Birds as prey of owls: an intra- and interspecific comparison

Aves como presas de rapinas noturnas: comparação intra e interespecífica

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ABSTRACT

A review on birds as prey of owls is presented based on 3639 prey lists from literature. The percentage of birds varied strongly between prey lists. Differences between owl species were moderate, only Eurasian Pygmy-owl (*Glaucidium passerinum*) and Eurasian Eagle-owl (*Bubo bubo*) showed over all higher percentages of birds in their prey. Differences between seasons were small. The variation within the same owl species (intraspecific variation) across the study regions was larger. In several cases, the percentage of birds as prey tends to have declined over the last decades. Although owls generally prey on mammals, birds are an important alternative prey.

Keywords: Food composition, birds as prey, Strigiformes

RESUMO

Uma revisão sobre as aves como presas de rapinas noturnas é apresentada, com base em 3639 listas de presas da literatura. A percentagem de aves variou muito entre listas de presas. As diferenças entre as espécies de rapinas noturnas foram moderadas, apenas o mocho-anão (*Glaucidium passerinum*) e o bufo-real (*Bubo bubo*) apresentaram no geral as percentagens mais elevadas de aves como presa. As diferenças entre as estações do ano foram pequenas. A variação dentro da mesma espécie de rapina noturna (variação intraespecífica) entre as regiões do estudo foi mais elevada. Em vários casos, a percentagem de aves enquanto presa tende a diminuir nas últimas décadas. Embora as rapinas noturnas geralmente se alimentem de mamíferos, as aves constituem uma presa alternativa importante.

Palavras-chave: aves como presas, composição da dieta, Strigiformes

Introduction

Food composition for many species of owls, regions and seasons is documented by hundreds of publications. Surprisingly, only a few syntheses about this topic have been published in the last three decades. There are some publications dealing with several species (Korpimäki & Marti 1995, Bó et al. 2007) and several on a single species, and most of them cover a restricted geographical range (Schönn et al. 1991, Birrer 2009, Obuch 2010, 2011, Korpimäki & Hakkarainen 2012, Roulin & Dubey 2012, Obuch et al. 2013, 2013, Roulin & Christe 2013, Roulin & Dubey 2013, Roulin 2015, Šotnár et al. 2015, Roulin 2016b, 2016a). The existing quantitative reviews on several species and regions present measures such as prey diversity, prey size or diet similarity but give no information on specific prey groups (Jaksić 1988, Marti et al. 1993).

Food of most owl species is composed primarily of mammals. Birds seem to be of minor importance and are often considered an alternative prey. Because food availability is a basic factor for ecology and conservation, it is important to have quantitative data not only on the main prey but on alternative prey species as well. The aim of this paper is to present data on birds as prey of as much owl species as possible based on a broad literature review.

Methods

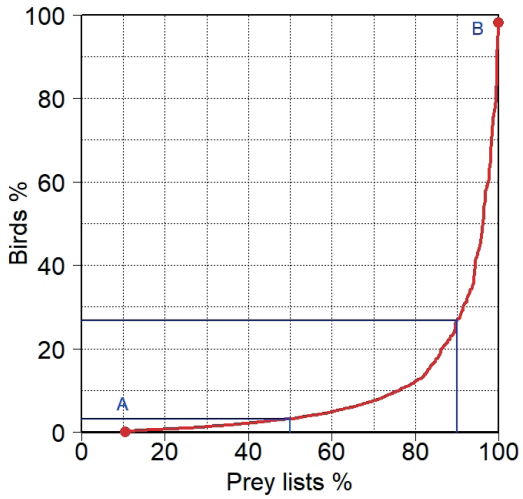
Various bibliographies, databases and entries in the library of the Swiss Ornithological Institute were searched for publications on owl diet. A total of more than 4300 references were found. Of these, 2262 publications were checked and if available, data on owl prey lists was entered into a database. Predator species, prey species or group and minimal number of items per prey species, date, country, place, and longitude and latitude were recorded. Where necessary, absolute numbers of prey items were calculated from published percentages. When a publication contained several sub-lists, i.e. several places, years or seasons, each list was entered separately (Birrer 2009). If the same data set was used several times in different publications, lists were entered only once. The owls' systematics and names follow the IOC World Bird List (Gill & Donsker 2017). Prey biomass was recalculated by multiplying the number of prey items with a mean weight of the prey species derived from literature. Each list was assigned to one major geographical region: North America (Canada, USA, Mexico), South America, Northern Europe (Scandinavia including Denmark, the Baltic States and northern Russia), the British Isles (including Ireland), Central Europe (Germany, Poland, Czech Republic, Slovakia, Austria, northern Switzerland, northern France, Benelux), Southern Europe (Spain, Mediterranean France, Italy, southern Switzerland), Southeast Europe (Slovenia, Hungary, Ukraine and countries south of it), Middle East and North Africa (Africa north of Sahara and Canary Islands), Africa (south of Sahara), Asia (excluding Middle East) and Australia.

