Importance of Prairie Wetlands and Avian Prey to Breeding Great Horned Owls (*Bubo virginianus*) in Northwestern North Dakota

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Abstract.—Prey use by Great Horned Owls (*Bubo virginianus*) is documented widely in North America, but not in the vast northern Great Plains. During spring through early summer 1986-1987, I recorded 2,900 prey items at 22 Great Horned Owl nesting areas in the prairie pothole farm- and rangelands of northwestern North Dakota. The owls relied heavily on wetland-dependent prey species (overall, 57 percent by number and 76 percent biomass) especially ducks (Anserinae) and rails (Rallidae). Far more avian (65 percent by number and 84 percent biomass) and less mammalian prey were used than typically reported. Variation in diet composition among owl families was not explained well by nesting area habitat, and was dominated by prey from wetlands regardless of wetland habitat availability.

Diets of Great Horned Owls (*Bubo virginianus*) are better documented than those of most other North American strigiforms. The owl preys mainly on small to mid-size mammals especially small rodents and leporids (Errington *et al*. 1940; Korschgen and Stuart 1972; McInvaille and Keith 1974; Marti and Kochert 1995, 1996; Voous 1988) although its list of prey includes diverse sizes and taxa (see Bent 1938). Despite broad knowledge of the Great Horned Owl's diet, little is known of its prey use in the vast northern Great Plains of midcontinent North America. Numerous studies of Great Horned Owl diets have been conducted in more wooded habitats of nearby Great Lakes States (Errington *et al*. 1940, Orians and Kuhlman 1956, Petersen 1979) and the boreal forest ecotone (McInvaille and Keith 1974, Rusch *et al*. 1972), but implications for predator-prey relationships in the Great Plains are only speculative.

Abundance and distribution of Great Horned Owls have increased in the northern Great Plains since the region was settled by Europeans about a century ago, due to increases in woodland breeding habitat associated with tree-planting and suppression of prairie fires (Murphy 1993, Sargeant *et al*. 1993). The increase in this generalist predator may have implications for population dynamics of species on which it preys. My objectives were to quantify diet composition of breeding Great Horned Owls in an area of mixed farm- and rangeland in the northern Great Plains, to assess variation in prey use among owl pairs, and to test whether such variation is explained by habitat makeup around nests.

STUDY AREA

Diets of nesting Great Horned Owls were examined during May to early July, 1986 and 1987 on 93 km^2 Lucy Township and about 100 km^2 of adjacent similar habitat and land use in Burke County, northwestern North Dakota (48°40'N; 102°35'W). The study area was within a rolling to hilly glacial moraine known as the Missouri Coteau (Bluemle 1977). Climate was semi-arid with cold winters and warm summers. Annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to a 42-cm average, and water levels in local wetlands were average and below average in respective years (Murphy 1993:155). Land use was a mix of grain farming and cattle ranching. Habitat composition on Lucy Township was 41 percent native (*Stipa-Agropyron*) prairie (about one-half grazed heavily by domestic livestock and one-half grazed lightly or idle) with scattered tall shrubs such as hawthorn (*Crateagus chrysocarpa*) or chokecherry (*Prunus virginiana*); 31

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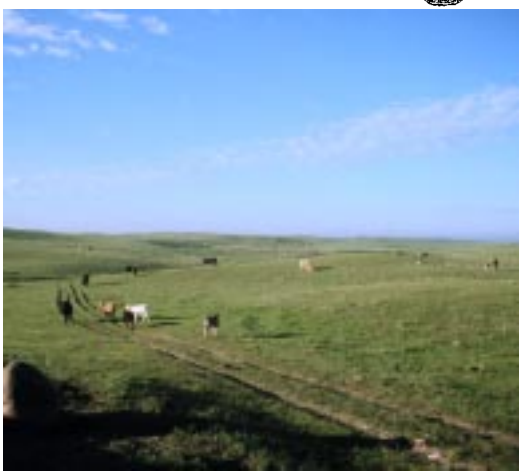
The study area was on the Missouri Coteau, a glacial moraine dotted with wetlands known as prairie potholes. Land use was a mix of grain farming and cattle ranching.



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Mixed grass prairie made up 41 percent of the study area. About one-half of this was grazed heavily each year by cattle, and the rest was grazed lightly or not at all. When ungrazed, average heights of the prairie vegetation reached about 10 cm on hilltops to 40 cm near wetland edges.

percent cropland, one-third of which annually was fallow; 19 percent seasonal, semi-permanent, and permanent wetlands (classification according to Stewart and Kantrud [1971]); 5 percent tame grass-alfalfa hay; 2 percent small (< 1 ha), scattered clumps of quaking aspen (*Populus tremuloides*) trees (mean = 4.7 clumps/km^2, SD = 3.4); and 2 percent roads, farmsteads, and shelterbelts. The area was sparsely inhabited by humans (one farmstead/8 km^2).

Raptors that nested commonly on the study area included Red-tailed Hawk (*Buteo jamaicensis*) (0.16 occupied nests/km^2), Swainson's Hawk (*B. swainsoni*) (0.08/km^2), Northern Harrier (*Circus cyaneus*) (> 0.2/km^2), and Great Horned Owl (0.11/km^2) (Murphy 1993). Great Horned Owls occurred year-round and nesting pairs hatched their eggs in early to mid-April.

