

Functional responses of the rough-legged buzzard in a multi-prey system

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Abstract The functional response is a key element of predator–prey interactions. Basic functional response theory explains foraging behavior of individual predators, but many empirical studies of free-ranging predators have estimated functional responses by using population-averaged data. We used a novel approach to investigate functional responses of an avian predator (the rough legged-buzzard *Buteo lagopus* Pontoppidan, 1763) to intra-annual spatial variation in rodent density in subarctic Sweden, using breeding pairs as the sampling unit. The rough-legged buzzards responded functionally to Norwegian lemmings (*Lemmus lemmus* L. 1758), grey-sided voles (*Myodes rufocanus* Sundevall, 1846) and field voles (*Microtus agrestis* L. 1761), but different rodent prey were not utilised according to relative abundance. The functional response to Norwegian lemmings was a steep type II curve and a more shallow type III response to grey-sided voles. The different shapes of these two functional responses were likely due to combined effects of differences between lemmings and grey-sided voles in habitat utilisation, anti-predator behaviour and size-dependent vulnerability to predation. Diet composition changed less than changes in relative prey abundance, indicating negative switching, with high disproportional use of especially lemmings at low relative

densities. Our results suggest that lemmings and voles should be treated separately in future empirical and theoretical studies in order to better understand the role of predation in this study system.

Keywords Predation · Rodent cycle · *Lemmus* · Subarctic

Introduction

Theoretical and empirical work suggest that predation can explain why certain prey populations fluctuate in time and space (Murdoch et al. 2003; Turchin 2003). In order to fully understand how predator–prey systems are structured, it is necessary to quantify two interactive processes—the functional and numerical responses of predators (Solomon 1949).

The functional response, defined as the predator consumption rate in relation to prey density, is the basic predatory response to changes in prey numbers, as energy for predator reproduction and growth is derived from consumed prey. The functional response involves the full range of foraging behaviours and occurs on a fast time scale. Holling (1959a, b) described three functional response types that are regarded as the theoretical basis for predator–prey interactions. The type I functional response illustrates a linear relationship between kill rate and prey density, whereas the type II response has a concave shape, and the type III functional response is sigmoid in shape. Given their dissimilar contributions to stability in a predator–prey system (Kuno 1987; Murdoch and Oaten 1975), it is of central importance to distinguish between different functional response curves.

However, despite functional response being an important concept in theoretical ecology, the number of empirical

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field estimates is relatively low compared to theoretical work (Abrams and Ginzburg 2000). This can partly be explained by difficulties in measuring functional responses under field conditions. For instance, it is not clear which temporal, spatial and population/individual scales that are most relevant in order to test predator–prey theory. According to Holling’s first principles (Holling 1959a), the functional response is the consumption rate of an individual predator measured over a short period of time and has an immediate effect on prey mortality. This is in contrast to the numerical response, which describe changes in natality and mortality rates—demographic processes that cause long-term effects in the predator and prey populations. The total effect of predation can be derived by multiplying the functional and numerical responses (Sinclair and Pech 1996), but the logical inconsistency of combining processes operating at different time scales has been pointed out (Inchausti and Ballesteros 2008; Oksanen et al. 1992). As a result, functional responses are often studied on the same temporal scale as predator population dynamics. An alternative to population-level functional responses is to study how individual predators or packs react to changes in prey density in their territories or home ranges. This approach is a closer approximation to underlying foraging theories and is likely to offer better mechanistic explanations and understanding of foraging decisions, but has only rarely been adopted for field studies (e.g. Jost et al. 2005; Koivunen et al. 1996; Moleón et al. 2012).

Further, the focus of many empirical studies has been on a single resource species, or similar resource species treated collectively as a functional group. But predators are often selective in their prey choice and kill some prey species disproportionately more often in relation to their abundance. Such prey selection can have effects on functional responses in multi-prey systems (Fryxell and Lundberg 1998; Messier 1995) and may also contribute to community dynamics. In multi-prey communities, predation patterns are therefore not only shaped by absolute prey densities, but also by relative densities of different prey, which may lead to switching behaviour (Murdoch 1969). The classic case is “positive switching” in which the predator directs disproportionately more attention to the more abundant prey—a behaviour that will have a stabilising impact on community dynamics (Oaten and Murdoch 1975). The opposite pattern, termed “negative switching” (Chesson 1984), has received less attention but is not uncommon (Rindorf et al. 2006), and increases the probability of local extinctions of rare prey. But although the concepts of different functional response types and switching are related, there is no generally applicable link or theoretical framework between them (Asseburg 2006).

A prerequisite for estimation of functional responses is that prey density is highly variable. This is a characteristic

feature of Arctic and boreal communities where many herbivores show fluctuations in population size with amplitudes ranging over several orders of magnitude (e.g. Krebs and Myers 1974; Stenseth and Ims 1993). These herbivores and their predators are therefore promising study systems (Boutin 1995). In northern Europe, interactions between predators and *Microtus* and *Myodes* voles have received particular attention (reviewed by Hanski et al. 2001; Henttonen and Hanski 2000). Population dynamics of voles in this region are primarily influenced by interactions between *Microtus* voles and mustelids *Mustela* spp. (Henttonen et al. 1987; Turchin and Hanski 1997), but there is also an important multi-species component involving *Myodes* voles and a guild of various rodent predators, both avian and mammalian (Korpimäki et al. 2002). Indeed, modelling suggests that differential prey vulnerability and species-specific functional responses are necessary to explain the complex community dynamics of boreal voles (Hanski and Henttonen 1996). These results can be extended to the Fennoscandian mountain region, where the rodent community is similar to the well-studied community in the boreal zone, but with different species involved. The key species in the mountain birch forest is the grey-sided vole *Myodes rufocanus* (Sundevall, 1846), whereas the Norwegian lemming (*Lemmus lemmus* L., 1758) is the most important species in mountain tundra (Henttonen and Wallgren 2001; Ims and Fuglei 2005). Population dynamics of the grey-sided vole are more likely to be caused by predator–prey interactions (Hansen et al. 1999; Turchin et al. 2000), whereas lemming dynamics are more consistent with a lemming–vegetation interaction in northernmost Fennoscandia (Oksanen et al. 2008). It has been proposed that the Norwegian lemming is a less suitable prey than voles (Hagen 1952; Taitt 1993), a suggestion that has received some experimental support (Andersson 1976; Barth et al. 2000). However, empirical studies describing functional responses and prey preference regarding grey-sided voles and Norwegian lemmings are, to our knowledge, lacking.