For this synthesis, the database was searched for prey lists which fulfilled the following conditions: a) all prey groups were mentioned if present, b) more than 90% of all vertebrates were determined to at least till the order level, c) the list contained more than 100 vertebrate prey items or more than 500 preys items (invertebrates and vertebrates). Furthermore, only owl species with more than 40 prey lists were taken into account for this synthesis.

Results are presented in graphs resembling Lorenz curves (Damgaard & Weiner 2000). Prey lists were first sorted by increasing proportion of birds on vertebrate prey. Then they were plotted along the x-axis. Such a curve allows to accurately visualizing various proportions of the prey list data

Figure 1 - Example of a graph showing the proportion of birds in the prey lists of Northern Long-eared Owl (N=1328) in relation to the proportion of prey lists and some important key metrics: Point A: percentage of prey lists with no birds (exact data point: 10.5 %); Point B: Maximum percentage of birds in a prey list (exact data point: 98.0 %); small rectangle: median (50 % on x-axis; exact data point: 3.2 %); larger rectangle: 90 %-quantile (exact data point: 26.8 %).

Figura 1 - Exemplo de gráfico da proporção de aves nas listas de presas de bufo-pequeno (N = 1328) relativamente à proporção de listas de presas, e algumas métricas importantes. Ponto A: percentagem de listas de presas sem aves (valor exato: 10,5%); ponto B: percentagem máxima de aves numa lista de presas (valor exato: 98,0%); retângulo menor: mediana (50% no eixo horizontal; valor exato: 3,2%); retângulo maior: quantil 90% (ponto exato de dados: 26,8%).



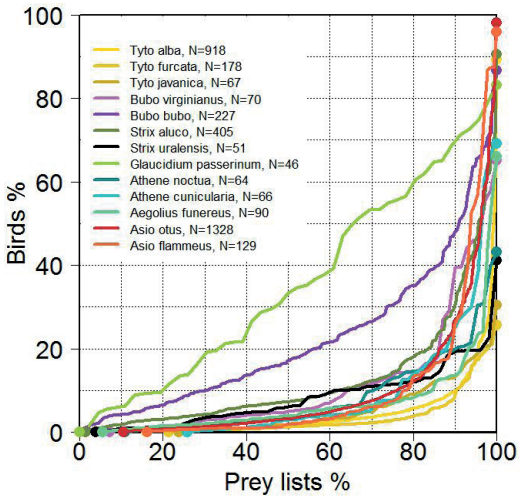
set, e.g. proportion of the median, of the 90%-quantile the maximum and minimum etc. (Fig. 1).

Results

After the selection, 3639 prey lists from 957 references were used for this review. The required 40 prey lists per species were available for 13 owl species. The distribution curves of birds as prey were quite similar for the different owl species: on the left-hand side, a slow increase is visible. At about 80%

Figure 2 - Percentage of birds in prey lists of different owl species.

Figura 2 - Percentagem de aves nas listas de presas de diferences espécies de rapinas noturnas.