METHODS

Each spring I systematically searched 80 km^2 of Lucy Township (access was denied on 13 km^2) for occupied nests of raptors (Murphy 1993) and subsequently monitored prey use by all successful Great Horned Owl pairs (those that produced nestlings at least 3 weeks old). I augmented this sample of owl diets with like data from all successful Great Horned Owl nests on similar land use and habitat within the Missouri Coteau, up to 10 km north, south, and east of Lucy Township.

Diet

In May, when owlets were 4 weeks old, I tethered them on platforms that were about 2 m above ground in sheltered sites < 9 m from nests (Petersen and Keir 1976). I subsequently visited the platforms every 3-4 days between 1000-2000 hours for 6-8 weeks after which young were released. During each visit I weighed owlets and collected all regurgitated pellets and discarded (inedible) prey remains. Fresh (edible) prey were identified, marked by cutting off a foot. I used standard techniques to analyze pellets (Marti 1987). I avoided duplicating the count of any prey item by conservatively choosing the lowest number of items represented collectively by pellets, discarded remains, and fresh items, including fresh items noted at the previous visit (Collopy 1983, Craighead and Craighead 1956, Marti 1987).

Mean weights of prey were obtained from specimens collected on the study area (Appendix 5 in Murphy [1993]) and from published literature (Dunning 1984, James and Seabloom 1969, Jones *et al*. 1983). For weights of prey represented by remains in owl pellets, I relied mainly on measurement of skeletal elements such as passeriform synsacra and tarsometatarsi (tarsi) to estimate approximate size and age of prey (Marti 1987). Ossification of major

skeletal elements and (for birds) presence of down versus emerging or fully developed contour feathers also were helpful in approximating age and size of prey in pellets. Weights were assigned to juvenile prey relative to those of adults of same species: (1) large juvenile (adult weight x 0.75), (2) two-thirds grown (adult weight x 0.66), and (3) one-half grown (0.5 x adult weight). For prey of undetermined age, I used prey observed at tether platforms as a reference and assigned the average weight of conspecific prey for which age could be determined. Weights of undetermined species of juvenile ducks were estimated by comparing tarsus lengths to a composite age-growth curve weighted according to relative abundance of small, medium, and large species among duckling prey of known identity that were observed on platforms (Murphy 1993:196). I assigned each invertebrate prey (e.g., Orthoptera) a weight of 1 g.

I report dietary makeup in terms of relative (percentage) frequency and biomass. Percentage frequency (i.e., the proportion by numbers) was calculated by dividing the number of individuals of each prey category by the total number of prey items observed. Percentage biomass was estimated by multiplying the number of individuals of each prey category by their respective mean weight, then dividing the subtotal of each prey category by the grand total prey weight (Marti 1987). For each prey category that comprised > 5 percent (frequency) of prey pooled from all owl tether platforms, I estimated the average biomass in g of prey killed daily by each Great Horned Owl pair. I refer to this estimate as a daily biomass consumption rate (DBC). DBC (g/day) was determined for a given owl family by multiplying the percentage biomass of each prey category times daily food needs (total g) of adults and young combined (Craighead and Craighead 1956:312). I assumed that composition of prey consumed by adults was the same as that delivered to owlets, and that each adult and juvenile Great Horned Owl required about 144 g of prey daily (McInvaille and Keith 1974). Last, I calculated food-niche breadth at a coarse level, using Levins' formula: $1/\Sigma\, p_i^2$, where p_is were frequency proportions of each prey class (Marti 1987).

Habitat Variables

I defined nesting area as the area within a 1 km radius of a tether platform and assumed this roughly defined a Great Horned Owl home range (Craighead and Craighead 1956:257, Marti and Kochert 1996, Petersen 1979). Habitat within each owl nesting area was classified into one of the following eight categories: aspen tree clump, seasonal wetland, semipermanent wetland, cropland, hayland (tame hay), pasture (moderately to heavily grazed native prairie), idle prairie (rested > 2 years), and miscellaneous (farmstead, road right-of-way); the proportion (percentage) of a nesting area that each habitat comprised was determined from area measurement on aerial photographs (1:15,840). Within each nesting area I also measured area (ha) of each of the eight habitats that was within 100 m of a perch > 6 m high because Great Horned Owls typically hunt from elevated perches (e.g., Petersen 1979). I also measured distance (m) from tether platform to nearest patch for each of the eight habitats (hereafter I refer to these simply as e.g., proximity or distance to cropland). Thus, at every owl nesting area there was a total of 24 habitat variables measured.

Statistical Treatment of Data

Null hypotheses regarding Great Horned Owl diets and relationships between diet and habitat were tested by ANOVA and contingency tests (Sokal and Rohlf 1981). Data sets were tested for homogeneity of variances using F-test procedures in BMDP (Dixon 1983). Hypotheses of no overall, between-year difference

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Prairie wetlands made up 19 percent of the area and were diverse in size and type (water permanency). Clumps of quaking aspen trees were widely scattered and typically occurred on wetland edges.

in frequency proportions of prey used by Great Horned Owls were tested by using the mulivariate analysis of covariance procedure in SAS (SAS Institute 1989). Univariate analyses of covariance were used if overall year effect was significant in the multivariate test. I convey exact probability levels for test results where P > 0.001 and consider P < 0.05 to be grounds for rejecting null hypotheses.

