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POPULATION ECOLOGY OF SNOWY OWLS DURING WINTER ON THE GREAT PLAINS OF NORTH AMERICA[1]

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Abstract. We used data from Christmas Bird Counts (1961–1984) and road counts (1983–1985) to study the winter population ecology of Snowy Owls (*Nyctea scandiaca*) on the Great Plains of North America. Numbers of owls wintering between 45°N and 53°N increased with latitude. Owl abundance fluctuated from year to year, but fluctuations were not synchronous among count localities across the Great Plains. Owls first appeared on our study sites in southwestern Alberta in early November and individuals continued to arrive until late December or early January. Spring departure occurred during late February and early March, with a few owls remaining until late March. During midwinter, the mean number of owls censused on four study sites ranged from 1.3 to 5.8 owls/100 km in 1983–1984 and from 1.7 to 10.2 owls/100 km in 1984–1985. Although all age-sex classes were represented on the Alberta study areas in both winters, adult birds predominated. Both the Christmas Bird Count data and our fieldwork indicate that owl dispersion is patchy, and that the abundance of owls within patches may vary markedly from year to year. We recommend that future studies of winter raptor populations select multiple study sites to permit detection of patterns that occur over areas larger than a single study site.

Key words: Snowy Owl; Nyctea scandiaca; *winter ecology; migration; Great Plains; raptor censuses.*

INTRODUCTION

The Snowy Owl (*Nyctea scandiaca*) has been depicted as a "cyclic" or "irruptive" species (Gross 1947) that leaves its Arctic breeding range only when populations of lemmings (*Lemmus* and *Dicrostonyx*) crash (Shelford 1945, Chitty 1950). However, recent studies suggest that large numbers of Snowy Owls migrate annually to the northern Great Plains of Canada and the United States. Kerlinger et al. (1985) used Christmas Bird Count data to show that Snowy Owls were present on the northern Great Plains every winter and that their numbers did not fluctuate in a cyclic fashion. In contrast to their general portrayal as nomadic, both adult and immature owls may defend territories for several months during winter (Keith 1964, Evans 1980, Boxall and Lein 1982a). Because the findings of these studies contrast so greatly with those of earlier studies (Shelford 1945, Gross 1947), further research is needed to clarify the population and migration dynamics of this predator.

Here we document patterns of abundance of Snowy Owls during winter within the northern Great Plains of Canada and the United States over a 24-year period and describe aspects of the population ecology of these owls in southwestern Alberta during two winters. Our fieldwork in Alberta attempted to determine: (1) the timing of autumn arrival and spring departure, (2) dispersion and abundance during midwinter, and (3) the age-sex class structure of the population.

METHODS

To determine the abundance and distribution of Snowy Owls within the northern Great Plains area we used Christmas Bird Counts (CBCs) published in *Audubon Field Notes* (later *American Birds*) for the winters of 1961–1962 through 1984–1985. We define the northern Great Plains to include the unforested areas of the provinces and states shown in Figure 1. Because Snowy Owls select nonwooded or prairie-like habitats during winter (Boxall and Lein 1982a), we excluded localities in mountainous or forested regions from our analyses. CBC localities south of

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TABLE 1. Summary of Snowy Owl abundance at Christmas Bird Count localities on the northern Great Plains from 1961 to 1984.

Locality[1]	Number of years with counts	Number of years with owls (%)	Number of owls reported $\bar{x} \pm$ SE
1. Calgary, AB	24	22 (91.7)	4.58 ± 0.99
2. Edmonton, AB	24	22 (91.7)	3.04 ± 0.76
3. Regina, SK	23	23 (100.0)	7.35 ± 1.04
4. Saskatoon, SK	24	19 (79.2)	2.38 ± 0.52
5. Delta, MB	9	7 (77.8)	4.56 ± 1.56
6. Oak Lake, MB	22	13 (59.1)	0.82 ± 0.18
7. Winnipeg, MB	23	18 (78.3)	3.87 ± 1.02
8. Arrowwood NWR,[2] ND	19	7 (36.8)	0.37 ± 0.11
9. Bismarck, ND	24	4 (16.7)	0.17 ± 0.08
10. Des Lacs NWR, ND	22	20 (90.9)	1.41 ± 0.22
11. Fargo-Moorhead, ND-MN	24	17 (70.8)	1.29 ± 0.26
12. Grand Forks, ND	22	16 (72.7)	1.23 ± 0.27
13. Jamestown, ND	21	10 (47.6)	0.95 ± 0.27
14. Leeds, ND	15	12 (80.0)	0.87 ± 0.13
15. J. Clark Salyer NWR, ND	24	13 (54.2)	0.67 ± 0.18
16. Sullys Hill NGP,[3] ND	16	4 (25.0)	0.25 ± 0.11
17. Tewaukton NWR, ND	12	2 (16.7)	0.17 ± 0.11
18. Upper Souris NWR, ND	11	4 (36.4)	0.64 ± 0.31
19. Valley City, ND	13	7 (53.8)	0.85 ± 0.27
20. Billings, MT	24	0	
21. Chester, MT	9	9 (100.0)	1.22 ± 0.15
22. Fort Peck, MT	9	4 (44.4)	0.67 ± 0.29
23. Aberdeen, SD	16	9 (56.3)	1.06 ± 0.32
24. Brookings, SD	24	1 (4.2)	0.04 ± 0.04
25. Huron, SD	11	2 (18.2)	0.27 ± 0.20
26. Lake Andes, SD	17	3 (17.6)	1.06 ± 0.69
27. Madison, SD	23	3 (13.0)	0.17 ± 0.10
28. Pierre, SD	14	1 (7.1)	0.14 ± 0.14
29. Sand Lake NWR, SD	9	7 (77.8)	1.22 ± 0.32
30. Sioux Falls, SD	23	0	
31. Waubay, SD	24	4 (16.7)	0.21 ± 0.10
32. Wilmot, SD	18	4 (22.2)	0.22 ± 0.10
33. Yankton, SD	22	3 (13.6)	0.18 ± 0.11