In this study, we studied interactions between a migratory avian predator, the rough-legged buzzard (*Buteo lagopus* Pontoppidan, 1763), and the key rodents in the Fennoscandian subarctic region, Norwegian lemmings, grey-sided voles, and field voles (*Microtus agrestis* L., 1761). We investigated prey density, diet choice and prey selection in separate territories of rough-legged buzzards within a single breeding season characterised by peak rodent densities, using a breeding pair as our focal unit. Our objectives are to investigate predation patterns of buzzards by (1) modelling prey-dependent functional responses, (2) analyse whether the buzzards exhibited different functional responses to each prey species, and (3) whether relative prey densities was related to prey selection, or whether non-random prey selection causes prey switching.

Materials and methods

Study area

This study was conducted in Stora Sjöfallet National Park with surroundings in NW Sweden (67°45'N, 17°30'E). The study area encompassed 150 km² of subarctic environment. The northern part of the study area comprised the alpine heaths surrounding the lakes Autajaure and Sitasjaure (altitudes ranging from 600 to 1,000 m a.s.l.). The vegetation was dominated by fresh and dry heaths, with mostly dwarf birch (*Betula nana* L., 1753), crowberry (*Empetrum hermaphroditum* Hagerup, 1927) and bilberry (*Vaccinium myrtillus* L., 1753). The southern part represented lower altitudes (450–700 m a.s.l.) along the northern shore of lake Akkajaure, where the main vegetation was moderately productive mountain birch (*Betula pubescens* ssp. *czerepanovii* Orlova, 1791) woodland.

Rough-legged buzzard monitoring

The rough-legged buzzard has a circumpolar distribution in the northern hemisphere (Hagemeijer and Blair 1997), and breeds in mountain regions, boreal taiga and on arctic tundra (Cramp and Simmons 1980). In peak rodent years, it is the most abundant avian predator in the Fennoscandian mountains, particularly in the transition zone between mountain birch forests and alpine tundra, where the nest usually is built on a cliff ledge. The rough-legged buzzard is widely considered as a specialist predator and shows strong aggregative and reproductive responses to fluctuations in small mammal populations (e.g. Hagen 1969; Potapov 1997; Sundell et al. 2004). Our study was part of a long-term study on raptors and owls in Stora Sjöfallet National Park, where the rough-legged buzzard population closely tracks the rodent cycle. The numerical response of the rough-legged buzzard at our study site is illustrated in Fig. 1, showing that density of breeding pairs was almost perfectly correlated with rodent density during 2001–2006.

The present study was conducted in a single year, 2001. Field surveys started in May 2001 shortly after the rough-legged buzzards had arrived in the study area. Of 32 occupied nesting territories, 9 were included in this study, representing breeders both on alpine heath ($n = 4$) and in the adjacent birch forest ($n = 5$). Occupied territories were visited 1–3 times during the summer to obtain data on brood size. Sampling from two habitat types was necessary for covering an adequate range of densities for functional response estimation. Territories included in this study were selected because adult hunting areas and roosting sites were observable (and not overlapping between territories) and partly also by topographic constraints (territories in boulder fields, steep slopes and on the border between the birch

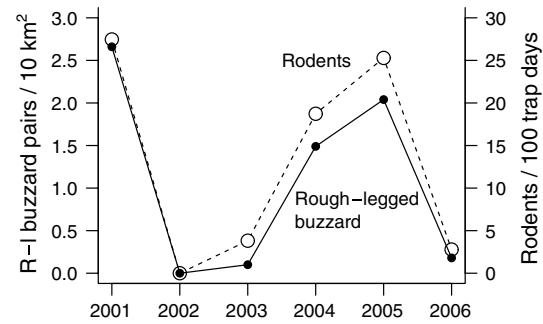


Fig. 1 Fluctuations in small mammal abundance (open circles, dashed lines, right y-axis) and the numerical response of rough-legged buzzards (*Buteo lagopus*) (filled circles, solid lines, left y-axis) to small mammals at Stora Sjöfallet National Park in northern Sweden 2001–2006. Rodent abundance was estimated by snap trapping, index values are presented as number of captures per 100 units of effort (trap days). Number of pairs that laid at least one egg were included in the rough-legged buzzard variable, density of breeding pairs expressed as the number of breeding pairs/10 km²

forest and heath habitats were not included). The minimum distance between two nest sites included in this study was 1.3 km (mean \pm S.E. 4.6 ± 1.8).

Rodent monitoring

We used the trapping protocol described by Krebs et al. (2002) to estimate density of rodent populations within buzzard territories. Two parallel snap-trap lines separated by 100 m were set out 300–500 m from the nest during the late nestling period of the buzzards in the period 14–27 July 2001. Each trap line had 20 stations placed at 15-m intervals. A small flag was placed at the centre of each station, and three traps were evenly distributed at a distance of 1–2 m from the flag. Traps were set for 48 h per territory and checked four times at 12-h intervals. We used peanut butter and raisins as bait. The trapping effort was 240 trap-nights per territory, and we used the number of captured individuals of each species per 100 trap-nights as an index of rodent density. The species-specific indices were calculated as $100 \times \text{number of captures/corrected effort}$. We took non-availability of sprung traps into account by calculating the corrected effort as (modified from Nelson and Clark 1973):

Corrected effort = Days

$$\times \left(\text{Traps} - \sum \text{Sprung traps} / [2 \times \text{Checks per trap}] \right) \quad (1)$$

which in our case meant that we subtracted 0.25 from the total effort for each trap sprung (sprung traps included all captures of all species as well as trap errors).

The rough-legged buzzards perched in top of trees or hovered while hunting, which allowed us to observe where each individual hunted. Consequently, the trap lines were

placed in the most frequently used hunting areas of each territory. Our rodent monitoring methods have been evaluated by an ethical committee and are licensed by the Swedish Board of Agriculture.

We have no information from our study regarding rodent abundance prior to 2001. But according to other monitoring studies in northern Fennoscandia, 2001 was a peak year for lemmings and voles at several sites (Kilpisjärvi, Cornulier et al. 2013; Ammarnäs and Stora Sjöfallet, Ecke et al. 2010; Sarek/Padjelanta, Nyström et al. 2006; Abisko and Vassijaure, Olofsson et al. 2009).