Linear regression models (Neter *et al*. 1985) were used to try to explain variation in use of important prey types among Great Horned Owl families (i.e., nesting areas). Either percentage biomass or DBC for each respective nesting area was entered as the dependent variable. I used biomass in this analysis because it may better convey relative importance of prey to raptors than frequency (Marti 1987, Rusch *et al*. 1972). The database randomly excluded data from 1 year for individual nesting areas monitored both in 1986 and 1987. All 24 habitat variables were candidates as independent (explanatory) variables in regressions. Also, abundance indices for prey used by owls in significantly different frequency proportions between years were derived from local surveys by the U.S. Fish and Wildlife Service (Murphy 1993), and were added as independent variables to account for year effect. I included number of tethered young as an independent variable when DBC was the dependent variable. The stepwise regression procedure in BMDP (Dixon 1983) was used to select five to eight potentially best independent variables. Then all possible one-, two-, and three-variable models were explored. Independent variables not normally distributed were log transformed. I checked for multicollinearity among independent variables by using correlation and examined residual plots for the assumption of constant variance. Standardized regression coefficients and associated P-values (probability of t in reduced model test for coefficient) were reported to convey relative importance and validity of independent variables in multivariate models. I accepted models for which F for the regression fit had an associated probability of P < 0.05.

RESULTS

I recorded 1,200 prey items at 12 Great Horned Owl tether platforms during 628 platform-days (i.e., a site monitored 1 day) in 1986 and 1,700 items at 12 tether platforms during 683 platform-days in 1987. Twenty-two different nesting areas were represented in this sample; two nesting areas were sampled both years. One to three owlets were tethered on each platform (means, 1.8 and 2.3 young/platform in 1986 and 1987, respectively). None of 49 tethered owlets died on platforms; all gained or maintained weight without need for supplemental feeding (Petersen and Keir 1976). Evidence of surplus prey on platforms was rare, however. Owlets were released while still being fed at a relatively constant rate by tending adults.

Overall Diet

Birds comprised most prey delivered especially in terms of overall biomass (subtotals, table 1); > 47 species were represented (all prey recorded, including scientific names, are listed in Appendix A). Mammals were far less important, particularly in biomass contribution. Other prey classes were insignificant (< 2 percent frequency and 1 percent biomass in aggregate, table 1). Mean prey mass was 196.6 g (range < 1 to 1,250 g, N = 2,900), and overall dietary diversity (food niche breadth) was 1.88 (N = five prey classes).

Ducks (10 species; 77 percent juveniles) were the most important prey category (table 1). Rails, especially American Coot (nearly all adults; 70 percent frequency, 94 percent biomass of rallid prey), were the second most important prey. Voles (mainly meadow vole), mice (mainly deer mouse), and passeriforms (mostly juvenile blackbirds) each contributed > 10 percent frequency of prey and, along with

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Great Horned Owls nested in aspen, usually in old Buteo *spp. nests.*

Table 1.—*Percentage composition of prey used by nesting Great Horned Owls (*Bubo virginianus*) in the Missouri Coteau of northwestern North Dakota during May to early July, 1986 and 1987, based on prey items pooled from all owl families.*[1]

Prey category[2]	Frequency		Biomass		Percentage of nesting areas where preyed on[3]
	N	Percent	kg	Percent	
Mammals					
White-tailed jackrabbit	95	3.3	43.0	7.5	63.6
Ground squirrel	42	1.4	10.1	1.8	81.8
Mouse	385	13.3	6.4	1.1	100.0
Vole	328	11.3	9.7	1.7	100.0
Muskrat	20	0.7	9.5	1.7	36.4
Norway rat	87	3.0	17.7	3.1	45.5
Miscellaneous	14	0.5	1.4	0.2	—
Subtotal		33.5		17.1	
Birds					
Grebe	99	3.4	35.4	6.2	95.5
Duck	1,010	34.8	256.5	45.0	100.0
Grouse and partridge	34	1.2	17.4	3.1	54.5
Rail	315	10.9	117.1	20.5	100.0
Shorebird	79	2.7	7.6	1.3	90.9
Passeriform	303	10.4	17.2	3.0	100.0
Domestic chicken	20	0.7	15.5	2.7	4.5
Miscellaneous	18	0.6	3.6	0.6	—
Subtotal		64.7		82.4	
Amphibian	38	1.3	1.9	0.4	50.0
Reptile	1	< 0.1	0.1	< 0.1	4.5
Insect	12	0.4	< 0.1	< 0.1	31.8
Total	2,900	100.0	570.1	100.0	

[1] Total of 12 and 12 nesting areas monitored in 1986 and 1987; two nesting areas were monitored both years.
[2] See Appendix A for names of prey species not specifically identified in table.
[3] Proportion of 22 nesting areas at which a given species or species group occurred as prey at least once during 1986-1987.

