

TROPHIC NICHE OF NEARCTIC SHORT-EARED OWLS

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ABSTRACT.—The trophic niche of Short-eared Owls (*Asio flammeus*) was analyzed using nine Nearctic studies reporting >500 prey items each. Of 20,416 prey items, 4136 were from the breeding and 16,280 from the non-breeding seasons. The owls preyed upon at least 62 species from four classes of animals. Mammals constituted >95% of prey from all but two sites. Food-niche breadth ranged from 1.23 to 5.20 ($\bar{x} = 1.87$), for combined studies, 1.31 to 1.87 ($\bar{x} = 1.50$) for breeding, and 1.23 to 5.20 ($\bar{x} = 2.00$) for non-breeding seasons. Dietary evenness values ranged from 0.315 to 0.703 ($\bar{x} = 0.435$), for combined studies, 0.331 to 0.404 ($\bar{x} = 0.365$) for the breeding season, and 0.315 to 0.703 ($\bar{x} = 0.458$) for the non-breeding season. Estimated prey masses ranged between 28 and 325 g. Most prey, however, weighed between 28 and 100 g. Short-eared Owls from coastal areas preyed more on birds than those at inland sites. Received 9 May 1992, accepted 24 Dec. 1992.

Despite numerous studies of the diet of the Short-eared Owl (*Asio flammeus*), there has been no quantitative review of their trophic niche in the Nearctic zoogeographical region. Clark and Ward (1974) calculated prey diversity for the Short-eared Owl, using the published literature but did not state the criteria they used for assigning prey categories or go into much discussion of its meaning. Here, I summarize the trophic niche of Short-eared Owls from nine Nearctic studies.

My objectives were to (1) compare trophic niche among studies, (2) compare trophic niche between breeding and non-breeding seasons, and (3) estimate prey size.

METHODS

I defined the trophic niche as the relationship between the owls and their food. I followed Marti's (1987) definitions for trophic diversity where a broad food-niche breadth has high prey species numbers which are nearly equally distributed and a narrow food-niche breadth has few prey species numbers unequally distributed. I estimated trophic diversity by calculating food-niche breadth and dietary evenness. I compared breeding season ($N = 3$) and non-breeding season ($N = 9$) diets from studies with >500 prey items. I combined crustaceans, insects, and birds to the class level because species or genera were not always identified. To compare trophic niche among studies, I used only mammals identified to species. I did so because they represented >95.0% of prey from all but two studies. Food-niche breadth (FNB) was calculated using the antilog of the Shannon-Wiener diversity index because it is related linearly to the number of prey categories in the sample and is easy to interpret (Marti 1987). Evenness was calculated using Alatalo's (1981) modification of Hill's (1973) equation: $\text{Evenness} = (N_2 - 1)/(N_1 - 1)$, where $N_1 = \exp H'$ and $N_2 = 1/\sum p_i^2$.

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TABLE 1
PERCENTAGES OF PREY CLASSES IN NORTH AMERICAN SHORT-EARED OWL DIETS

# prey	Insects	Crustaceans	Birds	Mammals	Source
Breeding season					
2948	4.7	0.1	12.0	83.2	Holt (1993)
664	—	—	1.4	98.6	Holt and Melvin (1986)
524	—	—	1.7	98.3	Clark (1975)
Non-breeding season					
4397	—	—	0.7	99.3	Banfield (1947)
3971	—	—	0.6	99.4	Clark (1975)
2185	—	—	0.7	99.3	Colvin and Spaulding (1983)
1489	—	—	0.2	99.8	Craighead and Craighead (1956)
1337	—	0.1	1.1	98.8	Stegeman (1957)
1025	—	—	1.2	98.8	Munyer (1966)
706	—	—	5.0	95.0	Holt (1993)
640	—	4.8	15.8	79.4	Johnston (1956)
530	—	—	1.1	98.9	Holt and Melvin (1986)

Evenness values range from zero to one. As prey proportions in the diet become more equal, the evenness value approaches unity. I compared the FNB and evenness values from breeding and non-breeding seasons among all studies (Mann-Whitney *U*-test, Sokal and Rohlf 1981).

