever there are satiation conditions and sizable handling time (traditionally defined as the time to capture, eat and digest the prey) (Jeschke et al., 2004). Moreover, theoretical and empirical studies showed that the food intake of consumers is expected to depend on interactions between prey, leading to the use of Multi-Species Functional Responses (MSFR) (Murdoch, 1972; Oaten and Murdoch, 1975; Gentleman et al., 2003; Smout et al., 2010; Morozov and Petrovskii, 2013; Vallina et al., 2014).

The first predator-prey models by Lotka-Volterra used linear rate of predation implying an unlimited feeding capacity per predator. For the more realistic Holling type II functional response, the predator’s ingestion rate increases and saturates with prey density (Holling, 1959). Prey switching, defined as a change of preference to a prey with a variation of its relative density, has been associated with foraging adaptation (Murdoch, 1969; Chesson, 1984). This led to a wide use of the switching functional response Holling type III modeling the adaptive change of a predator to over-consume a prey whose proportion increases (Holling, 1959; Morozov, 2010). This is called positive switching, which influences the stability of population dynamics (Pelletier, 2000; Kondoh, 2003; Williams and Martinez, 2004; Morozov, 2010). Negative switching refers to a change from being over-represented to under-represented in the diet compared to the relative density in the environment (Murdoch, 1969; Chesson, 1984; Kean-Howie et al., 1988; Gentleman et al., 2003). Since the definition of
Murdoch (1969), switching, positive and negative, has always been based on prey proportion availability (i.e. frequency-dependent) (Murdoch, 1969; Chesson, 1984; Gentleman et al., 2003; Van Leeuwen et al., 2007) (see Fig. 1.a,b). However, another kind of switching can be considered to account for a change of preference with the total density of all prey. This property we call “rank switching” is a change of the rank of species in the diet of the predator with a change of the total amount of prey. For instance, the prey A is preferred over B when the density of $A + B$ is smaller than 50 and prey B is preferred over A when density of $A + B$ is larger than 50. This rank switching might happen even if both prey are at equal proportion in the environment in both situations (see Fig. 1.c). As a consequence, the changes in preferences, which is traditionally frequency-dependent with switching (Murdoch, 1969; Chesson, 1984), may also include density-dependence with rank switching. To our knowledge, the distinction between both types of switching has never been taken into account in MSFR, and this paper is a first step in this direction.

The present study aims at first proposing a new modeling framework of MSFR that allows incorporating and testing the foraging properties of switching and rank switching. Second, we examined these MSFRs empirically with field data on two generalist predators, the red fox *Vulpes vulpes* and the barn owl *Tyto alba*. We used a Bayesian framework developed in Smout et al. (2010) to fit field data of those two generalist predators collected in the Jura mountains of eastern France. In this region, landscape composition and structure are favorable to population outbreaks of the water vole (*Arvicola scherman*) and the common vole (*Microtus arvalis*), two grassland rodents whose population biomasses are dominant in the landscape (Raoul et al., 2001; Berthier et al., 2014). Population declines of other small mammals species living in grassland and other habitats (e.g. the wood mouse *Apodemus sylvaticus* or the bank vole *Myodes glareolus*) are synchronous with the declines of grassland.

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species (Raoul et al., 2001; Bernard et al., 2010), strengthening the interest for the predator’s diet response to variation of total density of prey. As a consequence, this system offers a well-suited setting to comprehensively model functional responses of generalist predators in a context of fluctuating multi-prey dynamics. We predict complex change in preference of both predators including switching and rank switching as responses to, respectively, the variation in prey assemblage composition (i.e. species relative densities) and the highly variable availability of the total amount of prey, with population outbreaks and crashes.

In this study we first constructed a structural model of MSFR being able to include a large set of mechanistic rules that describe the foraging characteristics of generalist predators (i.e. preference, types of switching and overall feeding). Then, we adapted several MSFRs existing in the literature, from the classical Holling’s equations to more recent ones, to our new structural model. This led to 9 MSFRs. Finally, we evaluated the goodness-of-fit of those 9 MSFRs with Bayesian inference for the two predator-prey systems (i.e. the red fox and the barn owl).

