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Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators

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Specialist species, using a narrow range of resources, are predicted to be more efficient when foraging on their preferred food than generalist species consuming a wider range of foods. We tested whether the foraging efficiency of the pallid harrier *Circus macrourus*, a vole specialist, and of sympatric Montagu's harriers *C. pygargus*, a closely related generalist, differed in relation to inter-annual variations in vole abundance over five years (including two peak- one intermediate and two low vole abundance years). We show that the hunting parameters of pallid harriers strongly varied with vole abundance (higher encounter rates, capture rates and proportion of successful strikes in high than intermediate and low vole abundance years, respectively), whereas Montagu's harriers showed stable capture rates and hunting success (proportion of strikes that were successful), irrespective of vole abundance. Encounter rates and capture rates were higher for pallid than for Montagu's harriers when voles were abundant, but lower when voles were scarce. The hunting success of pallid harriers was also lower than that of Montagu´s harriers when voles were scarce, and when they had to target alternative preys, in particular birds. Overall, estimated biomass intake rate was 40% higher for pallid harriers than for Montagu's harriers when voles were abundant, but 50% lower when voles were scarce. Our results indicate that specialists predators, like pallid harriers, which evolve specific adaptations or breeding strategies, do better when their preferred prey is abundant, but may face a cost of specialisation, being not efficient enough when their preferred prey is scarce. These results have broader implications for understanding why specialist predators are, in general, more vulnerable than generalists, and for predicting how specialists can cope with rapid environmental changes affecting the abundance or predictability of their preferred resources.

The question of why predators specialise on certain prey types, and whether generalist and specialist tactics are equally profitable, is still unresolved (Recher 1990, Woo et al. 2008). In simple terms, a specialist uses a narrow range of resources and a generalist uses a wide range of resources, although there is a continuum from specialization to generalization both within- and between-species (Partridge and Green 1985, Durell 2000, Bernays et al. 2004, Egan and Funk 2006, Woo et al. 2008). Optimal foraging models predict that diet specialization should depend on the variety and abundance of available prey, and on the intrinsic energy qualities of these preys (e.g. handling time, search time per unit abundance, or caloric value, MacArthur and Pianka 1966). Specialisation may depend on: 1) the spatial-temporal heterogeneity and predictability in the abundance of resources, 2) cultural experience, and 3) the evolution of more efficient foraging adaptations (Partdrige and Green 1985, Sherry 1990, Durell 2000, Whitfield 1990). The latter implies that phenotypic characteristics (anatomical, morphological, behavioural or physiological) should confer greater foraging efficiency to specialists than generalists. For example, individuals that specialize on a single food type may form more effective search images and have greater foraging success linked with a reduced search time (Dukas and Kamil 2001). By exploiting a narrow range of foods, specialists are thus predicted to be more efficient on their preferred food than are generalists consuming a wider range of foods (MacArthur and Pianka 1966). In herbivorous insects, for example, the selection of host plants has been shown to be more accurate, and foraging more efficient, in specialist than in generalist species (Bernays and Funk 1999, Oppenheim and Goud 2002, Bernays et al. 2004, Egan and Funk 2006).

In vertebrates, several studies have evaluated the relative efficiency of different trophic strategies (Partridge and Green 1987, Annet and Pierotti 1999, Golet et al. 2000, Bolnick et al. 2003, Svanbäck and Evlov 2003, Tinker et al. 2008, Woo et al. 2008), mostly focusing on intra-specific individual specialization. Specialist individuals were often shown to be more efficient or to have higher fitness than generalist individuals (but see Woo et al. 2008, Whitfield et al. 2009). Other studies compared the foraging efficiency of closely related vertebrate species characterised by different levels of trophic specialization and showed that, between species, specialisation is also usually associated with a higher efficiency (Huckins 1997, Jones et al. 2001, Britt and Bennet 2008). However, a study on sunfish pointed out that there could also be a tradeoff associated with specialisation, as specialists could be less efficient than generalists on alternative resources, when the preferred food is scarce (Huckins 1997 but see Britt and Benet 2008 for contradictory results). This latter issue has, so far, received insufficient empirical attention, particularly in terrestrial top predators, despite strong implications for the conservation and population sustainability of specialist predators. The more specialized on a food resource a forager is, the more it is constrained to live in patches where that resource is abundant or to spend time and energy in searching for it among a mixture of resources (Begon et al. 2005). If specialists are less efficient than generalists when their preferred food is scarce, then specialisation might be costly under certain circumstances. This would help understand why specialists are often more vulnerable and at greater risk of extinction than generalists (Angermeier 1995, Shultz et al. 2005).

The Montagu's harrier *Circus pygargus* and the pallid harrier *Circus macrourus* are two closely related medium-sized ground-nesting raptors that breed in sympatry in northern Kazakhstan (Terraube et al. 2009). There, the abundance of small mammals (mainly voles *Microtus* ssp.) exhibits unstable dynamics with pronounced inter-annual variations in abundance (Bragin 2003, Davies et al. 2004). The Montagu's harrier is considered as a generalist raptor species that hunts for a wide variety of prey types, although it may favour certain prey in particular areas (Arroyo 1997), including voles in some parts of western Europe (Salamolard et al. 2000). In contrast, the pallid harrier is considered to be a vole specialist, behaving nomadically in response to fluctuations in abundance of this resource (Cramp and Simmons 1980, Ferguson-Lees and Christie 2001).

We tested whether the foraging efficiency of the two harrier species differed 1) among years in relation to vole abundance, and 2) between species in relation to variations in vole abundance. We predicted greater inter-annual variations in hunting success in the specialist (pallid harrier) than generalist species (Montagu's harrier), with the former showing high, intermediate and low success rates for peak-, intermediate and low vole abundance years, respectively. Furthermore, we predicted that pallid harriers would be better foragers than Montagu's harriers when voles (their preferred prey) are abundant, but worse foragers when voles are scarce.

