ARCTIC
VOL. 35, NO. 1 (JUNE 1982), P. 282-290

Feeding Ecology of Snowy Owls (*Nyctea scandiaca*) Wintering in Southern Alberta

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ABSTRACT. Food habits, habitat selection, and hunting behavior of snowy owls (*Nyctea scandiaca*) wintering near Calgary, Alberta were investigated during the winters of 1976-77 and 1977-78. The owls preyed extensively upon rodents. Gray partridge (*Perdix perdix*) were an important prey only in one winter. Dietary differences between years seem to be related to differences in weather. Male snowy owls preyed almost exclusively upon mice, whereas females utilized a wider range of prey, including much larger species. The owls appeared to respond to variation in habitat quality by selecting those habitats with the highest availability of prey. Snowy owls were successful in 43% of 51 attempts to capture prey. The success rate of attempts to capture birds was lower than for small mammals. Juvenile females had lower success rates and longer prey-handling times than did adult females.

Key words: snowy owl, *Nyctea scandiaca*, food habits, winter ecology, Alberta

RÉSUMÉ. Les habitudes alimentaires, le choix de l'habitat et le comportement de chasse des harfangs des neiges (*Nyctea scandiaca*) hivernant près de Calgary en Alberta, ont été étudiés durant les hivers 1976-77 et 1977-78. Les rongeurs furent le proie privilégiée des hiboux. La perdrix grise (*Perdix perdix*) fut une proie importante durant seulement un hiver. Les différences observées entre les années dans l'alimentation semblent être reliées à des différences climatiques. Le harfang des neiges mâle chassait presqu'exclusivement la souris, alors que les femelles jetaient leur dévolu sur une plus grande variété des proies incluant des espèces physiquement plus imposantes. Les harfangs semblent répondre aux variations de la qualité de l'habitat en choisissant les habitats offrant la plus grande variété de proies. Sur un total observé de 51 tentatives de capture d'une proie, les harfangs des neiges réussirent dans 43% des cas. Ce taux de succés était plus bas dans la capture d'oiseaux que des petits mammifères. Comparativement aux femelles adultes, les jeunes femelles eurent des taux de succès inférieurs et prirent plus de temps pour maîtriser leur proie.

Traduit par Pierre Bibeau, Arkéos Inc., Montréal.

INTRODUCTION

Although snowy owls (*Nyctea scandiaca*) are usually considered to be birds of the arctic tundra, they may actually spend the majority of their year on southern wintering grounds (Bird, 1972). The prairies of western Canada consistently support numbers of these owls during winter (Snyder, 1947, 1949; Keith, 1960; Lein and Webber, 1979; Boxall, 1980). However, the winter biology of this species is best known from studies in eastern North America where its periodic irruptions have generated numerous reports on numbers of owls, food habits, or unusual locality records (e.g., Gross, 1931, 1944, 1947; Bent, 1938; Meade, 1948). Food habit studies suggest that the snowy owl, although a specialist preying almost exclusively on lemmings (*Lemmus* and *Dicrostonyx*) while breeding (Pitelka *et al.*, 1955; Watson, 1957), is a more generalized predator in winter (e.g., Gross, 1944; Catling, 1973; Weir, 1973; James, 1980). Intensive investigations of snowy owls in areas where they regularly winter, such as the Canadian prairies, are lacking. This is unfortunate because the status of the food supply, and the age structure of owl populations, in such areas may be important in understanding the irruptive movements of this species into other areas.

This paper describes the food habits and foraging behavior of snowy owls in a regular wintering area (Bird, 1972; Lein, pers. obs.). It also analyzes habitat use by the owls in relation to major prey populations.

Common and scientific names follow Banfield (1974) for mammals and the AOU checklist (1957) for birds.

MATERIALS AND METHODS

Study Area

The study area is a 185 km^2 block of agricultural land on the southeastern border of Calgary, Alberta. A network of roads and the low relief in this area facilitated locating and observing owls. Human activity was concentrated along the western edge of the study area and in two small communities within it.

The predominant crop grown on the study area is barley; wheat and rye are grown in lesser amounts. Variation in agricultural practices, in grazing activity, and in drainage results in a patchwork of habitats. We classified habitats using eight categories: stubblefield, fallow, hayfield, pasture, slough, ungrazed grassland, residential areas, and industrial areas. These are described in detail in Lein and Webber (1979) and Boxall (1980).

The habitat composition of the study area was determined by inspecting each habitat unit each year and recording its classification on an aerial photo mosaic. The resulting habitat maps were digitized with a G.T.O. electronic coordinate digitizer, and the areas of each field or unit and of each habitat category on the area were determined with a Digital PDP 11/40 computer.

The habitat composition of the study area was similar during the two winters. The major habitats were stubblefield and fallow, which comprised about 37% and 34% of the study area respectively. Hayfields formed about 12% and pasture about 8% of the area. The other habitats together comprised only about 10% of the study area. "Edge"

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habitats such as roadside ditches and fence rows were not measured, but were important to the owls.