Methods

Construction of a structural model of functional responses

The mechanistic derivation of functional responses is inspired by the work of Holling (1959); Oaten and Murdoch (1975) and Van Leeuwen et al. (2007) where the predator population is divided into several foraging states. For a system with $n$ prey, we assumed $n + 1$ states for predators: a searching state when a predator is searching for prey, and $n$ handling states when predators have found and are currently handling (i.e. digesting) a prey of a certain type $i$. The density of the predator population $P$ satisfies $P = P_s + \sum_j P_{h_j}$, where $P_s$ is
the population of searching predators and $P_{hi}$ is the population of predators handling prey type $i$. We consider two steps in the searching process, that is the transition from $P_s$ to $P_{hi}$ (see Fig. 2). The first step is based on the assumption that a generalist predator is looking for any kind of prey in its foraging area, what we called the rate of accessibility to the prey community. And then, once a prey is detected, we assume in the second step that the predator choose to attack and eat according to its preference.

The first step is therefore the rate of accessibility to the set of all prey present in the foraging area referring to the benefit of the prey community in terms of the potential total prey ingestion (Tilman, 1980; Holt, 1983; Gentleman et al., 2003). In optimal foraging theory, Tilman (1980) and Holt (1983) studied how the combination of several prey species, that is the prey community, may increase (synergy) or decrease (antagony) the total amount of all prey ingested by the predator. This total of prey ingested results in what Jeschke et al. (2002) defined as a “predator’s hunger level”. For single-species functional response, Jeschke et al. (2002) proposed that our first step, the rate of accessibility (i.e. what they called “searching probability”), is a function of the predator’s hunger level itself depending on the prey density. The rate of accessibility is denoted $\alpha(x)$ where $x$ is the prey density. In a context of multi-prey species, we simply extend this theory by considering that the rate of accessibility is a function of the state of the prey community. Thus, the rate of accessibility is a generalized polynomial $\alpha(\vec{x})$ [time$^{-1}$] depending on each prey density in the foraging area, $\vec{x} = \{x_1, x_2, \ldots, x_n\}$:

$$\alpha(\vec{x}) = \sum_j a_j x_j^{n_j},$$  

(1)

where $a_j$ is the attack rate specific to prey $j$ (Chesson, 1984), and $n_j$ accounts for a non-linear
density-dependency of accessibility to prey community (Tilman, 1980; Holt, 1983).

The second step is the preference of the predator specific to every prey species $i$ modeled with a function $p_i(\vec{x})$ [probability] (Fig. 1), satisfying $\sum_j p_j(\vec{x}) = 1$. The transition rate from searching to handling a prey $i$ is the rate of prey $i$ successfully attacked (i.e. ingested). Therefore, the number of prey eaten per predator and per unit of time, that is the MSFR $\Phi_i(\vec{x})$, is the product of the transition rate with the proportion of predator searching for a prey:

$$\Phi_i(\vec{x}) = \alpha(\vec{x}) \times p_i(\vec{x}) \times \frac{P_s}{P}. \quad (2)$$

Then, the transition rate from handling state to searching state is denoted $1/h_i$ (Fig. 1), where $h_i$ [time] describes the time taken by the consumer to digest the prey item $i$ (the handling time). Solving the equilibrium of the dynamical system of predators’ states by means of (2) gives the structural formulation of the functional response (see Appendix S1, Eqs. S1-S7 for further details):

$$\Phi_i(\vec{x}) = p_i(\vec{x}) \times \frac{\alpha(\vec{x})}{1 + \alpha(\vec{x}) \sum_j p_j(\vec{x}) h_j} = p_i(\vec{x}) \times \Theta(\vec{x}) \quad (3)$$

In equation (3), $\Theta(\vec{x})$ is the total ingestion rate called overall feeding (Chesson, 1984; Vallina et al., 2014). With this formulation, it is of real interest to see how the predator’s hunger level, resulting from the total of prey ingested $\Theta(\vec{x})$, is linked with the rate of accessibility to the prey community $\alpha(\vec{x})$. This division of the MSFR in two parts is a common formulation (Gentleman et al., 2003; Morozov and Petrovskii, 2013; Vallina et al., 2014), and has the great advantage to distinguish what concerns the preference behavior of the predator (i.e. $p_i$), from the pattern of overall feeding depending on the composition of the prey community (see Fig. 1.d).
In the framework used by Chesson (1984) and Morozov and Petrovskii (2013), the overall feeding $\Theta(\vec{x})$ can be of “any functional form”. The generalized polynomial function of rate of accessibility to prey (i.e. $\alpha$ defined in equation (1)) allows different isoclines of total food ingested (Tilman, 1980; Holt, 1983) (see Fig. 1.d). Also, the formulation of the MSFR is a fraction of generalized polynomials as Holling’s functions or others more recent MSFRs (Morozov and Petrovskii, 2013; Vallina et al., 2014).