rails and ducks, were used by all owl families. White-tailed jackrabbits (all juveniles) and grebes (nearly all adults) contributed > 5 percent of overall biomass although jackrabbit prey was not used at many nesting areas. In contrast, shorebird and ground squirrel prey were used widely but infrequently by any one owl family and contributed little to biomass. One owl family switched from a diverse diet of wild prey to almost exclusively domestic chickens and Norway rats (means, 0.7 chickens and 1.2 rats found daily on the tether platform with three owlets) after 250 half-grown cockerels were released into an open pen lacking roosting shelter at a farmstead 0.5 km away. Galliform prey, composed equally of Sharp-tailed Grouse and Gray Partridge (nearly all adults), were used infrequently and by only about one-half of owl families. Tiger salamanders comprised nearly all amphibian prey; 46 percent were noted at a single tether platform.

Wetlands comprised 19 percent of habitat on Lucy Township and adjacent lands and averaged the same proportion of habitat in Great Horned Owl nesting areas, but wetland-dependent prey comprised 57 percent frequency and 76 percent biomass of prey in owl diets (pooled data, compared to 19 percent wetland composition; chi-square goodness-of-fit, both $P < 0.001$). These prey were ducks, rails, grebes, certain passeriforms (Yellow-headed Blackbird, Red-winged Blackbird) and shorebirds (e.g., Black Tern), muskrats, and tiger salamanders.

Variation in Diet

Year Effect

There was a difference between years in overall use (percentage frequency) of voles, mice, and passeriforms (table 2). The relative frequency of voles as prey was greater in 1987 when voles were more abundant in northwestern North Dakota (1986-1987 abundance indices: 0.1 and 12.4 captures/100 snap-trap nights [Murphy 1993]). Less significant was the decrease in frequency of mouse and passeriform prey from 1986 to 1987. Frequency of rallid prey appeared greater in 1987, but the difference was not significant ($P = 0.142$). Use of duck prey did not differ between years, even though duck abundance locally was below average in 1986 and about average in 1987 (May abundance indices: 54 and 104 ducks/km^2), a trend opposite that of local wetland conditions (Murphy 1993:155).

Variation Among Nesting Areas

I observed marked variability in use of prey among Great Horned Owl nesting areas (table 2). For example, percentage of dietary biomass represented by ducks ranged 28-90 percent in 1986. Habitat also varied among nesting areas (table 3), but was not dissimilar between

Table 2.—*Variation in relative diet composition[1] of Great Horned Owls (*Bubo virginianus*) between 1986 and 1987, and among nesting areas[2] within years, northwestern North Dakota.*

	Percentage frequency						Percentage biomass					
	1986			1987			1986			1987		
Prey category	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**
Mammals												
White-tailed jackrabbit	5.0	(3.7)	0-9.8	1.9	(2.5)	0-7.8	10.8	(9.5)	0-31.8	4.8	(6.4)	0-18.6
Ground squirrel	2.0	(2.5)	0-9.0	1.0	(0.7)	0-3.0	2.1	(2.6)	0-9.3	1.5	(1.6)	0-5.8
Mouse[3]	18.1	(9.4)	4.9-38.1	11.4	(6.7)	3.7-23.9	1.7	(1.1)	0.6-4.0	1.0	(0.6)	0.3-2.2
Vole[3]	7.0	(4.3)	1.9-14.3	14.3	(2.8)	9.0-20.2	1.0	(0.6)	0.3-1.9	2.2	(0.7)	1.3-3.7
Birds												
Grebe	3.2	(2.3)	0-7.4	2.9	(1.7)	0.7-5.4	5.7	(4.0)	0-12.7	5.5	(3.2)	1.1-11.2
Duck	35.5	(15.7)	16.7-71.3	32.5	(12.1)	8.5-59.3	51.4	(18.3)	27.8-90.2	42.3	(12.2)	17.0-66.9
Grouse and Partridge	1.3	(3.3)	0-11.4	1.2	(1.0)	0-3.1	2.3	(5.9)	0-20.9	3.4	(2.6)	0-8.8
Rail	7.6	(5.3)	0.8-19.6	14.4	(7.8)	6.3-32.2	15.9	(11.4)	0.4-42.0	25.7	(9.2)	8.7-36.5
Shorebird	3.2	(2.4)	0-7.1	2.4	(3.0)	0-10.9	1.6	(1.1)	0-4.0	1.2	(1.3)	0-4.7
Passeriform[3]	12.1	(5.1)	4.1-19.4	9.0	(4.4)	3.5-15.5	3.2	(1.8)	0.9-7.0	2.9	(2.0)	0.4-6.9
Amphibians	1.9	(3.9)	0-13.9	0.6	(0.7)	0-2.0	0.6	(1.3)	0-4.7	0.2	(0.2)	0-0.6
Between-year difference, overall diet				$P = 0.006$[4]						$P > 0.05$		

[1] Excludes prey or prey groups that comprised < 1 percent dietary composition by frequency during 1986-1987.
[2] Based on 22 separate nesting areas monitored: N = 11 in 1986 and N = 11 in 1987.
[3] Significant difference in relative (percentage) frequency composition between years; univariate analysis of covariance: mouse, $P = 0.019$; vole, $P = 0.005$; passeriform, $P = 0.047$.
[4] Significant difference in overall relative (percentage) frequency between years; multivariate analysis of covariance: Wilks' lambda = 0.014, F = 18.06, df = 16.

