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The diet of the Marsh Harrier *Circus aeruginosus* breeding on the isle of Hailuoto compared to other raptors in northern Finland

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The Marsh Harrier *Circus aeruginosus* population has expanded rapidly during the last decades in northern Finland. We studied the diet of Marsh Harrier during the breeding seasons 2002–2009 on the isle of Hailuoto in the Gulf of Bothnia in Finland. We compared these results to those of other raptors in the region, and attempted to relate potential differences in the diet composition to population trends. Birds accounted for 73–93% of prey numbers in the Marsh Harrier during the breeding season. Passerine birds were the most numerous during the nestling (63%) and fledging periods (21%), while ducks and gulls/terns had the highest biomass (29% and 12%, respectively). Muskrat (*Ondatra zibethica*) was the most important prey among mammals by number and weight (15% and 18%, respectively). Compositional analysis showed that the Marsh Harrier depredated water and shore birds opportunistically. Based on multidimensional scaling, the food niche of the Marsh Harrier was distinctive from those of five other raptor species. Analysis of diet breadth and annual change in population size suggested that Marsh Harrier diet breadth was wider and its annual population increase among the fastest, compared to other raptor species. Annual population change of raptors was positive among species that were rare in the beginning of monitoring, i.e., in the early 1970s, but was negative among species that were common at that time. No significant relationships were observed between diet breadth and population growth among the studied species.

1. Introduction

Concerns about the future of many raptor populations have led to special monitoring programs in many countries (Kovacs *et al.* 2008). These programs have detected both negative and positive long-term trends (Saurola 2008). Reasons for these trends may be changes in the availability of crucial resources, such as food and nesting sites (Korpimäki & Norrdahl 1991), competition (Hakkarainen *et al.* 2004), habitat quality (Widén 1997), environmental pollutants (Helander *et al.* 2002) and human persecution (Newton 1979). Some of these factors, especially pollution and human persecution, caused populations of some species to collapse during the early 20th century until the 1970s. But due to significant improvements in these factors the populations have often rapidly recovered (e.g., Stjernberg 2003).

Food is obviously a fundamental resource for all organisms to survive and reproduce. Raptors are an ideal group for studying the connection between food (prey) availability and population dynamics due to the relatively easy determination of diet and often reliable estimation of prey abundance by counting and trapping prey species (Korpimäki & Norrdahl 1991, Lewis *et al.* 2004; but see Redpath *et al.* 2001, Tornberg & Reif 2007). By calculating food-niche breadth based on known diets (e.g., Levins 1968, Korpimäki & Marti 1995) raptors can be classified to specialists and generalists (Reif *et al.* 2001, Valkama *et al.* 2005). Specialists use a narrow range of resources and are predicted to be more efficient when foraging on their preferred food than generalist species that are able to effectively utilize outbreaks of the prey they specialize on (Korpimäki & Norrdahl 1991). However, specialists may be more vulnerable to changes in habitat quality and food resources than generalists which may be able to flexibly switch between prey species (Angelstam *et al.* 1984, Suryan *et al.* 2000). Species with overlapping niches are often thought to compete with each other (e.g., Schoener 1982), while the intensity of competition depends on the abundance of the resources. For example, raptors feeding on voles whose numbers may fluctuate fiercely in northern latitudes may not significantly compete during peak years but do so during crash years of voles (Korpimäki 1987).

Populations of the Marsh Harrier *Circus aeruginosus* have being in recovery since the 19th century throughout Europe due to improvements in the quality of their habitats, ending of illegal hunting, and bans of toxic chemicals in farming (Cardador *et al.* 2011). The recovery has also involved an expansion of its northern distribution limits. The first nesting attempt in southern Finland was in 1922 (Hildén & Kalinainen 1968), and it reached its current northernmost breeding sites at the northern end of the Gulf of Bothnia in the 1950s (Törnroos 1956).

One of the key factors in the success of the Marsh Harrier is its relatively wide diet. The Marsh Harrier is a generalist predator, being able to hunt mammals, birds, reptiles, frogs and even fish (Hildén & Kalinainen 1966, Witkowski 1989, Blanco & Hiraldo 1990, Lange & Hofman 2002). It is also known to depredate eggs of other prey species, a rare foraging habit in raptors (Opermanis 2004). Despite the fact that the Marsh Harrier is among the most successful in terms of breeding numbers among Finnish raptors, its ecology is relatively poorly known at the northern parts of its distribution, i.e., in Fennoscandia.

In the present study, we describe the diet of the Marsh Harrier in one of its northernmost breeding sites, the isle of Hailuoto in Finland, based on an analysis of prey remains. We surveyed avian prey abundances to assess whether the diet composition in the March Harrierwas related to prey abundance. Finally, we compare the focal species food niche to that of other raptors in the region to analyze (1) the potential for food competition or food-niche partitioning (Korpimäki 1987, Garcia & Arroyo 2005), and (2) the possible relationship between food-niche breadth and population trends among common raptor species in the study area.

