FEEDING ECOLOGY OF FOUR SYMPATRIC OWLS

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Four species of owls, Great Horned (*Bubo virginianus*), Long-eared (*Asio otus*), Burrowing (*Speotyto cunicularia*), and Barn (*Tyto alba*), which occur together on the short-grass prairie and farmland of north-central Colorado, were selected for a study of feeding ecology. The purpose of this study was to assess the overlap in foods of the four owls and to examine feeding mechanisms which allow them to coexist. Primary objectives were (1) to analyze and compare the food habits of each owl species considering frequency of occurrence of prey species and biomass contributed by each prey species, and (2) to describe and evaluate the primary factors involved in capture of prey by the four owl species.

Few studies have been attempted in relation to the feeding of owls in this geographic area and none was a long-term study. Reed (1957) examined Barn Owl pellets from Larimer County, and Kelso (1938) and Hamilton (1941) noted Burrowing Owl foods in the Denver area. Catlett et al. (1958) studied foods of Long-eared Owls near Boulder, and Long and Kerfoot (1963) listed Great Horned Owl foods from east-central Wyoming.

Most abundant of these owls is the Great Horned. This species, a permanent resident of the area, is extremely versatile in both its nesting and feeding, allowing it to utilize a wide variety of habitats. The Burrowing Owl is abundant during summer. Burrowing Owls are restricted to open lands with available nesting and roosting sites in abandoned mammal burrows, chiefly those of black-tailed prairie dogs (*Cynomys ludovicianus*). Arriving by mid-April, they spend about 6 months in the area before returning south in mid- to late October. Barn Owls are less common. North-central Colorado is close to the northern limits of this species' range and some may move south in winter. However, some remain through the year. Rock cliffs or ditch banks are sought for nesting and roosting by Barn Owls. Long-eared Owls are also uncommon. They appear to be nomadic—there one year and gone the next. Low, dense coniferous or deciduous trees attract them for nesting and roosting.

A number of other vertebrate predators are present in this area whose diets may overlap with those of the four owl species. Other avian predators are the Golden Eagle (*Aquila chrysaetos*), Marsh Hawk (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), Swainson's Hawk (*B. swainsoni*), Rough-legged Hawk (*B. lagopus*), Ferruginous Hawk (*B. regalis*), American Kestrel (*Falco sparverius*), Prairie Falcon (*F. mexicanus*), and Loggerhead Shrike (*Lanius ludovicianus*). Mammalian predators include red fox (*Vulpes fulva*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), American badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), and long-tailed weasel (*Mustela frenata*). The more abundant reptilian predators are the gopher snake (*Pituophus melanoleucus*) and prairie rattlesnake (*Crotalus viridis*).

The research was carried out from December 1966 to June 1970.

STUDY AREAS

Field work was conducted in two areas. Most of the observations were made in a 200 km^2 area in the northeastern part of Larimer County, Colorado. Additional observations were made on a 120 km^2 area on the Pawnee National Grassland in Weld County, Colorado. These areas are characterized by short-grass prairie, with blue gramma (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) as dominant grasses. The Larimer County area has some farmland, both dry and irrigated, and is bordered on the west by hogbacks covered with shrubs, chiefly mountain mahogany (*Cerocarpus montanus*) and skunk bush (*Rhus trilobata*).

Climate is characterized by low humidity, low precipitation, typically concentrated in spring and summer, moderately high wind movement, a high per cent of intense sunlight, and a large daily range of temperatures. Summers are warm and winters cold. Snows are generally light and melt rapidly.

MATERIALS AND METHODS

FOOD HABITS

I located nests, roosts, and loafing sites of the four owl species to obtain food-habits information and comparative population sizes of the owls. Active nests were visited at intervals of 5–10 days to collect regurgitated pellets. Roosts used at times other than nesting were visited at less regular intervals to obtain pellets.

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Each whole pellet was broken apart and remains identified and recorded. Broken pellets were massed for each collection and handled in the same manner. Skulls and dentaries of mammals and skulls, feet, and feathers of birds were used in identification. Insect remains useful for identification were heads, jaws, legs and wing covers. Uncommon prey such as fish, snakes, crayfish, and spiders were identified by scales and pharyngeal arches, scales and vertebrae, various exoskeleton parts, and jaws, respectively.

Skulls only were used in counting small mammalian prey for it was found that the numbers of other bones did not indicate a larger number of individual prey in a sample. Different problems were encountered with large mammalian prey. Animals too large for a single meal were common prey of only the Great Horned Owl. Several alternatives are possible with large prey: (1) the owl may kill a large prey individual, eat its fill, and leave the remainder, never to return; (2) a pair of owls may feed from the same kill and not return to finish it; (3) one or a pair of owls may return to a kill and finish it; or (4) large prey may be brought to young in the nest and be completely consumed. It is evident, then, that remains of one large prey may be contained in one to several pellets. In order to estimate the numbers of these species, I separated all skull and leg bones in each collection sample and pieced together the numbers of individuals represented. This may be slightly less than the actual number in the case of adult owls for the first two reasons listed above but should be quite accurate for pellets of young collected at nests. Errington (1938) found, however, that Great Horned Owls usually eat all of a kill before making another, and Bowles (1916) listed several cases of Great Horned Owls returning to kills made the previous night. The same technique was used with the other three owls when necessary. Few prey, however, were larger than a single meal for the other three.

Skulls, legs, and feet, sternums and synsacrums of birds were grouped and pieced together to estimate the number of individuals in each daily collection. I found that whole heads for most insects and jaws for grasshoppers and crickets were the most accurate remains for counting. Wing covers and legs were often too fragmented or missing for accurate use in determining numbers of prey.

Uncommon prey were tabulated by assembling whatever remains were available. Seldom did it appear that more than one of these individuals was present in a particular sample.

Average weights of prey species were estimated from locally collected specimens (appendix I). Using these and prey numbers in the owl's diets, the proportion of biomass each prey group represented in each owl's food was estimated.

Chi-square contingency tables were used to compare diet compositions among owls, among years for each owl, and among different habitats for each owl.

To establish an index of their relative abundance, small mammals were trapped. Additionally, I obtained data from other small mammal studies done on or near the study area from 1959 to 1969. Combined, these data were used to rank the abundance of small mammals. Observations were made on abundance of other prey such as cottontails (*Sylvilagus* spp.) and pocket gophers (*Thomomys talpoides* and *Geomys bursarius*), but no specific techniques were used to rank them.

FACTORS AFFECTING PREY CAPTURE

Owl behavior and activity. Field observations with the aid of binoculars, a spotting scope, and sometimes a blind were used to study time of hunting activity and hunting behavior. An Esterline-Angus event recorder with triggers placed in nests was used to record times adults visited nests to feed their young. Time before or after sunset that foraging began was recorded from observations and event recordings.

Vision in low light. A room 2.1 × 3.1 × 2.4 m was light-proofed for use in testing captive owls for low-light vision and prey capture by hearing. I followed the system used by Dice (1945) to measure low-light vision. A frame to hold filters was attached to a light fixture in the center of the ceiling 2.1 m from the floor. During vision tests, one 7.5-watt bulb was the only light source. Dead mice were placed randomly on the floor of the room and light was reduced each test day by adding paper filters over the light. Light intensities were measured with a Science and Mechanics cadmium sulphide light meter near the source, converted to foot-candles, and the amount reaching the floor calculated by the inverse square method. A layer of sand on the floor was smoothed before each test to determine if the owls directly approached the mice or if they wandered about randomly until they happened to find one.

Prey capture by hearing. The same light-tight room was made ready by spreading dry leaves on the floor as in Payne (1962). Each owl was introduced individually to the room and allowed to acclimate to the surroundings. Live mice were then released under conditions of total darkness to determine if the owls could capture prey from auditory cues alone.

Morphological aspects. Body weights of owls were obtained from all birds handled on the study areas and from those reported in the literature (Craighead and Craighead 1956; Imler 1937). These were used for comparing predator and prey weights. Dice-Leraas diagrams of prey weight were constructed from complete prey lists to compare prey weights among the owls. Prey were also grouped in weight classes for comparisons.

Relative talon strength was compared among the four owls by allowing an owl to firmly grip an object in one foot and then hooking a ring over the two front toes and pulling against them with a spring balance until the grip could no longer be maintained. Feet were also measured for comparison.

Wing surface area was calculated by placing an owl dorsal surface down and tracing around the spread wings on 5-mm square graph paper. The portion of body directly between the wings was included. Numbers of whole squares included in the outline were then counted. Numbers of squares around the periphery which were only partially within the outline were counted separately, multiplied by 0.25, and added to the first figure. From this the wing surface in square centimeters was then obtained. Wing loading was calculated as the ratio of wing surface area in square centimeters over body weight in grams.