Diet composition

Diet composition was studied by analysis of regurgitated pellets and prey remains collected at nests and roost sites. Pellets of adult buzzards were collected at roosts and perches. Pellets from nestlings accumulated in and below the nest and were collected after the brood had fledged. Small mammals (voles, lemmings and shrews) were identified to species by molar teeth patterns or characteristic fur (Niethammer and Krapp 1982). The minimum number of ingested mammalian prey was estimated by counting the number of unique molar teeth in each pellet. Bird remains were identified to taxonomic order by using the keys of Brom (1986) and Day (1966). If a pellet contained only fur or feathers, it was assumed that one prey specimen had been ingested. Totals of each prey type were converted to biomass using mean values from all trapping sessions for rodents (grey-sided vole: 31.5 g; Northern-red backed vole, *Myodes rutilus* Pallas, 1779: 30.0 g; field vole: 31.3 g; Norwegian lemming: 48.6 g) and literature values for other mammals (Siivonen 1976) and birds (Huhtala et al. 1996; Pasanen and Sulkava 1971). Adult buzzards do not process small rodent prey before delivery at the nest (Hellström, unpublished data), a behaviour that is common in some raptor species (Korpimäki et al. 1994 and references therein). Therefore, our comparisons of adult and juvenile diets are not confounded by pre-delivery prey processing by adults.

Estimation of consumption rates

We estimated kill rates based on the combined adult and nestling diets. The number (NP) of grey-sided voles, field voles and lemmings killed by each rough-legged buzzard pair per day during the nestling period was calculated in accordance with Lindén and Wikman (1983), a formula that is widely used in the raptor literature:

$$NP_i = \frac{(2 \times \text{DER}_{\text{adults}} + \text{Brood size} \times \text{DER}_{\text{nestlings}}) \times \text{PP}_i}{\text{MMP}_i} \quad (2)$$

where DER is the daily energy requirements (average food intake in grams per day) of adults and nestlings,

respectively, and brood size is the number of fledged nestlings. PP is the proportion of the prey type (by biomass) in the diet of each buzzard pair and MMP is the mean mass (g) of a single prey item of species *i*. Daily energy requirements (DER) of rough-legged buzzards have been estimated in previous studies (Pasanen and Sulkava 1971; Potapov 1993; Reid et al. 1997). These three studies have found DER to be in the range 100–140 g/day under conditions with no food stress, with high agreement across studies. For adults, we therefore used DER = 110 g/day (average of estimates for males and females in the detailed study on energy budget in Potapov 1993, sect. 10.2), and for nestlings DER = 140 g/day (averaged from Pasanen and Sulkava 1971, sect. VII; Potapov 1993, fig. 9.25).

Prey selection and switching

We calculated two measures of prey selection or preference at both population and pair level—selection ratios (Manly et al. 2002) and standardised selection ratios. Selection indices are often referred to as preference indices. For our purposes, preference means any deviation from random use of prey, and thus not necessarily an active choice made by the predator.

Selection ratios are calculated as r_i/n_i , where r_i = proportion of species *i* in the diet and n_i = proportion of prey *i* available in the environment. Selection ratios from 0 to 1 reflect avoidance, and ratios from 1 to infinity relative over-representation or preference. Selection ratios can be standardised so that values range from 0 to 1 (and sum to 1) according to:

$$\alpha_i = r_i/n_i \times \frac{1}{\sum_{j=1}^m r_j/n_j} \quad (3)$$

Standardised selection ratios are equivalent to Manly's alpha index (Chesson 1978; Manly et al. 1972), and estimates the probability that the next prey item will be of class *i* if it were possible to make all resources equally available (Manly et al. 2002, p. 51). In the null case of no selective feeding, $\alpha_i = 1/m$, where *m* is the number of possible prey types. $\alpha_i > 1/m$ indicates preference.

Switching behaviour was evaluated with a graphical approach (Murdoch 1969; O'Donoghue et al. 1998) by comparing the percent of a given prey species in the diet with its relative availability. The null hypothesis is that the relative availability should fall on a line with unit slope, but at strong preference the null hypothesis is a curve (convex for preferred prey and concave for non-preferred prey; see Murdoch and Oaten 1975). If points fall below the null-hypothesis curve at low relative densities, and above the curve at high relative densities, this is taken as evidence for positive switching (Oksanen et al. 2001), while the opposite pattern indicates negative switching.

Statistical analyses

Diet composition was modelled with multinomial logit models (Venables and Ripley 2002), where the response matrix comprised counts of grey-sided voles, lemmings, field voles and birds in pellets. Habitat (birch forest or tundra heath) and age (nestling or adult) were included as predictor variables. Multinomial models were fitted with the multinom function in the nnet R-package (v.7.3-7; Venables and Ripley 2002). Territory A was excluded from this analysis, since diet data for adults could not be obtained as pellets were deposited on inaccessible cliff roosts.

Analyses of prey selection ratios and standardised selection ratios were calculated in accordance with Manly et al. (2002). Since prey availability and consumption was measured separately for each rough-legged buzzard pair, our study was of the design III sampling protocol (see chap. 4 in Manly et al. 2002). Selection ratios and associated standard errors were calculated with the widesIII-function in the R-package adehabitatHS (v.0.3.8; Calenge 2006), by assuming that proportions of each prey type available were estimated (and not accurately known). The null-hypothesis curve for prey switching was calculated following the approach by O'Donoghue et al. (1998).

Prey-dependent functional responses were modelled as Holling's functional responses (hyperbolic type II and two versions of the sigmoid type III), Lotka-Volterra (linear type I without intercept) and as constant (null model, type 0). We investigated three different sets of hypotheses: (1) no difference in the functional response to different prey species, (2) the functional response differs between species, but the type is similar for all prey species, and (3) the functional response differs between species and the predator shows different (non-linear) types of responses to different prey species.