Prey Populations and Habitat Use

Available prey species included meadow voles (*Microtus pennsylvanicus*), deer mice (*Peromyscus maniculatus*), white-tailed jack rabbits (*Lepus townsendii*), gray partridge (*Perdix perdix*), rock doves (*Columba livia*), and various passerine species. Richardson's ground squirrels (*Spermophilus richardsonii*) were available only in the fall and early spring. Because small rodents and partridge were more abundant than other prey, we concentrated on documenting their distribution and abundance throughout the study area.

We sampled relative rodent abundance in various habitats in 1977-78. Two lines of 25 snap-traps each were placed in each field to be sampled. The first line was set parallel to, and 10 m from, the edge of the field. The second line was set parallel to the first, and near the center of the field. Single trap-lines were used in linear habitats such as slough margins, roadside ditches, and fence rows. Three replicates were run in each habitat during each trapping session. Trapping sessions lasting 48 h were conducted at four intervals between October and April.

Trapping was restricted to five habitats: stubblefields, fallow, hayfields, sloughs, and roadside ditches and fence rows. Pastures and ungrazed grasslands were not sampled because of their relative rarity on the study area. Farmyards and other residential areas were impossible to sample because of human disturbance.

Tracking censuses of small mammals were conducted in the major habitats following light snowfalls to provide an independent check on the indices of abundance provided by snap-trapping. A census consisted of counting the number of rodent tracks crossing a 100 m transect located 10 m from the edge of a field.

Habitat use by owls and gray partridge was determined by recording the habitat in which each owl or covey of partridge was located when first sighted. If an owl or a covey was located on the boundary between two different habitat types, a value of 0.5 was assigned to each habitat.

Food Habits

Sex, age and individual identity of resident owls were determined by plumage characteristics (Fig. 1; Josephson, 1980; Lein, pers. obs.). Perches used regularly by these birds were visited approximately once every two weeks