RESULTS AND DISCUSSION

OWL POPULATIONS

Numbers of breeding pairs of owls on the Larimer County study area gave an indication

TABLE 1. Ranking of small mammal numbers in north-central Colorado from trapping data.

Year	Trap nights	Mammals trapped					
		Peromyscus	*Microtus*	*Mus*	*Reithrodontomys*	Others	Totals
1960	900	34	3	0	0	0	37
1961	1,512	125	15	9	6	1	156
1962	400	39	11	0	2	1	53
1963	2,370	106	15	8	0	10	139
1964	2,370	107	8	6	0	2	123
1965	1,995	213	4	5	3	0	225
1966	5,190	276	28	37	42	12	395
1967	4,694	306	3	6	6	3	324
1968	6,114	553	107	23	35	5	723
1969	6,508	110	12	8	2	8	140
Totals	32,053	1,869	206	102	96	42	2,315

of their relative abundance. In each year, I located about 10 pairs of breeding Great Horned Owls, 13 pairs of Burrowing Owls, and 5 pairs of Barn Owls. Long-eared Owls were much less consistent in numbers from year to year. In 1966, a flock of 8–10 wintered on the area but only one nest was found the following spring. In 1967, six to eight birds wintered and three nests were discovered the next spring. Only three to four Long-eared Owls spent the winter in 1968 and no nests were found in 1969.

I did not make an exhaustive census of all owls on the study areas. Considering the varied habitats, a density estimate would perhaps be misleading since much of the land was unsuitable for owl habitation. I believe these figures for the Burrowing, Barn, and Long-eared Owls represented most of the breeding birds because nesting habitat for them was limited and easily searched. Since the Great Horned Owl shows considerable adaptability in nesting, much more habitat was available and the breeding population was probably larger.

PREY POPULATIONS

Combined data on small mammal populations are shown in table 1. It was difficult to census small mammals adequately over large areas of diverse habitat in order to determine prey selection by owls. Problems arose from the fluctuating populations of some mammals and in lack of exact information on areas the owls forage. Certain biases such as differential trapping susceptibility among species, placement of traps, and bait choice may also have affected the results. I believe, however, that since the sample is so large, it can be used with confidence as a general ranking of the abundance of the species involved. Other prey species of importance which were not included in trapping data were cottontail rabbits and pocket gophers. Cottontails were particularly abundant in brushy areas bordering the foothills, in prairie-dog towns, and near abandoned homesites and intermittent streams on prairie lands. Pocket gophers were local in distribution on the study area. In certain areas along the foothills, *Thomomys talpoides* occurred in large concentrations. On the Pawnee Site, this species was more widespread but less concentrated. In most agricultural areas, *T. talpoides* was not found, and *Geomys bursarius* occurred only in low numbers, mostly along the flood plain of the Cache la Poudre River.

FOOD HABITS

Regurgitated pellets have been used in numerous studies to determine owl food habits. Errington (1930) established precedents in the techniques of pellet analysis which have been used with some modification by most investigators. I believe it has been adequately shown that pellet contents are reliable for the study of owl food habits—at least for the four species I have studied (Errington 1930; Glading et al. 1943; Moon 1940; Ticehurst

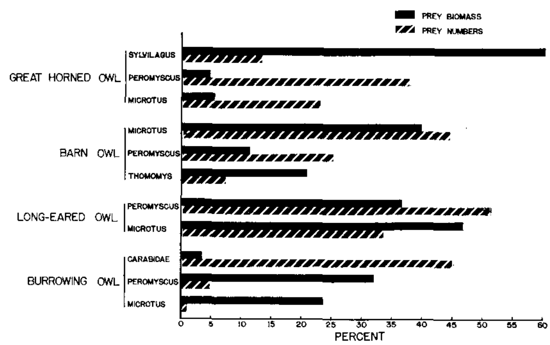

FIGURE 1. Comparison of major prey of four owl species from north-central Colorado.

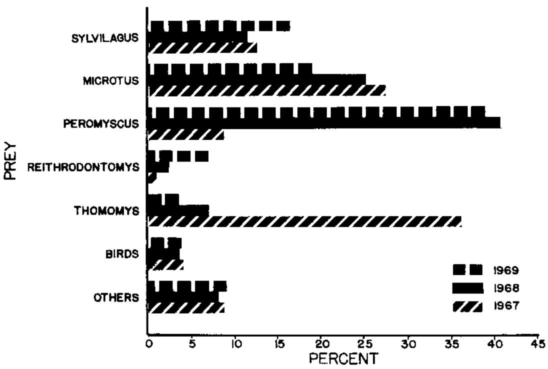

FIGURE 2. Comparison of Great Horned Owl prey for 3 years.

1935; Wallace 1948). Some prey may have been missed or not even represented in the pellets, but I believe that if this oversight existed, it was insignificant.

A potential problem in studying food habits from pellets is the possibility of some pellets lasting for a long time in the wild before decomposing. To test this, I placed groups of 10 pellets of each owl species in natural situations and visited them at intervals to evaluate their condition. Great Horned Owl pellets placed in June were badly disintegrated in 2 months and none remained whole. In 10 months only a few bones remained. Barn Owl pellets also put out in June were still whole but badly weathered in 2 months. No whole ones were left after 10 months. Pellets of Long-eared Owls planted in December remained whole but were distinctly weathered after 6 months. Burrowing Owl pellets, consisting of only vertebrate remains, were totally disintegrated after 2 months in summer. I observed many Burrowing Owl pellets, made only of insect parts, fall apart as they dried following ejection.

Similar results on pellet aging were obtained by Fairley (1967) and Wilson (1938). It is apparent then that few owl pellets will exist for a year under natural conditions in north-central Colorado. Pellets that remained whole

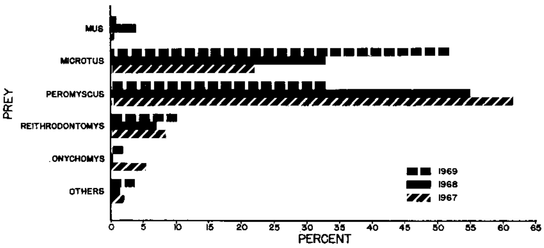

FIGURE 3. Comparison of Long-eared Owl prey for 3 years.

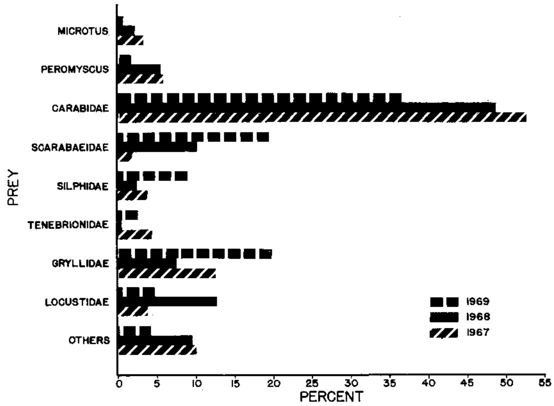

FIGURE 4. Comparison of Burrowing Owl prey for 3 years.

rapidly took on a weathered and loose appearance, easily separating them from darker, compact, fresh pellets. It is possible, however, that under certain climatic conditions owl pellets might remain whole for a long time, and caution should always be used, especially where monthly or yearly trends in food habits are of interest.

Pellets were collected during 1967, 1968, and 1969 at 71 sites. Two hundred and forty-six separate collections were made from these sites, yielding 14,263 prey individuals. Complete listings of prey are given in appendices II–V. Important prey of each owl are compared in figure 1. Three years of prey data were combined for each of the owls, compared among the four species, and found to be significantly different ($\chi^2 = 416.96$, $P < 0.005$, 27 d.f.). The per cent occurrence of major prey in all whole pellets collected for each owl species and in groups of pellets collected at the same time and place was also used to estimate importance of prey in the owls' diets.

A significant difference was indicated in prey composition among the 3 years for the

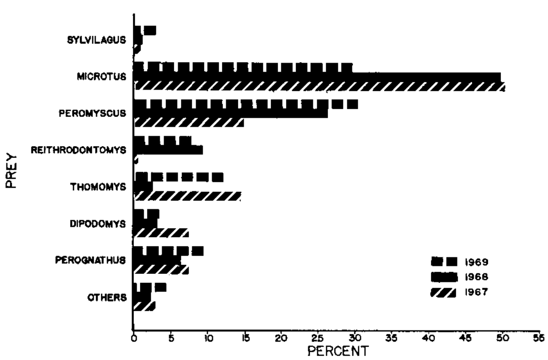

FIGURE 5. Comparison of Barn Owl prey for 3 years.

