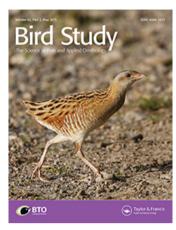
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On: 02 May 2015, At: 08:33 Publisher: Taylor & Francis

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Bird Study

Publication details, including instructions for authors and subscription information: http://www.tandfonline.com/loi/tbis20

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Published online: 27 Feb 2015.



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To cite this article: Alexandre Roulin (2015) Spatial variation in the decline of European birds as shown by the Barn Owl Tyto alba diet, Bird Study, 62:2, 271-275, DOI: 10.1080/00063657.2015.1012043

To link to this article: http://dx.doi.org/10.1080/00063657.2015.1012043

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SHORT REPORT

Spatial variation in the decline of European birds as shown by the Barn Owl *Tyto alba* diet

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Capsule The analysis of 635 papers about the diet of the European Barn Owl *Tyto alba* showed that 83751 birds were captured out of 3.44 million prey items (2.4%). Birds were more frequently captured on islands than mainland, in southern than northern Europe and in eastern than western Europe. Between 1860 and 2012, the consumption of birds decreased in northern and eastern Europe. Among avian prey, the House Sparrow *Passer domesticus*, the most frequently captured bird (65.7%), decreased in frequency during the last 150 years in eastern Europe.

Agricultural intensification has been responsible for the decline in bird populations over many years, particularly those species living in farmland (Engler & Bauer 2002, Donald et al. 2006, Wegrzynowicz 2013). Various factors are responsible for this decline including increased disturbance, land drainage, trampling by farm stock, earlier ploughing and a strong reduction in habitats and food supplies due to, for example, the use of herbicides (Chamberlain & Vickery 2002, Newton 2004). The rate at which these processes have taken place has varied across countries, partly because the Common Agricultural Policy, recommended by the European Union, has been applied at different rates (Donald et al. 2002, Báldi et al. 2005, Báldi & Faragó 2007, Pe'er et al. 2014). Determining the temporal decline in biodiversity at the scale of a continent is important to determine for how long a given agricultural policy has been negatively affecting ecosystems and trophic chains (Donald et al. 2001). For instance, predators that feed upon declining species may decline, modify their diet or move to regions where their staple prey is still abundant (Korpimäki & Norrdahl 1991, Hanson & Chouinard 2002, Millon et al. 2009).

Based on the fact that farmland birds declined during the last decades in Europe, I investigated whether this affected prey composition of the Barn Owl (*Tyto alba*). This bird, that forages in the open landscape and lives close to human beings, is a classical model system to perform diet analyses because bones of their prey are not fully digested and still present in regurgitated pellets (Taylor 1994). I performed a thorough literature survey of papers reporting diet analyses to test whether during the last 150 years the proportion of birds, the number of avian prey species and of the most frequent avian prey, the House Sparrow (*Passer domesticus*), decreased in the diet of Barn Owls. House Sparrow populations have indeed shown a dramatic decline throughout Europe (Robinson *et al.* 2005, Klok *et al.* 2006, Brichetti *et al.* 2008) and this might have affected Barn Owl diet. Thus, Barn Owl diet may be a useful indirect method for studying the decline of (farmland) birds at the scale of a continent.

The present article is based on an extensive collection of 635 papers reporting diet analyses performed between 1860 and 2012 (mean is 1975) (see Roulin & Dubey 2012 for further details; Table 1). If several pellet analyses in the same or different years were reported in a given paper, I calculated the sum of individuals for each prey species so that each paper appears only once per statistical analysis. This approach was used instead of calculating the sum of individuals for each separate year in each paper, a procedure that would have increased errors associated with small sample sizes. On average each paper reported the consumption 5428 vertebrate and invertebrate animals (range of sample sizes: 9-234991) of which 132 were birds (range: 0-4082). To obtain normal distributions, the total number of identified avian and non-avian prey items was log-transformed and the proportion of prey items

Table 1. Number of studies and sample sizes in different European regions.