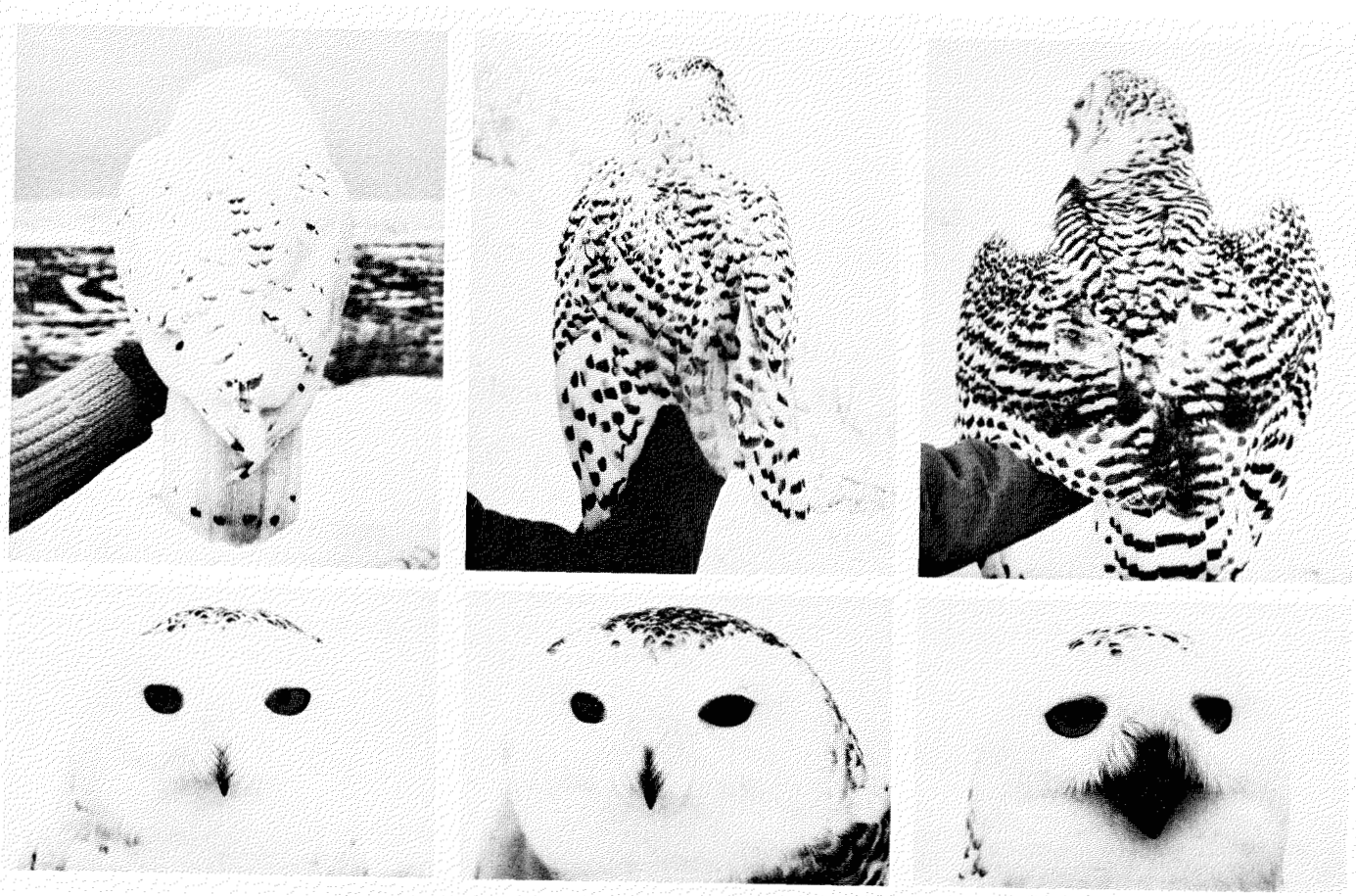

FIG. 1. The sex and age of snowy owls may be determined from variation in plumage markings. Adult males (top left) are lightly marked with dark bars, and may be almost immaculately white. Adult females (top centre) are more heavily barred. Juveniles (birds hatched during the preceding breeding season) are more heavily barred than their adult counterparts, and may be distinguished by the mottling of the covert feathers near the bases of the wings, as shown by a juvenile female (top right). In addition, individuals may be recognized by distinctive details of plumage marking, such as the differences in the brow markings of three females (bottom row).

during the winter to collect pellets. Analysis of owl pellets (Graber, 1962; Raczynski and Ruprecht, 1974) provides reliable estimates of the number of small prey items and the species composition of the diet (Glading *et al.*, 1943; Clark, 1975). Hunting ranges of resident owls were thoroughly checked for pellets following the spring snowmelt.

The contribution of each prey species to the total biomass of the diet was estimated from their numbers in the pellets. Mean weights of prey species were derived from specimens collected locally or taken from Banfield (1974) in order to calculate the biomass of prey eaten. Most prey individuals were small enough to be eaten in their entirety. However, the use of mean weights may overestimate the contribution of large prey species because the owl may not ingest the entire prey individual. We assumed that larger prey, such as jack rabbits and partridge, provided only a single meal because remaining meat froze rapidly under prevailing weather conditions. Pitelka *et al.* (1955), Watson (1957) and Gessaman (1972) calculated that the average meal size of snowy owls was about 284 g. We used this figure to estimate the amount of these larger prey that was consumed in a single meal.

Foraging Behavior

Snowy owls were observed from an automobile with 7 × 50 binoculars or a 20-40× telescope. Notes on behavior were recorded onto a cassette tape recorder. The duration of activities was timed directly with a stopwatch, or recorded notes were timed during playback. Most observations involved owls that remained on the study area for at least several weeks and which defended exclusive hunting ranges.

Resident snowy owls rarely fly except when attempting to capture prey or while interacting with another owl (Watson, 1975; Höhn, 1973; pers. obs.). Thus hunting flights were easily identified. For each capture attempt we recorded time of day, initial perch of the owl, habitat, prey type, estimated distance from perch to prey, and an estimate of the total elapsed time from the owl leaving the perch to the end of the hunting attempt. The feeding behavior of the owl, the time taken to ingest the prey, and the behavior following successful captures were also noted.

RESULTS

Food Habits

Remains of six mammalian species were recovered from 100 snowy owl pellets collected during the two winters (Table 1). In addition, the remains of gray partridge, short-eared owls (*Asio flammeus*), and several species of small passerine birds were found.

Peromyscus maniculatus was the most abundant species in the diet, comprising 61% and 51% of the total prey individuals in snowy owl pellets during 1976-77 and 1977-78, respectively (Table 1). *Microtus pennsylvanicus* was only about half as numerous as *P. maniculatus* in pellets. Together, these species comprised about 90% and 75% of the total prey individuals in the pellets of snowy owls in the two winters respectively. Other mammalian prey included Richardson's ground squirrels, weasels (*Mustela nivalis* and *M. frenata*), and white-tailed jack rabbits.

Numerically, birds were a minor component of the diet (Table 1). Passerines [snow buntings (*Plectrophenax nivalis*) and horned larks (*Eremophila alpestris*)] represented 2-4% of prey items during the two winters. Gray partridge remains were found in pellets collected during 1977-78, comprising 9% of prey individuals.

Mice and voles together formed 62% of the calculated prey biomass in 1976-77 but only 28% in 1977-78 (Table 1). Ground squirrels formed 14% and 28% of calculated prey biomass in the two winters respectively. Partridges comprised 33% of the calculated prey biomass in 1977-78.

