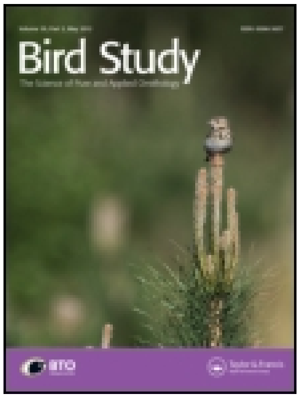

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SHORT REPORT

Geographic and temporal variation in the consumption of bats by European Barn Owls

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Capsule We report a review of the occurrence of bats in the Barn Owl diet *Tyto alba* in Europe. Based on 802 studies reporting 4.02 million prey items identified in pellets, 4949 were bats (0.12%). We found that bat predation decreased during the last 150 years, is more frequent on islands than mainland, and is higher in eastern than western Europe and in southern than northern Europe. Although Barn Owls usually capture bats opportunistically, they can sometimes specialize on them.

In Europe, the Barn Owl *Tyto alba* rarely consumes bats, although individuals can sometimes specialize on them (Bauer 1956). This specialization can be a consequence of owls and bats roosting or breeding in similar habitats such as buildings or cliffs. As a consequence, bats can sometimes abandon a site if Barn Owls depredate them or simply because of their mere presence (Boireau 2009). Although few data are available on population trends over decades, bats have apparently declined in Europe (Stebbings 1988). By reviewing the literature on the Barn Owl diet in Europe, we could, therefore, test whether Barn Owls have reduced bat consumption during the last 150 years (Uhrin *et al.* 2010). This review also allowed us to investigate whether there is geographic variation in bat predation or whether some bats are more vulnerable when displaying specific flying behaviour and so whether Barn Owls capture bats opportunistically.

As described in two previous reviews on Barn Owl diet obtained from pellet analyses (Roulin & Dubey 2012, 2013), we collected all papers published in international and local journals we could find. Among the 802 studies considered in the present review, 319 (39.8%) reported at least one bat prey item (Fig. 1). The highest percentage of bats was 54.2% in a study that reported 52 out of 96 prey items (Bauer 1956). Table 1 lists, for each European country and island, the total number of bats that were found in the Barn Owl diet. In total, 4 025 523 vertebrate and invertebrate prey items were identified of which 4949 were bats (0.12%). The highest proportion of bats was found in Crete (3.59%) followed by Sardinia (1.64%).

Using the entire sample of 802 studies, the distribution of the proportion of bats in the Barn Owl diet strongly departed from normality because of the large number of studies that did not report any bats ($n = 483$, Fig. 1). We, therefore, performed non-parametric analyses. The proportion of bats did not differ between islands and mainland (Wilcoxon matched-pair signed-rank, $z = 0.17$, $P = 0.86$) and was not significantly associated with latitude (Spearman's correlation: $r_s = -0.05$, $n = 788$, $P = 0.19$) but increased with longitude ($r_s = 0.15$, $n = 788$, $P < 0.0001$) and decreased between 1860 and 2010 ($r_s = -0.13$, $n = 763$, $P = 0.0002$). When considering only studies ($n = 319$) with at least one bat prey item, the log-transformed percentage of bats was normally distributed, and hence we could perform more powerful parametric analyses. In an ANCOVA, the percentage of bats in the Barn Owl diet was significantly higher on islands than mainland ($F_{1,295} = 4.4$, $P = 0.037$), decreased with latitude ($F_{1,295} = 5.8$, $P = 0.017$, Fig. 2a), increased with longitude ($F_{1,295} = 14.5$, $P = 0.0002$; Fig. 2b) and decreased between 1860 and 2010 ($F_{1,295} = 5.52$, $P = 0.019$; Fig. 2c: note a quadratic function of year to test whether this decline has slowed in recent years – see below – did not give a better fit). In this model, we statistically controlled for log-transformed total number of prey items identified ($F_{1,295} = 167.7$, $P < 0.0001$) because lower percentages of bats were found in larger samples (Pearson's correlation:

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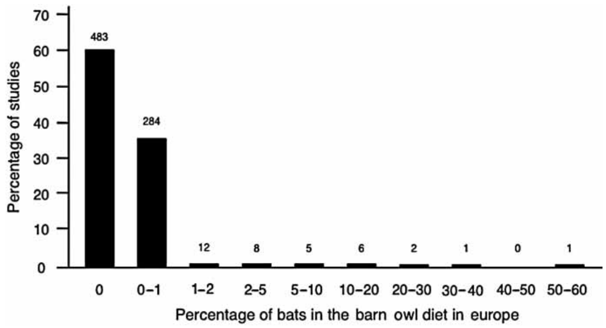

Figure 1. Frequency distribution of 802 studies reporting the percentage of bats in Barn Owl diet in Europe. Number above bars indicates the absolute number of studies.