Methods

Study area

We conducted fieldwork in the Naurzum National Nature Reserve area in north-central Kazakhstan (Kostanay Oblast, 51°N, 64°E) in June 2000, June 2006, May–July 2007 and 2008, and early June to mid-July 2009. The study area, located at the southern limit of Siberian forests and northern limit of Eurasian steppes, is characterised by a mosaic of dry steppes, riverbeds, bushy areas and woodland patches (Terraube et al. 2009). The two study species breed there in sympatry. They use slightly different vegetation types for nesting (Terraube et al. 2009, 2010), but both use the same habitats (mainly steppes) for foraging. We monitored an area of ca 700 km² (we estimated survey area by assuming a visibility of 1 km from the network of accessible tracks that we regularly travelled within the overall area, which totalled ca 350 km in length).

Vole abundance estimates

Small mammals (including voles) exhibit strong inter-annual fluctuations in abundance in Kazakhstan (Bragin 2003, Davies et al. 2004). We estimated vole abundance directly in 2006 (in June) and 2007–2009 (from late May to early July), using an index based on the occurrence of fresh vole droppings. This index is correlated with estimates derived from trapping methods (Tapper 1979, Madders 2003). Twenty-five quadrats (25 × 25 cm) were located every few meters along a transect in 11 (2006) and 25 (2007, 2008 and 2009) plots (each within a 1 × 1 km observation square located throughout the study site and stratified by habitat type), and sampled for the presence (1) or absence (0) of fresh vole faeces (moist and greenish in colour). Presence/absence scores were then summed across the 25 quadrats in each plot to obtain an index of vole abundance (Madders 2003). We located the plots in the main vegetation types present in the wider study area (steppes, marshlands and agricultural areas). 2006 was a high vole abundance year that preceded a strong population decline in 2007, followed by population increase in 2008 and then a population crash again in 2009 (Table 1).

We did not quantify vole abundance in 2000 (Table 1), but voles were very frequently observed even during daytime (unpubl.). Pallid harrier breeding densities (which we subsequently found to be highly dependent on rodent abundance, see below and Terraube 2010), as recorded by Bragin (2003) during transect surveys of the study area from 1997 to 2003, reached their highest level in 2000. Similarly, the breeding numbers of other rodent-eating species, such as kestrels *Falco tinnunculus* and short-eared owls *Asio flammeus*, were much higher in 2000 than in previous or subsequent years (Bragin pers. comm..). All these indirect data indicated that 2000 was a peak vole abundance year, rather than a year of increasing or decreasing vole abundance. We estimated the vole abundance index for 2000 in two ways: 1) from the relationships between our vole abundance index and pallid harrier density, i.e. number of pallid nests found divided by survey effort, for the other four study years (vole index = 11.352 × [pallid density] – 0.144; $R^2 = 0.989$; n = 4; see Table 1 for raw data) and 2) from the relationship between the vole abundance index and the % of small mammals in the diet of pallid harriers for the other four study years (vole index = 0.143 × [% small mammals] – 0.144; $R^2 = 0.958$; n = 4; see below and Table 1 for raw data). These relationships gave estimated vole abundance indices of 8.2 and 7.8 for year 2000, respectively. We used the average value (vole index = 8.0 for 2000) for analyses using vole abundance as a continuous variable. Given that one of our data points was estimated, and in order to check for consistency of results, we also analysed vole abundance as a categorical variable, pooling data from years characterised by same levels of vole

Table 1. Vole abundance estimates, foraging observation sample sizes and breeding parameters of pallid harriers (PH) and Montagu's harriers (MH) in each of the study years.

Year		2000	2006	2007	2008	2009
General sampling	Vole index[1]	[8.0][6]	8.8 ± 8.1	0 ± 0	4.2 ± 5.1	1.2 ± 2.9
	Survey effort (man-days)	52	57	104	94	79
	No. observations PH[2]	49	11	68	58	43
	No. observations MH[3]	17	18	59	53	61
	Vole abundance year class	High	High	Low	Interm.	Low
Pallid harriers	% small mammals in diet[4]	67.24	77.08	21.95	38.35	19.4
	Breeding pairs found	40	46	5	31	10
	% failed nests[5]	3.44 (29)	13.04 (46)	100 (5)	12.90 (31)	70 (10)
Montagu´s harriers	% small mammals in diet[4]	29.16	20.00	17.39	8.64	8.45
	Breeding pairs found	26	26	26	34	34
	% failed nests[5]	43.75 (16)	7.69 (26)	38.46 (26)	60 (30)	24.24 (33)

[1] mean ± SD presence/absence score per plot (n = 11 plots in 2006; n = 25 plots in 2007, 2008 and 2009)
[2] no. of hunting observations of pallid harriers
[3] no. of hunting observations of Montagu's harriers
[4] % based on numbers (prey items)
[5] sample size (in brackets) refers to the number of nests monitored
[6] estimated value (Methods)

abundance: 2000 and 2006 (hereafter 'high vole abundance' years); 2007 and 2009 ('low vole abundance' year); and 2008 'intermediate vole abundance' year (Table 1).