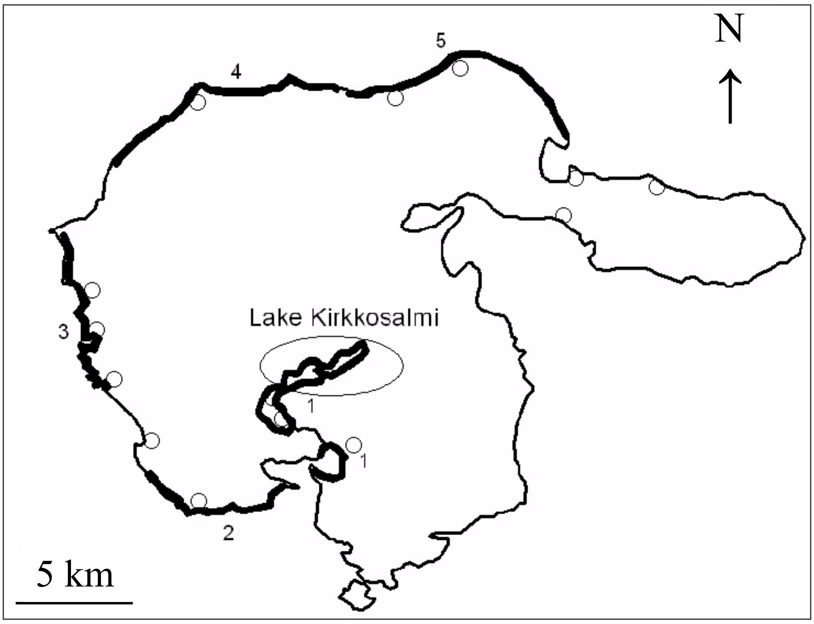
2. Material and methods

2.1. Study area and species

Our study area, the isle of Hailuoto, is situated in the northern Bothnian Bay in the Baltic Sea (65° N, 25° E). The area of the island is about 200 km^2. Approximately 33% of the area is covered by different-aged Scots pine (*Pinus sylvestris*) forests with lichens and *Vaccinium* dwarf shrubs as an understory, 19% is covered by deciduous and 15% by mixed-wood forests. The eastern part of the island (about 10%) is covered by a peat bog and the central part is dominated by cultivated fields (about 6%) growing mainly hay, barley and oats. The long, partly overgrown lake Kirkkosalmi is situated in the middle of the island. Large reed beds *Phragmites australis*, the main breeding habitat of Marsh Harriers in Hailuoto, surround the lake that is also one of the best waterfowl habitats in the island. The sea shores are mainly open or partly open sands and dunes (about 3%) or wet meadows (2%) sporadically overgrown by reed beds (Colpaert 1998). The largest sandy shores are situated along the northern and western sides of the island, while meadows predominate in the south (Fig. 1).

Marsh Harriers return from wintering grounds to Hailuoto in late April. Nest building is initiated soon after arrival, and first eggs are usually laid

Fig. 1. Map of the isle of Hailuoto in the Bothnian Bay, Finland. In area 1 (Lake Kirkkosalmi and Viinikanlahti) shores are overgrown by reed beds. In areas 2–3, shores are variably bordered by meadows, woodland and sands with scattered reed beds, while areas 4–5 are mainly sandy shores with scattered reed beds. Thick lines represent five shorebird census areas in 2004 and 2009. Open circles show territories of the Marsh Harrier in the shore area. Oval circle shows the nesting area of Lake Kirkkosalmi.



around 11–14 May (S. Haapala unpubl. data). Chicks hatch around mid-June and first chicks fledge around 15–20 July.

Our study was conducted during 2002–2009 (excluding 2003). During these years we found 62 Marsh Harrier nests. The number of nests discovered per year varied from 3 (2002) to 22 (2009). We started nest searching around mid-May in 2002 and 2007–2009 or early June during 2004–2006. The later start in 2004–2006 probably had little effect on the number of discovered nests, as the best time for finding nests was from mid-June onwards when chicks hatched. Nests were located by observing prey delivery trips of males to the nest. Male provisioning trips were most frequent and conspicuous when chicks had hatched in mid-June (Haapala 2008). All nests were situated in reed beds near seashore, except two with a distance to the shore a few hundred meters.

2.2. Diet-composition analysis

We collected prey remains and pellets from nests three times: when a nest was found, when the chicks were ringed (approx. 10–15 July), and after the chicks had fledged. We found relatively few prey remains per nest during nestling period, while these started to accumulate during the last days of the nestling period or early fledging period when chicks still used their nests as feeding sites. Mean number of prey specimens identified was 2.8 per nest during nestling period but it was 10.1 during fledging period. This is likely to be caused by an increase in the hunting activity of the female, when she no more removes prey remains from the nest (Witkowski *et al.* 1989). We therefore divided prey samples into two groups that coarsely reflect the diet during the nestling period and that of the late nestling/early fledging period. July the 15th was a priori set as the division between the periods. Note that because the timing of breeding differed among pairs and years, this division is necessarily arbitrary. Mean wing length of chicks between 13 and 17 July was 238 5.4 SE mm, with corresponding age of 28 days (Kjijgsveld *et al.* 1998). As Marsh Harriers fledge at the age of 35 days (Krijgsveld *et al.* 1998), they apparently stayed in or nearby their nests for approx. 1–2 weeks after 15 July.

