A REVIEW OF PREY SELECTION BY THE LONG-EARED OWL

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This paper describes variety and size of prey of the Long-eared Owl (*Asio otus*) from widespread parts of its range and develops a diet profile for the species. Compared to sympatric species, the Long-eared Owl has a restricted diet (Craighead and Craighead 1956, Errington 1932, Korschgen and Stuart 1972, Marti 1974, Maser et al. 1970). Food habits of this species have been extensively reported from North America and Europe. There are, however, large areas within its range from which no reports on diet are available.

The Long-eared Owl is Holarctic in north temperate regions of North America, Europe and Asia (see Grossman and Hamlet 1964). This is a strictly nocturnal species (Marti 1974) and apparently feeds almost exclusively in open lands (Getz 1961, Randle and Austing 1952, Smeenk 1972, Weller et al. 1963). However, it does require small, dense trees for nesting and roosting (Armstrong 1958, Bent 1938, Marti 1974).

This species is a medium-sized owl; mean weight of 66 specimens from North America was 262.3 g (Earhart and Johnson 1970). Several morphological adaptations point to efficiency of hunting in open areas. The long wings seem to be adapted to this habitat (Lack 1966), and compared to many other North American owls this species has rather light wing-loading, which indicates efficiency of hunting on the wing. Poole (1938) calculated wing-loading for the Long-eared Owl as 5.13 cm^2 of wing area per gram of body weight for males and 4.22 for females.

METHODS AND MATERIALS

The analysis of prey variety and size is based on data from studies listed in table 1. Most weights of prey were obtained from Craighead and Craighead (1956), Marti (1974), J. MacMahon (pers. comm.) and F. Hiraldo (pers. comm.). Weight of prey varies due to differences in sex, age, and geographical location. However, it was not possible to adjust for these variables, and the same weights were used uniformly for the calculation of mean prey size and its variation.

RESULTS

PREY SELECTED

Long-eared Owls feed upon small, nocturnal mammals that live in open lands, i.e., farmlands, grasslands, marshes and deserts. Mammals account for 98.2% of 23,888 prey surveyed from North America and 88.9% of 37,441 prey from Europe. In the Soviet Union, prey was reported to be 97.5% rodents (Dement'ev and Gladkov 1951). Species of voles (*Microtus*) are the most common prey of Long-eared Owls; 53.7% of all prey individuals from North America and Europe were *Microtus*. *Microtus* species were the most common prey in 31 studies ranging from 29.8 to 94.4% of the total prey (table 1). In contrast, in five studies, deer mice (*Peromyscus* spp.) and in two studies each pocket mice (*Perognathus* spp.), wood mice (*Apodemus* spp.) and birds were found to be the most numerous prey. At least 45 species of mammals have been reported as prey of Long-eared Owls in North America, and at least 23 species in Europe. In several genera of mammals, it is difficult or impossible to separate closely related species by the remains left in owl pellets so the total number of mammal species is undoubtedly greater.

Birds are preyed upon next in frequency to mammals but in much smaller numbers. Sixty-eight percent of the studies reviewed reported less than 3% birds by number in the diet. Two studies deviated extensively from this trend. Hartwig and Vauk (1969) reported that 86.2% of the winter diet of Long-eared Owls was avian and Hartley (1947) found 50.0% birds in food of Long-eared Owls in Iraq. Sample sizes in both of these reports were small. Birds were reported in higher numbers from Europe than North America (10.9% versus 1.7%). Glue (1972) indicated that Long-eared Owls in England often raided communal roosts of small birds during winter. The most abundant species in both areas was the House Sparrow (*Passer domesticus*). Thirty-five species of birds have been identified as prey from North America and 55 species from Europe.

Reptiles and amphibians occurred as prey in only three studies (Cahn and Kemp 1930, Tinbergen 1933, Uttendörfer 1952). Fish were reported three times (Korschgen, pers. comm., Tinbergen 1930, Uttendörfer 1952), and crayfish once (Randle and Austing 1952). Insects were reported in small numbers in many studies but amounted to only a small fraction of the overall prey numbers.

The Condor 78:331–336, 1976

TABLE 1. Most abundant prey in diets of Long-eared Owl.