$r = -0.60$, $P < 0.0001$). Note that if we do not control for this variable, we obtain qualitatively similar results. The higher proportion of bats found in the Barn Owl diet on islands may reflect the lower diversity and abundance of terrestrial small mammals on islands compared to the mainland (Alcover *et al.* 1998). The positive correlation between proportion of bats in owl pellets and longitude may be explained by higher bat population sizes in eastern European or/and by a closer proximity of Barn Owl roosts with bat colonies in eastern Europe, for example, if bat colonies are more often located in anthropogenic habitats than in natural caves. The higher proportion of bats reported in southern Europe may be explained by the less extreme weather conditions known to be detrimental to insectivorous bats and therefore higher density of bat populations and longer activity period during the year (Humphries *et al.* 2002 but see Sendor & Simon 2003). Clinal variation in bat depredation by Barn Owls had already been observed in Spain and Europe

Table 1. Proportion of Barn Owl diet composed of bats in different European countries and islands.

	Number of studies	Number of prey identified	Number of bats as prey	Percentage of bats in the diet
Albania	1	68	0	0
Austria	12	15 011	153	1.02
Balearic Islands	3	10 425	7	0.07
Belgium	11	159 384	64	0.04
Bosnia	2	2272	0	0
Bulgaria	5	41 787	40	0.10
Corfu	2	5888	20	0.34
Corsica	6	24 498	125	0.51
Cos	1	2277	0	0
Crete	4	4321	155	3.59
Croatia	3	8633	39	0.45
Czech Republic	27	115 516	99	0.09
Denmark	1	36 173	49	0.14
France	109	804 778	710	0.09
Germany	209	788 917	946	0.12
Greece	11	9630	2	0.02
Hungary	39	233 475	311	0.13
Ireland	19	28 442	60	0.21
Italy	93	150 954	231	0.15
Luxemburg	10	11 286	22	0.19
Malta	2	424	3	0.71
The Netherlands	13	150 131	37	0.02
Poland	28	201 870	477	0.24
Portugal	12	23 682	9	0.04
Romania	3	3283	0	0
Russia	9	2088	0	0
Sardinia	6	2619	43	1.64
Serbia	2	8576	1	0.01
Sicily	6	13 210	78	0.59
Slovakia	8	23 431	192	0.82
Slovenia	8	27 896	277	0.99
Spain	51	204 342	581	0.28
Sweden	2	3285	0	0
Switzerland	18	298 051	28	0.01
UK	61	572 714	155	0.03
Ukraine	4	34 128	35	0.10
Total	801	4 023 465	4949	0.12