Differences in Diet Between Sex and Age Cohorts

P. maniculatus and *M. pennsylvanicus* comprised 85.2% of prey individuals in the pellets of males; no remains of partridge were found (Table 2). *P. maniculatus* formed a

TABLE 1. Diet of snowy owls near Calgary in two winters

	1976-1977 (n = 28 pellets)		1977-1978 (n = 72 pellets)	
Prey type	No. of individuals (%)	Biomass in grams (%)	No. of individuals (%)	Biomass in grams (%)
Peromyscus maniculatus	57 (61.2)	1396.0 (35.0)	79 (51.0)	1935.5 (15.8)
Microtus pennsylvanicus	28 (30.1)	1070.0 (26.6)	39 (25.2)	1489.8 (12.2)
Spermophilus richardsonii	2 (2.2)	568.0 (14.2)	12 (7.7)	3408.0 (27.9)
Mustela nivalis	1 (1.1)	42.2 (1.0)	—	—
Mustela frenata	—	—	3 (1.9)	495.0 (4.0)
Lepus townsendii	3 (3.2)	852.0 (21.2)	—	—
Total Mammals	91 (97.8)	3928.2 (98.0)	133 (85.8)	7328.3 (59.9)
Perdix perdix	—	—	14 (9.0)	3976.0 (32.5)
Asio flammeus	—	—	2 (1.3)	680.0 (5.6)
Passerines	2 (2.2)	82.2 (2.0)	6 (3.9)	249.0 (2.0)
Total Birds	2 (2.2)	82.2 (2.0)	22 (14.2)	4905.0 (40.1)
Total	93 (100.0)	4010.4 (100.0)	155 (100.0)	12233.3 (100.0)

significantly greater proportion of the total of mice and voles found in pellets from males (71%) than they did in pellets from females (57%) [equality of proportions test, $p = 0.038$ (Sokal and Rohlf, 1969)].

Pellets from female owls contained a greater diversity of prey. Small mammals were important, forming 79.2% of the total prey individuals, but partridge and weasels were present in lesser numbers (Table 2). Three pellets from females contained remains of jack rabbits, the largest prey taken by snowy owls in this study. Females may utilize jack rabbits more often than suggested in Table 2. One female was observed to eat the shoulders and a portion of the neck of a jack rabbit. No bones appeared to have been ingested and no jack rabbit remains were found in 11 pellets collected from this owl. Males were not observed to attempt to capture jack rabbits and no jack rabbit remains were found in their pellets.

TABLE 2. A comparison of the diets of male and female snowy owls based on pellet analyses. Samples for both winters combined.

Prey type	% of total prey items	
	Male[1]	Female[2]
Mammals		
Peromyscus maniculatus	61.1	44.8
Microtus pennsylvanicus	24.1	34.4
Spermophilus richardsonii	7.4	6.2
Lepus townsendii	0	1.4
Mustela spp.	0	2.8
Birds		
Perdix perdix	0	7.6
Other birds	7.4	2.8
Total	100.0	100.0

[1]54 prey items in 20 pellets.

[2]145 prey items in 60 pellets.

There was no significant dietary difference between age cohorts of females based on pellet analysis (Chi-square test, $p>0.25$). The relative frequencies of *P. maniculatus*, *M. pennsylvanicus*, and gray partridge in the diets of adult and juvenile female owls were similar (Table 3). Only juvenile females were found to prey upon weasels and jack rabbits, while remains of passerines and short-eared owls were found only in pellets from adult females; these differences are probably due to small sample sizes. We did not obtain enough pellets from juvenile males to permit a similar comparison. We suspect, however, that there are no major differences in diet between age classes of males.

Habitat Use by Prey

Small mammal trapping success was high in roadside ditches and fence rows, and in sloughs, and lowest in fallow fields (Table 4). Stubblefields were more productive than hayfields.

TABLE 3. A comparison of the diets of adult and juvenile female snowy owls based on pellet analyses. Samples for both winters combined.

Prey type	% of total prey items	
	Adult[1]	Juvenile[2]
Mammals		
Peromyscus maniculatus	45.3	48.4
Microtus pennsylvanicus	31.3	31.3
Spermophilus richardsonii	9.4	3.1
Lepus townsendii	0	3.1
Mustela spp.	0	4.7
Birds		
Perdix perdix	7.8	9.4
Other birds	6.2	0
Total	100.0	100.0

[1]64 prey items in 29 pellets.

[2]64 prey items in 28 pellets.

TABLE 4. Snap-trapping indices of abundance of small mammals in different habitats during the winter of 1977-78

Habitat	No. of *Microtus* and *Peromyscus* captured /1000 traps/24 h				
	October	November	January	April	Total*
Roadside Ditch and Fence Row	75	5	0	61	141
Slough	39	14	0	**	53
Stubble	13	2	0	15	30
Hayfield	10	5	0	7	22
Fallow	0	0	0	15	15

*Indices differ significantly between habitats (Kruskal-Wallis ANOVA, $p<0.01$).

**Sloughs were all flooded in April and therefore none were sampled.

Capture rates declined as the winter progressed and rose again in the spring. *P. maniculatus* was the most common rodent trapped in the fall, but its proportion in the sample declined during the winter and was comparable to that of *M. pennsylvanicus* in April. Shrews (*Sorex vagrans* and *S. cinereus*) were trapped throughout the winter, but they were not represented in owl pellets (Table 1).