Location	Percent of total prey	Source
	Microtus species	
Oregon	87.8	Maser and Brodie 1966*
Oregon	73.9	Reynolds 1970*
Nevada	29.8	Johnson 1954*
Wyoming	41.1	Craighead and Craighead 1956*
Kansas	38.5	Rainey and Robinson 1954*
Missouri	45.2	Korschgen (unpubl. data)*
Iowa	80.0	Weller et al. 1963*
Iowa	67.6	Errington 1933*
Iowa	51.6	Scott 1948*
Illinois	85.2	Graber 1962
Illinois	49.9	Birkenholz 1958*
Indiana	75.7	Kirkpatrick and Conway 1947*
Ohio	63.7	Randle and Austing 1952*
Wisconsin	83.5	Errington 1932*
Michigan	86.5	Getz 1961*
Michigan	85.1	Craighead and Craighead 1956*
Michigan	85.4	Spiker 1933*
Michigan	84.3	Geis 1952*
Michigan	80.4	Armstrong 1958*
Michigan	75.3	Wilson 1938*
Ontario	94.4	Woods and Catling 1966*
New York	76.4	Eaton and Grzybowski 1969*
England	53.4	Wooller and Triggs 1968*
England	46.7	Flegg and Cox 1968*
England	36.1	Ticehurst 1939*
Netherlands	51.5	Tinbergen 1933*
Germany	76.0	Uttendörfer 1952
Germany	61.4	Wendland 1957*
Norway	52.3	Hagen 1965*
Sweden	49.9	Lundin 1960*
Sweden	52.6	Gerell 1968*
	Peromyscus species	
Colorado	71.0	Catlett et al. 1958*
Colorado	51.4	Marti 1974*
Missouri	45.7	Marti (unpubl. data)*
Illinois	56.5	Cahn and Kemp 1930*
Indiana	51.4	George 1955*
	Perognathus species	
Oregon	58.2	Maser et al. 1970*
Arizona	69.1	Lange and Mikita 1959*
	Apodemus species	
Ireland	82.5	Fairley 1967*
England	54.0	South 1966*
	Birds	
Germany	86.2	Hartwig and Vauk 1969*
Iraq	50.0	Hartley 1946*

* Studies used to profile Long-eared Owl diets and calculate prey size.

Complete prey lists for the Long-eared Owl are found in tables 2 and 3. In North America, two genera, *Microtus* and *Peromyscus*, provide 82.2% of the total prey. The distribution of *Peromyscus* overlaps completely with the distribution of the Long-eared Owl in North America, and the range of *Microtus* overlaps everywhere except at the southern limits of the Long-eared Owl's

TABLE 2. Prey of Long-eared Owls in North America.[1]

Species	Percent of total prey	Percent biomass	Mean individual weight, g
Mammals	98.2	98.3	
Sorex cinereus	tr.[2]	tr.	5
unidentified *Sorex* spp.	0.1	tr.	5
Blarina brevicauda	1.4	0.8	23
Cryptotis parva	3.0	0.4	5
Notiosorex crawfordi	tr.	tr.	5
unidentified shrew spp.	tr.	tr.	14
Neurotrichus gibbsii	tr.	tr.	11
Scapanus orarius	tr.	tr.	75
Condylura cristata	tr.	tr.	57
Myotis lucifugus	tr.	tr.	8
Lasiurus cinereus	tr.	tr.	8
Nycticeius humeralis	tr.	tr.	24
Lepus californicus (juv.)	tr.	tr.	7
Sylvilagus floridanus (juv.)	tr.	0.2	800
unidentified shrew spp.	tr.	0.3	400
unidentified *Sylvilagus* spp. (juv.)	tr.	0.5	400
Tamias striatus	tr.	tr.	60
Glaucomys volans	tr.	tr.	60
Thomomys talpoides	0.2	0.7	132
Thomomys bottae	tr.	tr.	132
Geomys bursarius	tr.	tr.	200
Perognathus parvus	0.3	0.2	20
Perognathus hispidus	tr.	tr.	39
unidentified *Perognathus* spp.	0.9	0.5	22
Dipodomys panamintus	0.1	0.1	68
Dipodomys ordii	tr.	0.1	68
unidentified *Dipodomys* spp.	0.1	0.2	68
Reithrodontomys montanus	tr.	tr.	12
Reithrodontomys megalotis	1.2	0.4	12
Reithrodontomys humulis	tr.	tr.	12
unidentified *Reithrodontomys* spp.	1.3	0.4	12
Peromyscus maniculatus	0.9	0.5	21
Peromyscus leucopus	2.6	1.5	21
unidentified *Peromyscus* spp.	17.9	10.1	21
Onychomys leucogaster	0.3	0.3	38
Onychomys torridus	0.1	0.1	26
Sigmodon hispidus	1.5	4.0	100
Neotoma albigula	tr.	tr.	217
Synaptomys cooperi	1.7	2.0	45
Cleithrionomys gapperi	tr.	tr.	25
Phenacomys longicaudus	tr.	tr.	28
Microtus pennsylvanicus	40.4	49.2	45
Microtus ochrogaster	16.4	17.7	40
Microtus montanus	0.4	0.5	47
Microtus townsendii	0.1	0.1	45
Microtus oregoni	tr.	tr.	18
unidentified *Microtus* spp.	3.5	4.1	43
Pitymys pinetorum	0.1	0.1	38
Lagurus curtatus	tr.	tr.	25
Rattus norvegicus	0.2	1.1	adult 220 juv. 100
Mus musculus	2.6	1.2	18
Zapus hudsonius	0.1	0.1	25
Zapus trinotatus	tr.	tr.	25
unidentifed rodents	0.3	0.3	35

