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A comparative study of Ural Owl *Strix uralensis* breeding season diet within its European breeding range, derived from nest box monitoring schemes

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ABSTRACT

Capsule: Voles are the main prey of the Ural Owl *Strix uralensis* in Europe, with larger prey and higher prey diversity being positively associated with owl breeding performance.

Aims: To assess the breeding diet and its influence on the breeding performance of the Ural Owl across a north–south gradient of its European range using nest box monitoring data.

Methods: Comparable monitoring of nest boxes in different biogeographical regions of Europe (Finland, Latvia, Slovenia) and diet analysis from nest samples to assess the taxonomic and trait influence of prey on owl breeding performance in different environments.

Results: High plasticity in the Ural Owl hunting behaviour under different prey availability conditions resulted in significant differences between regions and years. Voles formed the highest proportion of the diet in all studied regions. Owl brood size was positively associated with higher proportions of voles and mice in the diet, and with increasing proportions of seasonally available larger prey and consequently prey diversity. Brood size was negatively associated with the proportion of non-mammalian and predominantly forest-living prey.

Conclusions: The study highlighted the importance of comparative studies of raptor ecology across their geographical ranges in different environmental conditions to reveal undiscovered patterns, which may go undetected when conducting studies at the regional scale only.

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The relationship between raptors and their prey species is commonly studied in different parts of their geographical ranges (Herrera 1974, Korpimäki & Norrdahl 1991, Korpimäki 1994, Lehikoinen *et al.* 2011). Knowledge of raptor diets, coupled with information on the abundance and population fluctuations of their prey, is often seen as crucial for interpreting data from raptor monitoring schemes and explaining patterns and trends in raptor populations (Petty *et al.* 2000, Sundell *et al.* 2004, Millon *et al.* 2008, Tome 2009, Resano-Mayor *et al.* 2016). Just over half (57%) of the raptor monitoring schemes in Europe reviewed by Derlink *et al.* (2018) collected data on breeding success and monitored individual nesting attempts. Several also identified and recorded prey remains present during monitoring visits. This could provide an opportunity to monitor the influence of breeding season diet on breeding success. However, diet studies of raptors across their distribution ranges are rare (Obuch 2011) or mainly rely on compilations or meta-analysis of existing literature data (Mikkola 1983, Newton 1986, Village

1990, Taylor 1994, Sulkava *et al.* 1997, Watson 1997, Van Nieuwenhuyse *et al.* 2008, Birrer 2009, Korpimäki & Hakkarainen 2012). Studies based on comparable field samples from different parts of the species range are rare. Hole-nesting raptors, owls and falcons, which will use artificial nest boxes for breeding, are particularly appropriate for this kind of monitoring (Petty *et al.* 1994, Saurola 2008, Hardey *et al.* 2013), as the monitoring data (breeding activity, clutch and brood size, breeding diet samples) can be obtained over the whole species range in a similar way (Lambrechts *et al.* 2012).

Among raptors, the diet of owls is well studied since bone remains of prey are well preserved in the pellets and are, at least for predominant mammalian prey species, easy to identify (Mikkola 1983). During incubation and nestling development, the remains of the prey delivered by parents accumulate at the bottom of the nest. Thus, prey remains in nest samples provide a good overview of the diet in the most crucial part of the breeding cycle, that is from the start of incubation

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to when the chicks leave the nest, which in owls takes approximately two months (Hardey *et al.* 2013). However, nestlings in particular can digest part of the bones of their prey (Raczyński & Ruprecht 1974, Duke *et al.* 1975), which can introduce some bias in assessing diet from nest samples. Such bias may be larger in larger broods since, overall, more bones are likely to be digested and more prey items are thus missing from the nest sample. Differences in bone fragmentation and digestion have been found to be significant between owl species, between seasons and, to some extent, also between prey species (Mayhew 1977, Lowe 1980, Bochénski & Tomek 1994). Despite these biases, owl prey remains are considered a reliable source for owl diet composition assessment (Mikkola 1983, Bird & Bildstein 2007), and as a representative source for evaluation of the structure of small mammal communities in the ecosystem (Heisler *et al.* 2016, Solonen *et al.* 2016), even though owls do not behave opportunistically as predators (Derting & Cranford 1989, Birrer 2009, Korpimäki & Hakkarainen 2012). When comparing raptor diet between different areas, it is important to use data collected in a comparable way, however, to rule out the possible confounding influence of any biases in prey remains; the same predator in the same life cycle stage – breeding – might exhibit the same biases, such as species-age-sex specific bone digestion or the loss of prey remains due to feeding of adults.