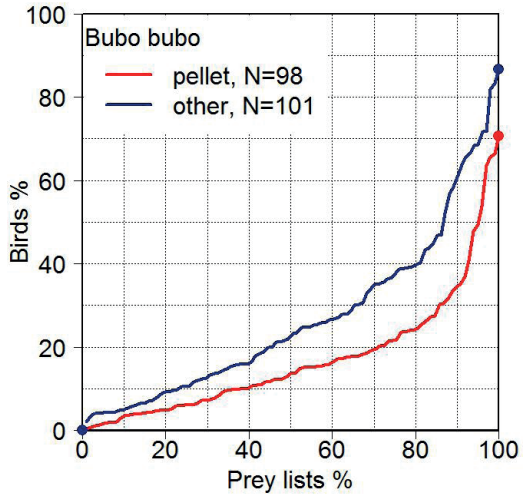


of all prey lists, the curve sharple increases and reaches 90 to 100% of birds at the right end (Fig. 2). In 11.1% of all prey lists no birds were found. The owl species with the most prey lists containing no birds was Burrowing Owl (*Athene cunnicularia*; 25.8%; Fig. 2), followed by Eastern Barn Owl (*Tyto javanica*; 23.9%), American Barn Owl (*Tyto furcata*; 21.3%), Short-eared Owl (*Asio flammeus*; 16.3%) and Common Barn Owl (*Tyto alba*; 16.1%). The fewest prey lists without any birds were found in Ural Owl (*Strix uralensis*; 3.9% of all lists) and Tawny Owl (*Strix aluco*; 1.5%). The prey lists of Eurasian Eagle-owl (*Bubo bubo*) and Eurasian Pygmy-owl (*Glaucidium passerinum*) all contained at least one bird.

Median percentage of birds was lowest in American Barn Owl (1.2%), Common Barn Owl (1.6%) and Short-eared Owl (1.8%). Most other owl species had a median lower than 7.5%, except Eurasian Eagle-owl (17.2%) and Eurasian Pygmy-owl (34.0%). The high proportion of birds in prey lists of Eurasian Eagle-owl and Eurasian Pygmy-owl

Figure 3 - Percentage of birds in prey lists of Eurasian Eagle-owl obtained by pellet analysis and other methods (including combination of pellet analysis and analysis of prey remains).

Figura 3 - Percentagem de aves nas listas de presas de bufo-real obtidas por análise de regurgitações e outros métodos (incluindo análise de regurgitações e restos de presas).



might have some methodological reasons: The vast majority of prey lists of all other species are based on pellet analyses, whereas prey lists of Eurasian Pygmy-owl and Eurasian Eagle-owl not only consider pellets but often prey remains too. It is well known that birds may be overrepresented in prey remains, because in many cases even a single feather of a prey species can be determined. When only pellet-based prey lists of Eurasian Eagle-owl were taken into account, the median proportion of birds dropped to 13.7% (N=98; Fig. 3). For Eurasian Pygmy-owl only 12 prey lists based on pure pellet analysis or on prey caching were available. In those lists, birds accounted for a median of 27.6%.

Intraspecific differences between prey lists of different regions were bigger than interspecific differences in some cases. In the Northern Long-eared Owl (*Asio otus*) there seems to be a latitudinal gradient in proportion of preyed birds across Europe: small proportions in Northern Europe, median proportions in Central Europe and high proportions in Southern Europe and even higher propor-

Figure 4 - Percentage of birds in prey lists of (A) Northern Long-eared Owl (*Asio otus*)and (B) Western Barn Owl (*Tyto alba*) suggesting a regional gradient.

Figura 4 - Percentagem de aves nas listas de presas de bufo-pequeno e coruja-das-torres, sugerindo um gradiente regional.