Diet

Pellets were collected each year at nests and perching sites of each species. As the pellets of each species have similar dimensions and appearance, we only included pellets collected in nests or perching sites identified as used by individuals of each species. A total of 276 pellets were analysed for this study (134 for Montagu's harriers and 142 for pallid harriers). For 2000, 2006 and for pallid harriers in the low vole abundance years (2007–2009), pellets analysed were the totality of those found. For 2008 (n = 30 for both species), and for Montagu's harrier in the low vole abundance years (n = 60 in 2007 and 25 in 2009), pellets analysed were a random sample of all pellets collected, to avoid too much discrepancy in sample sizes among years. Pellet contents were classified as 'birds', 'small mammals', 'reptiles', 'insects' and 'eggs'. We could not identify all pellet contents to the species level, but 95% of identified small mammals were *Microtus* sp. voles (sub sample size: n = 37). We assessed the minimum number of each prey category per pellet (highest number of different jaws, skulls or pairs of incisors in small mammals; upper or lower mandibles, left or right feet in birds; pairs of mandibles for insects). Diet data are presented both as the percentage of identified prey and their estimated biomass. For the latter, we used the estimated average biomass of each prey type (20 g for small mammals, 29 g for birds, 10 g for reptiles, 5 g for insects and 15 g for eggs) according to Arroyo (1997). Sample size was too small to analyse diet at the individual pair or nest site level (between 1 and 4 pellets per nest), so we pooled data across all individuals for a given year and species. Sampling was spread over the whole breeding population and study area, so a bias due to some pairs or areas being sampled more than others was very unlikely.

We also calculated an index of diet diversity for each species and year class (i.e. high, intermediate or low vole abundance). Diet breadth (B) was calculated according to Levins (1968), as $B = 1/\sum p_i^2$, where p_i is the proportion of the diet contributed by prey type i. Levin's index tends to weight in favour of abundant prey types, and was preferred over the Shannon Index, which tends to give more weight to rare groups (Krebs 1989).

Finally, we estimated the biomass of an average taken prey in a given year or vole abundance year class for each species by multiplying the frequency of occurrence of the different prey types in diet by the estimated average biomass of each prey type.

Foraging observations

Each year, the study area was surveyed daily, in conditions of good visibility, searching for Montagu's and pallid harriers breeding and monitoring the activity of each individual of the two harrier species exhibiting foraging behaviour during the survey. Thus, foraging observations were spread over one month in 2000 and 2006, over three months in 2007, two months and a half in 2008 and one month and a half in 2009. Each time an adult harrier was detected foraging, we recorded its behaviour using 10× binoculars and a stopwatch. When foraging, harriers typically fly at low (< 3 m) elevation above the ground, quartering to search for prey, a flight behaviour distinct from that of other activities (Schipper 1977, Madders 2003). Hunting from perches has never been observed. Behaviours clearly not aimed at capturing or locating prey (e.g. perching, territorial behaviours or prey transport) were ignored. During each foraging observation, we recorded the species observed (pallid or Montagu's harrier), length of foraging bout (in seconds), number of encounters, number of successful prey captures, and the habitat in which the bird was hunting (in no case did we record harriers hunting over more than one habitat during the same observation bout). We ended an observation bout when the hunting harrier's behaviour could no longer be determined accurately (e.g. when it was hidden from view or became too distant). Observation bouts lasted on average (mean ± SD)

157 ± 106 seconds (range 15–627; n = 437). Prey encounters were defined as unambiguous sudden changes in flight direction or speed directed towards a potential item on the ground. Observers undertook simultaneous watches of the same bird during training sessions at the beginning of each study year, with the aim of standardising the criteria that were used to define prey encounters. Prey strike attempts were defined as encounters in which the bird landed on the ground. Success rate was evaluated as the proportion of strikes that resulted in a capture. Whether strikes were successful or not was usually obvious from the harrier's subsequent behaviour. Failed strikes were generally followed by an immediate resumption of foraging, whereas captures resulted in harriers plucking prey at the capture site or flying with the prey to the nest. When harriers stayed out of sight on the ground for a very short period, it is difficult to assess whether they captured or not, because harriers can stay on the ground for a few seconds to rest after an unsuccessful strike (unpubl.). In such cases, harriers could have captured and quickly consumed a small prey, such as an insect, but including these could lead to an overestimation of successful strikes. These cases were rare (2.7% of all observations in 2000, and 2.1% of all observations in 2007, 0% in other years), but in order to be conservative, we considered those cases as unsuccessful, which was the most likely outcome based on our direct observations of birds after a successful capture. Over the course of the five year-study, we recorded 437 foraging bouts by individuals of the two species. Given that the observations were undertaken on unmarked individuals, there was a potential for sampling the same individuals repeatedly, for example on different days. Nevertheless, we sampled the whole study area (ca 700 km^2) homogeneously, including areas far from the breeding sites and probably used by non-breeding individuals, so we believe our sample is not biased with a disproportionate representation of some individuals. For each species, 90% of the recorded bouts occurred in dry steppes. Other habitats used for foraging were marshlands, fallow agricultural land and bushy areas. The proportion of habitats used for foraging did not differ significantly between species (χ^2-test, $p > 0.9$).

Statistical analysis

We used SAS 9.01 for analyses. We tested for differences in diet composition between species using χ^2-test on the number of individuals in each prey category. To analyse variation in encounter, strike and capture rates, and in capture success for each species, we used vole abundance either as a class variable (comparing high, intermediate or low vole abundance years) or as a continuous variable (regression on vole abundance index in each year). When testing for differences in study parameters between vole abundance year classes, we included in our generalized linear models two-by-two tests of the LS means differences. When using vole abundance as a continuous variable, we looked for possible non-linear relationships by trying different transformations of this variable in our models (non-transformed, log-transformed, or inclusion of a quadratic term). In all cases, the best models (in terms of explained deviance and significance levels) were those that included log-transformed vole abundance, and we show only the results of these models to simplify the presentation of the results. We tested for among-species differences in foraging variables using GLMs that included log-vole abundance (continuous), species (pallid vs Montagu's harrier) and the interaction between log-vole abundance and species as fixed effects. Number of encounters or strikes per observation bout were fitted to models using a Poisson distribution (and a log-link function), with the log-transformed duration of the observation bout included as an offset. Given that there was only one or no capture per observation bout, we fitted capture probability to models using a binomial error distribution (and a logit link function), using also the log-transformed duration of the observation bout as an offset. We fitted success rate (capture/strikes) to models using a binomial distribution and a logit link function. All tests were two-tailed, even though the predictions were directional.