The Ural Owl *Strix uralensis* is in general a northern boreal species with a distribution extending from Fennoscandia across Russia to the Pacific coast of Siberia (König *et al.* 1999). In Europe it inhabits the boreal and hemi-boreal regions, but an isolated population lives in the southern mountains of the temperate region, predominantly in Eastern Europe, and especially in the Carpathians, Dinaric Alps and Alps (Pietiäinen & Saurola 1997, Vrezec 2009). At least in the medieval period, the species was found more widely into Western Europe (Goffette *et al.* 2016). The northern population, described as a subspecies *liturata*, and the southern population, described as *macroura*, are clearly divergent with respect to some morphological features (Vrezec 2009), with the later subspecies being larger (mean \pm SD female wing length of *liturata* 366 ± 7 mm from Finland and *macroura* 385 ± 11 mm from Slovenia; P. Saurola and A. Vrezec unpubl. data). However, no genetic divergence between northern and southern populations has been found, so other mechanisms must govern north–south morphological differentiation of the species (Hausknecht *et al.* 2014). To date, no comparative study has been conducted on the species' breeding biology and diet across its range.

Several studies of Ural Owl diet during the breeding period have been published from different parts of the species range (older literature reviewed in Mikkola 1983). The species is predominantly a predator of small mammals and only locally do birds comprise more than 10% of prey items (Mikkola 1983). In all parts of the range, voles Cricetidae predominate in the diet, on average forming around 60% of all prey items (Mikkola 1983, Jäderholm 1987, Korpimäki & Sulkava 1987, Korpimäki *et al.* 1990, Czuchnowski 1997, Sidorovich *et al.* 2003, Shokhrin 2009, Kociuba 2012). This proportion decreases towards the southern part of the range in Central Europe and Japan, however, where higher proportions of mice Muridae in the diet were reported (Stürzer 1998, Obuch *et al.* 2013, Suzuki *et al.* 2013, Vrezec 2016). In some studies shrews Soricidae have also been reported in higher proportions, but never exceeding 20% of the prey items (Korpimäki & Sulkava 1987, Stürzer 1998). In the boreal region, Ural Owl breeding was found to be highly dependent on the abundance of voles in the environment (Lundberg 1976, Pietiäinen & Kolunen 1993), with breeding density and brood size dependent on the spring abundance of voles (Korpimäki 1994, Lehtikoinen *et al.* 2011) and laying date and clutch size on the autumn abundance of voles (Brommer *et al.* 2002).

The aim of this study was, for the first time, to assess comparable long-term monitoring data on the Ural Owl breeding population over the species' north–south range gradient in Europe, from boreal (Finland), hemi-boreal (Latvia) and temperate regions (Slovenia). In particular, the aim was to study Ural Owl diet shifts and their impacts on the breeding performance of the species within highly divergent habitats.

Methods

Study areas

Since the Ural Owl is distributed from north to south in the eastern part of Europe (Pietiäinen & Saurola 1997), we have taken into account three regions resembling different climatic, habitat and biogeographic conditions over the species' European range: Boreal region (southern Finland), Hemi-Boreal region (Latvia) and Temperate Region (Slovenia) (Figure 1). In all three regions, long-term monitoring of breeding Ural Owl populations was conducted using nest boxes (Reihmanis 2012, Saurola 2012, Vrezec 2012) and in all study areas the forest covering the major part of the area represented the most common characteristic forest assemblage in the region (Table 1).