We identified 702 prey specimens in the samples. The number of prey specimens identified during the nestling and the later nestling /fledging periods were 211 and 491 individuals, respectively. We identified prey specimens using the reference collection of the Zoological Museum of the University of Oulu, Finland. Avian specimens were classified to juveniles and adults based on feather shafts whose tips were open in juveniles but closed in adults, and color and shape. Bones of both birds and mammals were aged based on bone formation, i.e., whether the bone was porous or firm. We obtained the weight of prey specimens from Väisänen (1996).

The availability of prey animals was estimated based on shorebird and waterfowl counts carried out by the North Ostrobothnia Regional Environment Centre during May and early June in 2004 and 2009. These counts were done at protected areas of the Natura 2000 network, dispersed mainly at seashore areas (Fig. 1) by using standard count methods developed for waterfowl and shorebirds (Koskimies & Väisänen 1988). We did not collect estimates for mammals or terrestrial birds.

We used compositional analysis to compare Marsh Harrier diet to the availability of prey (Aebisher *et al.* 1993). In this method the proportion of each prey species or group in the diet and in the field is converted to log ratios by dividing the proportions of one prey type by another, and obtaining the natural logarithm of the ratio. By subtracting the log ratios of the availability of each prey pair from those of the prey used, we were able to determine whether a specific prey type was preferred over others, positive values denoting preference and negative values avoidance. By comparing log ratios of all used and available prey pairs, an anti-symmetrical matrix can be constructed. The sum of positive values on each row of the matrix gives the rank in an increasing order. We calculated the matrix for eight nesting areas, each including 1–9 nests; thus, cell values were means of these eight areas. Nesting areas denote five shorebird and waterfowl census areas, of which the areas 1, 3 and 5 were inventoried in both 2004 and 2009 (Fig. 1). The significance of values was tested by a randomization test using the Compositional Analysis Excel tool version 4.1. Due to the low number of some prey species, we grouped these prey specimens to the following categories. Firstly, grebes and ducks excluding Teal *Anas crecca* were grouped as aterfowl while Teal and Coot *Fulica atra*, as being relatively common, formed categories of their own. Other groups were waders, Common Gull *Larus canus,* Black-headed Gull *Larus ridibundus*, and terns (*Sterna paradisaea and S. hirundo* pooled). We used only waterfowl and shorebirds in the analysis because of the lack of comparable estimates from other prey types (mammals and land birds).

2.3. Diet composition of the Marsh Harrier and other raptor species

We compared the diet of Marsh Harriers with the diets of other, roughly similar-sized raptors: Hen Harrier *Circus cyaneus,* Sparrowhawk *Accipiter nisus*, Goshawk A*ccipiter gentilis*, Common Buzzard *Buteo buteo* and Peregrine Falcon *Falco peregrinus*. These species all breed on Hailuoto or nearby areas. Diet data for these other raptors were obtained from Tornberg (1997; Goshawk), Korpimäki et al. (2001; Peregrine Falcon), Reif et al. (2001; Common Buzzard) and own unpublished data (Hen Harrier and Sparrowhawk); see Appendix 1 and 2 for details.

We created a prey/raptor data matrix by first grouping prey into 21 groups: hares, red squirrel, muskrat, water vole, small rodents and shrews, weasels, waterfowl (including grebes, ducks and Coot), waders, shorebirds (gulls and terns), pigeons, the Cuckoo *Cuculus canorus*, raptors, owls, woodpeckers, corvidae, thrushes, small passerines, reptiles, frogs, fish, and insects. We then divided prey samples of each raptor species into these categories. For comparative reasons we used only samples collected from nests after fledging.

We analyzed the diet similarity by using multidimensional scaling (MDS) with proxscal procedure available in the SPSS 14.1 software. MDS applies Euclidean distances from standardized values of the matrix, and produces a two-dimensional space according to two main dimensions of data variation. The distance between the points is comparable to the similarity of the diets between raptor species.

2.4. Food-niche breadth and population trends

We categorized the ten raptor species as being either ommon or are based on their population numbers in the 1980s (Saurola 2008). We aimed to distinguish between species that (i) were not known to have remarkably declined or were not of conservation concern and (ii) were rare compared to their historical density decades earlier (Väisänen *et al.* 1998). For the latter, causal relationships between diet and population growth might be better perceivable. Because the recent rapid population growth of some of these species, they may no longer be considered rare. With common we refer to species whose density in the beginning of raptor monitoring was in some thousands of pairs.

We analyzed the species-specific relationship between food-niche breadth and population trends using data collected in or near the study area during 1982–2006; for five species, see above. We collected additional data for the Honey Buzzard *Pernis apivorus* (Mikkola & Itämies 1972), Kestrel *Falco tinnunculus* (Korpimäki 1985), Golden Eagle *Aquila chrysaetos* and the White-tailed Sea Eagle *Haliaeetus albicilla* (Sulkava *et al.* 1997, 1998), complemented with our own unpublished data.