To disentangle the preference $p_i$ from the overall feeding $\Theta$ using equation (3), we assumed the same handling time (i.e. $h_i = h$). This has no impact on $p_i$, modeling the changes in preferences, since $h_i$ is in the function $\Theta$ (see equation (3)). Nevertheless, we show in supporting information (Table S1) that considering different handling times for prey species does not alter the goodness-of-fit ranking of MSFRs when fitting to field data of the two predators considered in the application. As a consequence, the function of overall feeding obtained in (3) equals to:

$$\Theta(\vec{x}) = \frac{\alpha(\vec{x})}{1 + h\alpha(\vec{x})} = \frac{\sum_j a_j x_j^{n_j}}{1 + h \sum_j a_j x_j^{n_j}}$$

(4)

The focus of this paper is on the qualitative pattern of overall feeding isocline, what is controlled by the exponent $n_i$ in equation (1): if $n_i = 1$ for all $i$, then the isocline is monotonic (complementary overall feeding (Vallina et al., 2014)), otherwise, the patterns may be convex or concave (antagonistic or synergistic) (Fig. 1.d). The base attack rate $a_i$ and the assumption made previously of a same handling time do not change the qualitative shape of the isocline.
Formulation of 9 MSFRs

The equation (3) presents the structural model of MSFR used in this paper to study the foraging behavior of a generalist predator, and has the potential to include most of the MSFR widely used in ecology. The most classical one is the Holling type II MSFR (Murdoch, 1972) (denoted H2.1 in Table 1) which is well-known to not include the property of switching, and exhibit complementary overall feeding (see Fig. 1):

\[
\Phi_i(x) = \frac{a_i x_i}{1 + h \sum_j a_j x_j} \Rightarrow p_i(x) = \frac{a_i x_i}{\sum_j a_j x_j} \quad \text{and} \quad \Theta(x) = \frac{\sum_j a_j x_j}{1 + h \sum_j a_j x_j}.
\]

The attack rate \(a_i\) is also in the preference part of the equation \(p_i\). A classical extension of type II is Holling type III assuming that the attack rate varies with prey density \(a_i = a'_i x_i^{m_i-1}\) (denoted H3.1 in Table 1 where we use the notation \(a_i\) rather than \(a'_i\) for the sake of simplicity in the writing) (Murdoch, 1969; Chesson, 1983; Koen-Alonso, 2007). Many authors suggested \(m_i - 1 > 0\), and so \(m_i > 1\), but since \(\Phi_i\) is supposed to be an increasing function in \(x_i\), we only require \(m_i > 0\) to have \(\partial \Phi_i / \partial x_i > 0\). The parameter \(m_i\) is called the exponent of switching since it has the following properties: \(m_i > 1\) reflects positive switching where the most abundant prey is disproportionately more eaten, \(m_i = 1\) indicates no switching and \(0 < m_i < 1\) reflects negative switching where the most abundant prey is less consumed (see Fig. 1-b and Kean-Howie et al. (1988); Palma et al. (2006)). The development of the classical Holling III in equation (6) shows the occurrence of the switching exponent in the overall feeding part of the equation. As seen previously and in Vallina et al. (2014), this exponent directly induces a non-complementary pattern (Vallina et al., 2014): with \(m_i > 1\), H3.1 exhibits antagonistic overall feeding, and with \(m_i \in [0, 1]\), overall feeding is synergistic.
(see Fig. 1-b,d).

\[
\Phi_{i}(\vec{x}) = \frac{a_{i}x_{i}^{m_{i}}}{1 + h \sum_{j} a_{j}x_{j}^{m_{j}}} \Rightarrow p_{i}(\vec{x}) = \frac{a_{i}x_{i}^{m_{i}}}{\sum_{j} a_{j}x_{j}^{m_{j}}} \text{ and } \Theta(\vec{x}) = \frac{\sum_{j} a_{j}x_{j}^{m_{j}}}{1 + h \sum_{j} a_{j}x_{j}^{m_{j}}}. \tag{6}
\]

As proposed in many studies (Chesson, 1984; Morozov and Petrovskii, 2013; Vallina et al., 2014), we did the distinction between switching and overall feeding by considering different exponents in both parts (see equation (7) and MSFR H3.2 in Table 1). This distinction includes the alternative MSFR proposed by Vallina et al. (2014), called Kill-The-Winner, which preserve the switching of Holling III and the complementary isocline of Holling II by assuming \( n_{i} = 1 \), denoted KTW in Table 1.

\[
p_{i}(\vec{x}) = \frac{a_{i}x_{i}^{m_{i}}}{\sum_{j} a_{j}x_{j}^{m_{j}}} \text{ and } \Theta(\vec{x}) = \frac{\sum_{j} a_{j}x_{j}^{n_{j}}}{1 + h \sum_{j} a_{j}x_{j}^{n_{j}}}. \tag{7}
\]