Among these studies, I used Spearman rank correlation (Siegel 1956) to examine the relationship between number of mammalian species and FNB values. I did so to determine if wider FNB values were associated with increased numbers of prey species in the diet. Because FNB values can fluctuate with sample size and thus influence the results, I also examined the relationship between number of prey items and FNB. I used body mass estimates and size ranges of birds (Dunning 1984) and mammals (Burt and Grossenheider 1976) to derive a relative size class of prey species eaten by the owls. Standard prey biomass estimates were not calculated because of uncertainties associated with these calculations.

RESULTS

Data from nine studies yielded 20,416 prey items (Table 1) from six U.S. states and two Canadian provinces. Approximately 80.0% of the prey were from the non-breeding season. The owls ate at least 62 prey species from four taxonomic classes: Insecta, Crustacea, Aves, and Mammalia (Table 1). Mammals constituted at least 79.0% of the prey from each study. Only two studies reported <95.0% mammalian prey (Table 1).

The broadest food niche-breadth calculated (FNB = 5.20) was from data in Johnston (1956). In this study, mammals constituted 79.4% of the diet, of which voles accounted for only 42.5% (Table 2). Three other mammalian species constituted the remainder, while birds represented

TABLE 2
PERCENT OF DOMINANT PREY SPECIES AND TOTAL PERCENT MAMMALS, FROM NINE SITES

Dominant species	Dominant species (%)	Total mammals (%)	Source
Breeding season			
Meadow vole	78.1	83.2	Holt (1993)
Meadow vole	95.2	98.6	Holt and Melvin (1985)
Meadow vole	96.8	98.3	Clark (1975)
Non-breeding season			
Meadow vole	81.9	99.3	Banfield (1947)
Meadow vole	96.0	99.4	Clark (1975)
Meadow vole	95.4	99.3	Colvin and Spaulding (1983)
Meadow vole	87.7	99.8	Craighead and Craighead (1956)
Meadow vole	97.2	98.8	Stegeman (1957)
Meadow vole	93.1	95.0	Holt (1993)
Meadow vole	93.6	98.9	Holt and Melvin (1985)
Deer mouse	70.3	98.8	Munyer (1966)
California vole	42.5	79.4	Johnston (1956)

15.8%. The only non-microtine mammalian prey to dominate a study was *Peromyscus* with >70% occurrence (Munyer 1966, Table 2). Munyer felt that snow accumulation forced *Microtus* to become subnivean, whereas *Peromyscus* remained active on the snow surface. The number of mammalian prey species per study ranged from three to eight ($\bar{x} = 5.42$, $SD \pm 1.90$).

In general, the owls preyed upon only a few species of mammals, and usually a vole species dominated (Table 2). Overall, FNB values ranged from 1.23 to 5.20 ($\bar{x} = 1.87$, $SD \pm 1.12$). Food niche-breadth values for the breeding season (range = 1.31 to 1.87, $\bar{x} = 1.50$, $SD \pm 0.32$, $N = 3$) and non-breeding season (range = 1.23 to 5.20, $\bar{x} = 2.00$, $SD \pm 1.28$, $N = 9$) were similar (Table 3). The medians were not significantly different (Mann-Whitney *U*-test). Evenness values ranged from 0.315 to 0.703 ($\bar{x} = 0.435$, $SD \pm 0.127$), for all studies. Evenness values for breeding and non-breeding seasons ranged from 0.331 to 0.404 ($\bar{x} = 0.365$, $SD \pm 0.036$, $N = 3$), and 0.315 to 0.703 ($\bar{x} = 0.458$, $SD \pm 0.139$, $N = 9$) (Table 3). The medians were not significantly different (Mann-Whitney *U*-test).

There was a strong positive relationship between the number of mammalian species in the diet and FNB values ($r_s = 0.842$, $P < 0.001$). There was a weak negative relationship ($r_s = -0.335$, $P > 0.10$) between number of prey items and FNB values, which suggested that sample sizes were not influencing the results.