Table 3.—*Composition of seven major habitat types among 22 Great Horned Owl (*Bubo virginianus*) nesting areas, northwestern North Dakota, 1986-1987.*

Habitat type	Percentage of area within 1 km of nest		
	Mean	SD	Range
Quaking aspen tree clump	3.2	2.4	0.8-8.7
Seasonal wetland	10.1	4.6	2.3-19.8
Semi-permanent wetland	8.1	5.9	0.5-24.0
Cropland	28.4	15.4	3.1-56.7
Hayland	4.6	6.4	0-29.8
Pasture	22.8	14.4	1.9-55.5
Idle prairie	20.1	14.3	0.0-45.1

nesting areas on (N = 8) compared to off (N = 14) Lucy Township except semipermanent wetlands were slightly more prevalent on the township (means, 11 versus 7 percent; df = 21, F = 6.6, P = 0.022). Dietary diversity (food niche breadth, class level) ranged 1.38-2.07 among nesting areas (mean = 1.81, SD = 0.21, N = 22), and wetland-dependent prey species contributed up to 95.8 percent of dietary biomass (mean = 77.6, SD = 15.5). Next I present models for predicting use of prey categories that comprised > 5 percent overall frequency in table 1 except passeriforms (no models suitably explained variation in passeriform use), and for wetland-dependent prey collectively.

Mice and voles.—No models suitably accounted for variation in use of mouse prey among Great Horned Owl nesting areas. Use of mice in terms of mean biomass consumed daily (DBC) was weakly explained by percentage cropland in nesting areas (R^2 = 0.142, F = 3.31, P = 0.084). For voles, hayland was a common although not strong predictor of owl predation in multiple variable models (table 4), and alone it was nonsignificant (e.g., percentage hayland [log]: R^2 = 0.135, F = 3.31, P = 0.093). The functional response to changed vole abundance during 1986-1987 was indicated by a year-effect variable. Variation also was partly explained by the number of young owls being fed, a variable unimportant in models for other prey.

Rails.—Almost no suitable models were produced for rallids. Owls appeared to consume less rail biomass (nearly all represented by American Coot) as the amount of idle prairie near perches increased in nesting areas (table 4).

Ducks.—Models with relative biomass as the dependent variable inadequately explained variation in use of duck prey among owl nesting areas. However, nearly one-half of the variation in DBC of ducks was explained by pasture and distance to nearest road or farmstead (table 4). Owls consumed more duck prey when there was more pasture in nesting areas or when pasture was closer to nests, and less as roads and farmsteads became closer. I expected that main components of breeding duck habitat, wetlands and idle prairie (i.e., nesting cover), might explain most variation in use of duck prey among Great Horned Owl nesting areas, yet these variables were unimportant (e.g., percentage semi-permanent wetland in nesting area: R^2 = 0.004, df = 21, F = 0.08, P = 0.775).

Next I examined use of adult and juvenile duck prey separately (table 4). In the only model marginally suitable for adult ducks, extent of pasture and aspen tree clumps explained more than one-third of DBC variation. Duckling DBC did not relate to differences in pasture among owl nesting areas, and extent of semi-permanent wetland was a marginally significant predictor. From this second analysis, I conclude the positive relationship of pasture to overall use of duck prey (models I and II in table 4) pertained mostly to adult ducks.

Wetland-dependent Prey.—Perhaps use of either duck or rail prey was poorly explained by proximity or prevalance of wetlands because some owl families relied more on alternative wetland-dependent prey. If so, total wetland-dependent prey use should have reflected wetland availability if prey resources were used in proportion to their respective habitats in owl nesting areas. Distance to nearest semi-permanent wetland (inverse relationship) was only a marginally significant predictor of consumption of all wetland-dependent prey combined (table 4) and other wetland variables were poor predictors.

DISCUSSION

Importance of Wetland Habitats and Avian Prey

Prodigious use of wetland-dependent prey species by nesting Great Horned Owls in late

Table 4.—*Most parsimonius linear regression models that best explain variance in percentage biomass contribution or daily biomass consumption rates (DBC, g/day) of major prey of Great Horned Owls (*Bubo virginianus*), northwestern North Dakota, 1986-1987.*

Prey model	DV[1]	IV[2]	Coefficient Standardized estimate (b')	P[3]	Fit of model R^2	F	P
Vole I	DBC	No. juvenile owls	0.71	0.012	0.513	5.26	0.027
		Hayland near perches[4] (log)[5]	0.43	0.089			
Vole II	DBC	Year (vole abundance)[6]	0.51	0.015	0.689	8.86	0.002
		Number of juvenile owls	0.45	0.032			
		Percent hayland (log)	0.36	0.065			
Rails	DBC	Idle prairie near perches (log) (inverse)			0.265	6.14	0.024
Duck I	DBC	Percent pasture	0.55	0.003	0.492	9.19	0.002
		Distance to road or farmstead	0.39	0.028			
Duck II	DBC	Distance to nearest pasture (log)	-0.47	0.014	0.414	6.70	0.006
		Distance to road or farmstead	0.45	0.019			
Duck III (adult ducks)	DBC	Percent pasture	0.49	0.015	0.369	5.56	0.013
		Percent aspen	0.32	0.099			
Duck IV (juvenile ducks)	DBC	Percent semi-permanent wetland			0.175	4.23	0.053
Wetland prey[7]	DBC	Distance to semipermanent wetland (inverse)			0.177	4.31	0.051