To investigate the different patterns of change in preference either frequency-dependent, called switching (Murdoch, 1969) (see Fig. 1.b), or density-dependent, called rank switching (see Fig. 1.c), let introduce two new variables: the proportion of prey \( i \) in the environment \( \lambda_{i} = x_{i}/\sum_{j} x_{j} \) and the total density of prey in the environment: \( y = \sum_{j} x_{i} \). From verbal definition of switching and rank switching, it is clear that switching of the preference \( p_{i} \) depends only on the proportion \( \lambda_{i} \), while rank switching is a change of \( p_{i} \) with the total of prey \( y \) (see Fig. 1.b,c). The differentiation between both properties is made by separating the exponents for switching and rank switching in re-writting the preference as:

\[
p_{i}(\vec{x}) = \frac{a_{i}\lambda_{i}^{m_{i}}y_{i}^{r_{i}}}{\sum_{j} \lambda_{j}^{m_{j}}y_{j}^{r_{j}}}, \tag{8}
\]

where the exponent \( m_{i} \) is for switching of preference independent of rank switching and \( r_{i} \) the
exponent for rank switching (independent of switching). To obtain a continuum of MSFR combining all the properties of switching, rank switching and overall feeding, we derived several MSFRs: H2.2, H2.3, KTW.3 and H3.3, described in Table 1.

Study area and data sampling

Study sites, sampling periods and methods are fully explained in Raoul et al. (2010) for *V. vulpes* and in Bernard et al. (2010) for *T. alba*. We summarize the key points useful to parameterize the functional responses. For the *V. vulpes* system, data were collected in the winter period between 1995 and 2000 on 10 study sites in eastern France (Raoul et al., 2010). This resulted in the collection of 1,288 fox faeces for dietary analysis and the assessment of relative densities of grassland voles, the common vole *M. arvalis* and the water vole *A. scherman* (previously known as *A. terrestris*), by transects walked in grassland habitats (> 28 km) (Giraudoux et al., 1995; Quéré et al., 2000). Determination of vole remains in fox scats was carried out by examining teeth. Giving a number of voles of the same species per faeces is source of mistakes because jaws, skulls and teeth are fragmented what makes difficult to estimate if there is one or several individuals. Therefore, data are presence/absence in each faeces. For the *T. alba* system, sampling was carried out in the canton of Levier (eastern France) every season from 1987 to 1995. Pellets were collected in three church towers situated within a 5 km² area. A total of 17,950 vertebrate prey were identified using teeth and skulls. Four groups were identified: *M. arvalis, A. scherman*, Eurasian and Millet’s shrews *Sorex sp.*, and woodland rodents composed by yellow-necked mice *Apodemus flavicollis* and bank vole *Myodes glareolus*. Small-mammal sampling was carried out using traplines of 100 m long consisting in 34 INRA traps placed every 3 m, except for *A. scherman* whose relative density was estimated using a quantification of its
activity indices at landscape scale (Giraudoux et al., 1995). As the relative densities of prey in the field are indices (Giraudoux et al., 1995), every prey density was scaled from 0 to 100 where 100 is the historical maximum value. From the general equation (7) and as pointed out by Smout et al. (2013), this linear transformation is directly absorbed by the parameter of base attack rate $a_i$.

**Model fitting**

For the *V. vulpes* system, data are counts $C_{i,j}$ of occurrences of prey species $i$ in $N_j$ faeces collected in winter along a transect $j$. We modeled data with a Negative Binomial distribution as it generalizes the Poisson distribution and allows the mean and variance to be fitted separately (Smout et al., 2010; Gelman et al., 2013). For the *T. alba* system, data are counts $C_{i,j,k}$ of occurrences of prey species $i$ in pellet collection of site $j$ at season $k$. We built a hierarchical model to take into account variability in pellets number between sites described by a Poisson-log-normal model in the first level: $N_{j,k}$ (number of pellets collected at site $j$ season $k$) follows a Poisson distribution of parameter $\lambda_{j,k}$, with $\log(\lambda_{j,k}) = \alpha_k + \varepsilon_j$ and $\varepsilon_j$ is normally distributed. Since the parameters $a_i$ and $h$ are non-negative, and following previous works (Smout et al., 2010, 2013), we chose gamma priors for all of them. We used a weakly informative prior $a_i$ since we centered parameters to a null model (Holling type II without particular preference), and the same prior for the handling time $h$ based on robustness analysis and previous work (Smout et al., 2010). For exponent parameters ($m_i$, $r_i$ and $n_i$), we used a continuous uninformative uniform distribution from 0 to 10 as the range of those parameters is relatively small and the distribution shape is unknown.