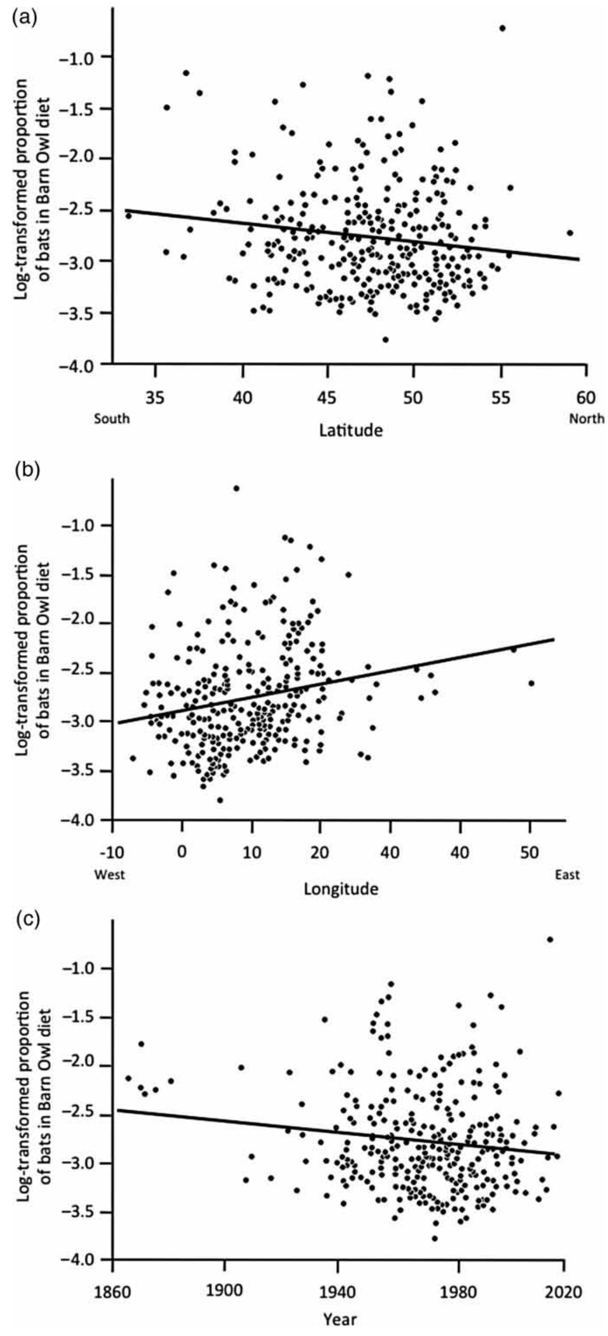

Figure 2. Frequency of bats in Barn Owl diet in Europe in relation to latitude (a), longitude (b) and year (c). Predicted lines from an overall model (see text) are plotted.

(Pérez-Barbería 1991) further indicating that this finding is robust. Finally, the long-term decrease in the proportion of bats in the Barn Owl diet may reflect historical declines of bat populations during the last century (Stebbings 1988). In Poland, Lesiński (2010) showed that Tawny Owls (*Strix aluco*) consumed fewer bats in the 1980s probably because of the intensive use of insecticides in those years. Bat populations recovered after the 1980s due to a lower use of insecticides, leading to an increase in bat consumption by Tawny Owls. We, therefore, tested whether in the Barn Owl bat consumption increased along the years after 1980. This was, however, not the case (similar model as above, year: $F_{1,110} = 0.06$, $P = 0.80$).

In many papers, the authors identified bats to the species level (supplementary online table shows the number of bats identified to the species level in different European countries and islands). Because in several papers, the authors reported only bats but not the other prey species, more bats were reported in Table 2 than in Table 1. We could thus examine whether bat depredation was related to bat body mass and measures associated with flying strategies (wing loading and aspect ratio). For instance, bats with long and narrow wings (high wing loading) fly rapidly and higher above the ground, whereas species with broad wings (low wing loading) fly slowly and are highly manoeuvrable (Norberg & Rayner 1987, Fenton 1990, Obrist *et al.* 2011). However, among the 23 species of bats identified as Barn Owl prey and for which we had data on wing loading, aspect ratio and body mass (Table 2), their log-transformed frequency in Barn Owl diet was not associated with these three variables (multiple regression analysis: P-values > 0.22). This suggests that bat flying behaviour does not play an important role on the probability to be preyed by Barn Owls. This is not surprising because Barn Owls frequently capture young bats that are not yet able to fly (Bauer 1956, Schmidt & Topal 1971, Glutz & Bauer 1980) and bats seem to be rarely captured in flight (König 1961). This suggests that most bats are captured at roosting and breeding sites in an opportunistic way, as shown in the Tawny Owl *Strix aluco* (Lesiński *et al.* 2012). In line with this statement, we found that bats foraging in open and semi-open landscapes were captured as often as bats foraging in forests (two-way ANOVA: $F_{1,27} = 0.07$, $P = 0.80$) and bats with more stable populations were more often captured ($F_{1,27} = 14.33$, $P = 0.0008$) indicating that bat abundance rather than some biological specificity is associated with their occurrence in the Barn Owl diet.

To conclude, our study suggests that Barn Owls opportunistically depredate bats. By reviewing the literature on Barn Owl diet, we could show that predation on bats decreased during the last century probably because bats declined. Predation was also

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Table 2. Number of individuals and of regions (see list in Table 1) (N/#) where bats (identified to the species level) were found in the Barn Owl diet in Europe. For each identified species, we give information on hunting habitat, location of roosts and colonies, size of colonies, population status, population trend and body mass. Information on population status and trends are from IUCN 2012 (IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>). Biological data are from Dietz *et al*. (2009) and data on wing loading and aspect ratio are from Norberg & Rayner (1987).