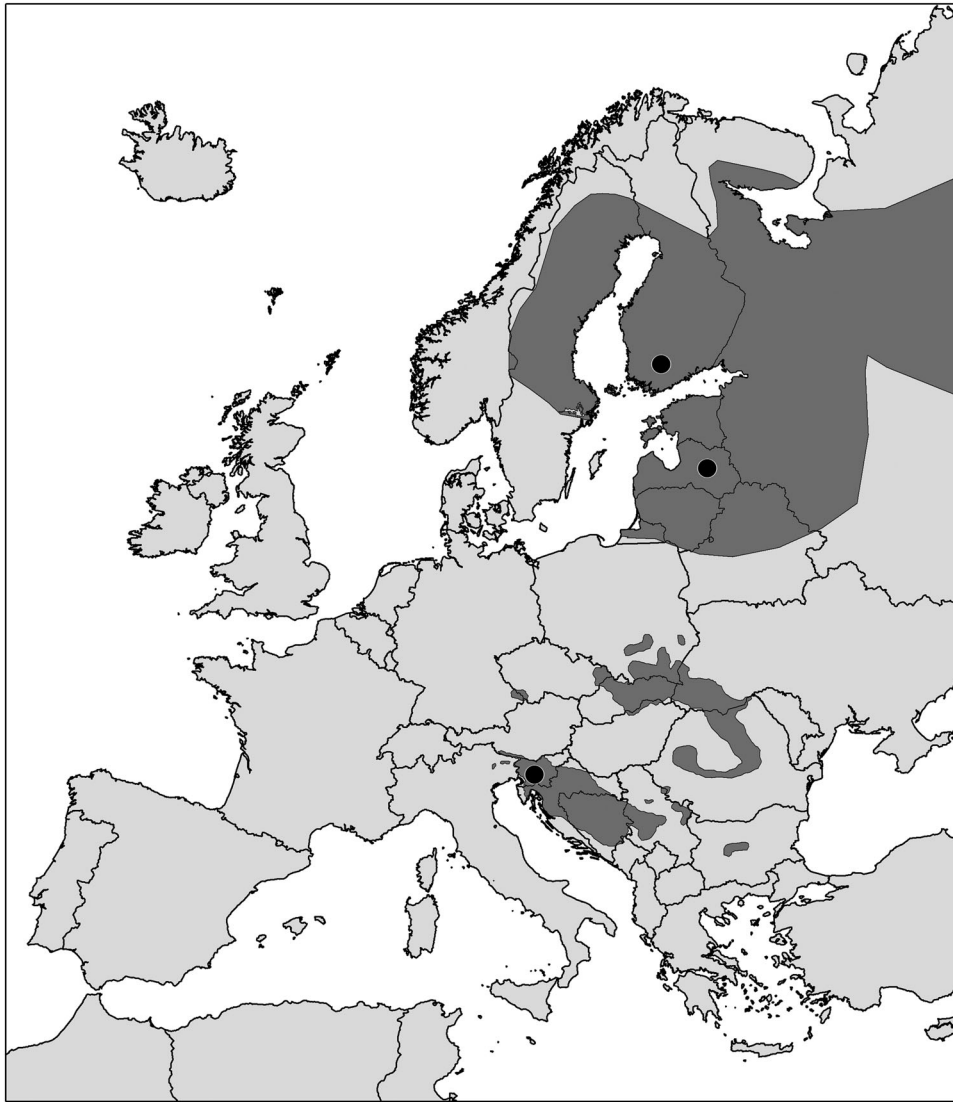


Figure 1. The breeding distribution of the Ural Owl in Europe (after König *et al.* (1999) and Vrezec (2009)) showing study sites from which nest samples were obtained (black dots).

Field methods

All nest boxes were regularly monitored each year in the period 2005–12 in Finland, 2005–16 in Latvia and 2005–12 in Slovenia. Nest boxes were first checked early in the spring (March and April) to establish breeding activity and to assess clutch sizes. Brood size was assessed in the period of 10 days before nestlings left the nest, when they were also ringed. A 10–20 cm layer of sawdust was put in each nest box before the breeding season and in the autumn the sawdust mixed with food remains was collected for the diet analysis and new sawdust was added ready for the next breeding season. The collected nest samples were dried and preserved in plastic bags until laboratory analysis. For the diet analysis, samples from all study years have been included from Latvia and Slovenia. In Finland there was a much larger sample size, so to obtain

comparable data set an equal subset of samples was selected for analysis; in order to include inter-annual diet variation, data were selected from two ‘good’ years (2005 and 2009), when the productivity of the Ural Owl was highest during the study period 2005–12, and three ‘bad’ years (2007, 2010 and 2012), when the productivity was lowest (Saurola 2012, Saurola & Francis 2018). Such a split into good and bad years was not possible in the other two countries due to lack of breeding in poor years in Slovenia or vanished owl breeding dynamics in Latvia.

Prey remains analysis

Prey remains samples were carefully examined and all bones and feathers were separated. Small mammals were mostly identified based on skull morphology (Pucek 1981, März 1987, Kryštufek & Janžekovič 1999,

Table 1. Description of study areas in which the Ural Owl diet was studied.

Region	Boreal	Hemi-Boreal	Hemi-Boreal	Temperate	Temperate
Country	Finland	Latvia	Latvia	Slovenia	Slovenia
Study area	Hauho area (southern Finland)	Lubana (Eastern Latvia)	Limbazi (Eastern Latvia)	Mt. Krim (central Slovenia)	Mt. Jelovica (Northern Slovenia)
Coordinates	61°10'N, 24°34'E	56°54'N, 26°29'E	57°34'N, 24°58'E	45°58'N, 14°25'E	46°18'N, 14°8'E
Altitudinal range (m asl)	90–140	90–120	80–120	290–1108	900–1678
Area size (km ²)	700	120	74	140	98
Forest cover	60%	91%	67%	77%	95%
Forest type	coniferous	mixed	mixed	mixed	mixed
Dominant trees	<i>Picea</i> , <i>Pinus</i>	<i>Pinus</i> , <i>Picea</i> , <i>Populus</i> , <i>Betula</i>	<i>Pinus</i> , <i>Picea</i> , <i>Populus</i> , <i>Betula</i>	<i>Fagus</i> , <i>Abies</i>	<i>Fagus</i> , <i>Picea</i>
Fields and grasslands	20%	6%	22%	20%	3%
Study plot establishment	1965	1994	2011	2002	2009
Nest box type	Figure S1A	Figure S1B	Figure S1B	Figure S1C	Figure S1C
No. nest boxes	120	62	40	32	21
Sources	Saurola (1989)	Avotins <i>et al.</i> (1999)	Avotins (2014)	Vrezec (2003), Vrezec & Tome (2004)	Božič (2003)