Results

Diet

Pallid harriers preyed mostly on small mammals in years of high vole abundance (72% of total biomass, Fig. 1) and

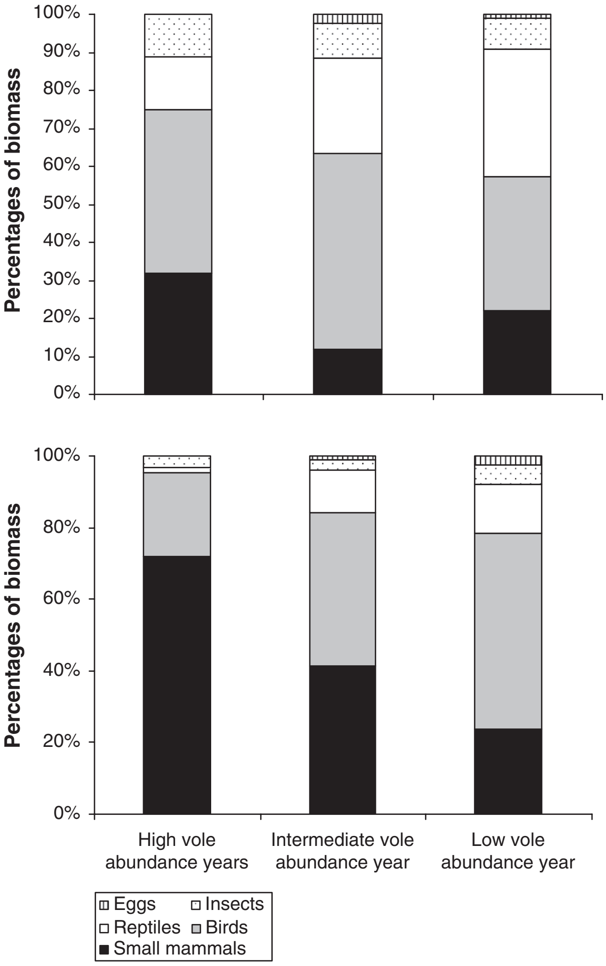

Figure 1. Diet composition (% of biomass) of Montagu's harriers (above), and pallid harriers (below) in high-, intermediate- and low-vole abundance years.

diet breadth (Levin's index) was very low in these years (Table 2). This change in diet breadth was associated with the progressive inclusion of more birds and reptiles (and a marginal higher inclusion of insects and eggs) in the diet. In particular, birds became increasingly important in intermediate (39% of total biomass) and low vole abundance years (59%; Fig. 1).

Montagu's harriers preyed upon three main prey types: birds, voles and reptiles (mainly lizards), and diet breadth was similar in all years (Table 2). For this species, the main prey in terms of biomass was birds (particularly in high vole abundance years) and reptiles (particularly in intermediate and low vole abundance years) (Fig. 1).

The relationship between diet breath (Levin's index) and log- vole abundance thus differed significantly between species (GLM: log-vole abundance: $F_{1,6} = 24.41$; $p = 0.003$; species: $F_{1,6} = 3.74$; $p = 0.101$; log-vole abundance × species interaction: $F_{1,6} = 10.47$; $p = 0.018$). Diet breath decreased with increasing vole abundance in Pallid harriers (slope: -0.25 ± 0.04, but not in Montagu's harriers (slope -0.05 ± 0.05). Diet breath of pallid harriers was half that of Montagu's harriers when small mammals were abundant, but was 20% higher than that of Montagu's harriers when voles were scarce (Table 2).

The percentage of small mammals in the diet of Montagu's and pallid harriers was significantly different in high ($\chi^2_1 = 6.15$; $p = 0.013$) and intermediate ($\chi^2_1 = 19.30$; $p < 0.0001$), but not in low vole abundance years ($\chi^2_1 = 0.46$; $p = 0.49$).

The average biomass of taken prey (according to the proportions found in pellets) was higher for pallid than Montagu's harriers in each vole abundance class year (Table 2).

Foraging efficiency and vole abundance

Prey encounter rates significantly differed between vole abundance years in both harrier species (Table 3). The pattern of variation was similar between species, with increasing encounter rates found with increasing vole abundance (log-linear relationship; Table 3, Fig. 2a). For both species, encounter rate was significantly higher in high than in low vole abundance years (Table 3). For pallid harriers, encounter rates were higher in intermediate than in low vole abundance years, and tended to be higher in high than in intermediate vole abundance years (Fig. 2a, Table 3). For Montagu's harriers, encounter rates were higher in high than in low or intermediate vole abundance years, but were not significantly different between intermediate and low vole abundance years (Fig. 2a, Table 3).

Strike rate significantly differed between vole abundance year classes, and significantly increased with increasing (log-transformed) vole abundance in pallid harriers, but not in Montagu's harriers (Table 3). In pallid harriers, strike rate in high vole abundance years was almost double that in either intermediate or low vole abundance years, and was also higher in intermediate than in low vole abundance years (Fig. 2b, Table 3). For Montagu's harriers, strike rate tended to be higher in high than in low vole abundance years (Table 3; $p = 0.072$).

Capture rate significantly differed between vole abundance year classes in pallid harriers, but not in Montagu's harriers (Table 3). In pallid harriers, capture rate was similar in high and intermediate vole abundance years, but was significantly higher in those years than in low vole abundance years (Fig. 2c, Table 3). Capture rate significantly increased with increasing vole abundance in pallid harriers, but not in Montagu's harriers (Fig. 3a, Table 3).

Success rate (captures per strike) significantly differed between vole abundance years in pallid harriers, but not in Montagu's harriers (Fig. 2d, Table 3). The success rate of pallid harriers increased with increasing vole abundance (Fig. 3b), being lower in low than in either high or intermediate vole abundance years, but did not differ significantly between intermediate and high vole abundance years (Fig. 2d, Table 3).