[1] Dependent variable = percentage dietary biomass (%) or total daily biomass consumption rate in g/day (DBC) represented by a prey category.
[2] Independent variable(s): measures of nesting area habitat, year effect, and number of young.
[3] Probability of $\underline{t}$ in reduced model test for coefficient.
[4] Area (ha) within nesting area $\leq$ 100 m from perches > 6 m tall.
[5] Data were log transformed.
[6] Year effect: 1986 and 1987 vole abundance index (0.1 and 12.4 captures/100 trap-nights [Murphy 1993]).
[7] Collectively: grebes, ducks, rails, certain passeriforms and shorebirds (e.g., Yellow-headed Blackbird, Black Tern), muskrat, amphibians.

spring and early summer was a major finding of this study. Such prey were far less important to nesting Great Horned Owls in the Great Lakes States (Errington *et al*. 1940, Petersen 1979) and boreal forest ecotone (Rusch *et al*. 1972). Use of grebes, Sora, Yellow-headed and Red-winged Blackbirds, juvenile muskrat, and especially ducks and coots was so extensive in this study that wetlands clearly were major foraging sites of adult Great Horned Owls. Some regression models suggested variation in use of duck prey related directly to the extent or, inversely, proximity of pasture (grazed native prairie). Some adult and juvenile ducks could have been captured in such uplands (e.g., hens at nests, broods traveling between wetlands), but others such as coots and grebes occur almost exclusively in wetlands (Kantrud 1985, Kantrud and Stewart 1984).

Few regression models adequately predicted owl use of wetland-dependent prey. For example, there was almost no relationship between use of ducks or coots and proximity and extent of wetlands within owl nesting areas. This suggests Great Horned Owls sought wetland prey regardless of proximity or abundance of wetland habitats. Thus, if abundance of wetland-dependent prey related directly to occurrence of wetland habitats, owls

did not consistently prey on what was locally most abundant, a relationship McInvaille and Keith (1974) also noted among Great Horned Owls, waterbirds, and wetlands in Alberta. Instead, my data support the assertion of Rusch *et al*. (1972) that wetlands are an exception to a direct, prey habitat-prey use relationship and that prey are more available and vulnerable to the owl in wetland sites than expected. Great Horned Owls may have used wetland-dependent prey extensively because quaking aspen comprised most elevated hunting perches on my study area and typically bordered wetlands. Prairie wetlands bordered by aspen probably are rich food patches (Krebs 1973, Pyke *et al*. 1977) for foraging Great Horned Owls due to high prey density and diversity (Kantrud and Stewart 1984, Kantrud *et al*. 1989).

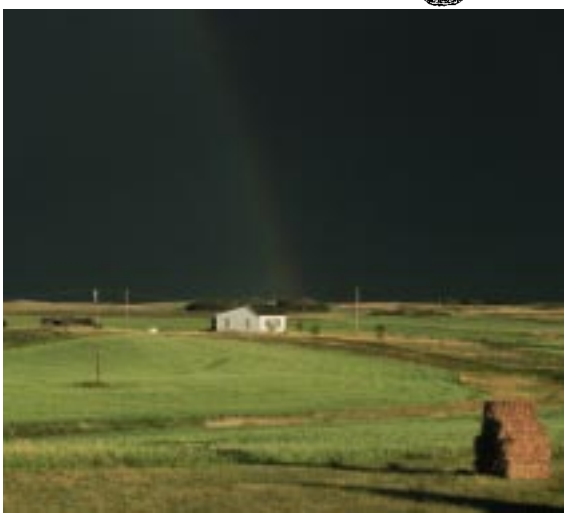
Overwhelming importance of avian prey to Great Horned Owls in my study was unusual although not unique. A cursory survey of Great Horned Owl diets in central North Dakota also suggested dominance by avian prey (Gilmer *et al*. 1983). Snyder and Wiley (1976) characterized Great Horned Owl diets in North America as 77 percent (frequency) mammalian and 6 percent avian prey, and subsequent reviews have closely corroborated this preponderance of mammalian prey (Marti and Kochert 1995). I attribute importance of birds in owl diets to relatively abundant avifauna associated with mixed grass prairie and numerous wetlands in the Missouri Coteau (Kantrud *et al*. 1989, Stewart 1975). At least 47 species of birds were prey of Great Horned Owls in this study, representing more than one-half of area breeding species (Stewart 1975). Scarcity of other, usually staple, prey especially leporids (Errington *et al*. 1940) also contributed to high use of avian prey. For example, nesting Great Horned Owls in the nearby Aspen Parkland region of Canada, where wetlands also abound, rely heavily on snowshoe hares (*Lepus americana*) and rodents (Bird 1929, Houston 1987). Decreased use of avian prey from eastern to western U.S. has been suggested (mean frequencies, 24 and 6 percent avian prey [Marti and Kochert 1995]). The northern Great Plains apparently form a gap in the knowledge of Great Horned Owl predation and trophic relationships and may supply further data that challenge generalizations about patterns in this owl's diet. Dietary diversity I recorded (overall food niche breadth, by prey class) exceeded that of most other Great Horned Owl populations studied in North America (Marti and Kochert 1995), a disparity that also can be attributed largely to the importance of avian prey in this study. Previously, Great Horned Owl trophic diversity was thought to be lowest in grassland biomes (Donazar *et al*. 1989).