The results of the tracking censuses (Table 5) show a pattern of rodent abundance similar to that shown by trapping. Roadside ditches and fence rows had the highest number of tracks. More tracks were found in stubblefields than in hayfields; no tracks were found in fallow.

The distribution of sightings of gray partridge coveys by habitat for each winter is shown in Table 6. The distributions for the two years differ significantly (Chi-square test, $p<0.01$), due to relatively heavier use of pastures in 1976-77, and of hayfields, sloughs and residential areas in 1977-78. The differences between the observed and expected distributions are significant in both years (Chi-square test, $p<0.05$ for both years), indicating a degree of habitat preference. Partridge were observed more frequently than expected in stubblefields and residential areas (farmyards).

TABLE 5. The numbers of rodent tracks counted crossing 100 m transects walked in various habitats

Date	No. of Rodent Tracks							
	Stubblefields		Fallow		Hayfields		Roadside Ditch and Fence Row	
	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*
November 19	3.2 ± 1.6	5	0.0	5	—		—	
November 24	5.3 ± 2.4	7	0.0	6	2.3 ± 0.6	3	10.1 ± 4.3	9
November 25	3.9 ± 1.3	7	0.0	4	2.6 ± 1.1	5	—	
November 27	3.5 ± 2.0	6	0.0	2	2.6 ± 1.1	5	6.0 ± 2.8	2

Pastures were apparently preferred in 1976-77 but not in 1977-78.

Habitat Use by Owls

The distributions of owl sightings by habitat (Table 7) differ significantly between 1976-77 and 1977-78 (Chi-square test, $p<0.025$). Relatively more owls were seen in pastures in 1976-77, and in hayfields in 1977-78. The observed and expected distributions of sightings differed significantly for both winters (Chi-square tests, $p<0.001$). Owls were observed more frequently than expected in stubblefields and sloughs in both winters, pastures in 1976-77 and hayfields in 1977-78. Fewer owls than expected were observed in fallow fields and residential areas in both winters.

Foraging Behavior

Snowy owls were observed in 51 hunting actions. The most common foraging method (50 of 51 hunts) was the "still perch" or sit-and-wait technique. Hovering, described by Watson (1975), was observed only once. Coursing, a low, searching flight lasting several minutes (Chamberlin, 1980), was not observed, although it is a common hunting technique on the breeding ground (Watson, 1957).

Hunting owls usually perched on tall objects, such as fence posts and utility poles, while visually scanning the surrounding area for 10-15 minutes (Fig. 2). If no prey was located, the bird often moved to another perch 100-200 m away and resumed searching. When prey was sighted, owls assumed an upright posture. Several head-bobs, which may facilitate the determination of the distance to the prey (Daanje, 1950), sometimes occurred, followed by a low flight directly toward the prey. In two observations, however, owls attempting to capture birds flew in a wide circle around the prey so that they approached from the direction of the sun. Both observed attempts were successful. In two other cases owls appeared to use bushes to screen their approach to avian prey; one of these attempts was successful.

Owls seized prey with their feet and killed it either by biting the head or by shaking the prey violently while holding it in the bill. *M. pennsylvanicus* and *P. maniculatus* were usually swallowed whole and head-first immediately after they were killed. This behavior varied, however, with the age class of the owl.

Most attempts to capture prey were directed at small mammals and birds (Table 8). This is consistent with the

TABLE 6. The distribution of sightings of gray partridge coveys by habitat category

Year	No. of Sightings (Expected No.)*						
	Stubble	Fallow	Hayfield	Pasture	Slough**	Residential	Total
1976-77	19.5 (14.7)	4.0 (12.6)	2.0 (4.7)	9.5 (3.2)	1.0 (2.5)	3.0 (0.9)	39
1977-78	22.0 (17.8)	3.5 (16.8)	9.0 (5.9)	0.5 (3.4)	5.0 (2.5)	8.0 (1.1)	48

*Expected values based on the distribution of habitats surveyed on the study area.

**Ungrazed Grassland is included in this habitat category.

TABLE 7. Distribution of owl sightings by habitat category

Year	No. of Sightings (Expected No.)*						
	Stubble	Fallow	Hayfield	Pasture	Slough**	Residential + Industrial	Total
1976-77	176.0 (131.6)	62.0 (113.7)	41.0 (41.2)	38.5 (28.9)	28.0 (20.3)	3.5 (13.3)	349
1977-78	165.5 (137.6)	90.0 (129.8)	63.5 (45.8)	25.5 (26.0)	26.5 (18.6)	1.0 (14.1)	372

*Expected values based on the distribution of habitats surveyed on the study area.

