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Synthesis of 312 studies on the diet of the Long-eared Owl *Asio otus*

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In this literature review, I examined 475 publications with information on the global diet of the Long-eared Owl *Asio otus*. Data within 312 publications were entered into a database, and quantitative diet data were available from 194 of these publications. The composite data set identified 477 different prey: 180 mammal, 191 bird, 15 reptile, 7 amphibian, and 1 fish species, and 83 invertebrate groupings. In 798 prey lists reflecting 813 033 prey items, small mammals accounted for 93.3% and birds for 6.4% of the vertebrate prey. Prey ranged from 1–500 g, with the vast majority of prey consisting of species ≤50 g. Twenty-three species predominate the prey in at least one species list. Diet composition at the family level was similar in different regions, but considerable differences were shown at the species level.

Key words: Long-eared Owl, food composition

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INTRODUCTION

The Long-eared Owl *Asio otus* is distributed over wide areas of North America, Europe, Middle East and Asia, and is relatively common (Mebs & Scherzinger 2000). While a large number of publications reporting on the owls' diet from pellet analyses exist, a quantitative synthesis is missing. Many diet papers are either of an older date, restricted to subregions of the species' range, or do not provide quantitative information (Uttendörfer 1939, Uttendörfer 1952, Smeenk 1972, Schmidt 1975, Marti 1976, Marks *et al.* 1994). For owls, brood sizes and fledging rates (which are crucial measurements in population biology) depend on food availability. Consequently, understanding of diet and the dynamics of prey species become key elements in conservation efforts. The aim of this paper is to compile a synthesis of the global diet of the Long-eared Owl, to aid in understanding this species' ecology.

METHODS

Various bibliographies and databases were searched for Long-eared Owl diet papers (e.g. Clark *et al.* 1978, Muller 1996, Mammen *et al.* 1997, Muller 2000; www.nisc.com, Ornithological Worldwide Literature OWL http://egizoosrv.zoo.ox.ac.uk/OWL). Entries into the library of the Swiss Ornithological Institute Sempach were also checked. Data on Long-eared Owl prey was entered into a database. Country, place, longitude and latitude, date, type of prey, proportions of biomass and absolute number of prey items were recorded. If necessary, absolute numbers of prey items were calculated from published percentages. Cases in which this conversion was not possible were excluded from the analysis, e.g. if only proportions of biomass were given. Obvious misprints were corrected before being entered into the database. When a publication contained several sub-lists, i.e. several places, years or seasons, each list was entered separately.

For analyses on the overall prey spectrum in the diet, all sources were included. If all sub-lists together constituted more than 75% of the items in the total list, the sub-lists were used. For qualitative analyses only complete lists including at least 100 prey items were used. I excluded lists in which the following situations occurred: (1) the number of unclassified vertebrate prey items exceeded 10%; (2) 'unclassified voles' made up more than 20% of all classified items; or (3) 'unclassified *Microtus*' made up more than 20% of all *Microtus* individuals.

Body mass of the prey species were derived from the literature. For species below 100 g, the mean adult body mass was used. For larger species, the minimal adult body mass was used because Long-eared Owls are known to prefer smaller prey items. For all invertebrates, a body mass of 1 g was assumed. Percentages refer to the sum of all vertebrate taxa unless stated otherwise. Invertebrates are given as proportion per 100 vertebrates. *Apodemus sylvaticus* and *A. flavicollis* were considered as one prey type as well as species of the genus *Mus, Peromyscus, Reithrodontomys* and bats, birds, reptiles, amphibians and invertebrates, since they were usually not differentiated in the publications.

Each list was assigned to one or more of eight major geographical regions: North 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), south-eastern Europe (Slovenia, Hungary, Ukraine and countries south of it), Africa including the Middle East (North Africa, Middle East and Canary Islands), and Asia (excluding Middle East).