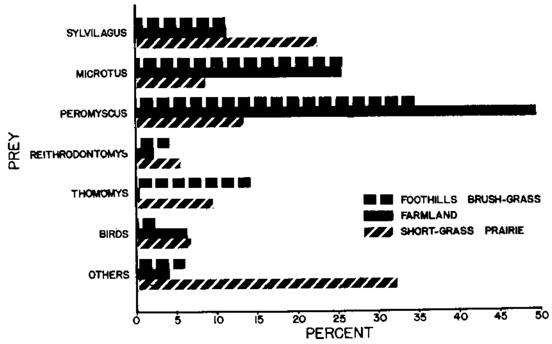

FIGURE 6. Comparison of Great Horned Owl prey from three habitats.

Great Horned Owl ($\chi^2 = 34.46$, $P < 0.005$, 12 d.f.) and for the Barn Owl ($\chi^2 = 32.24$, $0.01 < P < 0.005$, 16 d.f.), indicating prey were selected in different proportions. Neither the Long-eared Owl ($\chi^2 = 9.04$, $0.75 < P < 0.50$, 12 d.f.) nor the Burrowing Owl ($\chi^2 = 1.09$, $P > 0.995$, 18 d.f.) showed a significant difference in prey composition among the 3 years (figs. 2–5).

Food-habits data were also used to ascertain whether differences existed in each owl's prey from different habitat types. Collection sites for Great Horned and Barn Owls were classified as either (1) foothills brush-grass mixture, as found on and between hogbacks bordering the Rocky Mountain Front Range; (2) farmland with crops other than natural grasses; or (3) short-grass prairie. Sites where Long-eared and Burrowing Owls were found were classified as farmland or short-grass prairie. Tests of significance were also made of these data. A significant prey composition difference was found in Great Horned Owls ($\chi^2 = 31.29$, $P < 0.005$, 12 d.f.) and Barn Owls ($\chi^2 = 57.46$, $P < 0.005$, 16 d.f.) among the habitat types described. No difference was indicated for the Long-eared Owl ($\chi^2 = 8.03$, $0.25 < P < 0.10$, 6 d.f.) or the Burrowing Owl ($\chi^2 = 0.20$, $P > 0.995$, 9 d.f.) in this respect (figs. 6–9).

A number of other comparisons were made in prey composition where two to four collec-

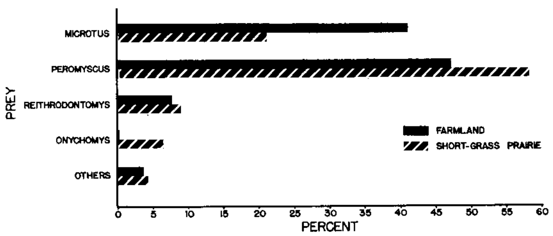

FIGURE 7. Comparison of Long-eared Owl prey from two habitats.

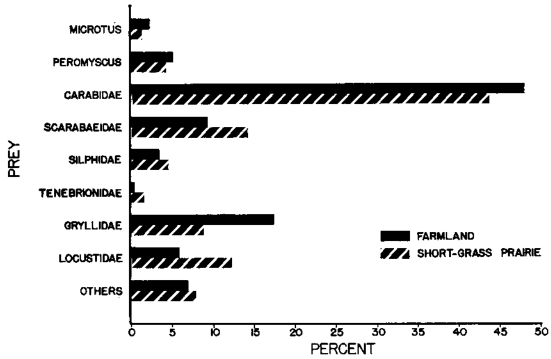

FIGURE 8. Comparison of Burrowing Owl prey from two habitats.

tion sites of different species or different pairs of the same species were located in close geographical proximity (table 2).

All prey data from known age pellets collected in 1968 and 1969 were used for determining prey variation through the year. Pellets were collected during all months of the year for the Great Horned Owl. August and September were combined as were October, November, and December because of small sample sizes in those months. Largest samples came from the nesting period, while late summer and winter provided the smallest numbers of pellets. Errington et al. (1940) also found it difficult to collect adequate prey data for periods other than the breeding season because young owls newly independent of their parents tended to wander erratically and adults used specific roosts less regularly at this time.

Seasonal variation of prey for Great Horned Owls in my study is listed in table 3. Fitch (1947) and Errington et al. (1940) gave seasonal prey distribution for Great Horned Owls from California and the north-central United States, respectively. Fitch found no marked changes in food habits for the California owls nor did Errington et al., but the latter lumped many prey species of similar weights together.

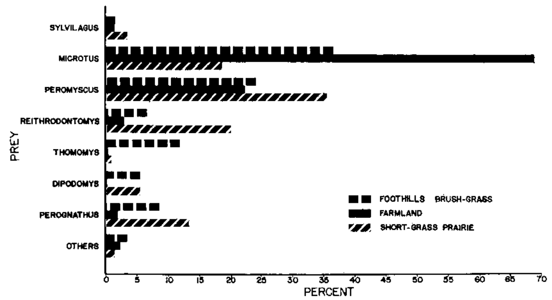

FIGURE 9. Comparison of Barn Owl prey from three habitats.

TABLE 2. Prey of owls compared from geographically close nest and roost sites.

Owl groups	Prey by per cent of numbers: *Sylvilagus*	*Peromyscus*	*Microtus*	*Perognathus*	*Thomomys*	Insects	Statistical comparison
Great Horned	21.7	44.8	18.8	2.0	—	—	$\chi^2 = 126.54$
Long-eared	0.4	45.8	42.8	0.1	—	—	$P < 0.005$
Burrowing	—	0.7	1.7	0.3	—	95.1	21 d.f.
Barn	0.6	20.1	72.1	3.1	—	—	
Great Horned	7.7	43.5	27.6	0.8	0.4	—	$\chi^2 = 52.17$
Long-eared	0.1	60.2	22.9	—	0.1	—	$P < 0.005$
Burrowing	0.1	4.8	1.5	0.3	—	93.3	27 d.f.
Barn	3.0	36.5	18.0	14.1	1.1	—	
Great Horned	23.1	13.9	8.5	0.7	8.8	9.5	$\chi^2 = 22.75$
Long-eared	6.2	32.3	3.1	9.2	1.5	—	$0.75 < P < 0.50$
Burrowing	0.6	3.7	5.0	—	—	81.5	27 d.f.
Barn	8.8	26.5	5.9	5.9	—	—	
Great Horned	13.5	39.8	27.4	1.1	0.7	—	$\chi^2 = 38.69$
Barn	0.8	24.4	49.3	6.5	—	—	$P < 0.005$ 5 d.f.
Great Horned	8.3	34.9	21.2	4.0	22.8	—	$\chi^2 = 68.22$
Barn	1.6	24.5	33.9	9.3	15.0	—	$P < 0.005$ 7 d.f.
Great Horned	8.9	61.5	20.5	—	—	—	$\chi^2 = 5.91$
Barn	1.6	33.5	57.3	—	—	—	$0.25 < P < 0.10$ 4 d.f.

I collected Long-eared Owl pellets from only 5 months with a period in spring, one in late summer, and one in winter. The results are shown in table 4. Graber (1962) found little variation in Long-eared Owl food from Illinois in three collections from 1 January to 1 April. In England, Fairley (1967) tentatively explained seasonal prey variation because of the changes that occurred in vegetative cover and because rodents moved over strange terrain at certain times of the year which made them more vulnerable to capture.

Burrowing Owl pellets were recovered for all months the birds were resident on the study area except October. Smaller samples were obtained early and late in their period of residency. At those times, before and after breeding, the owls did not use regular perches

TABLE 3. Seasonal variation in Great Horned Owl prey by per cent of numbers.