We fitted all our models within a Bayesian framework using Markov Chain Monte Carlo (MCMC) sampling by using STAN (Stan Development Team, 2014). For each model, 5
MCMC chains of 50 000 iterations were simulated with a burn-in of 20 000 runs. Convergence of Markov chains were assessed with chain traces and accepted when $\hat{R}$ values were under 1.1 (Gelman et al., 2013). We checked the validity of negative binomial posterior by comparing the posterior predictive distribution of replicated data to the observed data (Gelman et al., 2013) (see QQplots in Fig.S1,S2). The models of MSFR were compared using the Widely Applicable Information Criterion (WAIC) which is a fully Bayesian measure (Gelman et al., 2013).

Results

As reported in Table 1, for both *V. vulpes* and *T. alba*, the models combining switching and rank switching properties were the best-fitting models. Using WAIC, H3.1 functional response was the best to fit *V. vulpes* diet data set ($WAIC = 444.68; \Delta WAIC = 0.0$). For *T. alba*, the WAIC scores revealed that models disentangling switching and rank switching, H3.3 and KTW.3, were the best models (respectively $WAIC = 2748.27; \Delta WAIC = 0.0$ and $WAIC = 2748.65; \Delta WAIC = 0.38$). In both systems, H2.1, which was the only model without switching and rank switching, was the least suitable model (*V. vulpes*: $\Delta WAIC = 221.57$; *T. alba*: $\Delta WAIC = 139.14$), while it is the MSFR with the smallest degree of freedom (respectively 3 and 5 parameters to fit). Models with only switching or rank switching (H2.2, H2.3, KTW.1) did not yield a good fit. For *T. alba*, MSFR with switching without rank switching (i.e. KTW.1) had a better fit than those with rank switching without switching (H2.2 and H2.3). These results showed that switching and rank switching are two critical properties for a better fit of these predator-prey terrestrial systems. In the two trophic systems, the goodness-of-fit of MSFR in Table 1 is not driven by a particular
pattern of overall feeding. Indeed, complementary overall feeding is a property found in the best as well as in the worst models.

*V. vulpes* exhibited negative switching for both prey all along the gradient of total prey available (Fig. 3). For *M. arvalis*, the point of switching, i.e. the density at which the species turns from being over-represented to under-represented, was higher at low density of total prey and decreased with the increase of prey density. The opposite effect was observed for *A. scherman*: an increase of the switching point with the increase of total prey density. These changes in switching correspond to a rank switching, which consists in a change of the most eaten prey according to total of prey density, where *M. arvalis* was the most consumed prey at low total prey density while *A. scherman* was the most consumed prey at high total prey density.

*T. alba* behaved with a negative switching for three of the prey and aversion (“negative preference”) for the fourth (Fig. 4). At low total prey density, *Sorex* sp. was highly over-represented in the diet, then with the increase of total prey density, the point of switching decreased, referring to a reduction of *Sorex* sp. consumption (Fig. 4.a). The point of switching of *M. arvalis* was hump-shaped along the increase of total prey (Fig. 4.b): the switching point was maximal at an intermediate amount of total prey. Within this range of total prey density (i.e. [10, 400]), *Sorex* sp. and *M. arvalis* ingestion showed negative switching. At low density of total prey, *T. alba* had an aversion behavior (Fig. 1.a) for *A. scherman* (Fig. 4.c), but then a negative switching appears and the point of switching increased continuously, referring to the increase of the proportion of *A. scherman* in the diet of *T. alba*. Over the range of total prey density considered, there is no switching for woodland rodents but an aversion behavior (Fig. 4.d).
Discussion

Disentangling foraging properties

In this paper, we address a fundamental issue in ecology: revealing the shape of the multi-species functional responses of generalist predators. We propose a structural model of MSFR splitting up the properties of change of preference, switching and rank switching, and incorporating overall feeding which are two milestones in ecology as they contribute to the stability and the strength of food web links (Murdoch, 1969; Holt, 1983; McCann et al., 1998; Pelletier, 2000). Indeed, Drossel et al. (2004) used the feeding probability, that is the preference $p_i$, to investigate the pattern of food web links distribution, while Tilman (1980); Holt (1983) used the overall feeding, $\Theta$, as a common tool to study the benefit of prey diversity. The other main theoretical result is the distinction between switching (frequency-dependent) focusing on the adaptation of the foraging behavior to variations of prey proportion in the field, and rank switching, which investigates the change of foraging behavior when the overall amount of prey changes. This distinction is of real interest in a context of fluctuation, synchronous or not, of prey densities. To our knowledge, this is the first attempt to disentangle all these properties of MSFR, and we think this approach has the potential to be applied to a large variety of trophic networks from different ecosystems when the issue concerns the analysis of predator-prey interactions.