RESULTS

In this study, 475 publications with information on prey of Long-eared Owls were examined. Because of logistical constraints, I did not have access to, or necessary language translation support for another 198 references. A total of 312 publications with information on diet were included in the database. Quantitative data could be extracted from 194 publications with a total of 798 prey lists reflecting 813 033 prey items (Table 1; Appendix 1). The majority of prey information, 527 lists reflecting 509 955 prey items, came from Central Europe.

Prey spectrum

Worldwide, a total of 477 prey species of the Long-eared Owl were found (Table 2). Prey reflected 180 mammal, 191 bird, 15 reptile, 7 amphibian, and one fish species. Many invertebrate prey remains could not be classified to the species level, rather they were assigned to 83 different invertebrate groupings. The vast majority (99.6%) of identified prey items were vertebrates (Table 1). Among the vertebrates, mammals made up the majority of the prey, on average 93.5%. Birds were the second largest group with 6.2% (Table 3). The remaining vertebrate classes summed to a fraction of a percentage. In southern Europe 1.8 invertebrates could be found per 100 vertebrates. By contrast, in African prey lists, there were 26.9 invertebrates per 100 vertebrates. When related to the body mass of the prey species, however, invertebrates accounted for only 1% of the biomass.

The broadest prey spectrum (195 species) was found in Central Europe (Table 2). Prey spectrums from the other regions were: southern Europe (168 species), North America (133 species), south-eastern Europe (102 species), the British Isles (74 species), northern Europe (59 species), Africa/Near East (59 species) and Asia (45 species). However, only a few studies were available from these latter two regions.

Body mass of adult prey items ranged from less than 1 g (invertebrates) to over 500 g, with the majority of prey consisting of species ≤ 50 g (Fig. 1). When preying on heavier species, mostly juveniles were taken. The heaviest verified prey seized by a Long-eared Owl were two Ruffed Grouse *Bonasia umbellus* (Sutton 1926); female grouse average 575 g (Rusch *et al.* 2000) in their first winter, while males and older females are heavier.

Table 1. Number of prey lists and prey items of the Long-eared Owl grouped by regions.

Region	Prey lists	Number of prey items	Number of vertebrates
North America	24	16736	16522
Northern Europe	71	48761	48576
British Isles	31	15860	15838
Central Europe	527	509955	509206
Southern Europe	66	39132	38443
South-eastern Europe	63	162845	162797
Africa / Middle East	12	6211	4895
Asia	4	16756	16756
Total	**798**	**816256**	**813033**

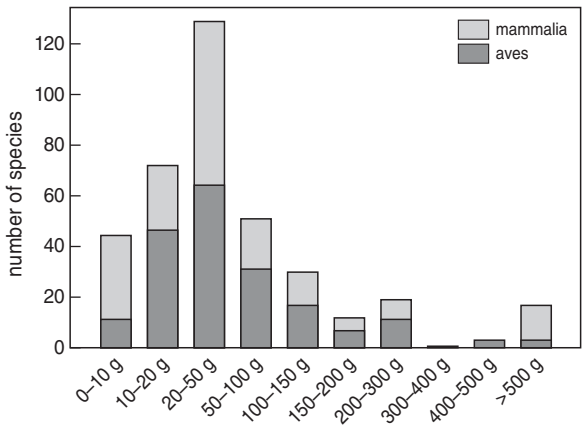

Figure 1. The global avian and mammal prey species of the Long-eared Owl, arranged by adult mass of the prey species. Black portion of bars reflect avian species, grey portions of bars, mammal species.

Diet composition in major regions

Frequency of Prey. Overall, regional differences in the frequencies of vertebrate prey were small (Table 3). The percentages of mammals in the diet for the various regions were: North America (98.1%), northern Europe (96.6%), Central Europe (94.2%), south-eastern Europe (93.0%), southern Europe (89.0%), the British Isles (87.9%), Africa/Middle East (86.4%), and Asia (80.9%). The percentages of birds in the diet for the regions were: North America (1.8%), northern Europe (3.4%), Central Europe (5.8%), south-eastern Europe (11.0%), southern Europe (5.9%), the British Isles (12.0%), Africa/Middle East (6.8%), and Asia (19.1%). The African prey lists contained a relatively large number of reptiles (6.8%) (Table 3).