Prey	Month of origin: J	F	M	A	M	J	J	A–S	O–D
Mammals									
Lepus spp.	2.0	1.3	0.8	0.1	0.3	2.4	—	2.1	10.2
Sylvilagus spp.	10.1	20.0	13.2	9.2	13.0	25.2	18.5	12.5	32.7
Thomomys talpoides	—	7.1	0.8	2.6	12.0	22.8	11.6	8.3	6.1
Dipodomys ordii	—	8.4	0.8	1.7	1.4	—	2.7	14.6	6.1
Perognathus spp.	—	0.6	1.2	1.5	4.8	1.6	4.8	—	2.1
Reithrodontomys spp.	22.2	5.2	1.2	4.5	1.4	—	0.7	—	4.1
Peromyscus spp.	46.5	29.7	47.1	52.0	27.4	18.9	21.2	12.5	14.3
Onychomys leucogaster	1.0	2.6	—	0.7	0.3	—	—	2.1	6.1
Neotoma spp.	—	0.6	—	0.3	—	0.8	0.7	—	—
Microtus pennsylvanicus	—	0.6	6.6	5.8	2.4	0.8	4.1	—	—
Microtus ochrogaster	15.2	20.6	19.8	15.4	29.8	23.6	15.0	22.9	10.2
Ondatra zibethicus	—	0.6	0.4	0.3	0.7	0.8	—	—	—
Other mammals	1.0	—	1.2	0.5	—	1.6	—	—	2.1
Birds	2.0	2.5	5.3	4.8	5.3	1.6	5.5	2.1	6.1
Fish	—	—	1.2	0.1	0.3	—	—	—	—
Arthropods	—	—	—	0.1	0.7	—	13.7	22.9	—
Total prey	99	155	242	952	292	127	146	48	49

TABLE 4. Seasonal variation in Long-eared Owl prey by per cent of numbers.

Prey	Month of origin				
	March	April	May	Aug.	Dec.
Mammals					
Sylvilagus spp.	2.4	—	0.6	17.4	—
Reithrodontomys spp.	5.9	10.3	7.0	17.4	8.1
Peromyscus spp.	29.4	33.2	55.3	34.8	44.4
Onychomys leucogaster	—	—	0.2	4.3	9.7
Microtus pennsylvanicus	10.6	2.8	4.8	—	4.8
Microtus ochrogaster	50.6	52.7	27.6	—	21.8
Mus musculus	1.2	0.7	4.3	—	0.8
Other mammals	—	0.4	0.2	17.3	8.0
Birds	—	—	0.1	8.7	2.4
Total prey	85	575	863	23	124

for any length of time; their pellets were widely scattered, making collection difficult. I found Burrowing Owls feeding heavily on insects during the entire time they were on the area (table 5). More data from the earliest and latest dates they were present might indicate more dependence on vertebrates when insects were fewer in number. In northern Iowa, Burrowing Owls were found to feed heavily on vertebrate prey from June to early August, on insects from mid-August to September, and then on vertebrates again (Errington and Bennett 1935).

I collected pellets of Barn Owls in 9 months, but samples from March and December were so small that they were combined with April and October, respectively. Seasonal variations I found in Barn Owls are shown in table 6. Many authors have listed seasonal prey changes in Barn Owl foods. Fitch (1947) found the changes in foods of California Barn Owls were related to prey activities such as hibernation of pocket mice and above-ground activity by pocket gophers. In Oregon, three prey species were predominant in Barn Owl diets except during summer when the variety of prey increased (Giger 1965). Evans and Emlen (1947) observed that fluctuations in prey composition of Barn Owls were related to seasonal changes in prey populations and seasonal activity changes of prey as well as to long-term prey fluctuations in some cases. Day-to-day fluctuations in food occurrence were compared to weather data by Evans and Emlen but no correlation was obtained. Barn Owls in Michigan were observed to feed on a relatively steady, unusually high percentage of *Microtus* during a year at which time *Microtus* populations were at their peak (Wallace 1948). Glue (1968) and Fairley (1966) also listed Barn Owl foods from England that showed trends in prey composition but did not discuss possible causes of variations.

TABLE 5. Seasonal variation in Burrowing Owl prey by per cent of numbers.

Prey	Month of origin					
	April	May	June	July	August	September
Mammals						
Sylvilagus spp.	1.1	0.1	0.1	0.1	—	—
Perognathus spp.	—	0.6	0.3	0.1	—	—
Reithrodontomys spp.	4.6	0.8	0.5	1.1	—	—
Peromyscus maniculatus	13.8	8.5	2.9	4.5	2.6	—
Microtus ochrogaster	4.6	1.8	1.5	2.6	1.7	—
Other mammals	—	0.4	0.2	0.1	—	0.6
Birds	—	0.1	0.5	0.1	—	—
Reptiles	—	—	0.1	0.1	—	—
Crayfish	—	0.2	0.4	0.8	0.9	—
Insects						
Gryllidae	8.0	2.9	16.2	8.7	8.6	14.3
Locustidae	9.2	8.9	10.0	15.5	1.7	10.9
Cicindelidae	—	0.8	0.6	0.4	—	—
Carabidae	50.6	45.9	41.9	48.4	47.4	67.4
Scarabaeidae	1.1	19.6	13.0	5.8	20.7	0.6
Silphidae	2.3	2.8	6.0	3.3	0.9	1.7
Tenebrionidae	—	—	1.3	0.1	12.9	4.6
Curculionidae	1.1	2.7	1.2	0.8	2.6	—
Other insects	2.3	3.6	3.4	6.2	—	—
Spiders	1.1	0.2	0.1	—	—	—
Total prey	87	1,204	2,468	737	116	175

TABLE 6. Seasonal variation in Barn Owl prey by per cent of numbers.

Prey	Month of origin						
	March–April	May	June	July	August	September	October–December
Mammals							
Sylvilagus spp.	1.1	4.2	2.2	1.7	0.7	1.1	2.7
Thomomys talpoides	3.3	7.6	8.2	11.0	4.6	0.8	—
Dipodomys ordii	2.8	5.5	3.8	5.3	2.7	1.9	—
Perognathus spp.	4.4	8.8	10.3	10.7	3.8	2.2	2.7
Reithrodontomys spp.	11.7	7.6	10.8	6.4	3.9	5.6	10.0
Peromyscus spp.	40.3	40.6	31.2	20.5	15.9	31.3	23.6
Onychomys leucogaster	0.6	0.9	1.8	1.4	0.4	0.5	2.7
Microtus pennsylvanicus	8.9	5.5	4.8	4.5	14.5	14.0	12.7
Microtus ochrogaster	25.6	18.2	25.6	35.5	51.4	37.1	43.6
Mus musculus	—	—	—	0.7	0.9	1.9	—
Birds	0.6	1.2	0.7	2.3	0.7	1.4	—
Total prey	360	330	683	702	564	358	110

I suspect that there are many causes for seasonal variation in prey of the various owls in north-central Colorado. Seasonal vegetational changes may make some species more available to owl predation for a time. Daily activity patterns of owls and certain prey may overlap at some times of the year and not at others. Longer daylight hours in summer together with young to feed may require owls to forage longer and thus make some prey available that are not at other times. A number of the prey species hibernate. Individuals which are unfamiliar with their surroundings are probably more vulnerable to predation, and during migration, when seeking mates and when young disperse, many prey individuals are in unfamiliar areas. Little is known about the specific ecology of most of the animals which serve as prey for owls in Colorado. This information is necessary before many of the above activities can be applied to a particular predator-prey situation.

I combined material from all habitat classifications for seasonal analysis and some variations may have been affected by the source of the majority of pellets for a particular month.

FACTORS AFFECTING PREY CAPTURE

Methods of hunting. I observed that Great Horned Owls hunt by perching on vantage points such as cliffs, poles, and trees. Generally, they would remain at one perch for 3–5 min and then move to another. If prey were sighted, a direct, low, rapid flight would be initiated in an attempt to capture it. These flights varied from 17 to 100 m in length. I did not see any harrier-like hunting flights, but this method has been seen in Great Horned Owls (Sherman 1912; Smith 1968). Baker (1962) reported that Great Horned Owls captured bats in flight by flying into a stream of bats emerging from a cave and thrusting with their talons. I believe, however, that the most common, and probably most efficient, hunting technique of Great Horned Owls is a flight from a perch.

Burrowing Owls were observed to hunt by direct flights to prey from a perch on the ground or fence post, by hovering flights of about 16 m in height, by running down prey on the ground, and by flights from a perch to flying insects. There was no apparent relation of type of hunting used to time of day. Both hovering flights and the capture of flying insects were commonly observed during daylight hours. Thomsen (1971), on the other hand, indicated that most hovering was seen after sundown and flycatching was rarely observed in California. In 60 hr of observation I saw only insects captured by all methods. Small birds often fed or flew close to foraging Burrowing Owls without being pursued. Most vertebrates must have been captured when light levels were low, giving the owl a visual advantage.