Table 2. Diets and estimated biomass intake rates of pallid and Montagu's harriers in years of contrasted vole abundance (high-, intermediate- and low-vole abundance years).

Vole abundance year classes:	High		Intermediate		Low	
Harrier species [5]	PH	MH	PH	MH	PH	MH
Sample size:						
no. of prey items	222	64	73	81	106	255
no. of pellets	65	19	30	30	47	85
Diet[1]:						
small mammals	69.4	23.4	38.4	8.6	20.8	14.9
birds	15.8	21.9	27.4	25.9	33.0	16.5
eggs	0	1.6	1.4	2.5	1.9	0.8
reptiles	3.0	20.3	21.9	37.0	23.6	45.5
insects	12.0	32.8	11.0	25.9	19.81	22.35
B index[2]	1.91	3.96	3.54	3.57	4.03	3.26
Biomass of average taken prey[3]	19.89	16.39	18.56	14.61	17.57	13.57
Biomass intake per h[4]	249.7	149.6	141.8	173.1	58.2	116.8

[1] diet data are given as a percentage of the total number of identified prey items.
[2] B index = Levin's diet breath index (Methods).
[3] estimated from the % of prey types in diet and the average weight of prey types (Methods)
[4] estimated by multiplying the Biomass of average taken prey by the capture rate (no. of captures per hr; data shown in Figures 2c and 3a).
[5] PH = Pallid harrier; MH = Montagu's harrier

Table 3. Results of the GLMs testing for the effect of vole abundance on the foraging parameters of pallid (PH) and Montagu's harriers (MH). Vole abundance was treated either as a class variable (comparing years of high-, intermediate- or low-vole abundance) or using estimated vole abundance (log-transformed) as a continuous variable (regressor).

		Vole abundance years (class)						Log-Vole abundance (continuous)		
Dependent Variable	Species[4]	DF	χ^2	p	LMS differences:	means ± SE	p	DF	Chi²	P
Encounter rate[1]	PH	2,226	54.46	< 0.0001	high vs int.	+0.244 ± 0.133	0.065	1,227	51.21	< 0.0001
					int. vs low	+0.716 ± 0.145	< 0.0001			
					high vs low	+0.960 ± 0.137	< 0.001			
	MH	2,205	7.98	0.019	high vs Int.	+0.378 ± 0.192	0.048	1,206	6.69	< 0.01
					int. vs low	+0.122 ± 0.161	0.450			
					high vs low	+0.500 ± 0.171	0.004			
Strike rate[1]	PH	2,226	7.00	0.0301	high vs int.	–0.012 ± 0.207	0.953	1,227	5.93	0.015
					int. vs low	+0.452 ± 0.200	0.029			
					high vs low	+0.439 ± 0.200	0.024			
	MH	2,205	3.25	0.197	high vs int.	–0.160 ± 0.287	0.577	1,206	1.67	0.197
					int. vs low	+0.228 ± 0.274	0.401			
					high vs low	+0.389 ± 0.216	0.072			
Capture rate[2]	PH	2,226	13.85	< 0.001	high vs int.	+0.325 ± 0.445	0.465	1,227	15.08	< 0.0001
					int. vs low	+1.296 ± 0.493	< 0.01			
					high vs low	+1.622 ± 0.482	< 0.001			
	MH	2,205	1.30	0.523	high vs int.	–0.466 ± 0.597	0.435	1,206	0.64	0.425
					int. vs low	+0.480 ± 0.433	0.268			
					high vs low	+0.014 ± 0.560	0.978			
Capture success[3]	PH	2,85	5.70	0.058	high vs int.	+0.333 ± 0.449	0.459	1,86	6.82	0.009
					int. vs low	+0.788 ± 0.503	0.117			
					high vs low	+1.121 ± 0.493	0.023			
	MH	2,79	0.13	0.939	high vs int.	–0.221 ± 0.633	0.762	1,80	0.03	0.865
					inter. vs low	+0.048 ± 0.463	0.776			
					high vs low	–0.173 ± 0.607	0.916			

[1] the dependent variable (number of encounters or strikes) was fitted to GLMs using a Poisson error distribution and a log-link function; the duration of the observation (log-transformed) was included as an offset.
[2] the dependent variable (capture = 0 or 1) was fitted to GLMs using a Binomial error distribution and a logit link function; the duration of the observation (log-transformed) was included as an offset.
[3] the dependent variable (success rate = capture / strikes) was fitted to models using a binomial distribution and a logit link function
[4] PH = Pallid harrier; MH = Montagu's harrier

Between-species differences in foraging efficiency and vole abundance

When comparing between species along a gradient of vole abundance, the relationship between encounter rate and (log-transformed) vole abundance differed between the specialist and the generalist species (Table 4; significant log-vole abundance × species interaction). Encounter rates were higher for pallid than for Montagu's harrier when voles were abundant, but lower when voles were scarce (Fig. 2a). For strike rate, there was no significant difference between species in relation to variation in vole abundance (Table 4: non significant log-vole abundance × species interaction). For capture rate, however, this interaction was significant (Table 4): capture rates were higher for pallid than for Montagu´s harriers when voles were abundant, but lower when voles were scarce (Fig. 3a). When comparing high and low vole abundance years only, there was a significant interaction between species and vole abundance year class explaining capture rate ($\chi^2_3 = 5.08$; p = 0.024), arising from the opposite differences in capture rate between species in low and high vole abundance years (Fig. 2c).

For success rate (% of strikes that were successful), differences between species in relation to vole abundance did not reach statistical significance (Fig. 3b, Table 4; log-vole abundance × species interaction: p = 0.110). However, success rate appeared lower for pallid than for Montagu's harriers in years of low vole abundance (Fig. 2d, 3b). Indeed, when considering between-species differences by vole abundance class years, success rate did not differ between species in high ($\chi^2_{1,37}$ = 0.29; p = 0.588) and intermediate ($\chi^2_{1,52}$ = 0.22; p = 0.635) vole abundance years, but was significantly lower for pallid than for Montagu´s harriers in low vole abundance years ($\chi^2_{1,75}$ = 4.13; p = 0.042; LMS difference: –0.966 ± 0.488).