	N/#	Wing loading (N/m^2)	Aspect ratio	Habitat	Roost colonies	Colony size	Population status	Population trend	Mean body mass (g)
Rhinolophidae									
Blasius' horseshoe bat (*Rhinolophus blasii*)	2/1			1	1, 2	30–500	1	1	12
Mediterranean horseshoe bat (*Rhinolophus euryale*)	9/4	8.1	6.2	2	1, 2	20–300	2	1	11
Greater horseshoe bat (*Rhinolophus ferrumequinum*)	133/6	12.2	6.1	2	1, 2	20–1000	1	1	21
Lesser horseshoe bat (*Rhinolophus hipposideros*)	28/8	7.1	5.7	2	1, 2	10–200	1	1	7
Mehely's horseshoe bat (*Rhinolophus mehelyi*)	1/1	11.6		1	1, 2	20–200	3	1	14
Rhinolophus sp.	3/2				1, 2				
Vespertilionidae									
Western barbastelle (*Barbastella barbastellus*)	47/8	9.1	6.0	2	2, 3	10–100	2	1	9
Northern bat (*Eptesicus nilssoni*)	17/4	8.1	6.6	2	2, 3	20–50	1	2	13
Serotine bat (*Eptesicus serotinus*)	920/15	12.2	6.5	1	2	10–60	1	4	25
Savi's pipistrellus (*Hypsugo savii*)	16/4			1	2	40–70	1	2	7
Bechstein's myotis (*Myotis bechsteinii*)	36/5	9.0	6.0	2	3	20–50	2	1	8
Lesser mouse-eared bat (*Myotis blythii*)	153/10	10.1	6.7	1	1, 2	50–500	1	1	21
Brandt's myotis (*Myotis brandtii*)	15/4			2	3	20–60	1	2	6
Long-fingered bat (*Myotis capaccinii*)	3/2			1	1, 2	30–500	3	1	8
Pond bat (*Myotis dasycneme*)	31/6	10.4	6.8	1	2, 3	20–300	2	1	15
Daubenton's bat (*Myotis daubentoni*)	107/7	7.0	6.3	1	2, 3	20–50	1	3	8
Geoffroy's bat (*Myotis emarginatus*)	45/7	7.1	5.9	2	1, 2	20–500	1	2	7
Greater mouse-eared bat (*Myotis myotis*)	1,278/17	11.2	6.3	2	1, 2	50–1,000	1	2	23
Whiskered bat (*Myotis mystacinus*)	56/8	7.1	6.0	1	2, 3	20–60	1	4	6
M. mystacinus or *M. brandtii*	1/1								
Natterer's bat (*Myotis nattereri*)	512/10	6.1	6.4	1	2, 3	20–50	1	2	8
Myotis sp.	68/11								
Giant noctule (*Nyctalus lasiopterus*)	2/1			1	3	Up to 80	2	1	44
Leisler's bat (*Nyctalus leisleri*)	21/4	19.3	7.9	2	3	20–50	1	4	15
Noctule bat (*Nyctalus noctula*)	363/10	16.1	7.4	1, 2	2, 3	20–60	1	4	26
Nyctalus sp.	1/1								
Kuhl's pipistrelle (*Pipistrellus kuhlii*)	178/7	8.5	6.3	1	2	20–100	1	4	7
Nathusius' pipistrelle (*Pipistrellus nathusii*)	130/11	9.8	7.2	2	3, 2	20–200	1	4	8
Common pipistrelle (*Pipistrellus pipistrellus*)	621/17	8.1	7.5	1	2, 3	50–100	1	2	5
Pygmy pipistrelle (*Pipistrellus pygmaeus*)	50/1			1	2, 3	15–800	1	4	6
P. pipistrellus or *P. pygmaeus*	36/1								
Pipistrellus sp.	143/10								
Brown big-eared bat (*Plecotus auritus*)	323/11	7.1	5.7	2	2, 3	5–50	1	2	8
Grey long-eared bat (*Plecotus austriacus*)	242/8	7.9	6.1	1	2, 3	10–30	1	4	8
Plecotus sp.	31/6								
Particoloured bat (*Vespertilio murinus*)	107/7	10.2	7.0	1	2	20–60	1	2	12
Miniopteridae									
Schreiber's bat (*Miniopterus schreibersii*)	54/8	10.2	7.0	1	1	100–20,000	2	1	12
Molossidae									
European free-tailed bat (*Tadarida teniotis*)	6/3			1	2	5–50	4	4	25
Pteropodinae									
Egyptian fruit bat (*Rousettus aegyptiacus*)	79/1			1	1	50–500	1–2	4	124
Total	5868								

Habitat – hunting habitat: 1 = open and semi-open landscape; 2 = forest. Location of roosts and colonies: 1 = caves; 2 = buildings cliff, crevasses; 3 = trees. Population status: 1 = least concern, 2 = near threatened, 3 = vulnerable, 4 = unknown. Population trend: 1 = Decreasing, 2 = stable, 3 = increasing, 4 = unknown.

more intense in southern and eastern Europe than in northern and western Europe, probably due to an opportunistic response to increased abundance.

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SUPPLEMENTAL DATA

A supplementary online table, showing the number of bats identified to species level in the Barn Owl diet in different European countries and islands, can be accessed http://dx.doi.org/10.1080/09593330.2013.847051.

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