**Ungrazed Grassland is included in this category.

FIG. 2. Snowy owls are regular winter residents in prairie habitats in southern Alberta. They show a variety of behavioral adjustments to this highly-modified environment, including the use of man-made structures such as utility poles and fence posts for hunting perches, and the concentration of hunting activity in those agricultural habitats with the highest availability of prey.

frequencies of prey categories in the diet as indicated by pellet analysis (Table 1). The overall success rate of snowy owls attempting to capture prey was 43% (Table 8). Adult females were significantly more successful (10 of 15 hunts) than were juvenile females (10 of 30 hunts) (Chi-square test, $p<0.05$).

Juvenile owls appeared to be inept at handling prey. On two occasions juveniles dropped prey while flying to a perch; in three other cases mice escaped after initial capture. Juveniles were also seen manipulating dead prey. We never observed adult owls manipulating or dropping prey. In addition, juveniles spent more time handling prey in preparation for ingestion than did adults. The duration between prey capture and ingestion was 12.3 ± 2.2 s for adults and 42.9 ± 14.0 s for juveniles (mean ± SE, n = 6 for adults, n = 8 for juveniles). This difference is significant (Mann-Whitney U test, P = 0.046).

Approximately two-thirds of all hunting attempts were initiated from perches over 5 m in height (utility poles and powerline towers) (Fig. 3a). Most prey were captured within 200 m of these hunting perches (Fig. 3b). Capture attempts at greater distances were rare and usually involved large, conspicuous prey such as jack rabbits or partridge. Most capture attempts occurred in stubblefields and hayfields (Fig. 3c). Of those capture attempts directed toward small mammals, 70% occurred in stubblefields and 18% occurred in hayfields. The majority of the remaining attempts to capture small mammals took place in sloughs.

TABLE 8. The number of attempts by snowy owls to capture various prey and their success in such attempts. Data from both winters combined.

Prey Type	No. of hunts (%)[1]	No. Successful (%)[2]
Small Mammals[3]	33 (64.7)	19 (57.6)
Passerines	2 (3.9)	1 (50.0)
Perdix perdix	11 (21.5)	1 (9.1)
Lepus townsendii	3 (5.9)	0 (0)
Spermophilus richardsonii	1 (2.0)	1 (100.0)
Unknown	1 (2.0)	0 (0)
Total	51 (100.0)	22 (43.1)

[1]Percent of all hunting attempts.

[2]Percent of hunting attempts on that prey type.

[3]*Peromyscus maniculatus* and *Microtus pennsylvanicus*.

DISCUSSION

Food Habits

Small mammals are the most important prey for snowy owls wintering near Calgary. They outnumbered other prey in the pellets recovered from owls and comprised about 30-60% of the total prey biomass in two winters. Small mammals are also important prey of snowy owls on the breeding grounds (Pitelka *et al.*, 1955; Watson, 1957) and in many wintering areas in eastern North America (Gross, 1944; Catling, 1973; Allan, 1977; Phelan and Robertson, 1978; Chamberlin, 1980).

The frequency of predation on gray partridge by snowy owls apparently varies from year to year, possibly in relation to weather conditions. The greater snow accumulation in 1977-78 resulting from persistently cold temperatures