Barns Owls hunted strictly after dark which made direct observation virtually impossible. Lack (1966) suggested that their long wings are suited for hunting on the wing in open areas. Unusual observations of Barn Owls hunting in daylight gave an actual indication of methods used (Harte 1954; Haverschmidt 1970). Harte saw a bird flying slowly at 2 to 6 m high for about 50 m. It would then climb rapidly to 10 m and hover for 20 sec with feet dangling and suddenly drop to the ground after prey. Haverschmidt's observations were of a Barn Owl quartering over open fields and of another which pounced to the ground several times in the course of a flight along a grassy roadside. Barn Owls were also observed, at a flood-lit area, to perch openly on a tree and then drop to bushes below in capturing sparrows at a communal roost (Sage 1962). Twente (1954) observed a Barn Owl preying on bats in the manner described above for Great Horned Owls.

I was also not able to observe Long-eared Owls hunting. The long wings of this species seem adapted to open area hunting as in the Barn Owl, and studies conducted where both open and forested areas were at hand support this (Getz 1961; Randle and Austing 1952; Weller et al. 1963). Since the closely related Short-eared Owl (*Asio flammeus*) is similar anatomically, and since both hunt open land, it might be assumed that their hunting techniques are similar. Armstrong (1958) found that courtship flights of the two are markedly alike. Short-eared Owls hunt by low, quartering flights. Terres and Jameson (1943) saw them hover, then drop to the ground after prey. Johnston (1956) reported that their most common foraging method was harrier-like flight, but they also occasionally chased prey from high perches when they were available.

Time of hunting. I observed three Great Horned Owl nest sites to determine time hunting began. Two other nests were monitored with an event recorder to record time of activity. Forty-eight hours of recordings were made at these sites (ca. 12 hr per night). Fifteen nests of Burrowing Owls were observed for time of hunting activity and 338 hr of event recorder tracings were made at two burrows (24 hr per day). One Barn Owl nest cavity was monitored with the event recorder resulting in 261 hr of recorded activity (ca. 9 hr per day). I observed two Barn Owl sites for the times that daily activity began. No recordings or observations were made on nests or roosts of Long-eared Owls as none was found during that part of the study. Glas and Nielsen (1967) observed that the average departure time of Long-eared Owls from a communal roost was 39 min after sunset.

Great Horned Owls began hunting long before full darkness. Departure averaged 20 min after sunset in spring. I did not observe any diurnal hunting as has been reported (Dixon 1914; Fitch 1947; Packard 1954; Sherman 1912; Vaughan 1954).

Barn Owls were strictly nocturnal in their activities in Colorado. I never found them leaving their roosts or nests before almost total darkness. First activities averaged 90 min after sunset in summer. However, Barn Owls have been observed to hunt in daylight (Harte 1954; Haverschmidt 1970), and Reed (1897) said they left their roosts before sunset when there were young to feed. Numbers and availability of prey are probably the chief determinants of the duration of hunting. Evidently in north-central Colorado, sufficient prey could be captured in the period of darkness.

Burrowing Owls were active in every hour of the day. Adults were seen foraging at all daylight hours even when there were no young to feed. However, there were three peaks of activity in a day: one of about 5 hr centered around sunrise; a short one of 2 hr just before midday; and another 5-hr period centered around sunset. In Minnesota, Grant (1965) found activity was concentrated in early morning and late evening, with little during the day. Coulombe (1971) said that, in southern California, Burrowing Owls were crepuscular in their foraging.

Vision in low light. The Great Horned Owl tested was able to directly approach dead mice under $13(10^{-6})$ foot-candles of illumination. Direct approach by sight was implied by tracks in sand. At $28(10^{-7})$ foot-candles, it found only one mouse and then by random searching. In complete darkness the Great Horned Owl did not attempt to search for mice. A rather distinct threshold at $70(10^{-8})$ foot-candles was found for the Long-eared Owl below which the bird no longer was able to find dead mice. Above that level the owl approached mice directly with little or no wandering. The Barn Owl took dead mice with no random searching at $13(10^{-6})$ foot-candles, at $70(10^{-8})$ foot-candles it was not able to. In total darkness, mice were still found by random searching. The Burrowing Owl was able to approach mice directly at illuminations of $11(10^{-5})$ foot-candles only. At $50(10^{-6})$ foot-candles, mice were found but some random searching was indicated. As in the Barn Owl, mice were found in total darkness by much searching.

Long-eared, Barn, and Great Horned Owls were able to see in quite low levels of light. Precise discrimination of their relative abilities to do so was not possible with the equipment available, but all three were apparently in a narrow range. Burrowing Owls, on the other hand, were not able to see in as low a light range. Only one bird of each species was used and it is not known what the extent of individual differences might be.

For a complete discussion of the adaptations of owls' eyes for nocturnal vision and prey capture, see Walls (1945) and Hocking and Mitchell (1961).

Prey capture by hearing. Virtually every part of the owl ear is modified for better hear-

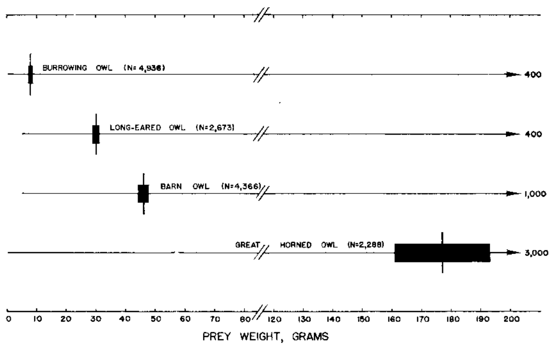

FIGURE 10. Prey weight of four owl species. Horizontal line = range; verticle line = mean; black rectangle = 95% confidence limits of the mean.

ing than other birds. See Pumphrey (1948) and Schwartzkopff (1955) for complete discussions of bird ears and owls' adaptations in hearing. Payne (1962), in his careful study of the Barn Owl's ability to locate and capture prey in total darkness, found that this ability was due to hearing only and not to echolocation, heat sensing, or infrared vision.

I determined that all four species in captivity were able to capture prey by hearing. The Great Horned Owl was least successful, possibly because of its lesser maneuverability in the relatively small space available.

It is likely that neither hearing nor vision functions entirely independently in prey capture by wild owls. Vision would not have to be supplemented by hearing when light levels were high, but hearing might serve to locate prey not directly in the line of sight. At very low light levels, and light must often fall below that in which small, hidden prey can be seen, hearing would be the most important sense in locating prey, with vision functioning only to avoid collision with large obstacles. Hearing may also be used when light levels are relatively high but prey is hidden or in a cryptic environment. Godfrey (1967) and Tyron (1943) cite examples of this in Great Gray Owls (*Strix nebulosa*).

Morphological aspects. Predator size is logically related to size of prey. Although the range in prey size an owl can subdue may be large, an optimum size that can be captured most efficiently probably exists because each prey individual must be found and caught separately. An average prey size was calculated for each owl species using total prey numbers and mean prey weights. Dice-Leraas diagrams were constructed which indicated a significant difference existed in mean prey size selected by the four owls (fig. 10). Table 7 lists prey classified into weight groups for the four owls. Storer (1955) postulated

TABLE 7. Estimated weight distribution of the prey of four owls in north-central Colorado.

Weight of prey, g	Per cent of prey in each class: Burrowing Owl	Long-eared Owl	Barn Owl	Great Horned Owl
0–1	91.2	—	—	1.3
1–9	0.5	0.4	4.5	1.6
9–20	0.8	10.2	7.8	4.0
20–30	4.9	52.2	25.8	39.4
30–50	2.2	36.6	48.3	24.7
50–80	0.1	0.3	4.0	2.5
80–140	0.2	0.2	7.8	9.9
140–210	—[a]	—	0.02	0.7
210–500	0.1	0.4[a]	1.6[a]	5.1
500–1,000	—	—	0.4	9.6
1,000–1,500	—	—	—	0.3[a]
1,500–2,000	—	—	—	—
2,500–3,000	—	—	—	0.9
Mean prey weight, g	3	30	46	177
(Mean prey weight / Mean owl weight) × 100 =	1.9%	11.1%	9.6%	11.4%

[a] Class containing the owl's weight.

that since the larger the bird the faster it must fly to remain aloft, a similar relationship between predator size and speed when striking prey must exist. If this were true, he said the force with which a hawk strikes (product of its weight and velocity) will be greater by more than the difference in weight between small and large avian predators. This, then, would make it relatively easier for a larger owl to stun and kill large prey.

Another factor allowing a predatory species to utilize a larger range of prey is sexual dimorphism in body size. Earhart and Johnson (1970) found a large difference in body weight between sexes in Great Horned Owls, a much smaller difference in Barn and Long-eared Owls, and a very small difference in Burrowing Owls. My food-habits data show that the Great Horned Owl, the species with the most pronounced sexual dimorphism, preyed on the largest range in size of prey while the other three species, with much less sexual dimorphism, tended to specialize on prey in smaller ranges in size.