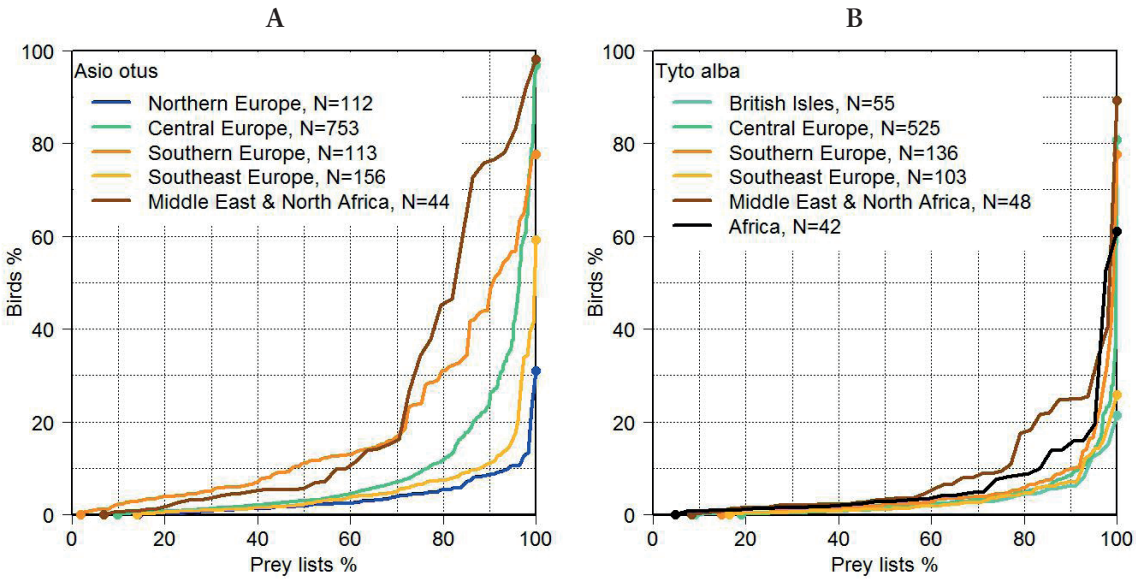
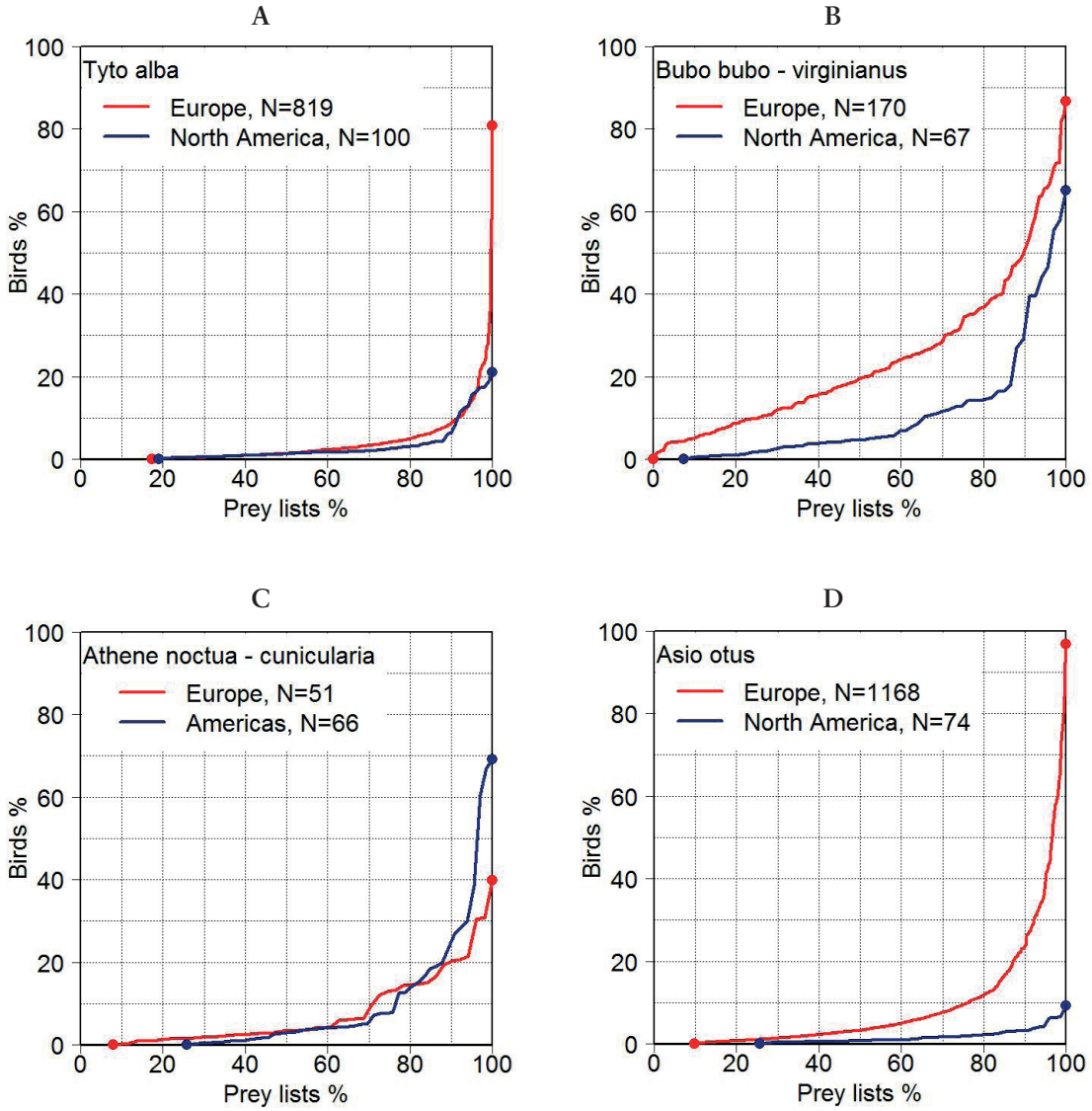