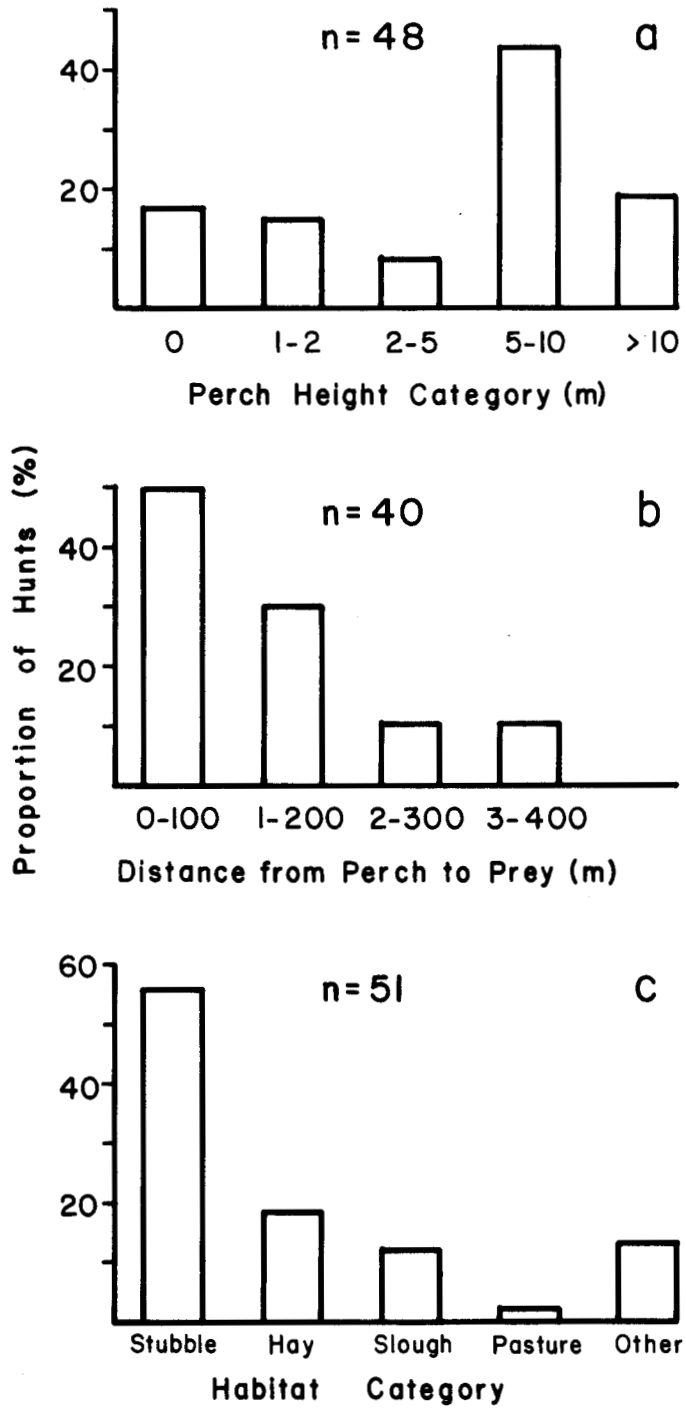

FIG. 3. Hunting behavior of snowy owls wintering near Calgary, Alberta. Data from both years combined. a. The relationship between perch height and capture attempts. b. Distances from hunting perches at which prey were captured. c. Partitioning of hunts among habitat categories.

(Boxall, 1980) may have reduced the availability of small mammals to the owls (see Craighead and Craighead, 1956). This suggestion is supported by the decrease in small mammals in the diet from 1976-77 to 1977-78. This decrease was offset by an increase in utilization of partridge during the second winter. Partridges may serve as buffers (*sensu* Errington, 1945) during periods of rodent scarcity in southern Alberta.

The success rate of attacks on partridge was low (9%) compared to that on small mammals (58%) (Table 8). This may be related to the tendency of partridge to form coveys in winter (Jenkins, 1960; Westerskov, 1966), or to the "sit-and-wait" hunting method of the owls. Only one successful attack on gray partridge was observed (Table 8), and this involved a single prey individual. All unsuccessful capture attempts were on birds in coveys. Covey formation may be an adaptive response to predation, permitting increased vigilance (Powell, 1974) or causing confusion in an attacking predator (Kenward, 1978).

Ground squirrels contributed significantly to total prey biomass in one winter but their importance is limited by their seasonal availability. Ground squirrels may emerge from hibernation as early as the middle of February and they may become an important food source for owls migrating to the Arctic.

Differences in Diet Between Sexes

One hypothesis regarding sexual dimorphism in size in birds is that it reduces intraspecific competition by permitting a partial non-overlap of the feeding niches of males and females (Selander, 1966; Earhart and Johnson, 1970). Snowy owls exhibit the pattern of reversed size dimorphism (with females larger than males) characteristic of most owls and hawks (Snyder and Wiley, 1976), and one would therefore predict that female owls take larger prey than do males, thus increasing the total size range of prey used.

Male snowy owls showed an apparent specialization for feeding upon *P. maniculatus*, in contrast to the wider range of prey captured by females (Table 2). Females also took much larger prey than did males. Both these results are consistent with the interpretation of sexual differences in body size as a means of reducing intraspecific competition (Selander, 1966; Schoener, 1969). However, the results reported here should be viewed with caution for two reasons. First, the sample of pellets from male owls was small (n = 20). Second, larger prey may not be well represented in snowy owl pellets because their bones may be ingested only infrequently (Brooks, 1929; pers. obs.).

The largest prey utilized by owls in our study were white-tailed jack rabbits. Only pellets from females contained remains of jack rabbits and only females were seen to attempt to capture jack rabbits. These observations support the suggestion that real sexual differences in the size range of winter prey of snowy owls exist.

Habitat Selection

Snap-trapping and tracking results (Tables 4, 5) suggest that highest concentrations of rodents existed in uncultivated areas with abundant cover. These habitats were in long, thin strips bordering fields (roadside ditches and fence rows), or were small patches surrounded by fields (sloughs). The major reason for the relative abundance of small mammals in these areas is probably the reduction of natural habitats by cultivation. Fence rows, roadside ditches and sloughs were virtually the only areas resembling natural habitat, and may represent "refugia" for small mammals (Ogilvie and Furman, 1959). Few captures of prey by owls were observed in these habitats, despite the presence of abundant prey. Such prey were probably not readily available to visual predators such as snowy owls because of the dense vegetation. Southern and Lowe (1968), Sparrowe (1972) and Wakeley (1978) have shown that a high density of vegetation decreases prey vulnerability to raptors. Therefore, hunting in these habitats would probably not be very profitable to snowy owls, regardless of the abundance of small mammals.