To calculate the diet width we applied Levins index (Levins 1968)

$$B = \Sigma\ 1/p_i^2 \qquad (1)$$

where p_i is the proportion of the *i*th prey or prey group. Population trends for raptor species during 1982–2006 were obtained from Saurola (2008). We applied a general linear model to examine the relationship between diet width and population change using R 2.13.1 (R Development Core Team 2012) software.

3. Results

3.1. Breeding-season diet of the Marsh Harrier

The Marsh Harrier diet during the nestling phase from hatching until late nestling was composed mainly of birds but in terms of biomass their share was less important. Later in the breeding season the proportion of birds declined and the proportion of mammals increased accordingly (Table 1). Passerine birds dominated the diet during the nestling phase, yet their biomass accounted only for 13.5% of the diet. Waterfowl (ducks and the Coot) and shorebirds (waders, gulls and terns) made up almost 50% of the biomass, ducks being the most important prey group.

During the fledging phase the proportions of the prey groups evened out. Waterfowl and shorebirds became the most important group. The most important prey species among the waterfowl were the Coot and the Teal (Table 1). Shorebirds (waders, gulls and terns), and especially their chicks, made up a significant part of the diet. Chicks constituted 82% of all gulls and terns found in the remains during the fledgling period. Generally, about 60% of bird prey was pulli or fledglings during both periods. All grouse, except one adult Willow Grouse *Lagopus lagopus,* were presumably chicks of the Black Grouse *Tetrao tetrix,* which is a stable part of the Marsh Harrier diet on Hailuoto. During the fledging period, passerine birds were a rather insignificant group in terms of weight, while the share of mammals, primarily muskrats *Ondatra zibethica*, increased both by number and weight from nestling to fledging periods. Hence, muskrats that were all juveniles were the most important single prey species in late summer. Leverets of *Lepus* species (*L. timidus* or *L. europeaeus*) were also important, accounting for 10–12% of the diet by weight during both periods. Small mammals, reptiles, amphibians and fish were rare in the diet. The mean prey weight increased two-fold from the nestling to the fledging period. The

Table 1. Proportions (%) of different components of the diet of the Marsh Harrier in the breeding seasons 2002–2009 in Hailuoto, northern Finland.

	Nestling period		Fledging period	
Group	Number	Weight	Number	Weight
Mammals, total	6.6	16.9	25.8	38.1
– Muskrat	1.4	5.0	14.9	24.3
– Leverets	2.8	9.9	7.5	12.2
– Other mammals	2.4	2.0	3.3	1.5
Birds, total	92.4	80.7	73.0	60.7
– Grebes	–	–	0.6	1.8
– Herons	0.5	4.1	–	–
– Ducks	10.9	33.8	8.7	10.9
– Grouse (juv.)	2.8	7.0	7.9	9.2
– Coot	0.9	3.4	8.5	14.4
– Waders	8.5	11.0	5.7	3.2
– Gulls and terns	3.3	4.6	17.1	16.1
– Passerines	63.5	13.5	20.9	2.5
– Other birds	1.9	3.3	3.5	2.7
Reptiles	0.5	1.7	0.2	0.0
Fish	0.5	0.7	1.0	1.1
Total (*n*)	211	–	491	–
Mean weight	–	143	–	307

Table 2. Cross-tabulation of water- and shorebirds determined by a compositional analysis. The first row for each species or group denotes the size and direction of the preference, and the lower row denotes SE. The number of positive values in the upper row indicates the preference rank of prey species or group, with peak values denoting the most preferred species.

	Teal	Other. waterf.	Coot	Waders	Black-h. Gull	Common Gull	Terns	Rank
Teal		–1.212	–2.124	–1.987	–0.101	0.379	–0.731	1
		1.304	1.680	1.264	2.222	1.466	1.081	
Other waterf.	1.212		–0.912	–0.775	0.768	1.591	0.480	4
	1.304		1.105	0.432	2.322	1.408	1.233	
Coot	2.124	0.912		0.138	1.984	2.503	1.393	6
	1.680	1.105		1.277	3.360	1.216	1.933	
Waders	1.987	0.775	–0.138		1.266	2.366	1.255	5
	1.264	0.432	1.277		2.269	1.590	1.139	
Black-h. Gull	0.101	–0.768	–1.984	–1.266		0.381	0.006	3
	2.222	2.322	3.360	2.269		2.958	1.564	
Common Gull	–0.379	–1.591	–2.503	–2.366	–0.381		–1.110	0
	1.466	1.408	1.216	1.590	2.958		1.591	
Terns	0.731	–0.480	–1.393	1.255	0.006	–1.110		2
	1.081	1.233	1.933	1.139	1.564	1.591		

compositional analysis did not detect significant differences between consecutively-ranked species indicated by the randomization test (all $p > 0.05$) between consumption and availability of shorebirds and waterfowl (Table 2).