When calculating an estimated biomass intake rate for each species (multiplying the capture rate per hr by the estimated average biomass of a taken prey for each year and species), the relationship between biomass intake rate and log-vole abundance also differed between species (Table 4; log-vole abundance × species interaction: p = 0.059; Fig. 3c). Biomass intake rate was lower for Pallid than for Montagu´s harriers when small mammals were scarce, by higher when voles were abundant (Fig. 3c). Overall, biomass intake rate was 40% higher for pallid than for Montagu´s harriers in years of high vole abundance, but was 50% lower in years of low vole abundance (data in Table 2).

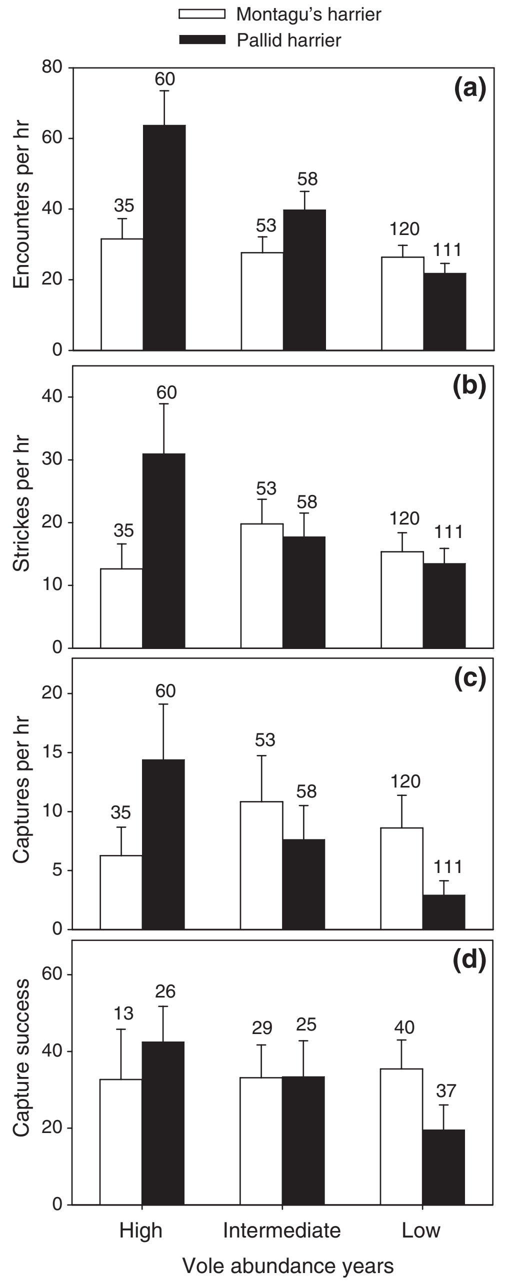

Figure 2. Mean ± SE (a) encounter rate (encounters per hour of hunting time), (b) strike rate (strikes per hour of hunting time), (c) capture rate (captures per hour of hunting time) and (d) capture success (% of strikes that are successful) of Montagu's and pallid harriers, according to vole abundance year classes (high-, intermediate- and low-vole abundance years). Sample sizes are given above the error bars.

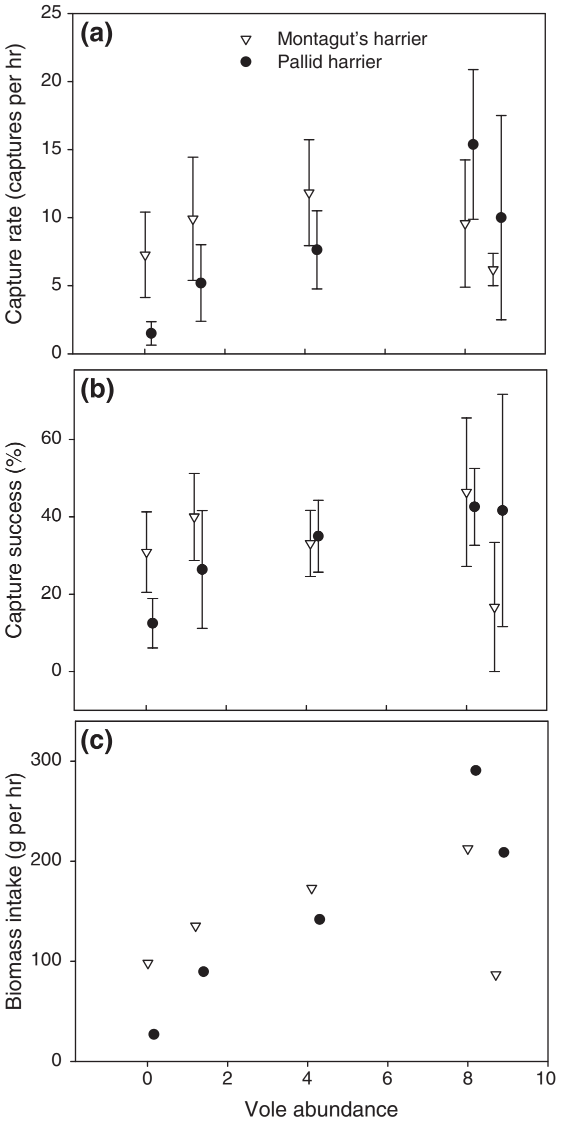

Figure 3. Mean ± SE (a) capture rate (captures per hour of hunting time), (b) capture success (% of strikes that are successful) and c) estimated biomass intake rate (g per h of hunting time) of Montagu's and pallid harriers, according to vole abundance as a continuous variable (1 data point per year).