Prey size ranged from <1 g (insects) to approximately 325 g (medium-

TABLE 3
TROPIC PARAMETERS FROM NINE STUDIES

Number of prey	FNB	Evenness	Location	Source
Breeding season				
2948	1.32	0.404	Massachusetts	Holt (1993)
664	1.31	0.331	Massachusetts	Holt and Melvin (1986)
524	1.87	0.362	Manitoba	Clark (1975)
Non-breeding season				
4397	1.66	0.645	Ontario	Banfield (1947)
3971	1.23	0.369	New York	Clark (1975)
2185	1.26	0.381	Ohio	Colvin and Spaulding (1983)
1489	1.62	0.458	Michigan	Craighead and Craighead (1956)
1337	1.83	0.315	New York	Stegeman (1957)
1025	2.69	0.539	Illinois	Munyer (1966)
706	1.14	0.360	Massachusetts	Holt (1993)
640	5.20	0.703	California	Johnston (1956)
530	1.39	0.358	Massachusetts	Holt and Melvin (1986)

sized mammals and birds). The medium-sized mammals, eastern cottontail (*Sylvilagus floridanus*) and muskrat (*Ondatra zibethicus*) rarely occurred in the diet, were juveniles, and probably weighed <325 g. The majority of prey weighed from 28 to 100 g, with *Microtus* dominant in all but one study (Table 2). The three dominant prey species from each study, meadow vole, California vole (*M. californicus*), and deer mouse (*Peromyscus maniculatus*) (Table 2), ranged in mass from 28 to 70 g, 42 to 100 g and 18 to 35 g, respectively.

Birds were not a major portion of the owl diets, although many species were eaten. Coastal and island Short-eared Owls (e.g., Johnston 1956, Holt 1993) ate more birds than Short-eared Owls at inland sites (Table 1). Body masses of avian prey eaten by the owls were divided into groups and ranged from: 11 to 106 g, passerines; 34 to 40 g, petrels; 20 to 230 g, shorebirds; 120 g, terns; and 271 to 323 g, rails (Dunning 1984). No weights were reported for nestling gulls. Most avian prey were passerines.

DISCUSSION

Short-eared Owls are generally considered to prey on small mammals of which usually one or two species predominate. The data herein support the conclusion that these owls are small mammal specialists having a narrow food-niche breadth with few exceptions.

Other open country owls such as the Barn Owl (*Tyto alba*) (Marti 1988),

Long-eared Owl (*Asio otus*) (Marti 1976), and Snowy Owl (*Nyctea scandiaca*) (Watson 1957), have a similar trophic structure as the Short-eared Owl. In areas where microtines were uncommon, however, Long-eared Owls fed on a wide variety of non-microtine prey (Marti 1974, Marks 1984). Mikkola (1983) also reported Short-eared Owls in Europe have a wider trophic niche when microtines were scarce or unavailable.

In other Nearctic coastal sites, results are similar to those reported here. In two consecutive seasons, Page and Whitacre (1975) reported 51.7% (N = 257) and 88.0% (N = unknown) birds in the Short-eared Owl diet. Tomkins (1936) reported 27.0% (N = 138) and Fisler (1960) 24.0% (N = 170) birds in the Short-eared Owl diet. Outside the Nearctic, on the Galapagos Islands, seabirds were the major prey of breeding Short-eared Owls (Abs et al. 1965, Harris 1969, Grant et al. 1975, De Groot 1983).

The narrow trophic niche of Short-eared Owls probably reflects several factors such as prey diversity, distribution, abundance, and availability through space and time. These factors could act independently or in combination. Abiotic factors affecting plant communities, which in turn influence prey communities, may also contribute to trophic diversity by affecting the above (Herrera 1974). In open habitats frequented by Short-eared Owls, one very common prey species usually occurs—most often a vole. The Short-eared Owls' narrow FNB may simply reflect where they most often forage. The Short-eared Owl appears to be a food "specialist." But, as suggested by Marti (1988) for Common Barn-Owls, Short-eared Owls may simply feed opportunistically in areas where prey species diversity is low, or they may be habitat specialists. Thus, these factors could all contribute to a narrow FNB.

The diversity equations presented here allow data to be computed into single values which can be compared from between studies and geographic areas (Hill 1973). Niches are multidimensional, however, and trophic dimensions are only one component.