3.2. Diet of the Marsh Harrier compared to other raptor species

The diet of the Marsh Harrier was most similar with that of the Sparrowhawk, the distance between the arithmetic means being 0.545 (Fig. 2). Distances to the Peregrine Falcon (0.710), Hen Harrier (0.756) and Common Buzzard (0.832) were of similar magnitudes, while it was considerably longer to the Goshawk (1.702). In one year the diet of the Common Buzzard was relatively close to that of the Marsh Harrier. This year was a crash year for voles, forcing Common Buzzards to shift from small mammals to thrushes and small passerines. Correspondingly, the Hen Harrier diet resembled that of the Common Buzzard during the two years when Hen Harriers specialized on *Microtus* voles.

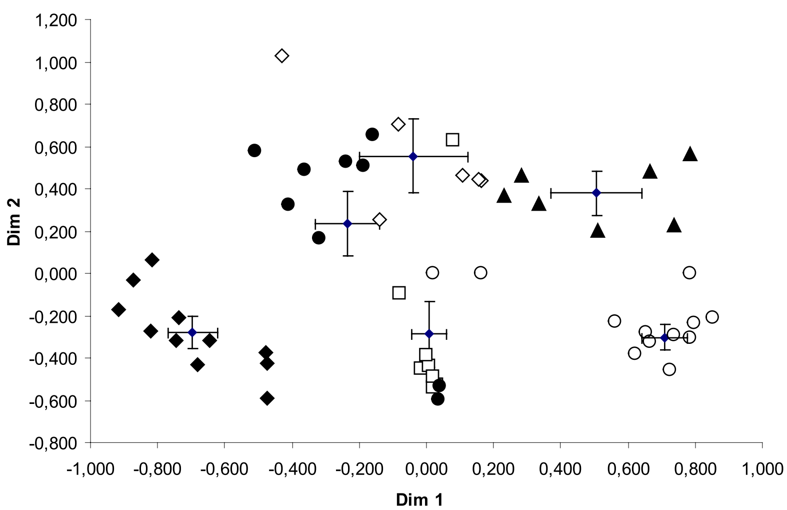


Fig. 2. Multidimensional scaling for six raptor species: Marsh Harrier (filled triangles), Hen Harrier (filled circles), Sparrowhawk (open diamonds), Goshawk (filled diamonds), Common Buzzard (open squares) and Peregrine falcon (open circles). Each symbol represents an annual food sample of a specific species. Black dots with error bars (95%CI) denote the arithmetic means of the locations of each species diet in the two-dimensional space.

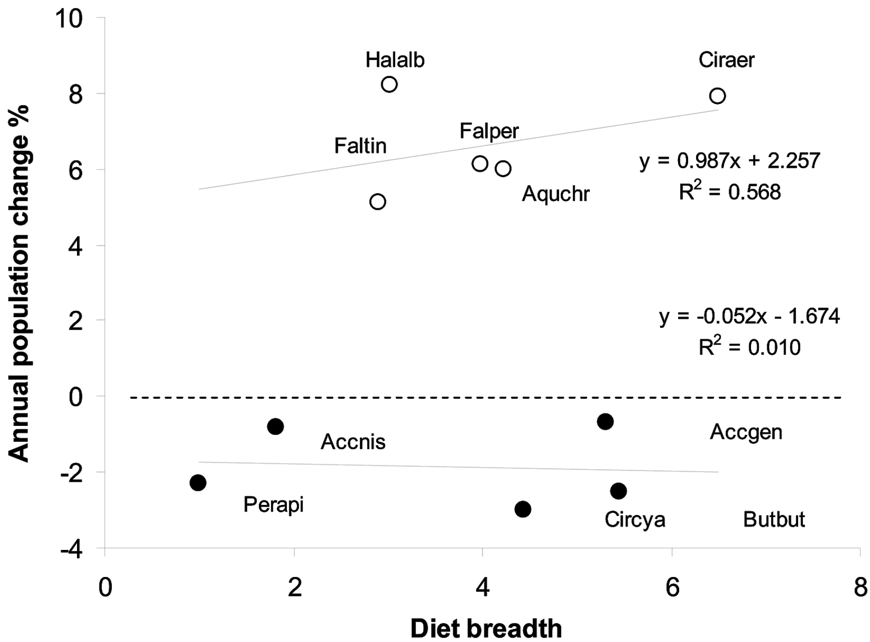


Fig. 3. Relationships between diet breadth and annual population change for ten raptor species (Ciraer = Marsh Harrier, Circya = Hen Harrier, Accnis = Sparrowhawk, Accgen = Goshawk, Butbut = Common Buzzard, Perapi = Honey Buzzard, Aquchr = Golden Eagle, Halalb = White-tailed Eagle, Faltin = Kestrel and Falper = Peregrine Falcon). The first five species are common (filled circles) and the remaining five are rare (hollow circles), the classification being based on their abundance according to raptor monitoring in the 1970s.

3.3. Food-niche breadth and population change in raptors

We plotted diet breadth against the annual mean of the population change for common and rare species separately. Common species showed weak negative population development for the diet breadth, while it was slightly positive in rare species. However, neither of these trends were significant. Instead, there was a significant difference between these two groups in that rare species had higher population growth than common ones (GLM; $F_{2,10} = 56.48$, $p < 0.001$; Fig. 3, Table 3).