Discussion

Our results are consistent with our initial hypotheses: 1) that specialist predators have overall higher inter-annual variation in foraging success, and 2) that diet specialization in a vertebrate predator was associated with greater foraging efficiency (higher encounter rates and capture rates, higher biomass intake rate) when the preferred prey was abundant. Most interestingly, our study also shows that the specialist had lower foraging success than the closely related generalist species when its main prey was scarce (lower encounter and capture rates, lower hunting success, and 50% lower biomass intake rate). We discuss below these results and their implications.

Consistent with our predictions, for the specialist pallid harrier foraging success (capture rate and success rate) was highly variable between years, being high when vole abundance was high, when diet data indicated a highly specialized diet (low trophic diversity and 67–77% of small mammals, mainly voles, in the diet). In contrast, foraging success was much lower during low vole abundance years, when diet data indicated a higher trophic diversity and a greater inclusion of alternative prey, in particular passerine birds. In contrast to pallid harriers, capture rate and success in the generalist Montagu's harrier (that had an overall greater diet breadth) did not vary between years of contrasted vole abundance.

Table 4. Results of GLMs testing for differences between pallid and Montagu's harrier in foraging parameters variation according to vole abundance (as a continuous variable, log-transformed).

Dependent-Variable:	Fixed effects	DF	χ^2	p
Encounter rate[1]	log-vole abundance	1,433		0.925
	species		0.01	< 0.001
	species × log-vole abundance		40.85 5.32	0.021
Strike rate[1]	log-vole abundance	1,433	1.02	0.312
	species		6.29	0.012
	species × log-vole abundance		0.22	0.639
Capture rate[2]	log-vole abundance	1,433	2.86	0.098
	species		10.19	< 0.01
	species × log-vole abundance		4.10	0.043
Capture success[3]	log-vole abundance	1,166	3.45	0.063
	species		4.18	0.041
	species × log-vole abundance		2.55	0.110
Biomass intake per h[4]	log-vole abundance	1,6	5.23	0.062
	species		13.23	0.011
	species × log-vole abundance		2.55	0.059

[1] the dependent variable (number of encounters or strikes) was fitted to GLMs using a Poisson error distribution and a log-link function; the duration of the observation (log-transformed) was included as an offset.

[2] the dependent variable (capture = 0 or 1) was fitted to GLMs using a Binomial error distribution and a logit link function; the duration of the observation (log-transformed) was included as an offset.

[3] the dependent variable (success rate = capture / strikes) was fitted to models using a binomial distribution and a logit link function

[4] biomass intake rate was estimated by multiplying the average biomass of taken prey by the capture rate of each species (1 point per year; data in Fig. 3c). The dependent variable was fitted to models using a normal error distribution and identity link function.

Furthermore, the observed between-species differences were in accordance to our predictions: pallid harriers tended to have higher capture rates and capture success than Montagu's when voles were abundant (Fig. 2, 3). Differences between species in encounter rates were even more pronounced (being higher in pallid than Montagu's harrier with increasing vole abundance), suggesting that pallid harriers were overall more efficient at finding and locating prey when voles were abundant (Fig. 2). Interestingly, we found that pallid harriers were worse foragers than Montagu´s harriers (lower capture success, resulting in lower capture rates) when they had to feed on alternative prey types (in low vole abundance years). The lower foraging success may arise if pallid harriers invest more time in hunting for voles but are less able to find them, or that they are less efficient in capturing alternative prey. Our results suggest that the second hypothesis is more likely: first, encounter rates were similar between both species in low vole abundance years, which would not be the case if they were searching only for voles; secondly, observed differences in capture success are consistent with the idea that pallid harriers are less efficient than Montagu´s harriers when they have to catch prey other than small mammals, and in particular passerine birds. Overall, capture rates of pallid harriers were higher and lower than those of Montagu´s harriers in high and low vole abundance years, respectively (Fig. 3a, Table 4; significant species × log-vole abundance interaction).

The pattern observed could be linked with the breeding status of pallid harriers in different years, as lower hunting effort may be expected in non-breeding than breeding individuals, due to their different energetic needs, and there was a higher proportion of the former in low vole abundance years. Nevertheless, the parameter that is more likely to be adjusted in relation to energetic needs is daily time spent hunting, not necessarily the foraging parameters considered on this study. On the other hand, inefficient foragers may not acquire enough energetic condition to become breeders, so it is more plausible to think that breeding status is a consequence of foraging parameters, and not the other way round.

As a result of their different foraging success and prey choice, biomass intake rate (estimated from capture rate and the average biomass of taken prey) differed between species in relation to vole abundance. Biomass intake rate of pallid harriers was 40% higher than that of Montagu´s harriers in high vole abundance years, but was half that of the generalist species in low vole abundance years (Table 2, Fig. 3c). Pallid harriers are noticeably heavier than Montagu's harriers (males are 8% heavier and females 30% heavier; authors, unpubl.), so adult pallid harriers need a higher biomass intake rate for self maintenance, in particular females. Also, nestling pallid harriers aged 20–25 days are 25% heavier than nestling Montagu's harriers (unpubl.), so the relative energetic needs for rearing a brood are higher for pallid than for Montagu's harriers. This helps understand 1) why fewer pallid harriers breed when voles are scarce, and why most fail to breed successfully (Table 1), and 2) the nomadic behaviour of the vole specialist pallid harrier. It might be more efficient to move to a different area rather than to stay in an area where the preferred prey is scarce, even when alternative prey are abundant. The lower foraging success on these alternative preys and the associated lower biomass intake rate perhaps might not allow adults to attain a body condition sufficient to breed, or to successfully raise a brood. Indeed, we found that breeding density in the low vole abundance year was extremely low: the species was virtually absent from the region as a breeder (Table 1), although pallid harriers were observed in the area early in the breeding season, but did not stay or bred. Moreover, the few pallid harrier pairs that bred in the study area in 2007 were all unsuccessful (Table 1). In contrast, Montagu's harriers, which took a variety of prey types and maintained foraging success independently of variations in vole abundance, did not show strong interannual variations in any breeding parameters (density or success; Table 1). Interannual variations in the diet composition of Montagu's harriers (Fig. 1) could suggest interannual variations in abundance and availability of alternative prey groups (mainly reptiles and passerine birds), possibly related to variations in the spring weather conditions (Terraube et al. 2010). An interesting result was the absence of significant differences in capture success between intermediate and high vole abundance years in pallid harriers. In this species, foraging success increased with increasing vole abundance, the relationship being log-linear. Thus, even at intermediate vole densities, like in 2008, pallid harriers were able to maintain high capture rates and foraging success. This suggests that the specialised foraging strategy may be a constraint only in low vole abundance situations.