Size and strength of talons are also related to the size of prey that can be held and killed. Goslow (1967) found that Barn and Burrowing Owls are adapted to pin prey to the ground rather than scoop it up in hawk-like fashion. This method of capture would be advantageous when attacking prey in dim light, or when the prey is concealed under grass. Aim would then not have to be as exact. Payne

(1962) found that the eight toes of Barn Owls were spread just before contact in a symmetrical pattern to maximize the area covered. Talon spread was 150 × 75 mm. Approximate talon spread for individuals of the other three species I measured was 200 × 100 mm for the Great Horned, 80 × 60 mm for the Long-eared, and 75 × 50 mm for the Burrowing Owl. I also found a great deal of difference in relative talon strength. A force of only 500 *g* was sufficient to open firmly clenched Burrowing Owl talons. Toes of the Long-eared Owl required 1350 *g* of force to open them. The Barn Owl foot required nearly 3000 *g* of force to open it. Great Horned Owls have extremely strong talons and 13,000 *g* of force were applied to open them.

Amount of weight carried per unit of wing surface area was measured as a means to compare the efficiency of hunting methods in the four owls. Great Horned Owls carry the most weight per unit of wing surface (ratio of wing surface area to body weight was 1.94, $n = 8$), and it appears that hunting on the wing would be less economical than in the other species. Long-eared Owls had the lightest wing loading (4.61, $n = 3$) and wing-hunting should be most efficient in that species. Barn and Burrowing Owls were intermediate in wing loading (3.62 and 3.67, respectively, both $n = 2$). Flight of Long-eared, Barn, and Burrowing Owls is bouyant and moth-like while that of Great Horned Owls is much more direct.

Flight feathers are modified in all four owls for silent flight. In the Barn and Burrowing Owls, the feather blades are soft, trailing edges of primaries and secondaries are fringed, and the upper surface of those feathers is downy. In addition to those characteristics, Great Horned and Long-eared Owls have comb-like projections on the forward edge of the leading primaries. All body feathers are also soft and downy in the four species. These muffling features are least developed in the Burrowing Owl and its flight noise is slightly audible to human hearing. Besides being silent to prey's ears, silent flight in owls would not interfere with locating prey by hearing. In view of the demonstrated ability of some owls to locate prey by hearing, this aspect may actually be more important than preventing potential prey from hearing the owl's approach.

FEEDING NICHE SEGREGATION

Gause's competitive exclusion principle states that no two species can occupy the same niche at the same time or place. Ashmole (1968), however, argued that ecological segregation does not necessarily indicate the operation of competitive exclusion and suggested that many natural habitats cannot be assumed to contain the greatest number of related species which could exist there if the opportunity to establish themselves were available.

Although many raptors overlap on certain food species, they usually do not on all their food species. Several raptors may feed on the same prey when it is abundant and then each turn to others when it is not. Species may compete for a while when one's normal prey is low, but the food supply usually changes before one predator is eliminated. Thus, competition is dynamic, not constant (Lack 1946).

Much overlap existed in prey consumed by the four owls considered here, but each owl specialized on different groups and sizes of prey. The Great Horned Owl in north-central Colorado fed on the widest range of prey, in both size and variety. Errington (1932) stated that choice plays a minimum role in horned owls' hunting and that they will take whatever is first encountered and can be caught. Obviously, from food-habits studies across the United States, Great Horned Owls are efficient predators. I believe, however, that their predation is not as completely random as Errington suggested. Density of the prey, overlap of time of activity between prey and predator, ease of killing and learning by individual owls must all be factors in determining what portions of the diet a particular prey will comprise. For the Great Horned Owl, very small prey would be inefficient, unless caught very easily, because each must be pursued and caught individually. Colorado Great Horned Owls appeared to select their mammalian prey in general relation to the prey populations. Cottontails, however, appeared to be selected as prey out of relation to their population status. Local populations such as pocket gophers were also heavily preyed upon by certain pairs of horned owls. The few insects included were from late summer pellets and may represent the first attempts at killing by newly independent young. No patterns were apparent in other prey and no other groups were of considerable importance.

Long-eared Owls were the most restricted in diet of the four owls. This has been reported elsewhere (Korschgen and Stuart 1972). Over 99% of Long-eared Owl prey in my study was mammalian, but only four or five species were represented in significant numbers. *Microtus* spp. have been the most important prey of Long-eared Owls in most published studies of their foods. The only other instance found where *Peromyscus* spp. were more important was also a Colorado study (Catlett et al. 1958). Long-eared Owls took their prey in accordance with the relative abundance, except that *Microtus* spp. must have been selected above their ranking. No prey was of large size. Largest were small, juvenile cottontails which are not difficult to kill. Evidence that Long-eared Owls can, and occasionally do, kill larger prey was given by Errington (1933) and Sutton (1926).

The prey of Burrowing Owls was variable in type but fairly limited in size. Majority of the biomass in their diet was from mammals. All cottontail remains were of small juveniles. Insects, however, were by far the most dominant in numbers. Grasshoppers appeared to be the most numerous large insects available to Burrowing Owls, but beetles occurred much more frequently in the diet. Similar results were reported by Kelso (1938). He found that Burrowing Owls preyed most heavily on the most available prey—grasshoppers. However, the per cent of grasshoppers in his data was also low in proportion to their availability; beetle numbers eaten were five times their percentage of the prey population. Parts of several jackrabbits (*Lepus* spp.), a large duck, and a domestic cat were found around Burrowing Owl burrows, evidently brought in as carrion to be eaten. These specimens were not reported with the food habits, but other food also may have been consumed as carrion. Remains of three immature Burrowing Owls were found in pellets at the same burrow and may have been eaten by their nest mates. Cases of possible cannibalism have been reported (Bent 1938; Robinson 1954). Even though insects are much smaller than the largest prey Burrowing Owls can subdue, it may be more economical to concentrate on them because of their abundance and ease of capture.

Barn Owls fed on a variety of mammals and several species of birds, mostly grassland species. No pattern appeared in predation on birds except that species which roost in open grassy areas were eaten most often. Again, mammals were the chief prey, with a number of species contributing significant percentages. *Microtus* spp. were dominant and evidently actively selected as prey. All but one of the cottontails found were juveniles. There are conflicting opinions in the literature on the ability of Barn Owls to utilize alternate sources of food. Some observers have thought that when Barn Owls are faced with a shortage of mammalian prey, such as under conditions of deep snow, they are unable to shift to birds as prey even though birds are plentiful (Errington 1931; Stewart 1952). However, Bonnot (1928) found Barn Owls feeding almost exclusively on young petrels and Carpenter and Fall (1967) reported a high percentage of Red-winged Blackbirds (*Agelaius phoeniceus*) in Barn Owl foods. This apparent conflict might be resolved when roosting habits of the birds in question are known. Birds roosting on the ground or in marsh vegetation may be more vulnerable to predation by Barn Owls than those in trees or shrubs. It may be that Barn Owls are not able to search out effectively and capture birds roosting individually in heavy cover, but they apparently are able to utilize large aggregations of roosting birds (Glue 1968; Sage 1962). Barn Owls observed feeding on grunion (*Leuresthes tenuis*) provided an example of adaptability (Gallup 1949).

MacArthur (1961) postulated that if a predator depends on a fluctuating food supply, it will be better off to switch its attentions to whatever food is available. If several food species alternate as most available, the specialization to feed on one or the other would often be harmful. I discovered there may be a differential ability to switch foods between years and habitats in the four owls. The fact that 3 years of food-habits data and data from different habitats were significantly different in composition reflects a degree of flexibility in feeding for Great Horned and Barn Owls. No significant fluctuations were found in Burrowing or Long-eared Owls from year to year or in different habitats. This may reflect a lack of change in prey populations or an inflexibility in the owl's foraging. The first possibility is more likely for the Burrowing Owl, judging from the variety of prey taken. The latter choice may be accurate for the Long-eared Owl since its choice of foods is restricted.

I believe the primary factor operating in feeding niche segregation among these four species is prey-size selection. The Great Horned Owl fills the niche of the large, powerful, nocturnal predator capable of capturing a wide range of prey in size and type. It is a sedentary species, hunting in small areas, and apparently able to do so because of its high versatility in prey capture. The niche of the Burrowing Owl is that of a small avian predator adapted for diurnal and crepuscular hunting on open lands. The feeding niches of

Barn and Long-eared Owls appear to be the most similar of the four species. A larger range of prey is available to the larger Barn Owls but both species are adapted for a similar mode of hunting and for capturing prey in very low light.