The largest prey class among the mammals were rodents which made up 91.7% of the vertebrates (lowest 79.5% in Asia, highest 93.3% in northern Europe).

Table 2. Number of prey species of Long-eared Owl grouped by systematic class and region.

	Total	Mammalia	Aves	Reptilia	Amphibia	Pisces	Insecta	Other Invertebrata
North America	133	78	39	5	2	0	5	4
Northern Europe	59	24	34	0	0	0	1	0
British Isles	74	20	51	0	1	0	1	1
Central Europe	195	50	97	3	3	0	38	4
Southern Europe	168	47	89	3	0	0	26	3
South-eastern Europe	102	42	51	0	0	1	8	0
Africa / Middle East	59	18	25	4	1	0	11	0
Asia	45	32	12	1	0	0	0	0
Total	**477**	**180**	**191**	**15**	**7**	**1**	**73**	**10**

Table 3. Number of prey items of Long-eared Owl grouped by class and region.

	Insectivora	Chiroptera	Arvicolinae	Cricetinae	Murinae	Other Rodentia	Other Mammalia	Aves	Amphibia, Reptilia & Pisces	Invertebrata
North America	502	10	6087	8431	308	767	109	300	8	214
Northern Europe	1547	2	31882	47	13384		59	1654	1	185
British Isles	550	8	6822		6431		114	1900	13	22
Central Europe	3792	33	407638	8	64234	21	3735	29565	118	749
Southern Europe	990	100	17377		15455	73	214	4231	3	689
South-eastern Europe	2497	8	81053	1307	66290	60	122	9536		48
Africa / Middle East	15	5	661	2	3500	8	36	331	337	1316
Asia	74	164	2187	887	10029	216	2	3197		
Total	**9967**	**330**	**553703**	**10682**	**179631**	**1145**	**4391**	**50714**	**480**	**3223**

The next common mammalian group were insectivores, reflecting 1.2% of the vertebrates. The insectivores were relatively scarce in prey lists from Africa/Middle East, Asia, and Central Europe (<0.7%), but slightly more frequent in North America (4.1%), northern Europe (3.2%) and the British Isles (3.5%).

At the taxonomic level of family, the pattern in the prey lists is less uniform. In Central Europe, Arvicolinae dominate with 80.1% of the vertebrate prey. In the rest of Europe, in North America and Asia, this family was also predominate, although the proportions were markedly lower (minimum 43.1%). The Murinae were second in Europe and the dominant family in Africa/Middle East (71.5%) and Asia (59.8%) while they are nearly absent in North America. In North America, the Cricetinae were the second largest family (51.0%).

Even more pronounced differences were apparent at the genus level. The genus *Microtus* was the most frequent prey in five regions: *M. arvalis* was the most common species in Central Europe and in south-eastern Europe (72.5%, 46.7%, respectively); *M. agrestis* in northern Europe and British Islands (48.8% and 37.0%, respectively); and *M. pennsylvanicus* in North America (23.8%). In south-eastern Europe, A*podemus* was the most numerous genus accounting for 21.0% of the prey frequency, while in the British Islands, northern Europe, and south-eastern Europe the same species accounted for 35.6, 24.7 and 22.1%, respectively. In Africa, 67.3% of the diet was comprised of the species *Mus*.

Worldwide, there are at least 23 species which appear as the most frequent prey in at least one list (Table 4). In Central Europe *Micotus arvalis* is the most common prey species in 81.6% prey lists. In other Central European lists, *Apodemus* sp. (8.5%), birds (7.2%), *Arvicola terrestris, Microtus agrestis, M. oeconomus* and C*lethrionomys glareolus* predominate.