Siivonen & Sulkava 2002) and the number of individuals of small species (e.g. *Microtus*, *Sorex*, small mice) was most often determined by counting mandibles (Korpimäki 1986). Numbers of individuals of *Rattus* and *Arvicola* (and larger) species were most often based on leg bones. In some samples, small species were additionally both identified and counted based on leg or pelvic bones (using reference collections). Birds were identified according to the humerus, beaks, feathers, metacarpus and tarsometatarsus to determine species or group (e.g. small bird of Great Tit *Parus major* size) by comparing with reference material from museum or own collections (Korpimäki 1986). Bones were used for identification of amphibians (März 1987) and reptiles, while exoskeleton remains were used for insects. According to the most numerous identified parts of the body of each taxon, the minimum count of the prey species in the sample was determined.

The biomass of prey was calculated according to region-specific body mass data on prey species (Kryštufek & Janžekovič 1999, Siivonen & Sulkava 2002, Balčiauskienė *et al.* 2006). The prey composition in the diet was analysed using taxonomic prey groups and using species trait groups of prey. Six species traits were considered and determined according to published sources (Kryštufek 1991, Snow & Perrins 1998, Kryštufek & Janžekovič 1999, Siivonen & Sulkava 2002): flying prey (yes/no), arboreality (arboreal/ semi arboreal and terrestrial), seasonal availability (whole year/half or less of the year), habitat (forest/generalist and open), predator (yes/no) and large prey (>100 g of body mass). Unidentified prey remains comprised 2.2–15.4% of prey per region, but were identified at least to the relevant group level (Table S1). The body mass for this prey was taken to be the average for the relevant group, and the species trait as the prevailing trait in

the group for that region. The diversity of prey composition was calculated as Simpson's diversity index (Krebs 1998), where unidentified prey groups were considered as separate groups according to Table S1. The breeding performance of Ural Owls was presented as the clutch and brood size. Nests in which the number of nestlings in a brood was unclear have been excluded from analyses of breeding performance.

Statistical analysis

When comparing diet composition between regions, only nest samples containing more than 10 prey item remains were considered. To compare the dietary patterns of breeding Ural Owls in boreal (Finland – good and bad years), hemi-boreal (Latvia) and temperate regions (Slovenia), discriminant function analysis was used (Tabachnick & Fidell 1996). To test for biogeographical and regional functional response patterns in Ural Owl diet we used taxonomic prey groups (% by biomass and diversity of prey species) and species trait groups of prey (% by number) as explanatory variables. To approach normality, the data were square root transformed prior to analysis. We performed backward-stepwise analysis in the program STATISTICA (StatSoft, Inc. 2011). Differences between regions were evaluated using squared Mahalanobis distances (D^2) between means of canonical variables, a measure of how well groups can be separated by the explanatory variables included (Tabachnick & Fidell 1996).

For analysis of the relationship between breeding performance (brood size) and diet, a new subset of samples were selected from nests with known clutch and brood size. For this analysis, the classical generalized linear modelling approach was used. We fitted Poisson family models using a log-link function.

Table 2. Clutch, brood and nest sample sizes in the Ural Owl nests across different regions and years. The median (minimum–maximum) values are shown and data were compared using Kruskal–Wallis tests. Between-group differences (*post hoc* Mann–Whitney test) are indicated with letters where the same letter indicates no significant difference.

	Finland (good years)	Finland (bad years)	Latvia	Slovenia	Kruskal–Wallis
Clutch size	6.0 ^a (3–6) (N = 17)	2.0 ^b (2–3) (N = 18)	3.0 ^c (2–4) (N = 39)	3.0 ^d (2–5) (N = 11)	$H = 47.29, P < 0.001$
Brood size	5.0 ^a (2–6) (N = 20)	2.0 ^b (1–3) (N = 19)	2.0 ^{b,c} (1–4) (N = 44)	3.0 ^c (2–5) (N = 11)	$H = 46.3, P < 0.001$
No. prey items per nest sample	167.6 ± 36.9 ^a (N = 20)	45.2 ± 20.8 ^b (N = 19)	76.8 ± 35.2 ^c (N = 44)	230.9 ± 166.4 ^a (N = 15)	$H = 56.1, P < 0.001$

To deal with uncertainty in the model selection process, we used an information-theoretic approach and multi-model inference. Instead of selecting only a single ‘best model’ for each species, we used a set of ‘competitive models’ to describe the relationship between species abundance and the explanatory variables (Burnham & Anderson 2002). All explanatory variables were scaled before use in the models. A correlation matrix was created to check for possible strong correlations between the explanatory variables. Out of 136 correlations, 19 exceeded 0.50. To reduce model overfitting and to maintain ecological meaning, we did not allow these highly correlated variables in the same model. We did not allow combinations of variables describing very similar effects in the same model even if the correlation between them was not strong. Different combinations of variables were tested using the automated model selection procedure in the R package ‘MuMIn’ (Barton 2016). We used Akaike information criteria adjusted for small sample size (AICc) for comparing model performance. We considered models with ΔAICc scores less than 2 to be similarly competitive (Burnham & Anderson 2002). We individually checked all competitive models for multicollinearity. The variance-inflation factor did not exceed three in any of the predictors of these models. For evaluating the performance of individual variables,

we used model averaging and the conditional average of competitive models in which the variable was present (Burnham & Anderson 2002).