Figure 5 - Comparison of proportions of birds as prey of the same or replacing species in Europe and (North) America: (A) Western Barn Owl versus American Barn Owl (*Tyto alba*), (B) Great Horned Owl versus Eurasian Eagle-owl (*Bubo bubo/virginianus*), (C) Little Owl versus Burrowing Owl (*Athene noctua/cunicularia*) and (D) Northern Long-eared Owl (*Asio otus*).

Figura 5 - Comparação das proporções de aves como presa de uma mesma espécie ou em espécies homólogas na Europa e na América do Norte: bufo-americano versus bufo-real, coruja-das-torres americana versus europeia, mocho-galego versus coruja-buraqueira e bufo-pequeno.

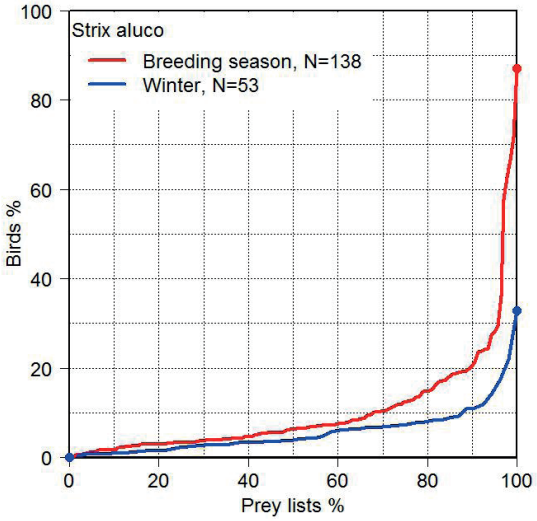


tions in Middle East/North Africa (Fig. 4). In prey lists of Southeast Europe, however, birds were relatively rare. Common Barn Owl prey lists of the region Middle East/North Africa also held higher proportions of birds than those in Europe. Prey lists south of the Sahara desert contained fewer birds. (Fig. 4).

For Northern Long-eared Owl, there were enough data for a comparison between prey lists from Europe and North America (Fig. 5). Such comparisons were also possible for the replacing species Common and American Barn Owl, Great Horned Owl (*Bubo virginianus*) and Eurasian Eagle-owl as well as for

Figure 6 - Comparison of proportions of birds as prey of Tawny Owl in the breeding season and winter.