Region	No. of studies	No. of birds as prey	No. of prey identified	No. of birds identified to species level	% House Sparrows
Albania	1	10	68	0	
Austria	8	325	11298	75	96.4
Belgium	10	5977	155883	130	96.2
Bosnia	1	68	1782	0	
Bulgaria	6	2133	60597	1966	51.4
Corfu	1	61	3097	42	21.4
Corsica	3	382	11295	27	0
Cos	1	227	2277	492	66.3
Crete	3	88	1359	75	24.0
Croatia	3	434	8633	429	98.4
Czech Republic	22	3365	103037	1230	81.0
Denmark	1	1967	36173	1737	68.2
France (mainland)	93	8266	722724	2092	57.2
Germany	154	14493	666036	12 726	67.8
Greece (mainland)	10	296	9508	314	46.3
Hungary	38	6886	140398	7001	81.6
Ireland	19	1081	28442	111	21.5
Italy (mainland)	60	4194	87 155	1332	57.2
Luxemburg	9	86	11003	241	74.4
Malta	2	29	424	33	0
Netherlands	10	2484	126070	0	
Poland	17	6395	114240	5109	78.2
Portugal	8	581	20343	92	64.8
Rumania	6	1433	31518	1571	89.2
Sardinia	6	364	2619	0	
Serbia	2	339	8576	321	19.6
Sicily	5	549	12555	30	0
Slovakia	8	1013	23431	969	85.5
Slovenia	6	195	6179	89	94.4
Spain	46	11314	176442	7970	47.3
Sweden	1	37	1661	0	
Switzerland	17	3566	291232	2805	85.1
Tenerife	1	19	2058	0	
Great Britain	57	5094	569 103	634	52.0
Total	635	83751	3447216	49 643	

that were birds was box-cox transformed. In a sample of 203 studies, at least ten birds were identified to the species level. The number of identified avian prey items was box-cox transformed and the proportion of birds there were House Sparrows was arc sine transformed. Two-tailed statistical analyses were performed with the software JMP (version 9.0.0; SAS Institute Inc., Cary, NC, USA) and *P*-values smaller than 0.05 considered significant.

Out of 635 studies, 3 447 216 prey items were identified of which 83 751 were birds (2.4%) (Table 1). The proportion of birds in the Barn Owl diet varied between 0% and 80.7% per study, with a mean of 4.1% and median of 1.7%. Owls consumed more birds on islands than mainland (estimates from the model presented in Table 2 are 3.3% and 1.2%, respectively), more in

southern than northern Europe and more in eastern than western Europe (terms latitude and longitude in Table 2). During the last 150 years, there was an overall decline in bird consumption (term 'Year' in Table 2), an effect that depended on latitude and longitude (interactions in Table 2). By defining two categories of studies based on median latitude, the decrease in bird consumption with year was detected in northern Europe (similar ANCOVA as in Table 2, year: $F_{1,312} = 16.5$, P <0.0001; island/mainland: $F_{1.312} = 16.6$, P < 0.0001; total number of prey analysed: $F_{1,312} = 2.3$, P = 0.13; longitude: $F_{1,312} = 13.6$, P = 0.0003) but not in southern Europe (ANCOVA, year: $F_{1,287} = 0.9$, P = 0.35; island/ mainland: $F_{1,287} = 16.3$, P < 0.0001; total number of prey analysed: $F_{1,287} = 0.3$, P = 0.57; longitude: $F_{1,287} =$ 1.6, P = 0.21) (Fig. 1). Similarly, by defining two

Table 2. Variation in the consumption of avian prey by Barn Owls in Europe. Two sets of analyses were performed, one on all available studies (n = 635, df = 1,601) and another on studies that reported at least one bird as prey (n = 560, df = 1,529). ANCOVAS were performed with latitude, longitude, year and log-transformed sum of avian and non-avian prey items identified as covariates and as a factor whether studies were performed on an island (n = 106) or on the mainland (n = 529). The dependent variable was the box-cox transformed proportion of consumed birds.