Results

Inter-regional comparison of the diet composition of the Ural Owl

We analysed prey remains from 98 Ural Owl nest samples: 39 from Finland (in the period 2005–12), 44 from Latvia (2005–16), and 15 from Slovenia (2005–12). The data set from Finland was further divided into diet in good years (20 samples from 2005 and 2009) and in bad years (19 samples from 2007, 2010 and 2012). The obtained nest sample sizes ranged from 12 to 657 prey items (median 86 prey items) with less than 10% of nest samples having fewer than 30 prey items. The highest numbers of prey items were found in the nests from Slovenia and from good years in Finland (Table 2). Nest sample sizes differed between regions, but correlated with brood size (Spearman $r_s = 0.49, P < 0.001$; Table 2). In all nest samples mammalian prey predominated, but higher proportions of birds were found in bad years in Finland and in Latvia (Table 3). Voles predominated in the Ural Owl diet in all regions, but in Slovenia a

Table 3. Overview of the breeding diet of the Ural Owl in three regions across the range gradient of the species in Europe. Detailed prey composition per prey species is given in Supplementary Table S1.

Region	% by number of prey items				% by biomass			
	Finland (good years)	Finland (bad years)	Latvia	Slovenia	Finland (good years)	Finland (bad years)	Latvia	Slovenia
Sciuridae	0.33	0.23	0.15	0.16	1.72	1.08	0.93	1.47
Gliridae	0.00	0.00	0.00	8.68	0.00	0.00	0.00	28.38
Dipodidae	0.18	4.53	1.84	0.00	0.03	0.55	0.29	0.00
Cricetidae	84.06	37.09	51.93	45.98	72.01	29.92	38.60	31.42
Muridae	2.00	2.91	2.22	34.23	7.92	5.75	1.69	28.19
Leporidae	0.57	1.86	0.04	0.00	5.79	15.97	2.41	0.00
Soricidae	3.46	13.37	10.02	1.18	0.65	2.04	2.10	0.32
Talpidae	1.10	1.63	9.83	4.42	1.25	1.55	12.30	8.25
Chiroptera	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Mustelidae	0.57	0.00	0.08	0.00	0.48	0.00	0.17	0.00
Mammalia, total	92.30	61.63	76.10	94.64	89.86	56.87	58.49	98.03
Aves	4.03	32.21	14.61	2.29	7.91	40.25	37.63	1.59
Amphibia	3.64	5.58	5.74	0.55	2.23	2.87	3.87	0.36
Insecta	0.03	0.58	3.56	2.44	0.00	0.00	0.01	0.01
Lumbricidae	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Total	3351 items	860 items	2615 items	1268 items	164 102 g	50 096 g	11 6144 g	43 721 g

Table 4. Significance of Ural Owl diet variables in discriminating between different regions and standardized coefficients for the three discrimination roots (Wilks' Lambda = 0.02, $F = 52.74$, $P < 0.001$). Only variables that contributed to the discrimination and were included in the model are shown.

Diet explanatory variable	Partial Wilks' Lambda	F	P	Root 1	Root 2	Root 3
Gliridae	0.35	56.14	<0.001	-0.910	0.662	-0.472
Talpidae	0.36	51.17	<0.001	0.471	1.029	0.232
non-Mamalia	0.42	41.62	<0.001	0.720	0.280	-0.594
Large prey	0.58	21.65	<0.001	0.822	0.355	1.155
Seasonal available prey	0.54	25.40	<0.001	-0.362	-1.226	-0.883
Proportion				0.70	0.22	0.08

higher proportion of mice and dormice Gliridae was noted, with the latter missing from the Finnish and Latvian samples (Table 3, S1).