Figura 6 - Comparação das proporções de aves como presa de coruja-do-mato durante o período reprodutor e o inverno.



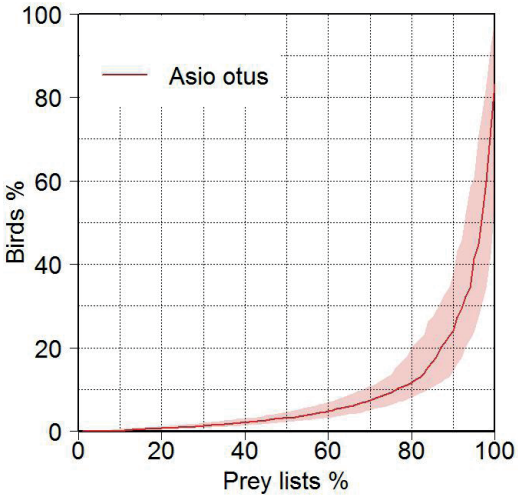
Little Owl and Burrowing Owl (subsequently compared with combined lists from North and South America). There was no difference in the proportion of birds between prey lists of Common and American Barn Owl and in prey lists of *Athene* species. However, European prey lists contained more birds than North American ones for *Bubo bubo/virginianus* and Northern Long-eared Owl (Fig. 5).

Seasonal differences in food composition are nearly nonexistent in Common Barn Owl and are small in Northern Long-eared Owl. Tawny Owl seemed to feed a bit more on birds during breeding season, but differences were marked only in the 40% of prey lists with the highest proportion of birds (Fig. 6).

In nine cases, there were enough prey lists to split them into two or more time series. In five of these nine cases, there was a lower proportion of birds in the most recent time series (Common Barn Owl in Southern Europe and Southeast Europe, Tawny Owl in Central Europe and Northern Long-eared Owl in Central Europe and in Southeast Europe, Fig. 7). In three cases there were no obvious

Figure 8 - Repeated sampling of prey lists (including degree of uncertainty): Out of the 1328 prey lists of Northern Long-eared Owls, 200 lists were randomly sampled 5000 times. The solid line shows the mean of all the samples. The shaded area represents the 95% confidence interval.

Figura 8 - Repetição da amostragem das listas de presas (incluindo grau de incerteza). Das 1328 listas de presas de bufo-pequeno, 200 listas foram amostradas aleatoriamente 5000 vezes. A linha sólida representa a média de todas as amostras. A área sombreada representa o intervalo de confiança de 95%.