The foraging properties of two predators

$V. vulpes$ and $T. alba$ are well known to be opportunistic consumers (see Sidorovich et al. (2006) and Hartová-Nentvichová et al. (2010) for $V. vulpes$ and Taylor (2004) for $T. alba$), and are probably the two mostly studied vertebrate generalist predators because of their
worldwide distribution and presence in many ecosystems. Despite this, the basic question of their predation patterns in a context of multiple prey, though a frequent situation, has never been reported. This might be the result of the difficulty in collecting long-term quantitative estimation of the prey community abundance variations. In our study area, common and water voles (respectively *M. arvalis* and *A. scherman*), woodland rodent species and shrews made up to more than 85% of the *T. alba* prey items (Bernard et al., 2010), and woodland rodent species and lagomorphs occurred in less than 5% of fox faeces and shrews were absent from *V. vulpes* diet (Raoul et al., 2010). One can therefore reasonably assume that no important prey, the predation of which would have significantly impacted predators’ functional response, was missed.

The first important result is the clear rejection of Holling type II functional response (H2.1) in both systems. It was the only model without the investigated foraging properties, let say the null model, and while it has the lowest number of parameters to fit, it has been the least suitable model for both predators. Among the other models, those combining switching and rank switching gave the best fits. These results highlight the complex predation behavior of these two predators.

**The necessity of rank switching**

Rank switching *per se* has never been studied previously while our results revealed the importance to include this property on both terrestrial food webs we studied. As rank switching is dependent on total prey density, this suggests that consumers have a pretty good image of the variations of the densities as a whole. A first hypothesis for rank switching is that the easiest prey to obtain ensures the feeding when the total prey density is low, followed by a switch to a more profitable prey when total prey density is higher (Palma et al., 2006).
This suggests that prey choice depends on the predator’s hunger level defined in Jeschke et al. (2002) as the “feelings of hunger and satiation in the predator”. In the words of Heatwole (2012), this means that “when hungry, eat what is available; when less hungry, be more choosy”. As already suggested by Raoul et al. (2010), *M. arvalis* is less subterranean than *A. scherman* and therefore likely easier to catch when the total amount of prey is low. In other circumstances, when prey are more abundant, *A. scherman* is taken more often as it is a more profitable species (more than 80g compared to 18.32g (n=4412) for *M. arvalis* (Bernard et al., 2010)). Also, when the density of *A. scherman* is high, the intraspecific competition makes its finding by predators easier.

We showed a high consumption of *Sorex sp.* by *T. alba* at low density of total amount of prey. *Sorex* species are common insectivores in a variety of habitats, including grassland, woodland, arable land, and hedges, and therefore may have a role of alternate prey taken opportunistically because of their large habitat niche. A slight increase of total prey density leads to a switch to more profitable prey (*M. arvalis* and *A. scherman*) (mean body mass of shrew = 8.57 g; n = 1454 (Bernard et al., 2010)). Woodland rodents are under-represented in the diet of *T. alba* compared to their availabilities in the field (Fig. 4.d). This pattern reflects that grassland is probably a more suitable habitat than woodland for *T. alba* foraging (Taylor, 2004; Askew et al., 2007).

**The occurrence of negative switching**

Contrary to most of the studies investigating functional responses, we showed that negative switching was a driving process of *V. vulpes* and *T. alba* foraging. The idea underlying a positive switching is that a consumer has a low preference (attack rate) for the least abundant item, which result in releasing the consumption pressure on rare species (Pelletier,
MULTI-PREY AND CHANGE IN PREFERENCES