The mean prey size I observed (197 g) was more than 2.5 times greater than a geometric mean reported for North American Great Horned Owls by Marti and Kochert (1995). I attribute this marked difference to the major contribution of relatively large, wetland-dependent birds (ducks, American Coot, grebes) as prey in this study, instead of small rodents typically predominant in the owl's diet elsewhere in North America. Relatively large prey from wetlands, especially ducks, may have been selected most often due to high bioenergetic profitability (Stalmaster and Gessaman 1982). Short nights (7 hours) during early summer in the far northern Great Plains may limit numbers of forays that can be made by Great Horned Owl pairs and thus preclude delivery of adequate numbers of smaller, less rich prey (e.g., mice, voles), especially for pairs tending several owlets.

Use of Upland Prey

Use of jackrabbits, deer mice, and ground squirrels indicated that Great Horned Owls did not hunt wetlands exclusively. Predation on spermophiles, especially thirteen-lined ground squirrels that are believed to be completely diurnal (Jones *et al*. 1983:144), suggested Great Horned Owl pairs hunted beyond dusk to dawn, or that the ground squirrels were crepuscular. Besides selecting relatively large prey, Great Horned Owls could compensate for a limited number of nocturnal hours in the northern Great Plains by extending their crepuscular activity. Relative low occurrence of leporid prey was expected because snowshoe hares and cottontails (*Sylvilagus* spp.) were lacking on the study area and white-tailed jackrabbits were scarce. Extent of predation on juvenile jackrabbits (N = 95 detected on platforms) despite their apparent scarcity, however, implied some selection for leporid prey. Leporids tend to be main prey of Great Horned Owls in temperate deciduous forests, whereas voles and a suite of other species of small rodents typically dominate diets in northern coniferous forests and deserts, respectively (Donazar *et al*. 1989)

Great Horned Owls also preyed heavily on meadow voles, another prey not strictly tied to wetlands. However, the vole inhabits dense, mesic vegetation (Jones *et al*. 1983:222) that typically occurs on wetland edges and within ephemeral and temporary prairie wetlands (Kantrud *et al*. 1989). Indeed, Great Horned Owl predation on meadow voles in southwestern Idaho appeared related to wetlands (Marti and Kochert 1996). But, regression models from my study suggested a link between vole use and hayland. Owls preyed on voles before hay was harvested, when it was relatively tall (to 45 cm). Although tall vegetation affords cover for small mammal prey of some raptors (Bechard 1982), Great Horned Owls can forage in vegetation up to 45-60 cm tall (Frounfelker 1977), especially when elevated perches occur nearby (Petersen 1979). A regression model in this study suggested a direct link between vole use and amount of hayland near hunting perches.



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Cropland, mostly wheat, and grass-alfalfa hayland comprised 31 and 5 percent of the study area, respectively. About one-third of croplands were fallowed. Hay was harvested during July.

Rare predation on Sharp-tailed Grouse was a startling result because the species was common and conspicuous. For example, I noted four leks each with 18-30 displaying male grouse, on about 25 km^2 of Lucy Township. These were within Great Horned Owl nesting areas I monitored beginning in May when grouse were active on leks at dawn and dusk. Rusch *et al*. (1972) suggested male Sharp-tailed Grouse in Alberta were vulnerable to Great Horned Owl predation in spring, but Houston (1960) found little evidence of owl predation on Sharp-tailed Grouse in Saskatchewan and Berger *et al*. (1963) noted raptors seldom preyed on cogeneric Greater Prairie Chickens (*T. cupido*) on leks in Wisconsin. Perhaps owls rarely preyed on grouse because wetlands were attractive foraging sites.

SUMMARY AND CONCLUSIONS

Great Horned Owls nesting on mixed farm- and rangelands in the Missouri Coteau of northwestern North Dakota relied heavily on avian prey associated with prairie wetlands during late spring through early summer. High diet diversity and mean prey weight relative to reports from previous studies of the owl's diet were attributed to this predominance of avian, wetland-dependent prey. Adult and juvenile ducks, American Coots, passerines especially juvenile blackbirds, and meadow voles and deer mice were most important prey overall. Dietary composition varied among owl pairs, but the variation was not always clearly related to habitat or land use because wetlands probably were selected as foraging sites regardless of prevalence or distance from nests. Availability of adjacent perches likely was an important determinant of opportunistic use of wetlands by owls, although this was not consistently suggested among regression models. Differences in prey preference among owl pairs also may have clouded prediction of owl diet based on wetland habitat within nesting areas. Reliance on avian prey, especially that from wetlands, may not be as strongly evident in other physiographic subregions of the northern Great Plains, which have lower wetland abundance than the Missouri Coteau and far fewer wetlands with adjacent perches than on the Coteau in northwestern North Dakota. Also, wetland-dependent prey may be more or less available during years of abundant moisture or drought, than they were in near average wetland conditions during this study. I suspect vulnerability of such prey to Great Horned Owl predation is elevated by rapid drying of seasonal and some semipermanent wetlands that often occurs as summer progresses (Kantrud *et al*. 1989). Regardless, results of this study contest assertions that the owl is essentially a mammal predator across its range in North America (Marti and Kochert 1995, 1996; Snyder and Wiley 1976) and suggest exceptions