Nonlinear functional responses were modelled as:

$$y_{ij} = N \left(\frac{a_j \times x_{ij}^{\theta_j}}{b_j^{\theta_j} + x_{ij}^{\theta_j}}, \sigma_j^2 \right) \quad (4)$$

where subscripts denote observation i of prey species j (in our analysis, j had two levels, 1 = lemmings and 2 = grey-sided voles) and x is prey density. We used calculated kill rates and % of prey biomass as the response variable y in separate analyses. Equation 4 belongs to the family of Michaelis–Menten equations, and can be re-parameterised to Holling's original notation (Real 1977). Parameter a represents the asymptotic kill rate, and b (the half-saturation constant) is the prey density at half the maximum kill rate a . θ controls the shape of the curve (concave down or sigmoid). The type II response was obtained by setting $\theta = 1$. If $\theta = 2$, we obtain the most commonly used (sigmoid) type III response (hereafter referred to as type IIIa). The phenomenological

form of the type III response (hereafter type IIIb), where θ is an estimated parameter was also modelled. Hypothesis 1 (a single curve describes the functional response to both species) was evaluated by dropping the subscripts j in Eq. 4. Hypothesis 2 corresponded to fixing the parameter θ to the same value for both prey species for type II ($\theta_j = 1$) and IIIa ($\theta_j = 2$) responses, while having no constraints on θ_j for type IIIb. Finally, different response types (hypothesis 3) to different prey species was evaluated by fixing θ_j at a particular value (1 or 2) for at least one prey species and not allowing $\theta_1 = \theta_2$. The linear type I functional response was described as $y_{ij} = N(a_j \times x_{ij}, \sigma_j^2)$ where a equals search rate, and the constant null model as $y_{ij} = N(\mu_j, \sigma_j^2)$.

From our set of hypotheses, we constructed 14 candidate models (Table 1). The functional response models were fitted to the data with (nonlinear) generalised least squares (Pinheiro and Bates 2000) by using the gnls-function in the R-package nmls (Pinheiro et al. 2013). In all models, the variance was estimated separately for each prey species.

Territory I was excluded from analyses of prey selection ratios and the functional response to lemmings, as we could not estimate lemming density in this territory. The hunting territory of the male in this pair was divided between a high ridge, where lemmings were abundant, and the adjacent birch forest (grey-sided vole habitat). Trap lines could only be placed in the birch forest due to the impassable terrain, and lemming density was consequently underestimated. This territory was included in the analyses of functional responses to grey-sided voles, as both adults were observed to frequently catch this species in the area where our traps were set.

The information-theoretic approach (Burnham and Anderson 2002) was used to select the best model among candidate models, defined as the model with the lowest information criteria, in this case AIC_C (Akaike's Information Criterion corrected for small sample size). All statistical analyses were performed in R 3.0.2 (R Development Core Team 2013).

Results

Rodent density

The population estimates of the four arvicoline rodent species in the study area (grey-sided vole, Northern red-backed vole, field vole and Norwegian lemming) indicated a high degree of both intra- and interspecific spatial variation in density within the same summer season. The most abundant species, the grey-sided vole, was trapped in all territories, but density estimates decreased along the productivity gradient from birch forest to heath vegetation. There was a 41-fold difference in density between highest

Table 1 Model-selection of functional responses to the data in Fig. 3

Set	Type	Parameters	Constraints	(a) Biomass ($n = 17$)						(b) Kill rates ($n = 17$)					
				LogL	K	AIC _c	Δ_i	w_i	Rank	LogL	K	AIC _c	Δ_i	w_i	Rank
1	0	μ		-71.81	3	151.47	13.88	0.0005	11	-41.60	3	91.04	24.17	<0.0001	9
	I	a		-73.93	3	155.71	18.12	0.0001	13	-44.65	3	97.15	30.28	<0.0001	11
	II	a, b	$\theta = 1$	-69.01	4	149.36	11.78	0.0013	10	-34.14	4	79.61	12.74	0.0007	7
	IIIa	a, b	$\theta = 2$	-68.07	4	147.47	9.88	0.0033	7	-39.98	4	91.30	24.43	<0.0001	10
	IIIb	a, b, θ		-66.86	5	149.17	11.59	0.0014	9	NA					
2	0	μ_j		-68.34	4	148.01	10.42	0.0025	8	-39.28	4	89.89	23.02	<0.0001	8
	I	a_j		-70.76	4	152.86	15.28	0.0002	12	-44.16	4	99.66	32.79	<0.0001	12
	II	a_p, b_j	$\theta_1 = \theta_2 = 1$	-60.67	6	141.73	4.15	0.0586	5	-25.78	6	71.97	5.10	0.0331	5
	IIIa	a_p, b_j	$\theta_1 = \theta_2 = 2$	-59.16	6	138.72	1.13	0.2648	2	-23.57	6	67.54	0.67	0.3030	2
	IIIb	a_p, b_p, θ_j		NA						NA					
3	II & IIIa	a_p, b_j	$\theta_1 = 1, \theta_2 = 2$	-58.59	6	137.59	0.00	0.4662	1	-23.23	6	66.87	0.00	0.4242	1
	II & IIIb	a_p, b_p, θ_2	$\theta_1 = 1$	-57.04	7	140.53	2.94	0.1070	3	-21.43	7	69.30	2.43	0.1256	3
	IIIa & II	a_p, b_j	$\theta_1 = 2, \theta_2 = 1$	-61.23	6	142.86	5.28	0.0333	6	-26.12	6	72.64	5.77	0.0237	6
	IIIa & IIIb	a_p, b_p, θ_2	$\theta_1 = 2$	-57.61	7	141.66	4.08	0.0608	4	-21.77	7	69.98	3.11	0.0897	4

The nonlinear functional response model (Type II, IIIa, IIIb) was $y_{ij} = N(a_j \times x_{ij}^{\theta_j} / (b_j^{\theta_j} + x_{ij}^{\theta_j}), \sigma_j^2)$. Type I was modelled as $y_{ij} = N(a_j \times x_{ij}, \sigma_j^2)$ and Type 0 as $y_{ij} = N(\mu_j, \sigma_j^2)$. j denotes prey species, 1 = lemmings and 2 = grey-sided voles. Set 1 contained models with shared parameters across prey species, while set 2 and 3 estimated species-specific responses. All responses were of the same type in set 2, while set 3 evaluated responses of different types. Alternative models were defined by constraining parameters (see column *Constraints*). The model with the smallest AIC_c-value (Akaike’s information criterion, corrected for small sample size) had most support. LogL is the negative log-likelihood (NA indicates non-convergence), and K the number of estimated parameters (regression coefficients + 2 variance estimates). Δ_i is AIC_c for the model of interest – min(AIC_c). w_i is the weight, or the relative likelihood

and lowest density estimates. Lemmings were trapped in all territories except one, but showed less intraspecific variation in density (a 14-fold difference) than grey-sided voles. Highest lemming indices were obtained above the tree line, particularly in high-altitude territories dominated by fresh heath vegetation. Field voles and Northern red-backed voles showed a patchy distribution pattern. High densities of field voles were recorded in two territories in a mosaic landscape with a high proportion of dry fens and low herb meadows. The Northern red-backed vole was restricted to low altitudes in the birch forest, and occurred at very low densities.