2000; Van Leeuwen et al., 2007). This process is expected to increase the robustness and stability of the prey and to promote the coexistence of prey species (Pelletier, 2000; Morozov, 2010). However, in both systems, we observed clear evidence for negative switching, which is likely to have a destabilizing effect (Chesson, 1984). This destabilizing effect is susceptible to accentuate population cycles in small-mammals, a demographic pattern occurring in the areas under study (Berthier et al., 2014). Several empirical studies showed that negative switching may be observed in marine (Kean-Howie et al., 1988; Rindorf et al., 2006) and terrestrial ecosystems (Weale et al., 2000; Palma et al., 2006; Hellström et al., 2014). There are numerous explanations for negative switching coming from those empirical studies. In our context, the combination of inter-specific competition and predator confusion may be relevant. *M. arvalis* and *A. scherman* are two subterraneous species living in grasslands. The predator may be attracted by the most abundant prey but because of their similarity, confusion may happen and lead to higher ingestion rate of the less abundant one (Kean-Howie et al., 1988). Negative switching was also observed with lemmings and grey-sides voles preyed by the rough-legged buzzard (Hellström et al., 2014), what could also be a reasonable explanation in our context. Authors suggested that the inter-specific competition for habitat between species may increases the vulnerability of the less abundant which is pushed in the high consumption risk area (Hellström et al., 2014). Confusion and competition need a shared habitat and, for *T. alba*, prey species occupying a different habitat (i.e. *M. glareolus* and *Apodemus* sp.) did not exhibit any frequency-dependent switching (only aversion). An other explanations is given by Chesson (1984) who showed that a prey switching (positive or negative) at the population level may also be explained by high individual variation in prey preferences.

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Changes in preferences and optimal foraging

Optimal foraging theory assumes that prey choice is driven by the maximization of energy gain by the predator, mainly based on the energy yields from a prey per handling time unit (Emlen, 1966; Charnov, 1976). The review of Sih and Christensen (2001) showed that while the use of optimal foraging theory seems very efficient for immobile resources (e.g. leaves, seeds, nectar, meal-worms), it often fails on mobile resources as those considered in the present study (i.e. small-mammals). Therefore, optimal foraging is limited to the energetic balance, and releases other components of predator-prey interactions which may be important for mobile prey (e.g. inter-specific competition, prey refuge, prey taste) (Loeuille, 2010).

Our findings on rank switching leads us to propose that the predator’s hunger level, developed by Jeschke et al. (2002) and used to build the MSFR model, is one of these other components influencing the foraging behavior. We can reasonably assume that optimal foraging is more or less used along a gradient of predator’s hunger level. When the overall prey density is low, the predator’s hunger level is likely to be high and therefore, the predation should satisfy optimal foraging theory. But in the case of high overall prey density, leading to a low predator’s hunger level, then the predator foraging behavior is less constraint by an optimization of the energetic balance. Our approach disentangling frequency-dependent and density-dependent switching gives new tools to explore the limitation of optimal foraging theory in the case of mobile prey as raised by Sih and Christensen (2001). However, in the two applications with *V. vulpes* and *T. alba*, we have no direct access to the biomass of prey ingested which is necessary to test the optimal foraging theory (Charnov, 1976).
Conclusion

The comparison of multiple MSFRs with empirical data showed that switching between prey was frequency dependent, as commonly thought, but also dependent on the total amount of prey (i.e. rank switching), which has never been tested. Our results contrasted with the traditional assumption of positive switching since, for both predators, switching was highly used but in its negative form, which may tend to have a destabilizing effect on prey dynamics. This work gives insights on the non-linear frequency and density dependent interactions that arise in food-webs.

Acknowledgments

We thank D. Michelat for barn owl data collection. We are particularly grateful to M. Gauthier-Clerc and L.-F. Bersier for reviewing earlier versions of the manuscript, and to F. Barraquand and A. Massolo for constructive discussions. We also express our gratitude to the editor, S. Schreiber, and the two anonymous reviewers whose remarks and suggestions greatly improved the manuscript. This research was undertaken within the framework of the Zone Atelier (LTER site) Arc Jurassien (zaaj.univ-fcomte.fr).

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**Supporting information**

Supporting information of Appendix S1 provides: (1) mathematical details of the derivation of multi-species functional responses, Eqs. S1-S7; (2) WAIC score and ranking of model considering different handling time between prey species, Table S1; (3) results of Bayesian

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estimates of MSFR parameters for the two food webs \textit{V. vulpes} and \textit{T. alba} (means and 95\% credible intervals), respectively Tables S2 and S3; and (4) QQplots for assessing the goodness-of-fit of the best models for \textit{V. vulpes} in Fig. S1 and \textit{T. alba} in Fig. S2.
Table 1: Derivation of MSFR from the structural model (3) with $p_i(\vec{x})$ the probability to feed on prey type $i$, and $\Theta(\vec{x})$ the total food intake. For switching and rank switching, NO means that the property is impossible. H2 stands for Holling type II, H3 for Holling type III (Holling, 1959), KTW stands for Kill-The-Winner (Vallina et al., 2014). For overall feeding, NO means that overall feeding is always complementary. Exponent letters $a$, $b$ and $c$ on YES refers to dependence between properties: properties sharing a same letter are controlled by the same parameter. $n.p$ refers to the number of parameters to fit and WAIC is a Bayesian measure of goodness of fits (Gelman et al., 2013). Models are ranked according to $\Delta WAIC$ (difference with the smallest WAIC).