4. Discussion

The diet of the Marsh Harrier was diverse, consisting of prey species from both aquatic and terrestrial habitats. Passerines dominated the diet during the early nestling period by number, whereas ducks were the most important prey group by weight. Later in the breeding season the importance of mammals, grouse, the Coot and gulls increased. When compared to other diet studies, our results deviate mostly in terms of the share of small mammals. While these account for between 20 and 70 percent in other studies (Hildén & Kalinainen 1966, Witkowski 1989, Lange & Hofman 2002), we found them to account for a low percentage. Clearly, young muskrats had taken the role of small mammals in our study area. We did not find any small mammals in the pellets that tend

Table 3. Parameter estimates of a general linear model explaining population changes in ten raptor species. Species classification to rare and common species was used as a fixed variable and diet breadth as a covariate. For details, see text.

Parameter	Estimate	SE	*t*	*p*
Intercept	–10.656	1.486	–7.173	<0.001
Species	8.473	0.813	10.422	<0.001
Diet breadth	0.090	0.252	0.357	0.731

to give them higher percentages than prey remains (Lange & Hoffman 2002). The reason for that might be an exceptionally long-lasting low population phase in the field vole *Microtus agrestis* and the water vole *Arvicola terrestris* during the study years in Hailuoto.

Passerines commonly dominated the avian part of the diet in Marsh Harriers, accounting for about 20–30% in the diet (Hildén & Kalinainen 1966, Witkowski 1989, Lange & Hofman 2002). In our sample from the nestling phase, passerines accounted for over 60% of prey items by number, which may be due to a low share of small mammals in the diet that are sometimes replaced by passerines in the Marsh Harrier diet (Lange & Hoffman 2002) but also due to the timing of our diet sampling. If prey are sampled only after fledging, the diet composition differs from that obtained in the middle of the nestling period when only the male delivers prey to the nest. Witkowski (1989) observed that males hunted mainly in terrestrial, whereas females predominantly hunted in aquatic habitats. During the breeding season, males seem to have larger home ranges than females, enabling them to encounter terrestrial species more often, while females hunt near their nests in wetlands, which could be one reason for the habitat separation and hence for different prey choice between the mates (Cardador *et al.* 2009). Another explanation may be a change in the availability of different prey species. Young growing individuals of muskrat, leveret, grouse and gull become more beneficial and visible prey for hunting raptors in mid and late summer, while at the same time fledglings of passerines disperse and are more difficult to detect. Increased food demand by harrier chicks may also force parents to hunt larger prey, especially if small mammals are not abundant (Cardador *et al.* 2012), which was the case in Hailuoto.

The compositional analysis showed that Marsh Harriers hunt opportunistically among waterfowl and shorebirds. We found no significant differences between successively-ranked prey types, except for the first (the Coot) and last rank (the Common Gull). Coots were mainly found in nests situated in the luxuriant Lake Kirkkosalmi where we also found the highest density of nesting Marsh Harriers. Also many earlier studies have reported the Coot to be the most important waterfowl species in the diet of the March Harrier (Hildén & Kalinainen 1966, Witkowski 1989, Blanco & Hiraldo 1990, Lange & Hofman 2002). The low rank of gulls may reflect the aggressive nest defense in gull colonies against Marsh Harrier attacks, although some pairs subsisted on juvenile gulls living on sandy dunes of the shores of Hailuoto.

We did not find diet overlap between the Marsh Harrier and other raptors. This suggests that the Marsh Harrier has adopted a relatively distinct food niche as compared with other raptors. Although the Sparrowhawk had quite similar diet to the Marsh Harrier, they may not significantly compete with each other as they generally occur in different habitats (forest vs. open). The same is true for the Common Buzzard that shares the diet of Marsh Harriers in years of low vole abundance (Reif *et al.* 2001). During low vole years Marsh Harriers and Buzzards may potentially compete for the same food resources. However, this was not apparent in Hailuoto, as the Common Buzzard is an extremely rare breeder in the island. Competition may also be avoided through habitat segregation (Garcia & Arroyo 2005). Although the breeding and hunting habitats of the Marsh Harrier coincide virtually only with those of the Hen Harrier, these two species have distinctive food-niches. The fairly high proportion of grouse chicks and leverets in the Marsh Harrier diet, on the other hand, suggests that in our study area the species frequently hunts in forested habitats, thereby potentially overlapping with the Goshawk and the Sparrowhawk. In central and southern Europe, however, Marsh Harriers almost exclusively use open habitats (Witkowski *et al.* 1989, Lange & Hoffman 2002, Cardador *et al.* 2011). Interestingly, although being a common breeder in Hailuoto, the Goshawk has not been found to kill any Marsh Harriers, young or adult (authors pers. obs.).