SUMMARY

Great Horned, Long-eared, Burrowing, and Barn Owls were studied in north-central Colorado from 1966 to 1970 to determine niche segregation in feeding ecology. Mechanisms which contribute to niche segregation are described and discussed.

Food habits were studied for each owl by pellet analysis. Great Horned Owl prey totaled 2288 individuals; Long-eared Owl prey, 2673; Barn Owl prey, 4366; and Burrowing Owl prey, 4936. Great Horned Owls preyed on the widest variety of species, with *Sylvilagus* being most important in biomass consumed. Long-eared Owls fed on a much smaller array of prey, almost entirely mammalian, with *Peromyscus* and *Microtus* the most important. Barn Owls fed largely on small mammals, with *Microtus* most important. Prey of Burrowing Owls included insects as most numerous but mammals contributed more biomass.

The four species of owls selected significantly different frequencies of prey ($P < 0.005$). Mean prey size selected by each owl was also found to be significantly different ($P < 0.05$).

Significant differences in prey composition from different years and different habitats were found for the Great Horned and Barn Owls ($P < 0.005$). Nonsignificant differences were found for the Long-eared and Burrowing Owls.

Barn and Long-eared Owls were found to be strictly nocturnal in their hunting. Much of the Great Horned Owl's hunting was crepuscular. Burrowing Owl foraging was both diurnal and crepuscular.

Great Horned Owls hunted primarily by flights from observation perches. Wing loading in Great Horned Owls was 1.94 cm^2 of wing surface area per gram of body weight. Long-eared and Barn Owls both had lower wing loading ratios—4.61 and 3.62, respectively—apparently being adapted for hunting on the wing. A variety of hunting methods was used by Burrowing Owls. Wing-loading ratio was 3.67 in this species.

The Great Horned Owl tested was able to find dead mice by sight under an illumination of $13(10^{-6})$ foot-candles. The Barn Owl also found mice at $13(10^{-6})$ foot-candles. Only $70(10^{-8})$ foot-candles were required by the Long-eared Owl to find dead mice, but the Burrowing Owl was unable to locate dead mice by sight at light levels less than $50(10^{-6})$ foot-candles.

All four species successfully captured live mice in complete darkness by hearing.

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APPENDIX I. Estimated weights of prey species used to determine biomass consumed by owls and average prey size captured.

Species	No. of records	Mean weight g	Source
Mammals			
Lepus spp. (adult)	15	2,800	Seidensticker 1968; CSU[a]
Lepus spp. (juv.)	0	1,400	estimated
Sylvilagus spp. (adult)	193	1,000	Seidensticker 1968; Craighead and Craighead 1956; CSU[a]
Sylvilagus spp. (juv.)	0	400	estimated
Microtus ochrogaster	50	40	CSU[a]
Microtus pennsylvanicus	50	45	CSU[a]
Ondatra zibethicus	10	700	CSU[a]
Peromyscus spp.	50	21	CSU[a]
Reithrodontomys spp.	41	12	CSU[a]
Onychomys leucogaster	37	38	CSU[a]
Neotoma spp.	15	217	CSU[a]
Marmota flaviventris	?	3,000	Burt and Grossenheider 1964
Cynomys ludovicianus	?	1,200	Burt and Grossenheider 1964
Mus musculus	15	18	CSU[a]
Rattus norvegicus	14	221	CSU[a]
Dipodomys ordii	129	68	Desha 1967; CSU[a]
Perognathus hispidus	4	39	CSU[a]
Perognathus small spp.	13	8	CSU[a]
Thomomys talpoides	649	132	Hansen 1960
Geomys bursarius	5	200	CSU[a]
Zapus princeps	9	25	CSU[a]
Mustela frenata	8	178	CSU[a]
Cryptotis parva	3	5	CSU[a]
Myotis spp.	3	8	CSU[a]
Birds			
Aythya americana	46	1,247	Kortright 1943
Anas crecca	198	312	Kortright 1943
Phasianus colchicus	135	1,133	Craighead and Craighead 1956
Columba livia	8	330	Clait Braun unpublished
Asio otus	7	262	Craighead and Craighead 1956; CSU[a]
Speotyto cunicularia	8	140	Imler 1937; CSU[a]
Colaptes auratus	4	145	R. A. Ryder unpublished
Eremophila alpestris	79	31	R. A. Ryder unpublished
Corvus brachyrhynchos	3	461	CSU[a]
Pica pica	7	200	CSU[a]
Sialia currucoides	5	45	R. A. Ryder unpublished
Sturnus vulgaris	12	80	R. A. Ryder unpublished
Sturnella neglecta	15	94	R. A. Ryder unpublished
Agelaius phoeniceus	13	55	R. A. Ryder unpublished
Calamospiza melanocorys	16	33	R. A. Ryder unpublished
medium passerine	38	100	R. A. Ryder unpublished
small passerine	132	30	R. A. Ryder unpublished
Reptiles			
Thamnophis spp.	9	64	Craighead and Craighead 1956
Phrynosoma douglassi	2	20	CSU[a]
Fish			
Catostomidae	19	20	Seidensticker 1968
Cyprinus carpio	3	800	CSU[a]
Crustaceans			
Cambarus spp.	4	6.5	Craighead and Craighead 1956
Insects			
Carabidae	19	0.2	locally collected specimens
Scarabaeidae	2	0.3	locally collected specimens
Silphidae	2	0.3	locally collected specimens
Cicindelidae	2	0.3	locally collected specimens
Curculionidae	2	0.1	locally collected specimens
Tenebrionidae	10	0.6	locally collected specimens
Gryllidae	11	0.4	locally collected specimens
Locustidae	10	0.6	locally collected specimens
Diptera	4	0.3	locally collected specimens
Vespidae	2	0.3	locally collected specimens
Formicidae	3	0.01	locally collected specimens
Spiders			
Araneae	3	0.4	locally collected specimens

[a] Specimens in Colorado State University collections collected in north-central Colorado.

APPENDIX II. Total prey identified for Great Horned Owls in north-central Colorado.

Prey	1967 % No.	1967 % Biomass	1968 % No.	1968 % Biomass	1969 % No.	1969 % Biomass	Total No.
Mammals	(93.2)	(98.4)	(94.5)	(93.1)	(94.9)	(96.3)	(2,141)
Lepus spp.	—	—	0.2	4.4	2.0	23.1	17
Sylvilagus spp.	12.9	48.1	11.7	62.3	16.5	61.6	303
Marmota flaviventris	1.1	14.0	0.1	1.6	—	—	3
Cynomys ludovicianus	0.6	2.8	—	—	—	—	1
Thomomys talpoides	36.5	20.0	7.1	6.9	3.7	2.0	191
Dipodomys ordii	0.6	0.2	1.4	0.7	4.3	1.2	50
Perognathus hispidus	—	—	0.9	0.3	0.3	0.05	15
Perognathus smaller spp.	—	—	1.6	0.1	0.7	0.02	28
Reithrodontomys spp.	1.1	0.1	2.4	0.2	7.0	0.3	85
Peromyscus spp.	9.0	0.8	40.9	6.3	38.9	3.4	865
Onychomys leucogaster	—	—	0.1	0.04	2.1	0.3	17
Neotoma spp.	1.1	1.0	0.3	0.5	0.3	0.3	8
Microtus pennsylvanicus	3.4	0.6	5.2	1.7	1.8	0.3	92
Microtus ochrogaster	24.7	4.1	20.1	5.9	16.2	2.7	441
Ondatra zibethicus	2.2	6.5	0.4	1.8	0.4	1.2	12
Rattus norvegicus	—	—	0.2	0.3	—	—	3
Mus musculus	—	—	0.3	0.04	0.4	0.03	7
Mustela frenata	—	—	0.1	0.1	0.3	0.2	3
Birds	(4.0)	(1.5)	(4.4)	(6.8)	(4.9)	(3.2)	(103)
Aythya americana	—	—	0.2	2.0	—	—	3
Anas crecca	—	—	0.1	0.2	—	—	1
Phasianus colchicus	—	—	0.2	1.8	0.1	0.7	4
Columba livia	—	—	—	—	0.6	0.8	4
Asio otus	—	—	0.1	0.1	0.1	0.1	2
Colaptes auratus	—	—	0.7	0.8	0.3	0.2	12
Pica pica	—	—	—	—	0.3	0.2	2
Corvus brachyrhynchos	—	—	0.1	0.5	—	—	2
Sturnus vulgaris	0.6	0.2	0.1	0.04	0.1	0.04	3
Sturnella neglecta	—	—	—	—	0.1	0.1	1
Agelaius phoeniceus	—	—	0.3	0.1	—	—	4
unidentified passerine	3.4	1.4	2.6	1.3	3.3	0.7	65
Fish	(1.1)	(0.1)	(0.3)	(0.04)	(0.1)	(0.5)	(7)
Cyprinus carpio	—	—	—	—	0.1	0.5	1
Catostomidae	1.1	0.1	0.3	0.4	—	—	6
Crustaceans	(1.7)	(0.04)	(0.3)	(0.01)	(0.1)	(tr.[a])	(8)
Cambarus	1.7	0.04	0.3	0.01	0.1	tr.[a]	8
Insects	—	—	(0.5)	(tr.[a])	—	—	(29)
Carabidae	—	—	0.1	tr.[a]	—	—	2
Scarabaeidae	—	—	1.5	tr.[a]	—	—	21
Locustidae	—	—	0.4	tr.[a]	—	—	6
Total number and estimated biomass (g)	178	42,811	1,405	191,733	705	169,939	2,288

[a] Less than 0.01%.