[1] From studies in table 1.
[2] Less than 0.1%.

TABLE 2. *Continued.*

Species	Percent of total prey	Percent biomass	Mean individual weight, g
Birds	1.7	1.7	37
Amphibians	tr.	tr.	
Ambystoma sp.	tr.	tr.	40
Rana pipiens	tr.	tr.	25
Reptiles			
Storeria dekayi	tr.	tr.	20
Fish (unidentified sp.)	tr.	tr.	30
Arthropods	tr.	tr.	
unidentified crayfish	tr.	tr.	6.5
unidentified insects	tr.	tr.	0.5
total number	23,888	total biomass	883,086.5 g

distribution. A similar situation exists in Europe where *Microtus* and *Apodemus*, a genus ecologically very similar to *Peromyscus*, provide 79.5% of all prey.

PREY SIZE AND ITS RELATIONSHIP TO DAILY FOOD CONSUMPTION

In North America, prey weights of the Long-eared Owl have been reported ranging from less than 1 g to 800 g, and in Europe from less than 1 g to 300 g. The mean weight of 23,888 prey from North America was 37.0 ± 0.13 g; in Europe the mean of 37,441 prey was 32.2 ± 0.12 g. The largest prey reported were blacked-tailed jackrabbits (*Lepus californicus*) from Nevada (Johnson 1954). Prey of this size would be undoubtedly very difficult for Long-eared Owls to kill and probably were immature hares. No details were given, and it is possible that the animals were killed by another predator. Sutton (1926), however, documented the capture of two adult Ruffed Grouse (*Bonasa umbellus*) by Long-eared Owls. The actual captures were not seen, but circumstantial evidence strongly indicated that Long-eared Owls killed the grouse. Adult Ruffed Grouse weigh over 600 g (Edminster 1954). These examples are unusual. The range and mean of prey weights are given by geographical areas in table 4. In all but two of these areas, the variation about the mean weight is small. The two areas with large variation in prey weight were represented by small sample sizes and one contained the heaviest prey reported overall.

Daily food consumption rates for wild Long-eared Owls have been calculated by several investigators. Graber (1962) estimated that daily consumption was 47–53 g during winter in Illinois. In Colorado, it was

TABLE 3. Prey of Long-eared Owls in Europe (including Iraq).[1]