Discriminant function analysis successfully separated the Ural Owl diet composition between study regions, but out of 14 explanatory diet variables, only five contributed to the discrimination between groups; the others were excluded as redundant using a backward-stepwise procedure (Table 4, S2). The first two discriminant roots explained most of the discrimination between regions (92%; Table 4). Squared Mahalanobis distances indicated high dissimilarity in the Ural Owl diet between regions as well as between years in Finland (Table 5). The most deviant diet composition was found in the temperate region (Slovenia), and the most similar were the good and bad year diets from Finland (Table 5). The first discriminant root effectively separated the Ural Owl breeding diet in Slovenia from that of the northern regions (Figure 2(a)), with the proportion of dormice, large, and non-mammalian prey contributing the most to this separation (Table 4). The second discriminant root separated boreal (Finland) and hemi-boreal (Latvia) samples (Figure 2(a)), with the proportion of seasonal available prey and moles Talpidae contributing the most to the discrimination (Table 4). The third discriminant root separated sample groups from the boreal region (Finland) between good and bad years (Figure 2(b)). This root was influenced most by the proportion of large prey in the diet (Table 4).

Breeding performance in relation to diet conditions

The breeding performance of the Ural Owl differed significantly in relation to region (Table 2). The highest breeding success was in the boreal region, followed by temperate and hemi-boreal, although there was also a significant difference between good and bad years in the boreal region. To explain the importance of certain prey on brood size, 1696 generalized linear models considering 15 diet variables were compared. Of those, 14 models considering 11 variables were similar:

$\Delta AIC_c < 2$ from the best model found with $AIC_c = 302.49$ and significantly different from the null model with $AIC_c = 319.59$ (Tables S3, S4) and these were conditionally averaged (Table 6) to describe variation and diet influences on brood size. Larger broods were related positively to the proportion of voles and mice in the diet. However, the positive effect of increasing the average prey weight suggested that, at least in parts of the chick rearing period, larger prey was important. This is supported by a near significant positive effect of the proportion of large prey in the diet (>100 g of body mass) on the brood size (Table 6). The proportion of forest prey species in the diet was negatively associated with the brood size at least in part of the species range (Table 6). We found a positive effect of superpredation on breeding performance, although predators taken as prey were mainly vole-eaters, such as *Mustela* species (Table S1) and were found in fairly low abundances in diet samples, mostly only in broods with at least four young.

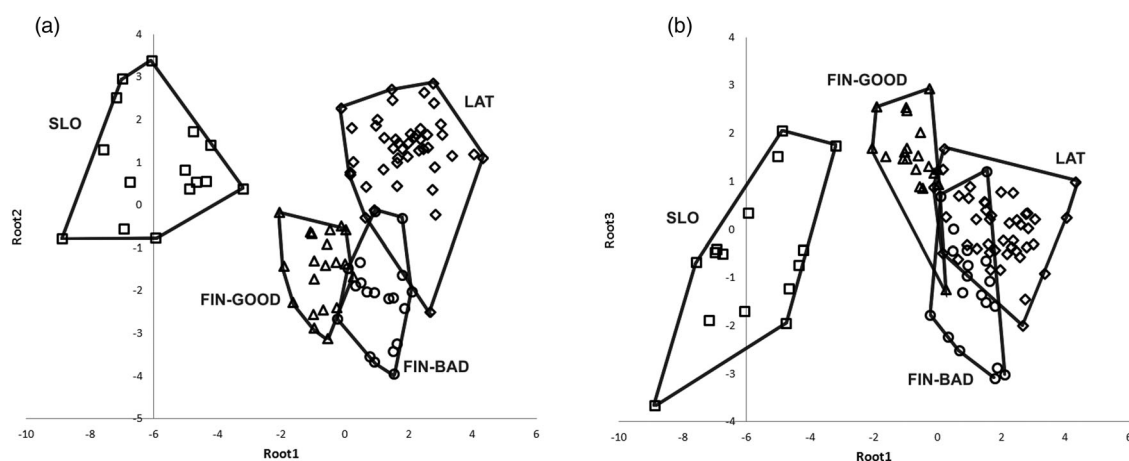
Discussion

Across its European range, the Ural Owl faces very different environmental conditions, but nevertheless voles were the main prey in all regions. A similar situation was found also in Japan, where the proportion of voles was much higher in the Ural Owl diet than in small mammal traps in the field (Imaizumi 1968). In contrast to voles, mice tend to be more agile and have larger eyes and ears, suggesting they are better equipped to evade owl capture (Derting & Cranford 1989). This might explain the relatively higher proportion of voles in different parts of the Ural Owl distribution range.

The overall diet composition was found significantly divergent among regions and even between years, as shown in the case of Finland. These differences were evident when considering taxonomic as well as trait classification of the prey, indicating high plasticity in Ural Owl hunting behaviour under different prey availability conditions. As expected, the most deviant was diet composition in the temperate region, and

Table 5. Evaluation of discriminating differences in the diet of the Ural Owl between regions and years by squared Mahalanobis distances (D^2).