	All studies			Studies with at least one bird as prey		
	F	Р	Estimate ± se	F	Р	Estimate ± se
Island/mainland	38.0	< 0.0001	-0.0083 ± 0.0013	29.5	< 0.0001	-0.0060 ± 0.0011
Sum of prey	5.1	0.025	0.0028 ± 0.0012	13.0	0.0003	-0.0040 ± 0.0011
Latitude	42.3	< 0.0001	-0.0014 ± 0.0002	37.7	< 0.0001	-0.0011 ± 0.0002
Longitude	26.2	< 0.0001	0.0005 ± 0.0001	24.2	< 0.0001	0.0005 ± 0.00009
Year	14.1	0.0002	-0.0002 ± 0.00004	11.9	0.0006	-0.0001 ± 0.00004
Latitude × Year	3.8	0.05	-0.00002 ± 0.00001	3.8	0.05	-0.00002 ± 0.000009
$Longitude \times Year$	11.1	0.0009	-0.00002 ± 0.000005	12.4	0.0005	-0.00002 ± 0.000004

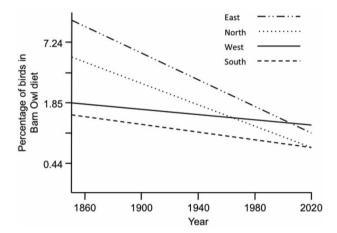


Figure 1. Relationship between year and proportion of birds in the Barn Owl diet. Lines are predicted relationships extracted from linear regression analyses with year, island/mainland and log-transformed total number of prey items identified. Studies are assigned to the categories 'southern Europe' vs. 'northern Europe' and to the categories 'western Europe' vs. 'eastern Europe' based on median latitude and median longitude, respectively.

categories of studies based on median longitude, the temporal decrease in bird consumption was stronger in eastern Europe (ANCOVA, year: $F_{1,298} = 26.6$, P < 0.0001; island/mainland: $F_{1,298} = 3.6$, P = 0.059; total number of prey analysed: $F_{1,298} = 4.4$, P = 0.037; latitude: $F_{1,298} = 18.5$, P < 0.0001) compared to western Europe (ANCOVA, year: $F_{1,301} = 4.4$, P = 0.04; island/mainland: $F_{1,301} = 32.9$, P < 0.0001; total number of prey analysed: $F_{1,301} = 1.7$, P = 0.19; latitude: $F_{1,301} = 40.1$, P < 0.0001) (Fig. 1). These results were similar if considering the full sample of studies, if restricting the statistical analyses to studies for which at least one bird was found as prey (Table 2), or if considering only studies published after

1900 or 1940 (not shown). The results are, therefore, robust.

The 51561 birds identified in the Barn Owl diet belonged to 149 species (Online Supplementary Material, Table S1). The most common group was Passeridae (81.51%) followed by Hirundinidae (2.85%), Fringillidae (2.72%), Muscicapidae (1.90%), Alaudidae (1.86%), Apodidae (1.73%), Sturnidae (1.45%), Emberiziidae (1.17%) and Turdidae (1.10%). The number of avian prey species decreased with latitude (ANCOVA on box-cox transformed values: $F_{1.196} = 10.2$, P = 0.0016, estimate \pm se: -0.25 ± 0.08) and was higher on islands than the mainland ($F_{1.196}$ = 6.2, P = 0.014; ten vs. six bird species) but was not significantly related to longitude ($F_{1.196} = 0.5$, P =0.49) and year ($F_{1.196} = 1.7$, P = 0.19) after controlling for the box-cox transformed number of avian prey identified $(F_{1.196} = 72.1,$ P < 0.0001); interactions between year, latitude and longitude were not significant and were removed from the final model.

Among avian prey species, the House Sparrow was more frequently preyed upon on the mainland than islands (ancova with 71% vs. 46%) and in northern than southern Europe (Table 3; Fig. 2a). The significant interaction between year and longitude (Table 3) was explained by the significant temporal decrease in the proportion of avian prey that were House Sparrows in eastern Europe (similar linear regression analysis as in Table 3, year: $F_{1,97} = 5.4$, P = 0.02, Fig. 2b; I included in the model the factor 'island/mainland' and the covariates 'latitude' and 'box-cox transformed total number of birds identified') but not in western Europe (similar model, year: $F_{1,96} = 0.1$, P = 0.80); eastern and western Europe were defined by the median longitude.