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LITERATURE CITED

- ABS, M., E. CURIO, P. KRAMER, AND J. NIETHAMMER. 1965. Zur Ernährungsweise der Eulen auf Galapagos. *J. Ornith.* 106:49–57.
- ALATALO, R. V. 1981. Problems in the measurement of evenness in ecology. *Oikos* 37: 199–204.
- BANFIELD, A. W. F. 1947. A study of the winter feeding habits of the Short-eared Owl in the Toronto region. *Can. J. Res.* 25:45–65.

- BURT, W. H. AND R. G. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston, Massachusetts.
- CLARK, R. J. 1975. A field study of the Short-eared Owl, *Asio flammeus* (Pontoppidan) in North America. Wildl. Monogr. 47:1-67.
- , AND J. G. WARD. 1974. Interspecific competition in two species of open country raptors *Circus cyaneus* and *Asio flammeus*. Proc. Penn. Acad. Sci. 48:79-87.
- COLVIN, A. B. AND S. R. SPAULDING. 1983. Winter foraging behavior of Short-eared Owls (*Asio flammeus*) in Ohio. Amer. Midland Natur. 110:124-128.
- CRAIGHEAD, J. J. AND F. C. CRAIGHEAD. 1956. Hawks, owls, and wildlife. Stackpole Books, Harrisburg, Pennsylvania.
- DE GROOT, R. S. 1983. Origin, status and ecology of the owls in the Galapagos. Ardea 71:167-182.
- DUNNING, J. B. 1984. Body weights of 686 species of North American birds. West. Bird Band. Assoc. Mono. No. 1.
- FISLER, G. F. 1960. Changes in food habits of Short-eared Owls feeding in a salt marsh. Condor 62:486-487.
- GRANT, P. R., N. M. SMITH, I. J. ABBOTT, AND L. K. ABBOTT. 1975. Finch numbers, owl predation and plant dispersal on Isla Daphne Major, Galapagos. Oecologia 19:239-257.
- HARRIS, M. P. 1969. The biology of storm-petrels in Galapagos Islands. Proc. Calif. Acad. Sci. 37:95-166.
- HERRERA, C. M. 1974. Trophic diversity of the Barn Owl (*Tyto alba*) in continental western Europe. Ornis Scand. 5:181-191.
- HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432.
- HOLT, D. W. 1993. Breeding season diet of Short-eared Owls in Massachusetts. Wilson Bull. 105:490-496.
- , AND S. M. MELVIN. 1986. Population dynamics, habitat use, and management needs of the Short-eared Owl in Massachusetts. Mass. Div. Fish and Wildl. Nat. Her. Prog., Boston, Massachusetts.
- JOHNSTON, R. F. 1956. Predation by Short-eared Owls on a salicornia salt marsh. Wilson Bull. 68:91-102.
- MARKS, J. S. 1984. Feeding ecology of breeding Long-eared Owls in southwestern Idaho. Can. J. Zool. 62:1528-1533.
- MARTI, C. D. 1974. Feeding ecology of four sympatric owls. Condor 76:45-61.
- . 1976. A review of prey selection by the Long-eared Owl. Condor 78:331-336.
- . 1987. Raptor food habits studies. Pp. 67-79 in Raptor management techniques manual (B. A. Giron Pendleton, B. A. Millsap, K. W. Kline, and D. M. Bird, eds.). Nat. Wildl. Fed. Sci. & Tech. Ser. No. 10, Washington, D.C.
- . 1988. A long-term study of food-niche dynamics in the Common Barn-Owl: comparisons within and between populations. Can. J. Zool. 66:1803-1812.
- MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, South Dakota.
- MUNYER, E. A. 1966. Winter food of the Short-eared Owl in Illinois. Ill. Acad. Sci. 52: 174-180.
- PAGE, G. AND D. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77: 73-83.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.
- SOKAL, R. R. AND F. J. ROHLF. 1981. BIOMETRY. FREEMAN AND CO., NEW YORK, NEW YORK.

- STEGEMAN, L. C. 1957. Winter food of the Short-eared Owl in central New York. *Am. Midland Nat.* 57:120-124.
- TOMKINS, I. R. 1936. Notes on the winter food of the Short-eared Owl. *Wilson Bull.* 48: 77-79.
- WATSON, A. 1957. The behavior, breeding and food ecology of the Snowy Owl (*Nyctea scandiaca*). *Ibis* 99:419-462.