Species	Percent of total prey	Percent biomass	Mean individual weight, g
Mammals	88.9	86.4	
Sorex araneus	0.3	tr.[2]	10
Sorex minutus	0.1	tr.	4
unidentified *Sorex* spp.	1.1	0.3	8
Neomys fodiens	tr.	tr.	16
Crocidura russula	tr.	tr.	10
Pachyura etrusca	tr.	tr.	10
Talpa europaea	tr.	0.1	92
Myotis spp.	tr.	tr.	8
Lepus timidus (juv.)	tr.	0.1	300
Oryctolagus cuniculus (juv.)	tr.	0.2	200
Sciurus vulgaris	tr.	0.1	255
Lemmus lemmus	0.1	0.2	43
Cleithrionomys glareolus	2.7	2.1	25
Arvicola terrestris	1.0	4.3	142
Microtus arvalis	28.9	27.9	30
Microtus agrestis	12.5	13.6	35
Microtus oeconomus	1.1	1.8	50
Microtus ratticeps	5.6	7.5	43
unidentified *Microtus* spp.	tr.	tr.	43
Micromys minutus	0.1	tr.	10
Apodemus spp.	30.3	19.8	21
Rattus norvegicus	1.1	6.8	adult 220 juv. 100
Rattus rattus	tr.	tr.	200
Mus musculus	2.5	1.4	18
Mus or *Apodemus*	0.1	0.1	19
unidentified mammals	tr.	tr.	35
Birds	10.9	13.5	37
Amphibians	tr.	tr.	
Rana temporaria	tr.	tr.	25
Fish (unidentified)	tr.	tr.	30
Insects	0.2	tr.	0.5
total number	37,441	total biomass	1,205,112.5 g

[1] From studies in table 1.
[2] Less than 0.1%.

estimated that food consumption was slightly under 60 g per day (Marti 1973). Long-eared Owls in Germany were thought to consume 43 g per day (Uttendörfer 1939), whereas those in the Soviet Union were said to need only 30 g of food per day (Dement'ev and Gladkov 1951). It is, of course, difficult to accurately measure food intake of owls in the wild because it usually is not possible to adequately control or study variables such as the weight of the owl, ambient temperature or the owl's activity level. I found that a captive female Long-eared Owl consumed an average of 37.5 ± 1.1 g (12.7% of its body weight) per day over 1 year (Marti 1973). This bird was held outdoors in a cage that allowed only limited activity. A wild, active bird would undoubtedly consume more food. The available evidence indicates that Long-

TABLE 4. Size characteristics of Long-eared Owl prey from various areas.[1]

Area	Prey weight $\bar{x} \pm 1$ S. E.	Prey weight range, g	Number of prey
Oregon	35.3 ± 0.74	0.5–132	469
Nevada	53.8 ± 9.69	12–800	114
Arizona	26.9 ± 1.07	5–217	307
Colorado, Wyoming	39.0 ± 0.51	5–400	2,932
Kansas, Missouri	36.9 ± 0.41	5–400	3,271
Iowa	39.2 ± 0.84	0.5–220	795
Michigan, Wisconsin	42.0 ± 0.11	0.5–400	10,375
Illinois, Indiana, Ohio	31.7 ± 0.28	0.5–400	5,195
New York, Ontario	42.4 ± 0.88	21–400	430
British Isles	32.1 ± 0.53	0.5–300	3,265
Germany, Netherlands	31.2 ± 0.13	0.5–255	25,937
Norway, Sweden	35.3 ± 0.31	0.5–300	8,161
Iraq	31.5 ± 4.33	10–220	78
World (all combined)	34.0 ± 0.09	0.5–800	61,329

[1] From studies in table 1.

eared Owls consume on the average between 40 and 60 g of food per day depending on several variables. Since 90% of the identified prey weighs 20–45 g, a typical night's foraging would consist of one to three successful captures. For instance, two or three deer mice or one or two voles would supply biomass within the range of daily food consumption.