to current thought on the species' trophic relationships may occur in the relatively understudied Great Plains, at least where prairie wetlands are an important landscape feature.

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Appendix A.—*Prey recorded at 22 Great Horned Owl (*Bubo virginianus*) nesting areas in the Missouri Coteau of northwestern North Dakota, 1986-1987.*

Mammals

Leporids
White-tailed jackrabbit (*Lepus townsendii*)

Ground squirrels
Richardson's g. squirrel (*Spermophilus richardsonii*)
Thirteen-lined ground squirrel (*S. tridecemlineatus*)
Franklin's ground squirrel (*S. franklinii*)[1]

Mice
Deer mouse (*Peromyscus maniculatus*)
Western or meadow jumping mouse (*Zapus* spp.)
Olive-backed pocket mouse (*Perognathus fasciatus*)[1]
N. grasshopper mouse (*Onychomys leucogaster*)[1]
House mouse (*Mus musculus*)[1]

Voles
Meadow vole (*Microtus pennsylvanicus*)
S. red-backed vole (*Clethrionomys gapperi*)[1]

Other Rodents
Muskrat (*Ondatra zibethicus*)
Norway rat (*Rattus norvegicus*)

Miscellaneous mammals
Short-tailed shrew (*Blarina brevicauda*)
Masked shrew (*Sorex cinereus*)
Least weasel (*Mustela nivalis*)[1]
Striped skunk (*Mephitis mephitis*)[2]

Birds

Grebes
Horned grebe (*Podiceps auritus*)
Eared grebe (*P. nigricollis*)
Pied-billed grebe (*Podilymbus podiceps*)

Ducks
Green-winged teal (*Anas carolinensis*)
Mallard (*A. platyrhynchos*)
N. pintail (*A. acuta*)
Blue-winged teal (*A. discors*)
N. shoveler (*A. clypeata*)
Gadwall (*A. streptera*)
American wigeon (*A. americana*)
Redhead (*Aythya americana*)
Lesser scaup (*A. affinis*)
Ruddy (*Oxyura jamaicensis*)

Grouse and Partridge
Sharp-tailed grouse (*Tympanuchus phasianellus*)
Gray partridge (*Perdix perdix*)

Rails
American coot (*Fulica americana*)
Sora (*Porzana carolina*)
Virginia rail (*Rallus limicola*)[1]

Shorebirds
Killdeer (*Charadrius vociferus*)
American avocet (*Recurvirostera americana*)[1]
Upland sandpiper (*Bartramia longicauda*)
Willet (*Catoptrophorus semipalmatus*)[1]
Common snipe (*Gallinago gallinago*)[1]
Wilson's phalarope (*Phalaropus tricolor*)
Black tern (*Chlidonias niger*)

Passeriforms
E. kingbird (*Tyrannus tyrannus*)
Horned lark (*Eremophila alpestris*)
American crow (*Corvus brachyrhynchos*)
House wren (*Troglodytes aedon*)
Brown thrasher (*Toxostroma rufum*)
Unknown warblers (Parulinae)
Unknown sparrows (Emberizinae)
Bobolink (*Dolichonyx oryzivorus*)
Red-winged blackbird (*Aeglaius phoeniceus*)
Western meadowlark (*Sturnella neglecta*)
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)
Brewer's blackbird (*Euphagus cyanocephalus*)
Common grackle (*Quiscalus quiscula*)
Brown-headed cowbird (*Molothrus ater*)
Baltimore oriole (*Icterus galbula*)
Unknown blackbirds (Icterinae)

Domestic chicken

Miscellaneous
American bittern (*Botaurus lentiginosus*)[2]
Black-crowned night heron (*Nycticorax nycticorax*)[2]
Canada goose (*Branta canadensis*)[2, 3]
Mourning dove (*Zenaida macroura*)[1]
N. saw-whet owl (*Aegolius acadicus*)[2, 4]
N. harrier (*Circus cyaneus*)[2]
Yellow-shafted flicker (*Colaptes auratus*)[1]

Amphibians

Tiger salamander (*Ambystoma tigrinum*)
N. leopard frog (*Rana pipiens*)[2]

Reptiles

Plains garter snake (*Thamnophis radix*)[2]

Insects

Grasshoppers, crickets (Orthoptera: Oedipodinae)
Giant water bug (Hemiptera: Belostomatidae)[1]

[1] Less than five individuals recorded.
[2] One individual recorded.
[3] Juvenile.
[4] Probably a spring migrant instead of a local breeding species (Stewart 1975:161).