<table>
<thead>
<tr>
<th>Model</th>
<th>$p_i(\vec{x})$</th>
<th>Switching</th>
<th>Rank switching</th>
<th>$\Theta(\vec{x})$</th>
<th>Overall feeding n.p.</th>
<th>Vulpes vulpes</th>
<th>Tyto alba</th>
</tr>
</thead>
<tbody>
<tr>
<td>H2.1</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>NO</td>
<td>NO</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>NO</td>
<td>3</td>
<td>666.25</td>
</tr>
<tr>
<td>H2.2</td>
<td>$\frac{a_i a_j x_i x_j}{\sum_i a_i a_j x_i x_j}$</td>
<td>NO</td>
<td>YES</td>
<td>$\frac{\sum_i a_i a_j x_i x_j}{1 + h \sum_i a_i a_j x_i x_j}$</td>
<td>NO</td>
<td>5</td>
<td>501.12</td>
</tr>
<tr>
<td>H2.3</td>
<td>$\frac{a_i a_j x_i x_j}{\sum_i a_i a_j x_i x_j}$</td>
<td>NO</td>
<td>YES</td>
<td>$\frac{\sum_i a_i a_j x_i x_j}{1 + h \sum_i a_i a_j x_i x_j}$</td>
<td>YES</td>
<td>7</td>
<td>494.22</td>
</tr>
<tr>
<td>KTW.1</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>NO</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>NO</td>
<td>4</td>
<td>500.86</td>
</tr>
<tr>
<td>KTW.2</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>YES</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>NO</td>
<td>5</td>
<td>462.19</td>
</tr>
<tr>
<td>KTW.3</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>YES</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>NO</td>
<td>7</td>
<td>458.99</td>
</tr>
<tr>
<td>H3.1</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>YES</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>YES</td>
<td>5</td>
<td>444.68</td>
</tr>
<tr>
<td>H3.2</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>YES</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>YES</td>
<td>7</td>
<td>451.28</td>
</tr>
<tr>
<td>H3.3</td>
<td>$\frac{a_i x_i}{\sum_i a_i x_i}$</td>
<td>YES</td>
<td>YES</td>
<td>$\frac{\sum_i a_i x_i}{1 + h \sum_i a_i x_i}$</td>
<td>YES</td>
<td>9</td>
<td>459.00</td>
</tr>
</tbody>
</table>
Figure 1: Graphical illustration of predator’s change in preference properties. (a) Preference: the solid line indicates no-preference (equal representation in diet and environment). A preference (dotted line) is an over-representation of the item in the diet, conversely, aversion (dashed line) is an under-representation of the item in the diet. (b) Switching: the dashed line is positive switching where the proportion of prey eaten is under-represented compared to prey availability until a switching point where the prey switches to being over-represented in the diet, and dotted line is a negative switching. (c) Rank switching: the rank of species in the diet changes with an increase of the total amount of prey. (d) Overall feeding isocline: total ingestion of two prey, $\Theta(x_1, x_2)$, depending on their relative proportion $x_1/(x_1 + x_2)$, with a constant sum $x_1 + x_2$. 

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Figure 2: Diagram depicting the mechanistic method used to derive the MSFR. The predator population is divided into several states: searching predator and handling predator (here with only 2 prey). The rate of accessibility $\alpha$ reflects the potential benefit of the prey assemblage for the total ingestion rate. The preference for prey $i$ denoted $p_i$ depends on the characteristic of prey $i$ compared to all other prey. The rate from handling prey $i$ to searching state is $1/h_i$, where $h_i$ is the handling time.
Figure 3: Switching graphs for *V. vulpes* according to the best MSFR Holling type III H3.1 (Table 1). Figure (a) stands for *M. arvalis* and (b) for *A. scherman*. z-axis is the proportion of the prey in the fox diet, x-axis is the proportion of the prey available, and y-axis is a range of total prey density. Grey plans represent no-preference (then no-switching). Both switching are negative all along the gradient of total prey available.
Figure 4: Switching graphs for *T. alba* system and H3.3 MSFR. The z-axis stands for the proportion of a prey ingested, x-axis is the proportion of that prey available in the environment, other prey are evenly distributed; y-axis stands for the total prey density. Grey plans represent no-preference (then no-switching). (a,b) Switching graphs for *Sorex* sp. and *M. arvalis* show negative switching all along the gradient of total prey available. (c) *A. scherman* presents a part without switching (with aversion) at low total prey, and then a negative switching setting up with the increase of total prey. (d) There is no switching for woodland rodents on this range of total prey density, but aversion.