Biomass of Prey. The 394 vertebrate and 83 invertebrate groups were organized by categories, based on the mass of the adult for each species/group. Weight categories for bird and mammal species are shown in Fig. 1, as these were the major prey. The majority (66.5%) of the vertebrate species were <50 g. Overall, the percentages by biomass correspond largely to the percentages of prey items. Even at the level of prey

Table 4. Maximum proportion of prey species in Long-eared Owl diet. Prey species which reached at least 50% by frequency in at least one list were included. The number of lists in which a certain prey species is dominant is given between parentheses.

Prey species	North America	Northern Europe	British Isles	Central Europe	Southern Europe	South-eastern Europe	Africa / Middle East	Asia
Perognathus parvus	58.7 (1)							
Peromyscus eucopus	51.8 (1)							
Clethrionomys glareolus				58.0 (1)				
Clethrionomys rufocanus								87.2 (1)
Microtus agrestis		92.9 (41)	79.1 (9)	58.0 (1)		59.1 (1)		
Microtus arvalis		70.8 (3)		99.7 (389)		94.1 (28)		
Microtus oeconomus				75.8 (2)				
Microtus guentheri							71.3 (1)	
Microtus ochrogaster	59.5 (1)							
Microtus pennsylvanicus	95.0 (11)							
Microtus socialis							98.9 (1)	
Microtus rossiaemeridionalis		51.3 (1)						
Pitymys lusitanicus					53.5 (1)			
Pitymys savii					84.1 (10)			
Arvicola terrestris				70.7 (3)				
Apodemus spec.		58.9 (3)	87.5 (15)	97.2 (16)	86.3 (7)	66.4 (4)		
Mus spec.					68.6 (5)	59.2 (2)	90.9 (7)	77.4 (2)
Thomomys talpoides	56.9 (1)							
Meriones meridianus								54.1 (1)
Aves		87.4 (1)		96.9 (26)	77.6 (9)			

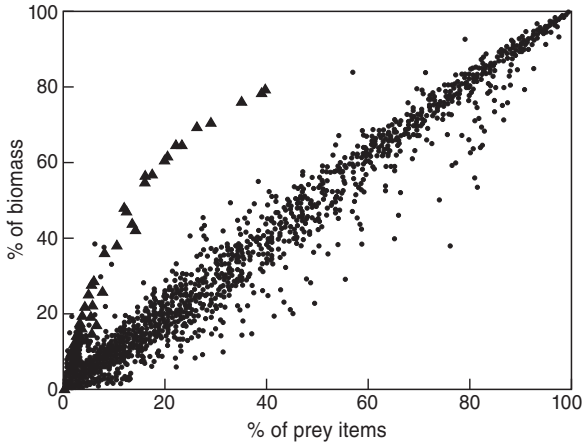

Figure 2. Percentages of prey items compared to percentages of prey biomass. Triangles = *Rattus* spec. n = 6072 prey items from 798 prey lists of the Long-eared Owl.

types, the differences between percentages of prey items and biomass are usually small. In half the cases, this difference is below 3.5% and in 90% of cases it is less than 11.1% (Fig. 2). The only exception to this pattern is found in prey lists in which the genus *Rattus* is frequent. The largest differences between the percentages of biomass and prey items at the class level occur in Asia. Mammalia account for 73.1% of the biomass but make up 80.9% of the prey items; birds account for 26.5% of biomass and 19.1% of prey items.

DISCUSSION

Representation of diet studies

Compared to the estimated global distribution of Long-eared Owls, diet studies are strongly reported in some areas, and under-represented in others. Data from Central Europe (especially Germany) is most strongly represented. There are only relatively few lists with quantitative data from North America. Diet lists from Africa and Asia are limited and likely under-represent actual prey arrays (however, lists from Asian areas exist but were logistically difficult to obtain, and language translation was not available to this researcher). Diet lists within a certain region are not necessarily representative either, with some papers reporting dietary exceptions, e.g. data from severe winters or special habitats such as islands.