Diet composition

A total of 959 prey items were identified from 505 pellets and occasional larger prey remains. The dietary analysis confirmed that the rough-legged buzzard relied heavily on small mammalian prey, as rodents constituted 79–98 % of all prey items and 69–98 % of prey in terms of biomass. Overall, lemmings (41 %) and grey-sided voles (36 %) constituted three-quarters of biomass intake on a population level. An additional 11 % of the diet was made up by field voles. The remaining proportion of the diet was shared between other small mammals (0.2 %) and birds (13 %). Diet composition (in terms of proportion of all prey

items) was best explained by an interaction between habitat (birch forest or tundra heath) and age of bird (nestling or adult) (Fig. 2), as this model (AIC_c = 1,814.55, $K = 12$, weight = 0.65) was (weakly) supported over the model with additive effects of habitat and age (AIC_c = 1,815.55, $K = 9$, weight = 0.35). Remaining models including only age or habitat as predictors had very low AIC_c-weights (<0.0001). As expected, based on the distribution pattern of prey species, grey-sided voles were more common in the diet in the birch forest than in tundra heath, while the opposite was observed for lemmings, field voles and birds. Further, in both habitats, adults had a higher proportion of lemmings and field voles in the diet than nestlings, while nestling diet comprised a larger share of grey-sided voles and birds (Fig. 2). The interaction effect between habitat and age was likely caused by the larger difference between the proportion of birds in nestling and adult diets in the heath habitat than in the birch forest habitat (Fig. 2).

Functional response

The rough-legged buzzards exhibited strong functional responses to both grey-sided voles and lemmings (Fig. 3). They also responded functionally to field voles (not shown), but since we only have two estimates of field vole density >0, the shape of this response could not be analysed. We

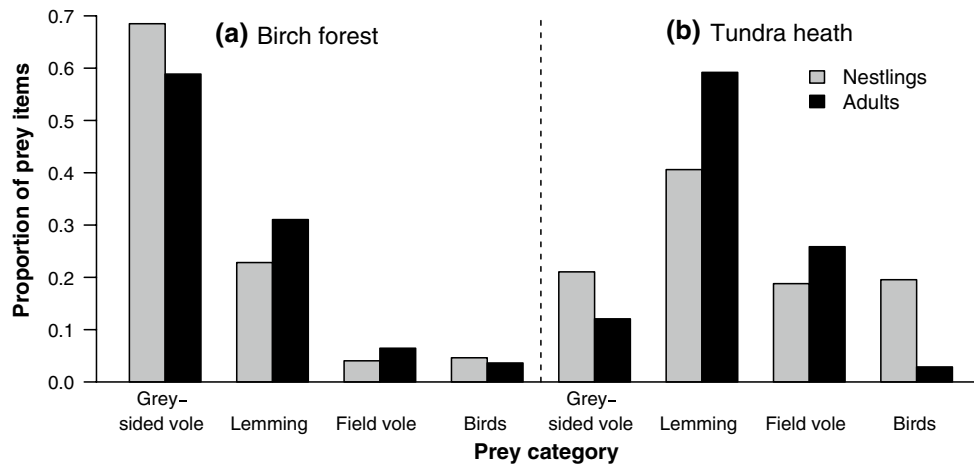


Fig. 2 Diet composition of rough-legged buzzards in relation to habitat (birch forest, tundra heath) and age class (nestling, adult). Pooled data from 8 territories (4 territories in each habitat type). Proportions

refer to proportions of prey items per habitat and age class. Number of identified prey items: birch forest $n_{\text{nestlings}} = 346$, $n_{\text{adults}} = 248$, and in tundra heath $n_{\text{nestlings}} = 133$ and $n_{\text{adults}} = 174$

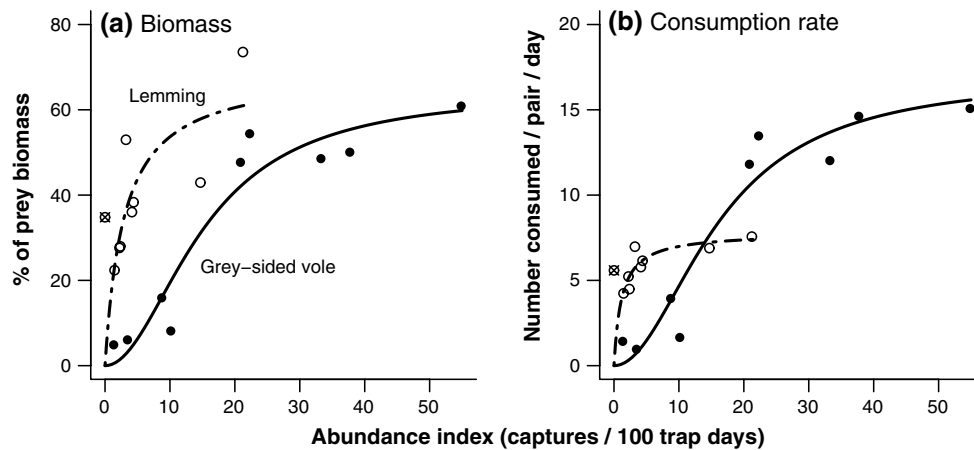


Fig. 3 Prey-dependent functional responses of rough-legged buzzards to grey-sided voles (*Myodes rufocanus*) and Norwegian lemmings (*Lemmus lemmus*). **a** Percentage of ingested prey biomass in relation to prey density index, compositional data that was converted to: **b** the estimated number of killed prey individuals by a single breeding pair (including prey items fed to their nestlings) per

day. Density estimates of respective prey species were obtained by snap-trapping. The functional response to grey-sided voles (filled circles, solid line) was best described by a type IIIa response, and the response to lemmings (open circles, dashed line) was of type II (open crossed circle data point not included in the analysis; see “Materials and methods” for explanation)

therefore focused on the functional response to grey-sided voles and lemmings.