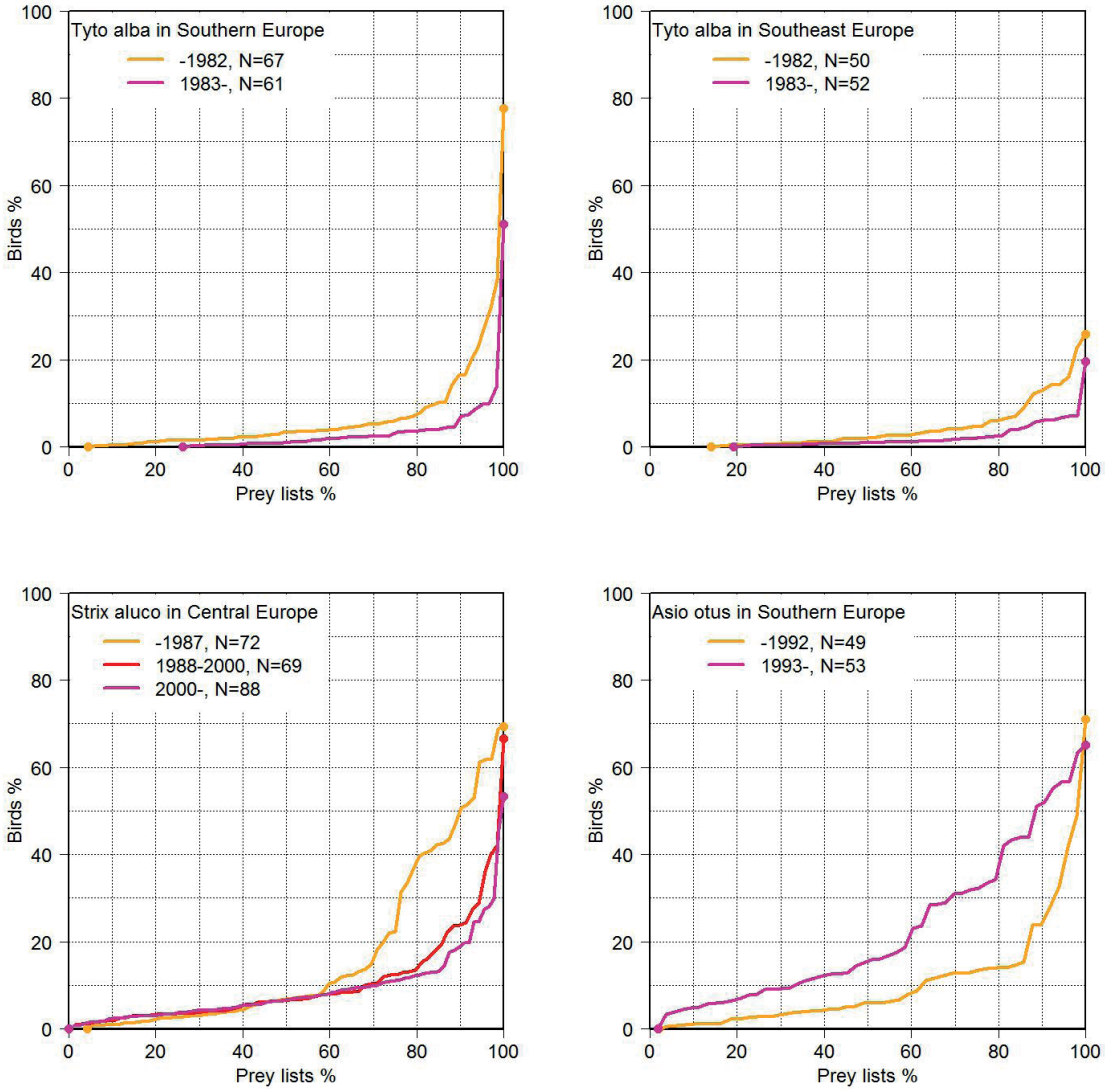
differences (Common Barn Owl in Central Europe, American Barn Owl in North America and Northern Long-eared Owl in Northern Europe) and only in Northern Long-eared Owl prey lists from Southern Europe did the most recent prey lists show higher proportions of birds than in older ones.

Instead of the percentage of prey items it is also possible to calculate the percentage of biomass. Differences between percentage of prey items and percentage of biomass were generally small in this data set. They were nearly nonexistent in Common Barn Owl and Northern Long-eared Owl. The most prominent differences were found in Great Horned Owl and Ural Owl.

To get an impression on how precise the graphs are, a random sample of 200 out of the 1327 prey lists of Northern Long-eared Owl was taken. This procedure was repeated 5000 times. The mean and 95% interval of all these

Figure 7 - Some examples of comparisons of proportions of birds as prey in different periods.

Figura 7 - Alguns exemplos de comparações das proporções de aves como presa em diferentes períodos.



lists are shown in Fig. 8. It is obvious that all lists lie close together in the left-hand part, while uncertainty becomes larger in the 20 % of lists with the highest proportions of birds.