We found no correlation between population trends and food-niche -breadths of either rare or common raptor species, but the former had significantly positive and steeper trends than common species, which all had negative trends. Among the ten species, the Marsh Harrier had the widest diet breadth and the second-fastest population growth. The Marsh Harrier is also quite opportunistic in its foraging habits and may avoid interspecific competition either for food or breeding sites. The latter may be an important limiting factor especially among forest-living raptors (Hakkarainen *et al.* 2004). The Marsh Harrier has benefited from the expansion of reed beds, their preferred breeding habitat (Stanevicius 2004, Haapala 2008), which has taken place on the shores of Hailuoto due to enrichment of waters and cessation of cattle grazing (since 1956 in Hailuoto). One reason for the success of the Marsh Harrier may be the generally high productivity of their breeding habitats where polygyny may be an effective breeding strategy (Altenburg *et al.* 1982). We found apparent cases of polygyny mostly on Lake Kirkkosalmi, where the polygyny rate varied among years between 0% and 10%.

The strongly-increasing tare species have benefited from vast areas having become vacant during the largely human-caused population collapses in the 1960s and 1970s (Newton 1979, Stjernberg 2003). The Marsh Harrier, on the contrary, is a newcomer that has adopted an open niche, the shores. In spite of its wide diet breadth, it is also well adapted to man-made habitats and may even benefit from certain human activities (Witkovski *et al.* 1989, Lange & Hoffman 2001, Cardador *et al.* 2011). The same concerns some other species such as the Peregrine Falcon although its natural breeding habitats, open bogs, are declining due to draining and turf industry. Among common species that showed negative populations trends, the Goshawk probably suffers from loss of habitat (mature forests) and main prey (forest grouse; Widén 1997). The Honey Buzzard may face the same problem as it seems to be even more engaged with mature forests than the Goshawk (P. Byholm, pers. comm.). Vole specialists the Common Buzzard and Hen Harrier on the other hand, may have been adversely affected by the irregularity of vole fluctuations. Especially if spring densities of voles remain low, e.g., due to mild winters with poor snow cover not providing sufficient shelter for voles, the reproduction of vole specialists may fail (Solonen & Karhunen 2002, Sundell *et al.* 2004, Lehikoinen *et al.* 2009). It is noteworthy that the Marsh Harrier, although basically having a preference for voles (e.g., Lange & Hoffman 2002), seems not to depend on voles either in spring or in summer, thus avoiding many dangers the vole specialists may face. The Marsh Harrier has also other sources of food, such as eggs of other birds that are plentiful in late spring (Opermanis 2001) and, as our results showed, a wide variety of birds.

The observed diet breadth of the Marsh Harrier suggests flexibility against environmental changes, although this did not seem to explain the success of the examined ten raptor species. Some of the successful, rare species have apparently adapted to man-made environments, even urban areas, while many losers live in mature forests. Northern forests, although still covering large areas, may still become poorer for top predators although human-modified landscapes may provide an increasing food source for them (Cardador *et al.* 2011).

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Hailuodossa pesivien ruskosuohaukkojen ravinto suhteessa muihin Pohjois-Suomessa pesiviin päiväpetolintuihin

Ruskosuohaukka on yleistynyt voimakkaasti Pohjois-Suomessa viimeisten vuosikymmenten aikana. Tutkimme ruskosuohaukkojen ravinnonkäyttöä ja -valintaa Hailuodossa vuosina 2002–2009. Lintujen osuus vaihteli pesimäkauden kuluessa välillä 73–93 %. Pienten varpuslintujen osuus oli pesäpoikasajalla 63 %, mutta saaliin kokonaismassasta niiden osuus oli vain 13 %. Nisäkkäistä piisami oli tärkein, sen lukumääräosuuden ollessa 15 % ja massaosuuden ollessa 24 %.

Rakenneanalyysin mukaan ruskosuohaukat saalistivat vesi- ja rantalintuja opportunistisesti. Moniulotteisen skaalauksen perusteella ruskosuohaukan ravintolokero oli erilainen kuin viiden muun petolintulajin lokerot. Ravintolokeron leveys ja vuotuinen populaatiokasvu kymmenellä päiväpetolintulajilla osoitti, että ruskosuohaukan ravintolokero oli levein ja populaatiokasvu toiseksi nopein. Vuotuinen populaation muutosnopeus oli positiivinen lajeilla, jotka olivat vähälukuisia petolintujen kannanseurannan alettua 1970-luvulla, mutta negatiivinen tuolloin runsaslukuisilla lajeilla.

Merkitsevää suhdetta ei ollut havaittavissa ravintolokeron leveyden ja populaation vuotuisen muutoksen välillä vähä- tai runsaslukuisilla lajeilla.

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Appendix 1. Prey species identified in food samples collected from the Marsh Harriers' nests in Hailuoto, northern Finland during 2002–2009. Numbers are individuals.