Models with species-specific parameters were strongly supported over global models in which grey-sided voles and lemmings shared parameters. All five global models had Akaike-weights <0.001 (Set 1 in Table 1) and the species-specific models thus received almost all support. Analyses with different response variables (kill rates and % of prey biomass) gave very similar results regarding the overall shapes of the functional responses (Table 1). The highest ranked model contained a type IIIa response to grey-sided voles and a type II response to lemmings. However, the model with type IIIa responses to both species received

similar support (Table 1). The functional response to grey-sided voles was weak at low densities and clearly sigmoid in shape. The inflection point of the type IIIa response to lemmings was at very low density. Such a functional response is density-dependent only over a narrow spectrum of low densities, and probably of limited importance in reality. The type II response was therefore the more likely predation pattern on lemmings.

For the analysis with kill rates as the response variable, both asymptotic kill rates and half-saturation constants differed between responses to grey-sided voles and lemmings. Asymptotic kill rate of grey-sided voles was 2.17 times greater than the corresponding asymptote for lemmings,

whereas the half-saturation constant for lemmings was 13.94 times lower than the half-saturation constant in the response to grey-sided voles. The difference in the asymptote of the functional response was not evident when % of prey biomass was analysed as the response variable (as the functional response leveled out at ~65 % for both species), but half-saturation constants differed in the same direction as for kill rates (ratio grey-sided voles/lemmings: 5.19). The two functional responses thus differed markedly in the rate of approach to the asymptote, which was expressed as a substantially steeper functional response to lemmings than to grey-sided voles (Fig. 3; Table 2).

Prey selection and switching

According to selection ratios, different rodent prey categories were not utilised in accordance with relative availability, neither on the population (Table 3) nor territory (Fig. 4) levels. On the population level, grey-sided voles occurred half as often in pellets compared to alternative prey (i.e. lemmings and field voles) as would be predicted from their relative abundance. Selection ratios for lemmings versus alternative prey (all vole species combined) showed that lemmings were taken 1.7 times more often than suggested by relative availability. However, this pattern was not consistent at the individual (or pair) level. Analyses of data obtained from each pair showed that grey-sided voles were taken in proportion to relative abundance at low relative densities (Fig. 3a), but that standardised selection ratios declined with relative abundance (GLM, Gaussian error structure with logit-link: $\text{logit}(\text{selection ratio}) = -0.26 - 1.58x$, analysis of deviance $\chi_1^2 = 0.08$, $p = 0.0009$). At low relative densities, lemmings were apparently more vulnerable to predation than grey-sided voles (Fig. 3b), but as for grey-sided voles, standardised selection ratios for lemmings declined as relative density increased [GLM, Gaussian error structure with logit-link: $\text{logit}(\text{selection ratio}) = 1.55 - 2.90x$, analysis of deviance $\chi_1^2 = 0.28$, $p < 0.0001$]. The graphical analysis presented in Fig. 4 indicated that the predation patterns on grey-sided voles and lemmings were not consistent with positive switching, but rather with negative switching.

Discussion

In this study, we demonstrated that an avian predator, the rough-legged buzzard, showed different functional responses to its two most important prey species, Norwegian lemmings and grey-sided voles. The response curve to lemmings was noticeably steeper at low-to-intermediate prey densities than the response to grey-sided voles. The rough-legged buzzard can thus be categorised as a rodent

Table 2 Parameter estimates from the most supported functional response models (selected as the model with smallest AIC_C value in Table 2)

Response variable	Model	Parameter	Estimate	SE	95 % CI
Biomass	Table 1a, II and IIIa	a_{lemming}	69.37	12.55	42.25–96.48
		b_{lemming}	2.93	1.47	−0.26–6.11
		a_{vole}	64.38	6.71	49.89–78.87
		b_{vole}	15.21	3.08	8.55–21.87
Kill rate	Table 1b, II and IIIa	a_{lemming}	7.80	0.55	6.61–8.99
		b_{lemming}	1.16	0.35	0.41–1.92
		a_{vole}	16.94	1.77	13.11–20.76
		b_{vole}	16.21	3.17	9.37–23.05

Parameter names refer to Eq. 4

specialist with an opportunistic foraging strategy, which has also been observed in Siberian rough-legged buzzards (Wiklund et al. 1998). But we also observed that grey-sided voles and lemmings were not preyed upon according to relative abundance, and further that diet composition differed between adults and nestlings.

We analysed functional responses to spatial heterogeneity in prey densities, rather than to temporal variation. Spatial within-year heterogeneity of rodents is common in taiga and tundra landscapes of Fennoscandia, and is related to productivity patterns and habitat preferences of different rodent species (Oksanen and Henttonen 1996; Oksanen et al. 1999). Thus, this high degree of within-year variation was not a consequence of our sampling protocol and selection of specific predator territories, and long-term studies in our study area have shown that the habitat-related pattern of vole and lemming abundance observed here was consistent over three cycles from 2001 to 2011 (Taylor 2009; Hellström, unpublished data). We assumed that density indices obtained by snap-trapping was highly correlated and linearly related to true densities, a suggestion supported by previous studies on *Myodes* and *Lemmus* species (Gruyer et al. 2008; Hanski et al. 1994). However, the relationship between snap-trap indices and density estimates might differ depending on species and habitats (e.g. Øvrejorde 2007), which can potentially bias calculations of particularly prey preference. But various removal estimators (White et al. 1982) applied to snap-trapping data for lemmings and grey-sided voles in our study area yield abundance estimates that are linearly related to density indices and further do not support a species-dependent relation between snap-trap indices and abundance estimates (Hellström and Angerbjörn, unpublished data). Current data therefore indicate that removal trapping using snap-traps reflects true abundance (both absolute and relative) without major biases and differences between species.