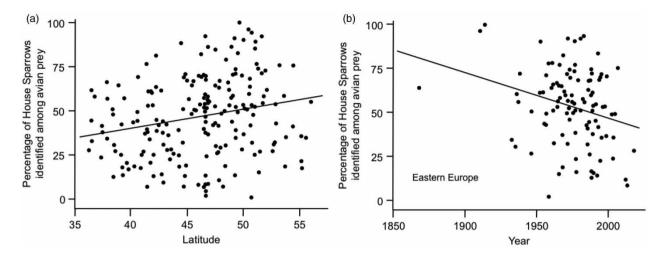


Figure 2. Percentage of House Sparrows among the avian prey of the European Barn Owl with latitude and year. (a) Predicted latitude from an ANCOVA including, as a factor, island/mainland and as covariates latitude, longitude, year and box-cox transformed total number of identified avian prey items. (b) Predicted year when pellets were analysed from an ANCOVA with island/mainland as a factor and as covariates year, longitude and box-cox transformed total number of identified avian prey items. This figure represents samples collected in Eastern Europe defined as the median latitude of the entire sample of studies in which avian prey were identified to the species level.

Table 3. Variation in the percentage (arc sine transformed) of House Sparrows among the avian prey in the diet of the European Barn Owl. An ANCOVA (df = 1,195) was performed with latitude, longitude, year and box-cox transformed sum of avian prey items (i.e. House Sparrows and other birds) identified as covariates and as a factor whether studies were performed on an island (n = 25) or on the mainland (n = 178). The dependent variable was the arc sine transformed proportion of House Sparrows that were consumed.

	F	Р	Estimate ± se
Island	10.2	0.001	0.1460 ± 0.0456
Latitude	7.2	0.008	0.0182 ± 0.0068
Longitude	6.4	0.012	0.0076 ± 0.003
Year	4.0	0.046	-0.0029 ± 0.0014
Sum of avian prey	13.0	0.0004	0.001 ± 0.0003
Latitude \times Year	1.0	0.31	0.0003 ± 0.0003
$Longitude \times Year$	4.0	0.047	-0.0003 ± 0.0002

The present study shows that Barn Owls consume fewer birds nowadays than before. Although Barn Owls eat more birds in southern than northern Europe, a pattern opposite to what was observed in North America (Johnston & Hill 1987), the temporal decline in bird consumption was more pronounced in northern Europe (Fig. 1). Because Barn Owls forage primarily in the open landscape, these results mirror recent findings showing that farmland birds have experienced pronounced declines in Europe. This is in part the consequence of the Common Agricultural Policy aimed at improving agriculture efficiency but, unfortunately, at the cost of biodiversity

(Donald et al. 2006). Because the staple prev of the Barn Owl, small mammals, also declined during the same time period (Cornulier et al. 2013), the present study suggests that the temporal decline in birds is more pronounced than in small mammals. The stronger decline of avian prey in northern Europe is consistent with the finding that farmland birds declined to a larger extent in this part of the continent (Väisänen et al. 2007). With regards to longitude, Barn Owls consumed more birds in eastern than western Europe and the temporal decline in bird consumption was more pronounced in the east (Fig. 1). This is somewhat surprising because the Common Agricultural Policy was implemented earlier in western than eastern countries (Donald et al. 2001). This decline may, therefore, be explained by other factors than this Policy, which affect primarily House Sparrows. Indeed, I observed a strong temporal decline in the consumption of House Sparrows in eastern countries (Seress et al. 2012; Fig. 2b), a finding that did not apply to western countries.

Barn Owls consumed approximately twice as many birds on islands than on the mainland (Table 2), as observed in North America (Johnston & Hill 1987). This is concordant with the reduced species diversity on islands than mainland implying that predators have to rely on fewer mammalian prey species and in turn on more birds (Crowell 1962, Alcover *et al.* 1998, Grant 1998).

To conclude, this study shows that the decline in bird populations is pronounced and detectable in the diet of a predator, the Barn Owl. Interestingly, the temporal decline in bird consumption is more pronounced in north-eastern Europe. Impoverishment in prey diversity and abundance implies that global changes affect all trophic levels further demonstrating the major biodiversity changes that are occurring currently. This crisis may be caused not only by the Common Agricultural Policy but also by other factors that affect our farmland.

ACKNOWLEDGEMENTS

I am grateful to the Swiss Ornithological Institute for opening their library to me, and to Will Cresswell and two anonymous reviewers for useful comments.

SUPPLEMENTAL DATA

Table S1 (the different species recorded as consumed by Barn Owls studies in Europe) can be accessed at 10.1080/00063657. 2015.1012043.

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(MS received 24 November 2014; revised MS accepted 20 January 2015)