Discussion

For this study 2262 publications were checked. This is about half of the known references on prey of owls. The majority (79.3%) of these lists are based on pellet analyses. The rest is based on analysis of prey remains in the nest, analysis of plucking remains, photo or video surveys of nests and on combinations of these methods. The checked publications are not a random sample, and publications in European journals and more recent publications might be overrepresented because of easier access

in the library of the Swiss Ornithological Institute and online respectively. Furthermore papers on Northern Long-eared Owl were clearly overrepresented because of an earlier work by Birrer (2009). After reaching more than one hundred prey lists per region, searching effort on publications on Barn Owl, Eurasian Eagle-owl and Tawny Owls was reduced. Despite a considerable effort to get data for as many owl species as possible, enough data for a quantitative analysis was only retrieved for relatively few combinations of species and regions. Therefore, even if literature on owls' diet is rather extensive, it would be worth publishing further studies, especially for species and/or regions where knowledge has remained poor. Unfortunately there are several publications which could not be used for this review due to methodological problems. For example, some authors publish percentages of each prey but no total number, so that prey items cannot be calculated (e.g. Thal et al. 2014, Wadatkar et al. 2016). Others only present graphs but no tables (e.g. Clulow et al. 2011, Żmihorski et al. 2011), or only the percentage of pellets in which certain prey items were found (e.g. Lavazanian 1996, Zade et al. 2011) or only list prey of some groups but not of all (e.g. Andrade et al. 2016, Lesiński & Beuch 2016).

There is a large body of literature available comparing owl diet between species, regions, seasons, and time. Most papers are based on only a few prey lists and results were contradicting between papers. Some authors found higher percentages of birds in prey lists of Northern Long-eared Owls in winter especially when snow cover was high (Korpimäki & Hakkarainen 2012), whereas others found higher percentages in the breeding season (Manganaro 1997, Bertolino et al. 2001). Our data do not indicate a general difference between seasons in Northern Long-eared Owl and Barn Owl. This is not surprising, because season is a proxy for different factors such as prey abundance or different prey availability (e.g. because of snow cover: Elvers et al. 1979, Canova 1989). Nevertheless, this review shows a somewhat higher proportion of birds in Tawny Owl in the breeding season.

The most pronounced differences were visible between continents and/or regions in one species or related species. Such differences have been described before for birds as food of Barn Owl in Europe (Roulin 2015) and for Northern Long-eared Owl (Birrer 2009).

Roulin (2015) found a decrease of birds as prey of Barn Owl between 1860 and 2012 in Northern and Eastern Europe. Such a decrease is also observed in the presented data for Common Barn Owl in several European regions as well as for Tawny Owl in Central Europe, and Northern Long-eared Owl in Central and Southeast Europe. In Southern Europe, on the other hand, Common Barn Owl prey lists from 1993 and older contained a higher proportion of birds than more recent ones.

An interesting result of this review is the similarity of the Lorenz curves of the different analysed owl species. Only Eurasian Pygmy-owl and Eurasian Eagle-Owl's curves were distinctly higher. For all other species, in more than half of all prey lists birds accounted for less than 10% of prey items. However, for all but Ural Owl, Burrowing Owl, Eastern Barn Owl, and American Barn Owl, birds can be an important prey and can make up more than 50 % of vertebrate prey items.

The distribution of birds in owl prey was very uneven. Such high proportions of birds are often a result of specific situations, e.g. low density of small mammals due to cyclic population changes (Potapov & Sale 2012, Chandler et al. 2016) or unfavourable conditions on islands. Another situation which can lead to high bird proportions in owl prey is low mammal availability, caused e.g. by dense and high ground vegetation in summer or snow cover in winter (Elvers et al. 1979, Ancelet 1987, Canova 1989). Furthermore, an extraordinarily high local bird density can be exploited by owls and can thus also lead to elevated proportions of birds in their prey. Owls are known to hunt

in colonies of waterbirds like terns and gulls (Kayser & Sandoul 1996), or they can exploit concentrations of migrating birds attracted by lighthouses (Moritz & Schonart 1976, Canário & Tomé 2012) or resting places during migration (Reglade 1985, Kiat et al. 2008).

Even though high proportions of birds in owl prey lists are not very common, the flexibility of owls to switch their diet to birds in certain situations might be important for their survival.

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Supporting information

Appendix S1 contains additional figures comparing prey numbers with percentage of biomass, per region, in winter and breeding season, and at different time series; Appendix S2 contains the complete list of references included in the analysis; and Appendix S3 contains raw data.

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