Other habitats may be ranked in descending order on the basis of rodent abundance as follows: stubblefields, hayfields, and fallow fields. As mentioned previously, pastures were not intensively sampled, but limited trapping data suggest that they rank below hayfields in rodent abundance. The lack of vegetative cover and food in fallow excludes it as a profitable habitat for mice, voles and partridge, and hence for owls. This is borne out by the poor trapping success (Table 4), the absence of rodent tracks (Table 5), the scarcity of partridge sightings (Table 6), and the relatively low numbers of owl sightings (Table 7) in fallow fields. Snowy owls showed a preference for pastures in 1976-77 (Table 7), as did partridge (Table 6). The low snow cover in 1976-77 may have enabled partridge to forage in pastures; the owls may have responded to this increased use by hunting more frequently in these areas. The relatively low abundance of prey and the relatively dense vegetative cover in hayfields seem to eliminate this habitat as a primary hunting site.

Overall trapping and tracking success of small mammals and sightings of partridge were higher in stubblefields than in any other cultivated habitat. In addition, the vegetation in stubblefields was less dense than in other cultivated areas (except fallow), suggesting that rodents were probably detected more easily by owls in this habitat than in others. Stubblefields would thus appear to provide snowy owls with favorable hunting sites.

Peromyscus maniculatus was the most common species in the diets of owls (Table 1), and most hunting attempts were observed in stubblefields (Fig. 3c). We suggest that the abundant supply of seeds left in stubblefields following harvest (pers. obs.) attracts mice and voles from adjacent ditches, fence rows and sloughs. One might expect such foraging movements to involve *P. maniculatus* more than

Microtus pennsylvanicus because *P. maniculatus* is granivorous (Hamilton, 1941; Jameson, 1952) while *M. pennsylvanicus* is mainly herbivorous (Thompson, 1965). In addition, *M. pennsylvanicus* range over smaller areas than do *P. maniculatus* (P.K. Anderson, pers. comm.); they are also most abundant in areas of dense vegetative cover and apparently avoid more open areas if possible (Eadie, 1953; Getz, 1961; Birney *et al.*, 1976).

Snowy owls were observed in stubblefields, hayfields, sloughs and ungrazed grassland more often than expected (Table 7). Fewer owls than expected were seen in fallow, and in residential and industrial areas. The avoidance of residential and industrial areas may be due to human disturbance (Lein and Webber, 1979). Our observations suggest that owls were selecting stubblefields as habitat in which to hunt. Stubblefields appear to be more profitable than other habitats because of the availability of prey, as described above. Lein and Webber (1979) also observed a preference for stubblefields by wintering snowy owls, and suggested that this was related to hunting success.

Age and Hunting Success

The ability of birds to obtain food likely improves with age and experience, especially in predatory species with specialized techniques of capture (e.g., Ashmole, 1963; Lack, 1966).

We found a significant difference between the hunting success of adult and juvenile female snowy owls. Direct observations of hunting owls suggested that juveniles had more difficulty in subduing prey than did adults. The manipulation of prey by juvenile owls following capture may be a mechanism whereby they acquire skill in handling prey (Ficken, 1977; Bildstein, 1980).

Our observations suggest that juvenile snowy owls may be less efficient hunters than adults, and thus may be subject to a higher mortality rate than adults because they are less adept at meeting their energy requirements. A high mortality rate among first-year birds has been reported for several other species of owls, presumably due to starvation (Honer, 1963; Stewart, 1969; Southern, 1970; Adamcik and Keith, 1978; Hirons *et al.*, 1979). Knowledge of the sex and age structure of wintering snowy owl populations therefore may be valuable in relating population fluctuations to age-dependent mortality.

CONCLUSION

Our findings demonstrate some of the close relationships of the behavior of the snowy owl to the winter environment of the Canadian prairies. The adaptability of this species is evidenced by the obvious adjustments that it has made in the past 80 years to the extensive modification of the prairie environment by human activity. The owls respond to the variations in prey density in the "artificial" habitats created by modern agricultural practices, and apparently prefer man-made objects such as utility poles for hunting perches. Snowy owls have also adapted to an introduced prey species, the gray partridge. The latter may assume a role as a "buffer" species in the diet of snowy owls that was formerly occupied by native grouse such as the greater prairie chicken (*Tympanuchus cupido*), which have declined in numbers since settlement. Our findings contradict the popular myth that snowy owls are winter nomads that are forced into an "alien" environment in southern Canada and the northern United States, and which may never return to their arctic breeding grounds (Downs, 1979; Walker, 1974).

ACKNOWLEDGEMENTS

We thank R.M. Fisher, B. Free, C.C. Mamo and G.A. Webber for assistance in the field. P.K. Anderson made valuable suggestions regarding the small mammal work. L.O. Sinkey assisted with the computer analyses of habitat data. M.C. Conway provided assistance in the preparation of the manuscript. P.K. Anderson, J.B. Doran, and G.R. Holton improved the manuscript with critical comments. This study was supported by grants from the Canadian Wildlife Service, the University of Calgary, and the Natural Sciences and Engineering Research Council of Canada to MRL.

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