Differences in foraging efficiency between generalist and specialist species could be explained by neural limitations in relation to diet breadth: specialist species appear to be more sensitive to key stimuli, whereas generalists respond equally to large quantities of sensory neural inputs (Dukas and Real 1991). This implies that generalists need higher attentiveness and learning to be able to narrow their resource choices (Bernays 1998). This phenomenon of limited attention helps to understand why specialists tend to forage more efficiently than generalists, through a search image formation on a given food type (Dukas and Kamil 2001). Specialization may be also associated with morphological or behavioural adaptations to handle certain resources. Harriers, along with *Elanus* kites, are the only diurnal raptors to have evolved a parabolic cowl of feathers surrounding their eyes, suggesting that hearing is enhanced to locate small mammal prey concealed in dense vegetation (Rice 1982, Simmons 2000, Negro et al. 2006). Consistent with this, the trait is more pronounced in the pallid harrier than other harrier species, the facial disc encircling the ears and meeting below the bill (Forsman 1999). In contrast, the facial disc of the Montagu's harrier is confined to an arc just behind the ear opening, suggesting its hearing capacities might be less well developed than that of the rodent specialist species. Such adaptations (physiological and morphological) could explain the higher encounter rates of pallid harrier when voles are increasingly abundant. In contrast, adaptations for vole predation could be detrimental when alternative preys have to be targeted. The later was supported by our results: pallid harriers had lower encounter rates and lower capture rates, and also had a lower capture success than Montagu´s harriers in years of low vole abundance.

Additionally, it is worthwhile recalling that some populations of Montagu's harriers behave as vole specialists, feeding mainly on voles and presenting strong numerical responses to their abundance, even when alternative prey are present (Salamolard et al. 2000), which suggests that adaptations for capturing certain prey may also be learnt behaviours. For example, Warburton and Thomson (2006) showed that silver perch *Bidyanus bidyanus* can change from a specialist to a generalist phase over very short time intervals. By learning through experience, these fish could adapt to changes in the profitability of different prey types. Mechanisms determining interspecific (or inter-population) differences in foraging success on different prey types remain however barely understood.

The results of this study have broader implications for understanding why specialists are often more vulnerable than generalists (Angermeier 1995, Shultz et al. 2005). Recent studies have shown that specialist bird species could exhibit a behavioural syndrome, i.e. a suite of correlated behaviours reflecting between-individual consistencies in behaviour across situations (Sih et al. 2004). For example, specialist species are usually less innovative and more stressed than generalists (Clavel 2007). This could lead specialist species to be less adaptable and therefore more vulnerable to new environmental conditions (Shultz et al. 2005, Devictor et al. 2008). Specialists may therefore pay a price for their specialisation through lower efficiency when conditions are not optimal. Thus, our results may have implications for the sustainability and conservation of the vulnerable pallid harrier, whose populations have declined in different parts of the breeding range (Birdlife International 2003). Their specialization on voles, low success in capturing alternative prey, and nomadic behaviour could have negative consequences for the species at a large geographical scale, particularly if the frequency, amplitude and predictability of vole outbreaks varies for example through land use or climate change. Climate changes have been shown to affect vole dynamics in the Mongolian steppes (Zhang et al. 2003) and have been predicted to have deep impacts in the Arctic ecosystem (Gilg et al. 2009). On the other hand, agricultural intensification and land use change has also been shown to have effects on vole dynamics in Europe (Huitu et al. 2003). Land use in Kazakhstan has changed through recent agricultural intensification (Bragin 2003). Similarly, climate change in the area is predicted to be characterized by a decrease in precipitations level and an increase in summer temperatures (Lioubimtseva and Henebry, 2009), which may decrease vole numbers (Zhang et al. 2003). Thus, it is possible that current and future changes may have negative impacts on voles in Kazakhstan. As stated above, in pallid harriers, the relationship between foraging and vole abundance appeared to be not linear (even at intermediate vole densities the species is able to maintain high capture rates), and the detrimental effects of low foraging efficiency (in terms of breeding success) were mainly apparent in years of lowest vole abundance. At the population level, these detrimental effects could be compensated for by high values in breeding parameters at other phases of the vole cycle (e.g. higher breeding success than the sympatric Montagu's harrier during high vole abundance years, Terraube et al. 2009, 2010), and by moving to other areas where vole abundance is relatively higher. However, if land use or climate changes increase the frequency and spatial synchronicity of vole population crashes, detrimental effects at the local level may influence population sustainability at a larger scale. To fully evaluate possible costs of specialisation, it would be necessary to compare the lifetime fitness outcomes of generalist and specialist strategies, and their sensitivity to spatio-temporal variations in abundance of the preferred food at a large scale. This is a challenging task for specialist vertebrate predators, especially when they are nomadic (large scale movements, with breeding populations tracking the fluctuations in abundance of their preferred prey), as compared with generalist species, which exhibit more limited breeding dispersal. Disentangling the interactions between food availability, dietary specialization, foraging success and contrasted demographic strategies (and associated variations in survival, reproduction and dispersal) would greatly help in setting conservation priorities for threatened specialist predators in rapidly changing environments.

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