D^2/p	Finland (good years)	Finland (bad years)	Latvia	Slovenia
Finland (good years)	–	11.30	16.84	35.79
Finland (bad years)	<0.001	–	14.30	58.03
Latvia	<0.001	<0.001	–	59.80
Slovenia	<0.001	<0.001	<0.001	–

**Figure 2.** Plots (a – Root 1 vs. Root 2; b – Root 1 vs. Root 3) of the individual scores for the two roots discriminating between breeding Ural Owl diet from different regions across the species' range gradient in Europe (SLO – Slovenia, FIN-GOOD – Finland in good years, FIN-BAD – Finland in bad years, LAT – Latvia).

differences between it and the boreal and hemi-boreal regions were largely generated by the proportion of dormice (only present in the temperate region) and of flying prey (larger proportion in the boreal and hemi-boreal regions), that are mainly alternative prey groups (Korpimäki *et al.* 1990). Although the Ural Owl can be considered a generalist predator, its diet is still almost exclusively dependent on voles and only partly on mice (see also literature review in the introduction) and apparently the species is not able to shift its feeding habits as much as, for example, the closely related Tawny Owl *Strix aluco*, for which even the main prey may differ between regions (Obuch 2011). We are

aware of only one study of Ural Owl diet from southern Japan (Morii & Shioiri 1996) in which birds were reported as the most numerous prey (79%). In our study, birds as the main group of alternative non-mammalian prey were found in higher proportions in Latvia and in bad years in Finland, and were also associated with smaller brood sizes. In the absence of the main and profitable prey, Ural Owls can compensate with birds (Korpimäki *et al.* 1990), but with the consequence of lower breeding performance. In temperate Slovenia, for example, the proportion of non-mammalian prey was low, but the nest samples that were analysed originated mostly from good years

Table 6. Summary of generalized linear models explaining the relationship between diet and brood size in the Ural Owl across the species' distribution range in Europe. Variables in the best model are marked in bold. (Intercept only $AIC_C = 319.5913$)

Variable	Conditional averaged model				Variable importance			AIC_C Best model
	Coefficient	SE	Z-value	P	No. models with variable	Relative importance		
(Intercept)	0.3885	0.4965	0.78	0.436	14		302.4874	
Average prey weight	0.9342	0.4911	1.881	0.060	8	0.65		
Cricetidae (biomass ratio)	0.9497	0.4017	2.348	0.019	12	0.90		
Muridae (biomass ratio)	0.8247	0.3824	2.128	0.033	7	0.54		
Non-Mammalia (biomass ratio)	–0.7166	0.3653	1.942	0.052	7	0.46		
Talpidae (biomass ratio)	0.4371	0.3403	1.267	0.205	2	0.15		
Predators (abundance ratio)	0.3753	0.2952	1.254	0.210	5	0.33		
Large prey (abundance ratio)	0.7614	0.4234	1.777	0.076	4	0.23		
Forest prey (abundance ratio)	–0.9348	0.4623	2.002	0.045	2	0.10		
Diversity index value	1.0776	0.2577	4.125	<0.0001	1	0.05		
Soricidae (biomass ratio)	–0.3358	0.5047	0.656	0.512	1	0.05		

since breeding activity was found to be very low or completely suppressed in poor vole/mice years in Slovenia (A. Vrezec, unpubl. data). Therefore, the functional response to prey availability appears to have a detrimental effect on Ural Owl breeding performance, reflected in lower breeding frequency and breeding abstinence of some pairs (Saurola 1989).

The breeding performance of the Ural Owl, in terms of clutch and brood size, was found to be significantly different among regions, and in the boreal region also among years. This was expected since owl breeding performance is highly dependent on the fluctuating and regionally different prey populations (Sundell *et al.* 2004). In the generalist Eagle Owl *Bubo bubo*, Lourenço *et al.* (2015) proposed that high breeding performance is associated with profitability and size of the prey. Our data representing large geographical scale on the Ural Owl diet support this hypothesis. First, the main prey, voles in the case of the Ural Owl, is expected to be also the most profitable due to greater foraging efficiency of the predator (Lourenço *et al.* 2015). As a vole-specialized predator, the breeding performance (in our case brood size) of the Ural Owl was higher with a higher proportion of voles in the diet, and this was evident in all studied regions. Additionally, the hypothesis was supported by higher superpredation detected in larger broods in which the remains of vole-eating predators, especially weasels *Mustela* sp., were found (but only in boreal and hemi-boreal regions; Table 2, S1). We argue that superpredation in the Ural Owl is unlike superpredation in the Eagle Owl (Lourenço *et al.* 2011) since the former is not as large and since vole-eating predators appear in the diet as a by-catch in good vole years, which support high populations of other vole-eating predators (Korpimäki *et al.* 1991). In contrast, in the case of the Eagle Owl, predators appear in the diet as an alternative prey in years of lower availability of the main prey (Lourenço *et al.* 2015). Secondly, the larger prey (>100 g) was found to be highly associated with larger brood sizes in Ural Owls, presumably as it reduces the number of nest visits or hunting sessions, and therefore the costs of repeated flights. This larger prey comprised mainly Water Voles *Arvicola amphibius* in boreal and hemi-boreal regions, and Fat Dormice *Glis glis* in the temperate region. Both these large prey species exhibit high seasonally limited exposure to owl predation due to their subterranean lifestyle or hibernation in winter (Siivonen & Sulkava 2002, Kryštufek 2010). Therefore, such prey are probably important in later phases of nestling development in defining brood size before fledging, but not for clutch size determination which is influenced