Table 3 Selection ratios and standardised selection ratios for grey-sided voles versus alternative prey and for lemmings versus alternative prey

Comparison	Prey category	Selection ratio	Stand. selection ratio	SE	95 % CI	Diff. selection ratio	95 % CI Diff. selection ratio
Grey-sided vole vs. Alt. ^a	Grey-sided voles	0.71	0.32	0.05	0.61–0.82	−0.80	−0.70 to −0.88
	Alternative	1.51	0.68	0.25	0.96–2.06		
Lemming vs. Alt. ^b	Lemmings	1.44	0.63	0.38	0.59–2.29	0.59	0.42–0.77
	Alternative	0.84	0.37	0.05	0.73–0.96		

Selection ratios are calculated at the population level, standard errors and confidence intervals refer to estimates of selection ratios. Standardised selection ratios (equivalent to Manly’s alpha) are shown for comparison. Differences between selection ratios are also presented. Confidence intervals around the differences do not include zero, and therefore show that different rodent prey were not preyed upon in direct relation to relative availability

^a Alternative = lemming + field vole

^b Alternative = vole = grey-sided vole + field vole

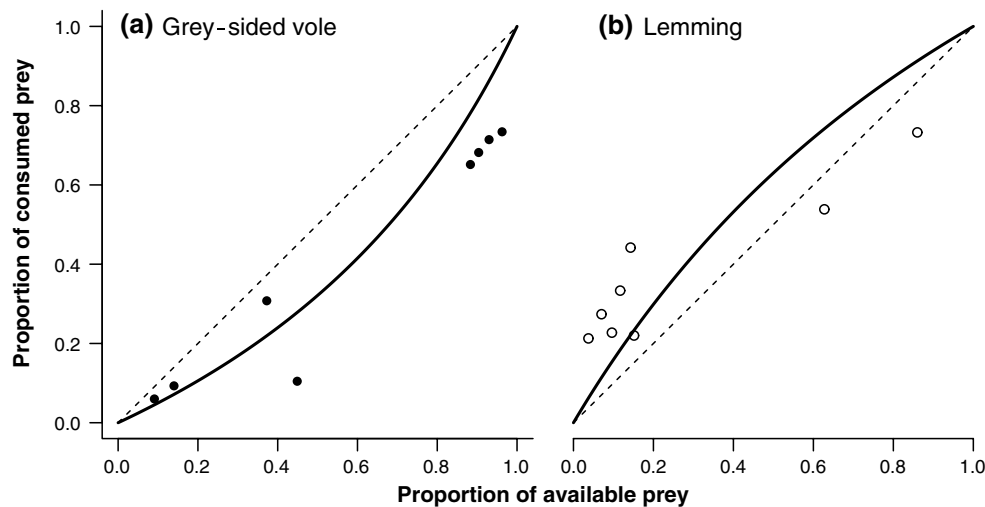


Fig. 4 Selection of prey by each rough-legged buzzard pair in relation to relative prey abundance. **a** Grey-sided voles versus alternative rodent prey (lemmings + field voles), **b** lemmings versus alternative prey (grey-sided voles + field voles). The *dashed line* indicates equal

representation in diet and environment, the *solid line* represents the null hypothesis calculated from population-level selection ratios. Proportions are proportions of prey items

Scaling issues and functional responses

It is necessary to test predictions from foraging theory using various observational scales. Arditi and Ginzburg (1989) suggested that functional responses should be studied on the same temporal scale as population dynamics (i.e. numerical responses), otherwise predator–prey models are contradictory due to the combination of fast and slow processes. This is in contrast to mechanistic explanations for the functional response, which was derived from behaviours of individual predators (Holling 1959a, b). Population level responses are indeed the cumulative effects of individual responses occurring on a behavioural time scale, and both the population and individual level approaches are thus necessary for finding scale-independent features of predation. Researchers concerned with regulation of prey populations have primarily adopted the population scale

approach, usually by averaging kill rates and prey density within a breeding interval and then repeating the sampling over several seasons (Abrams 1994). But the variation in both predator and prey behaviour would be lost by such averaging of important parameters, and can lead to unexpected results (Chesson 1984). Instead, the “individual scale approach” allows for a detailed study of how individuals vary in their response to prey density.

Patterns detected on longer time scales may further be obscured by changes in densities of other species other than the focal predator–prey unit. For instance, the rough-legged buzzard responds numerically mainly to vole fluctuations, and lemmings are not a pre-requisite for successful breeding (Hellström 2007). Although vole and lemming cycles are generally tightly coupled, lemmings repeatedly fail to reach peak densities when voles do (Henttonen and Kailusalo 1993). It is possible that the functional response to

grey-sided voles would shift from a type III curve in simultaneous lemming and vole peaks to a steep type II function in years when only voles peak. Such context-dependent responses could have interesting consequences on population dynamics, but have so far largely been over-looked.

Time-scale averaging of functional responses further excludes the possibility to take spatial variation in predation pressure into account, a factor that is often ignored in investigations of predator–prey systems, but might be an important component of vole and lemming dynamics (Ekerholm et al. 2001). Oksanen et al. (1999) found that the dynamics of tundra-living grey-sided voles were characterised by dynamics with more truncated peaks than grey-sided vole dynamics in more productive patches. The functional response of buzzards to grey-sided vole is one plausible explanation to this pattern, as the type III response indicates that buzzard functional response can be density-dependent at low densities (i.e. on tundra heath vegetation), and hence could dampen population peak densities in less preferred habitats of grey-sided voles. In birch forests, where grey-sided voles are highly abundant, per capita rates of predation pressure from buzzards on grey-sided voles were likely less important as the functional response reached saturation level at intermediate densities. Predation on lemmings followed a different pattern, and was characterised by negative switching where the proportion of lemmings in the diet of buzzards were higher than expected at low relative abundance and lower than expected in mountain tundra heaths where lemmings are the dominant prey. Low absolute and relative densities of lemmings largely coincided with productive patches such as birch forest or grasslands. Oksanen (1993) suggested that lemmings could not establish populations in forested areas due to apparent competition mediated by least weasel (*Mustela nivalis*) predation, a hypothesis that can be refined to also include avian predators given the negative switching by buzzards presented here (but see Ims et al. 2011 for an alternative hypothesis). Negative switching is likely to have a destabilising impact on community dynamics (Chesson 1984) and has been observed in other raptors (e.g. Palma et al. 2006). There are several proposed explanations for negative switching, including confusion of predator's search by more abundant (and less preferred) prey (Kean-Howie et al. 1988), changes in behaviour under high predation risk (Abrams and Matsuda 1993), differences in nutritional status between prey types (Abrams 1987), and a need for information-sampling of the availability of different prey types. In relation to foraging theory, negative switching does not support the classic energy-maximising model (i.e. optimal diet or contingency models; Fryxell and Lundberg 1998; Stephens and Krebs 1986), but the observed dietary conservatism instead supports the balanced diet hypothesis. In terms of raw energy content, the larger lemmings are more profitable prey, and