COMPARISON WITH SYMPATRIC SPECIES

Craighead and Craighead (1956) classified the Long-eared Owl in Michigan and Wyoming as a restricted feeder along with Short-eared Owls (*Asio flammeus*), Marsh Hawks (*Circus cyaneus*) and all buteos except Red-tailed Hawks (*Buteo jamaicensis*). Great Horned Owls (*Bubo virginianus*) and Screech Owls (*Otus asio*) were classified as general feeders along with Red-tailed and Cooper's hawks (*Accipiter cooperi*) and American Kestrels (*Falco sparverius*). Errington (1932) studied Great Horned, Long-eared, Short-eared Screech, Saw-whet (*Aegolius acadicus*), Barred (*Strix varia*) and Barn owls (*Tyto alba*) in Iowa. He considered the Long-eared Owl inflexible in its prey, whereas the much smaller Screech Owl was termed opportunistic. In Missouri, Korschgen and Stuart (1972) found the Long-eared Owl to be more restricted in diet than Great Horned, Barred and Screech owls and Red-tailed Hawks. Maser et al. (1970) considered the Long-eared Owl to be more restricted in diet throughout the year than to Great Horned and Short-eared owls. They found that Short-eared Owls were more restricted than Long-eared Owls in diet in the summer only. In Colorado, Long-eared Owls fed on fewer prey species than Great Horned, Burrowing (*Speotyto cunicularia*) and Barn owls (Marti 1974). Woods and Catling (1966) found 94.4% *Microtus* by number in the diet of Long-eared Owls in Ontario. Saw-whet Owl diets in the same area were about 60% *Microtus* and 40% *Peromyscus*.

VARIABILITY OF THE DIET

The data on seasonal, annual, and environmental variations in diet are often incomplete and inconclusive. Graber (1962) in Illinois found that prey species changed little from year to year in the same locality. Birkenholz (1958), also in Illinois, discovered a large increase in *Microtus* as prey from December to March and a concurrent drop in least shrews (*Cryptotis parva*). In England, South (1966) found small variations in prey with season and locality. Armstrong (1958) found little change in prey between summer and winter in Michigan, but Fairley (1967) mentioned significant seasonal fluctuations in Ireland between the two major prey species. Wood mice (*Apodemus sylvaticus*) were most abundant except in the fall when Norway rats (*Rattus norvegicus*) became more common in the diet. Smeenk (1972) indicated that striking differences in diet occurred from different areas in the Netherlands, but in Colorado no significant differences in prey composition were found from three consecutive years or from two habitats (Marti 1974). Most studies seem to indicate that the Long-eared Owl does not greatly vary its diet over time. Diets of Long-eared Owls in different habitats are notably consistent. Although prey species vary, the diet is typically concentrated on a relatively few species of small mammals regardless of location or habitat. Long-eared Owls have never been known to adopt a primarily arthropod, reptilian or amphibian diet. Occasionally, birds are heavily preyed upon but apparently not for long periods.

DISCUSSION

Earhart and Johnson (1970) pointed out that the sexual dimorphism in wing-loading in this species could mean less maneuverability for the female and, thus, different feeding behavior creating differential use of niches between the sexes. Data to test this are needed. Earhart and Johnson discovered that in North American owls, sexual dimorphism

is greatest in species that feed heavily on vertebrates and least in those that specialize on arthropods. The Long-eared Owl deviates from this trend and exhibits less dimorphism in body weight than most other North American owls. Earhart and Johnson suggested that the small degree of sexual dimorphism might indicate specialization on prey of a uniform size. The results presented here support that idea.

Much of the extensive literature on food habits of Long-eared Owls is summarized here. I suggest that future research on the feeding of this species investigate the following areas: (1) sexual differences in prey selection, (2) food consumption rates, (3) the relationship between diet and prey availability, and (4) seasonal and long-term changes in diet.

SUMMARY

A diet profile is presented for Long-eared Owls, based on original field study and examination of other food studies from North America and Europe. Long-eared Owls appear to be adapted for hunting small nocturnal mammals in open areas. Mammals constitute 98.2% of all prey in North America and 88.9% in Europe. Birds are only 1.7% of the prey in North America, compared to 10.9% in Europe. Amphibians, reptiles, fish and arthropods are taken occasionally but in very low percentages. Average weight of prey is 37.0 g (r = < 1 g–800 g) in North America and 32.2 g (r = < 1 g–300 g) in Europe. Studies from widespread geographical areas reveal that Long-eared Owls are more restricted in diet than sympatric owl species. Most studies find little seasonal variation in Long-eared Owl foods, and diets from different habitats are notably consistent. Prey species differ but the diet is typically concentrated on a relatively few species of small mammals regardless of the type or location of the habitat.

ACKNOWLEDGMENTS

Dale Hein and Keith Dixon read drafts of this paper and improved it by their suggestions. I am grateful to James MacMahon and Fernando Hiraldo for the weights of many European mammals and to Leroy Korschgen for his unpublished food data from Missouri.

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