by autumn and overwinter prey availability (Brommer *et al.* 2002). In experimental enclosures it is shown that Ural Owls could adjust their hunting strategy to the patches where larger-sized prey were available (Nishimura 1991). When larger and abundant prey are available, the Ural Owl switches its hunting strategy and consequently its diet, which leads to a higher diversity of prey taken. In the Eagle Owl, Lourenço *et al.* (2015) found the opposite effect, with higher prey diversity associated with lower brood size. This is a consequence of compensation of the main prey with less profitable prey, what can be an effect of trophically specialized raptor populations, and not actual switching to more profitable large prey as is found in other less specialized raptor populations (Penteriani *et al.* 2002) as well as in our studied Ural Owl populations. For example, in the areas where large and profitable prey are available only for a limited time of the season (e.g. Fat Dormice in Beech temperate forests), large shifts in the diets of Ural Owls and other coexisting large predators have been recorded (Krofel *et al.* 2011, Vrezec 2016) leading to an overall increase in the diversity of prey taken. The latter corresponds well with the prey availability hypothesis, in which high availability of profitable prey may lead to increased reproductive success because of enhanced opportunities for profitable prey captures (Whitfield *et al.* 2009). Higher diversity of prey could, therefore, reflect both poor prey availability with low breeding performance, when profitable main prey is compensated with less profitable alternative prey (Lourenço *et al.* 2015), or enhanced prey availability with high breeding performance, when profitable prey is available only for limited periods in the season so the predator switches its diet from main but less profitable prey, as shown in our study.

According to the prey habitat associations in the Ural Owl diet, and despite the species being a forest-dwelling predator, it appears to rely largely on non-forest prey, such as *Microtus* voles. The proportion of forest prey species in the diet was actually negatively associated with brood size. Open habitat prey was of particular importance in boreal and hemi-boreal regions, but not in the temperate region, at least during the breeding season. This was probably a consequence of habitat structure, with large and continuous forest complexes with very few isolated open patches in the south, and more fragmented forest with many larger clear-cuts in the north (Savola *et al.* 2013). In the temperate region, the Ural Owl breeding population is mostly confined to the montane forests, but birds can move to lowlands and open areas in the winter period, when *Microtus* voles (*M. agrestis*, *M. arvalis*) may prevail in the diet

(Vrezec 2001). In the breeding period, the lower availability of voles in temperate forests, especially the Bank Vole *Myodes glareolus* is compensated by mice *Apodemus* sp. and, later in the season, by the Fat Dormouse. Multi-annual cycles of voles in northern regions of Europe govern breeding populations and breeding success of Ural Owls (Sundell *et al.* 2004), but in the south mice and dormice may also affect Ural Owl breeding populations through interacting cycles, which might not be synchronized between species, and warrant further study. Our study highlighted the importance of comparative and explanatory studies of raptor biology and ecology across the geographical ranges of species in different environmental conditions to reveal undiscovered patterns which would remain undetected when conducting studies only at a regional scale. The standardization of pan-European monitoring protocols as far as possible, and their adoption across raptor monitoring schemes, could therefore greatly facilitate the filling of this research gap.

Our study has shown the importance of including prey monitoring in raptor monitoring schemes as a key explanatory variable for raptor breeding performance and consequently for raptor population trends. The value of the prey availability monitoring has proven to be an important parameter in explaining raptor population fluctuations (see overview and references in introduction), but the value of monitoring raptor diet composition in connection with breeding performance has been rarely assessed (Lourenço *et al.* 2015). Our study is the first, to our knowledge, that has assessed the relationship between raptor diet composition and breeding performance across the north–south geographical distribution gradient of a species. This was possible only by applying comparable monitoring scheme protocols that include: (1) established study plots of similar sized nest boxes (the nest box bottom measurements in our study was similar between regions with 35–45 × 35–50 cm; Figure S1; see also Lambrechts *et al.* 2012), (2) annual inspection of nest boxes for assessing nesting frequency, clutch and brood size of breeding owls (Saurola 2003), (3) annual collection of nest samples after the breeding season (Korpimäki & Sulkava 1987) and, additionally, (4) annual field trapping of small mammals targeting the main raptor prey species, in spring, but preferably also in the autumn and in different hunting habitats (Lehikoinen *et al.* 2011). Many such comparable data probably already exist at a pan-European level (see Derlink *et al.* 2018) and combining these data at inter-regional scale would add new insights and knowledge of raptor ecology, as we have demonstrated in this study.

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