Taxon		2002	2003	2004	2005	2006	2008	2009	Total
Erinaceus europaeus juv.	500		1						1
Sciurus vulgaris	270					1			1
Arvicola terrestris	150	3	1	1	1	2	1	3	12
Ondatra zibethica juv.	500		9	5	10	41	9	2	76
Microtus agrestis	20		1						1
Microtus/*Myodes*	20				1		2	2	5
Lepus sp juv.	500	3	6	4	9	10	6	5	43
Mustela erminea	156						1		1
Large mammal sp.	500			1					
Mammals, total		**6**	**18**	**11**	**21**	**54**	**19**	**12**	**141**
Podiceps cristatus	930	1							1
Podiceps sp.	900		1			1			2
Botaurus stellaris	1230							1	1
Anser anser juv	500						1		1
Anas platyrhynchos	1,100						2	1	3
Anas crecca	300		4	1	3	12	9	3	32
Anas querquedula	300		1		1	1	1		4
Aythya marila	603							1	1
Aythya fuligula	720		1	1	1	1	1	2	7
Bucephala glangula	750			1			1		2
Anseriformes	300		2	2	3	5	4		16
Accipiter nisus	200					1		1	2
Falconiformes	200		1						1
Lagopus lagopus	585						1		1
Tetraonidae juv.	350	3	5	1	16	4	13	2	44
Fulica atra	520			2	21	10	6	5	44
Haematopus ostralegus	480			2		1	1		4
Charadrius hiaticula	58					1			1
Vanellus vanellus	206		1	1	4				6
Tringa totanus	107	1	2		3	1			7
Tringa nebularia	180			1	2	1	1		5
Tringa glareola	60						1	3	4
Tringa ochropus	80							1	1
Scolopax rusticola	300	1			2			1	4
Gallinago gallinago	95				1				1
Philomachus pugnax	150	1			1				2
Charadriformes	206		2	2	1	2	2	2	11
Larus ridibundus	265	1	9	5	6	4	5	1	31
Larus canus	415	1	8	1		3	23	0	36
Sterna sp.	110		13	3	1	2	4	1	24
Columba palumbus	500		1					1	2
Columba sp.	300							1	1
Asio flammeus	315						1		1
Aegolius funereus	123					1			1
Dendrocopos major	88		1		1	1	2		5
Hirundo rustica	19						1		1
Anthus trivialis	23			2	17	1	6	14	40
Anthus pratensis	18	1			1				2
Motacilla alba	20					1			1
Motacilla flava	20				1				1
Bombycilla garrulus	56				2				2
Saxicola rubetra	16				1		1		2
Turdus merula	101				1		1		2

Appendix 1, continued

Turdus pilaris	105			2	2				4
Turdus iliacus	60	1		1	6		1		9
Turdus philomelos	69			2	5				7
Turdus sp.	80		3	2	2	1	1		9
Acroc. schoenobaenus	12			6	2				8
Sylvia borin	20		2		5				7
Phylloscopus trochilus	9	1		1	11	3	2	1	19
Ficedula hypoleuca	13		1		2				3
Muscicapa striata	16	1			2				3
Parus montanus	11							1	1
Parus caerulaeus	11			1	3		1		5
Parus major	20		1	1	8		2	2	14
Lanius collurio	29							1	1
Pica pica	235				3			1	4
Corvus corone cornix	525					1			1
Fringilla coelebs	22	3	2	1	18	2	6	2	34
Fringilla montofringilla	22				2				2
Carduelis spinus	13	1	1		3	1	1	4	11
Carduelis chloris	29	1			1		1		3
Pyrrhula pyrrhula	31				3			1	4
Carpodacus erythrinus	23				1				1
Loxia curvirostra	41	1		1				1	3
Emberiza citrinella	31						1		1
Emberiza schoeniclus	19				4			1	5
Passeriformes	20	1	6	2	9	3	2	4	27
Middle-sized bird	210		1	2		2	1		6
Large bird	510				1	1			2
Birds, total		**20**	**69**	**47**	**183**	**68**	**107**	**60**	**554**
Lacerta vivipara	9	1							1
Vipera berus	500							1	1
Esox lucius	500				2				2
Abramis brama	300						1		1
Unidentified fish	200		1			1	1		3
Total		**27**	**88**	**58**	**206**	**123**	**128**	**73**	**703**

Appendix 2. (a) Sample size, number of study years and number of nests collected for six raptor species in Hailuoto and nearby areas. (b) Numbers of water and shorebirds found in the diet of Marsh harriers and counted in five different areas in Hailuoto during 2004–2009, denoted by numbers 1–5 (see Fig. 1). Diet data of areas 1, 3 and 5 were split into two periods (2004–06 and 2007–09) according to counts done in 2004 and 2009.

(a)

Variable	Sparrowhawk	Common Buzzard	Marsh Harrier	Hen Harrier	Goshawk	Peregrine Falcon
No prey	240	1,869	706	197	1,224	805
Nests	9	113	69	9	85	41
Years	6	8	7	7	11	9

(b)

Area	Teal	Other wf	Coot	Waders	Black-h. Gull	Common Gull	Terns
Birds in diet							
1		25	17	36	23	9	3
2	0	1	0	7	4	1	2
3	2	5	0	7	4	1	2
4	0	3	0	1	1	24	3
5	0	8	1	5	0	2	1
Total	**27**	**34**	**37**	**43**	**18**	**31**	**13**
Birds counted							
1	73	373	61	155	140	41	67
2	7	194	0	92	0	31	82
3	40	291	5	156	141	210	154
4	28	156	0	122	6	146	191
5	23	221	0	125	396	46	305
Total	**171**	**1,235**	**66**	**650**	**683**	**474**	**799**