APPENDIX III. Total prey identified for Long-eared Owls in north-central Colorado.

Prey	1967 % No.	1967 % Biomass	1968 % No.	1968 % Biomass	1969 % No.	1969 % Biomass	Total No.
Mammals	(99.0)	(98.9)	(99.8)	(99.8)	(99.5)	(99.2)	(2,657)
Cryptotis parva	—	—	0.2	0.04	0.3	0.04	4
Myotis sp.	—	—	—	—	0.1	0.03	1
Sylvilagus spp.	0.01	1.5	0.5	7.3	0.8	9.7	12
Thomomys talpoides	0.01	0.5	—	—	0.6	2.1	5
Dipodomys ordii	0.7	1.8	0.1	0.2	0.1	0.3	9
Perognathus hispidus	0.01	0.1	—	—	0.1	0.2	2
Perognathus smaller spp.	—	—	—	—	0.8	0.2	6
Reithrodontomys spp.	8.5	3.8	7.0	2.9	9.9	3.5	223
Peromyscus spp.	61.7	48.7	54.9	40.0	32.7	20.1	1,375
Onychomys leucogaster	5.4	7.7	0.2	0.3	1.8	2.0	69
Microtus pennsylvanicus	7.4	12.5	4.9	7.8	3.4	4.5	146
Microtus ochrogaster	14.6	21.9	27.8	38.6	48.0	56.2	757
Mus musculus	0.5	0.3	4.0	2.5	0.7	0.4	48
Birds	(1.0)	(1.1)	(0.2)	(0.2)	(0.5)	(0.8)	(16)
unidentified passerine	1.0	1.1	0.2	0.2	0.5	0.8	16
Total numbers and estimated biomass (g)	1,003	26,678	945	27,224	725	24,761	2,673

APPENDIX IV. Total prey identified for Burrowing Owls in north-central Colorado.

	1967		1968		1969		
Prey	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	Total No.
Mammals	(12.8)	(84.4)	(9.6)	(86.8)	(3.1)	(62.1)	(388)
Sylvilagus spp.	—	—	0.1	14.0	0.1	25.5	6
Thomomys talpoides	0.7	19.6	0.1	4.6	—	—	5
Dipodomys ordii	—	—	0.1	1.2	—	—	2
Perognathus hispidus	—	—	0.1	1.4	0.1	2.5	6
Perognathus smaller spp.	—	—	0.2	0.4	0.2	0.8	9
Reithrodontomys spp.	2.7	7.1	1.0	3.6	—	—	38
Peromyscus maniculatus	6.0	28.0	5.8	36.0	1.8	17.4	231
Microtus pennsylvanicus	—	—	0.1	0.8	—	—	2
Microtus ochrogaster	3.4	29.7	2.1	24.8	0.8	15.3	88
Mus musculus	—	—	—	—	0.1	0.6	1
Birds	(1.3)	(9.8)	(0.4)	(3.5)	(0.6)	(19.5)	(24)
Speotyto cunicularia	—	—	—	—	0.2	13.4	3
Eremophila alpestris	—	—	0.1	0.5	0.1	1.0	3
Calamospiza melanocorys	1.3	9.8	0.1	1.4	0.2	3.2	10
unidentified passerine	—	—	0.2	1.6	0.1	1.9	8
Reptiles	—	—	(0.1)	(1.1)	(0.2)	(2.6)	(4)
Thamnophis spp.	—	—	0.1	1.1	0.1	2.0	3
Phrynosoma douglassi	—	—	—	—	0.1	0.6	1
Crustaceans	—	—	(0.2)	(0.5)	(0.8)	(2.3)	(19)
Cambarus	—	—	0.2	0.5	0.8	2.3	19
Insects	(85.8)	(5.7)	(89.6)	(8.3)	(95.2)	(13.7)	(4,495)
Gryllidae	12.8	1.2	7.6	0.9	20.0	3.6	560
Locustidae	4.0	0.6	12.8	2.4	4.8	1.4	503
Cicindelidae	1.3	0.1	0.7	0.1	0.4	0.06	31
Carabidae	53.0	2.7	48.7	3.3	36.8	3.9	2,240
Scarabaeidae	2.0	0.1	10.3	0.9	19.6	2.7	629
Silphidae	4.0	0.3	2.5	0.2	9.0	1.2	218
Tenebrionidae	4.7	0.6	0.5	0.1	2.7	0.7	62
Curculionidae	4.0	0.1	1.9	0.1	0.6	0.03	78
unidentified beetles	—	—	3.3	0.3	1.0	0.1	126
Diptera	—	—	0.5	0.03	0.2	0.03	21
Formicidae	—	—	0.7	tr.[a]	—	—	24
Vespidae	—	—	0.1	tr.[a]	0.1	tr.[a]	3
Spiders	—	—	(0.1)	(0.02)	(0.1)	(0.03)	(6)
Araneae	—	—	0.1	0.02	0.1	0.03	6
Total numbers and estimated biomass (g)	149	674	3,356	11,447	1,431	3,142	4,936

[a] Less than 0.01%.

APPENDIX V. Total prey identified for Barn Owls in north-central Colorado.

	1967		1968		1969		
Prey	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	Total No.
Mammals	(98.2)	(98.8)	(99.1)	(99.4)	(97.9)	(97.7)	(4,305)
Cryptotis parva	—	—	0.1	0.01	0.5	0.04	7
Sylvilagus spp.	1.0	6.9	1.1	10.8	3.0	23.3	67
Thomomys talpoides	14.7	34.1	2.7	9.2	12.1	29.4	319
Geomys bursarius	—	—	—	—	0.1	0.3	1
Dipodomys ordii	7.4	8.8	3.1	5.4	3.4	4.2	173
Perognathus hispidus	4.3	2.9	2.9	2.9	1.9	1.4	128
Perognathus smaller spp.	3.2	0.4	3.4	0.7	7.5	1.1	191
Reithrodontomys spp.	0.5	0.1	9.3	2.8	7.9	1.7	318
Peromyscus spp.	15.0	5.5	26.2	14.1	30.2	11.7	1,097
Onychomys leucogaster	0.4	0.2	0.8	0.8	1.3	0.9	37
Neotoma spp.	0.7	2.8	—	—	—	—	6
Microtus pennsylvanicus	15.2	12.0	9.5	11.0	5.2	4.3	415
Microtus ochrogaster	35.4	24.8	39.4	40.3	24.4	18.0	1,523
Ondatra zibethicus	—	—	—	—	0.1	1.2	1
Mus musculus	0.1	0.04	0.7	0.3	0.4	0.1	21
Zapus princeps	0.1	0.1	—	—	—	—	1
Birds	(1.8)	(1.2)	(0.9)	(0.5)	(2.1)	(2.3)	(61)
Eremophila alpestris	0.2	0.1	—	—	—	—	2
Sialia currucoides	—	—	0.04	0.04	—	—	1
Sturnus vulgaris	0.1	0.2	—	—	—	—	1
Sturnella neglecta	—	—	0.04	0.1	0.7	1.3	9
Agelaius phoeniceus	0.2	0.2	—	—	—	—	2
Calamospiza melanocorys	0.2	0.1	—	—	—	—	2
unidentified passerine	1.1	0.6	0.8	1.4	1.4	1.0	44
Total numbers and estimated biomass (g)	814	46,450	2,459	96,052	1,093	59,293	4,366

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