Proportions and biomass

In this study, I refer to proportions of prey items because uncertainties are involved in the calculation of body mass proportions. In many prey species, body mass varies considerably with geographical location, sex and individual traits. Often body mass of the lightest adults is only half of that of the heaviest. Also, it has been shown that Long-eared Owls prefer smaller items of the larger prey species. Further publications containing data on sex, age classes and a species mean (and range) of mass for prey would be very helpful for biomass calculations (Tome 2000, Pirovano *et al.* 2000).

The composition of the Long-eared Owls' diet depends on an array of interacting factors (Fig. 3). Season and geographical location of the diet samples, which are usually indicated in the publications, both have an effect on prey diversity. Some papers mention various other factors. Usually, the most abundant species available are preyed upon most often (Canova 1989, Guidoni *et al.* 1999). The proportion of *Microtus* in the prey lists increases with increasing density of this species (Schmidt 1971, Veiga 1981, Wijnandts 1984, Korpimäki 1992, Tome 1994, 2003).

Aspects of predation

Prey abundance does not necessarily explain the degree of predation, as prey need to be accessible to the owls. Factors like vegetation, weather and prey behaviour can influence accessibility (Fig. 3). The Long-eared Owl prefers low and sparse vegetation for hunting (Nilsson 1981, Aschwanden *et al.* 2005). Therefore, prey lists from habitats with different vegetation structure and from different cultivation stages (e.g. before or after harvest of cereal grains) can vary considerably (Tinbergen 1932). *Apodemus*, for instance, is captured more frequently in or near woods (Wijnandts 1984).

Accessibility is influenced indirectly by the season (Fig. 3). Some authors reported no seasonality (Graber 1962, Marti 1974, Armstrong 1958 in Marti 1976) while others found differences between winter and summer (Degn 1976, Nilsson 1981, Wijnandts 1984, San Segundo 1988, Bertolino *et al.* 2001, Rubolini *et al.* 2003).

Weather has an influence on the accessibility of prey items. Many prey species profit from snow cover and this is mirrored in the diet lists (Elvers *et al.* 1979, Wijnandts 1984, Schmitz 1987, Ancelet 1987, Canova 1989). Hunting sites and hence prey composition differ in nights with and without wind (van Manen 2001). In America, however, wind did not influence hunting site selection in radio-tracked breeding Long-eared Owls (Craig *et al.* 1988).

The behaviour of a prey species can influence its availability for an owl. Young males of otherwise subterranean rodents display a dispersal pattern during

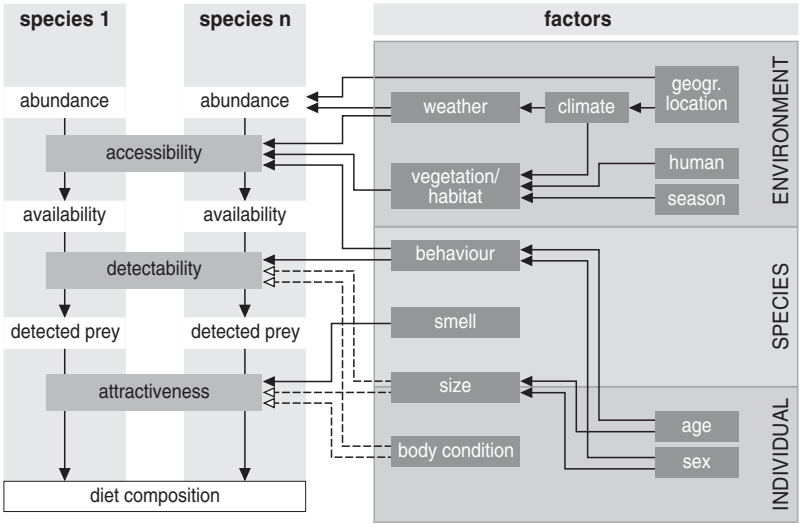

Figure 3. Possible factors influencing diet composition of the Long-eared Owl.