energy-maximising models would predict that buzzards should ignore other prey types at high lemming densities, but we instead found that voles comprised a large share of the diet even at the highest lemming densities. For a full evaluation of contrasting hypotheses, we would however need to obtain direct estimates of handling times of lemmings and voles, as measures of profitability should also take species-specific handling time into account. Balanced diets are typically attributed to herbivores as plants often differ in chemical composition. Carnivores, on the other hand, mostly feed on prey species with similar nutrient and chemical composition, but a difference between voles and lemmings in this aspect has long been discussed (see below).

Prey selection and provisioning

Our study contrasts with the common view that lemmings are inferior prey, a viewpoint largely based on Hagen's large collection of prey items (Hagen 1952) that has been repeatedly cited in the literature (e.g. Framstad et al. 1997). On a population level, lemmings were captured more often than expected based on relative availability, whereas voles were underrepresented in buzzard diet. Hagen (1952, pp. 539–540) reported that lemmings were a surprisingly rare prey in his studies of the diets of raptors and owls in Norway, and further that lemmings were frequently regurgitated by raptors only partially digested. Taitt (1993) suggested that lemmings might be distasteful because of substances emitted by their dorsal skin glands (Wallin 1967). There are, however, other alternate explanations for why lemmings may be more vulnerable to predation than voles.

First, encounter rates with different prey depend on prey density and overlap in predator/prey habitat selection. Rough-legged buzzards mainly hunt in open areas or in patches with sparse vegetative cover (Sonerud 1986; Sylvén 1978), which is the typical habitat for lemmings during summer (Heske and Steen 1993). Grey-sided and field voles on the other hand mainly occupy habitats with a high proportion of shrub cover or boulder fields (Hambäck et al. 1998; Johannesen and Mauritzen 1999; Magnusson et al. 2013), where the risk of encounters with avian predators supposedly is lower. Several studies of selective predation by birds of prey have demonstrated that a preference for a prey type can be explained by coincident habitat choice, both in space and time, of the predator and its preferred prey (e.g. Dickman 1992; Dickman et al. 1991; Norrdahl and Korpimäki 1993; Rohner and Krebs 1996). It is also possible that predators detect lemmings more easily than voles in most habitats. Lemmings, in their “bright yellow, reddish brown, white and contrasting jet black hues” (Andersson 1976) are certainly more conspicuous than both grey-sided and field voles, whose pelage is reddish brown.

Second, rodent-eating avian predators seem to attack different prey species in proportion to their relative densities (Hakkarainen et al. 1992; Nishimura and Abe 1988; Temple 1987), rather than actively select to attack or ignore certain prey types. Prey utilisation patterns therefore seem to be also governed by differences in capture success between prey types. Lemmings are larger and much slower than voles (Oksanen 1993), which suggests that lemmings are easier to catch. Lemmings are also known for their aggressive anti-predator behaviour (Koponen et al. 1961) and often try to ward off predators (Myllymäki et al. 1962), a tactic that can be successful at least against long-tailed skuas (*Stercorarius longicaudus* Viellot, 1819) (Andersson 1976). Voles have adopted another behaviour by outright fleeing when approached by a predator (Sundell and Ylönen 2008), a strategy that is less likely to result in being captured (Shifferman and Eilam 2004).

The overall higher vulnerability of lemmings is thus probably a result of a high encounter rate due to similar habitat choice and high capture success due to their slower mobility and behaviour. The cause of selective predation on lemmings needs further investigation, but seems to lie with the prey rather than with the predator. Prey vulnerability is also likely related to habitat, as we found that selection ratios were variable at the predator-pair level, with both grey-sided voles and lemmings having lower selection ratios in their respective favoured habitat. The cause for this shift in vulnerability warrants further study, but can be caused by intra-specific processes and unfamiliarity with a non-preferred habitat, but also by competitive interactions between lemmings and voles where the inferior competitor is forced to occupy patches with high predation risk.

It is important to note that the functional responses and prey selection ratios would have been different if we had analysed pellets and prey remains collected only at nests, since there was a consistent difference between adult and nestling diets. For instance, lemmings occurred more frequently in the diet of adults, and predation rates on lemmings would have been biased low if the functional response analysis had been based only on nestling diet. Grey-sided voles were found more often in nestling diet, and this pattern does not support a load-size effect (Orlans and Pearson 1979; Sonerud 1992), since the expected outcome under such a scenario is that lemmings should be more frequent in nestling pellets than voles. This difference in prey selection can be a consequence of differential patch use (Markman et al. 2004) or foraging behaviour (e.g. Davoren and Burger 1999) during self-feeding and nestling provisioning, tactics that can be explained by adaptive foraging (Ydenberg 2007). An alternate hypothesis not invoking adaptive behaviour is that nestling size and development determine provisioning decisions and delivery of prey of different sizes to the nest. This is partly supported

by direct observations of nestling feeding behaviour (Hellström, unpublished data), as lemmings are frequently difficult to handle, process and swallow for nestlings until the very latest stage of the nestling period.

To conclude, there is a need for further theoretical and empirical work on community interactions with species-specific or multi-species functional responses to different prey (Hanski and Henttonen 1996; Koen-Alonso 2007; Matthiopoulos et al. 2007; Sinclair et al. 1998). We advocate that, in studies and analyses of the rodent community in subarctic Fennoscandia, species should be treated separately and not as a collective unit, which has been a debated issue (see discussions in Falck et al. 1995; Turchin 2003). The novel approach adopted in this study also revealed that functional responses can vary depending on within-year variation in the density of different prey species. An alternative individual-based approach in which processes occurring on different spatio-temporal scales are both coupled and compared (e.g. Englund and Leonardsson 2008) therefore seems to be necessary to bridge the gap between theoretical and empirical studies of functional responses.

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