which they can be found on the surface and are therefore more vulnerable to predation by owls. This is a possible reason for the preference of young *Arvicola terrestris* (Saucy 1988, Tome 2000) and *Thomomys talpoides* (Bull *et al.* 1989). Behaviour may also explain the vast differences in the genera *Microtus* and *Pitymys* in the prey lists of Long-eared Owls in Europe. While *Microtus* can be seen regularly on the surface, most *Pitymys* species, e.g. *P. multiplex*, live much more subterraneously (Hausser 1995).

Not all species are equally attractive prey for Long-eared Owls. The attractiveness of a prey species depends on species-specific and individual qualities. Most important is probably size. Generally, vertebrates ≤ 300 g are potential prey items for Long-eared Owls (Fig. 1), with the dominate prey consisting of species ≤ 50 g. The larger prey items reported were probably weakened or injured at the time they were seized. It was assumed several times that owls fed on carcasses. Of the larger species, the smaller individuals are often preferred, e.g. in *Arvicola terrestris* (Saucy 1988, Tome 2000), *Rattus norvegicus* (Gawlik & Banz 1982, Hillis *et al.* 1988, Ekins & Steward 1994, Pirovano *et al.* 2000) and *Thomomys talpoides* (Janes & Barss 1985, Bull *et al.* 1989, Marks *et al.* 1994). In medium-sized prey species, i.e. *Clethrionomys* and *Apodemus*, immature individuals also tend to be taken more often (Lodé 1994). Tome (2000) found a significant size difference between individuals captured as prey by owls and those from trapping efforts in all prey species except for *Apodemus sylvestris*.

Shrews are avoided by Long-eared Owls (Gross 1943) and items caught are sometimes even dropped (Thiollay 1968) presumably because of their smell (or taste). Correspondingly, compared to the prey lists of other owls, especially the Barn Owl, collected in the same place at the same time, there were fewer shrews found as Long-eared Owl prey (Uttendörfer 1939, López-Gordo *et al.* 1977, Veiga 1980, Erfurt & Stubbe 1987, Roulin 1996). Individuals with poor body condition could also be easier prey for Long-eared Owls. In the pellets, prey items with deformed bones are regularly found and their proportion decreases over the winter (Manegold 2000). Yet, it is not known whether such items are preyed upon selectively. In a lab experiment, a Long-eared Owl hunted more lab mice which were infected with *Sarcocystis dispersa* (Vorisek *et al.* 1998).

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SAMENVATTING

In dit literatuuronderzoek worden 475 publicaties met informatie over de voedselsamenstelling van de Ransuil *Asio otus* op een rij gezet. De gegevens van 312 publicaties werden in een database ingevoerd. Uiteindelijk werden 194 publicaties geselecteerd die een goed kwantitatief beeld van het voedsel gaven. In de publicaties tezamen ging het om 813 033 prooien die verdeeld waren over 477 verschillende prooitypes: 180 zoogdieren, 191 vogels, 15 reptielen, 7 amfibieën, 1 vissoort en 83 taxa van ongewervelde dieren. Kleine zoogdieren waren veruit de meest aangetroffen prooien (93,3% van de gewervelde prooien). Vogels werden veel minder vaak aangetroffen in het voedsel (6,4%). Het gewicht van de prooien lag tussen de 1 en 500 g, maar de meeste prooien waren lichter dan 50 g. Er waren 23 prooisoorten die in minstens één van de onderzoeken het grootste deel van het voedsel uitmaakten. De voedselsamenstelling op het niveau van familie van de prooidieren was vergelijkbaar in de verschillende regio's over de wereld, maar er waren grote verschillen op soortniveau.

Appendix 1. In addition to the citations in the list of references, the following abbreviated citations reflect publications that contained Long-eared Owl *Asio otus* diet data which were input into the diet database for this project.

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