[1] Numbers refer to Figure 1.
[2] National Wildlife Refuge.
[3] National Game Preserve.

Montana and South Dakota were also excluded because they reported few owls. Because we were concerned with long-term patterns of abundance, only localities reporting nine or more years of counts during the period were used. Thirty-three CBC localities met these criteria (Table 1, Fig. 1).

For each CBC we recorded the number of owls seen on the count, or during the count week. We also recorded the number of observer parties, party-miles driven, party-hours, and weather conditions, and used simple linear regression to examine the influence of observer effort and visibility conditions on the number of owls reported. Observer effort may be important in some places and for some species (Raynor 1975), including owls (Smith and McKay 1984). For our analysis of the effects of observer effort and visibility conditions we used only localities with >20 years of counts and where owls occurred in >5 years. For visibility analyses we used the following scale: 0 = clear sky (excellent visibility); 1 = partly cloudy (excellent–good visibility); 2 = cloudy–overcast (good–fair visibility); 3 = overcast with intermittent flurries (fair–poor visibility at times); 4 = overcast with snow through much of the day, patchy fog (poor visibility); and 5 = steady snow (poor to no visibility).

Because observer effort was not a consistent predictor of the number of owls recorded (see below), we used the following measures of owl abundance at each locality for our analyses (Table 1): the percentage of count years in which owls were reported (arcsine transformed for sta-

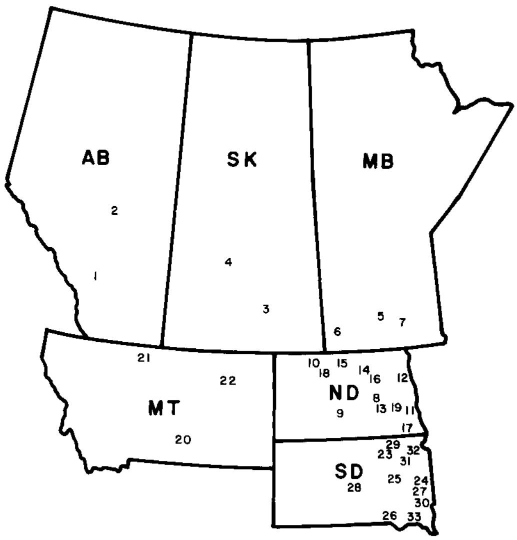

FIGURE 1. The northern Great Plains (Alberta [AB], Saskatchewan [SK], Manitoba [MB], Montana [MT], North Dakota [ND], and South Dakota [SD]), showing the locations of the Christmas Bird Counts used in this study. Numbers on the map correspond to the numbers of Christmas Bird Count localities in Table 1.

tistical analyses) and the mean number of owls reported per year. Bock and Root (1981) have discussed why observer effort might not influence the number of individuals reported on CBCs for species that are either rare, conspicuous, or occur in large flocks. To determine whether year-to-year fluctuations in owl numbers were synchronous across the northern Great Plains, we calculated pair-wise correlations among all combinations of localities. If owl numbers tended to be high (or low) at many localities in the same years, this would produce positive correlations among localities. Eleven localities with >20 years of observations and that reported owls in at least 5 years (Table 1) were included in this analysis.

In the winters of 1983–1984 and 1984–1985 we sampled populations of Snowy Owls at four study sites near Calgary, Alberta (51°03′N, 114°05′W) using the road-count method (Fuller and Mosher 1981). One site (hereafter the MRL-site) is the location of a long-term study of Snowy Owls (Boxall and Lein 1982a, 1982b; M. R. Lein, unpubl.), and is situated on the southeastern edge of the city of Calgary. It was chosen because of its proximity to Calgary and its history of use by Snowy Owls. Land use on the site was predominantly agricultural with >70% of the area being cultivated for cereal grains (Boxall and Lein 1982a).

The other three sites were located near Airdrie, about 20 km N of Calgary; near Lyalta, about 20 km ENE of Calgary; and near Mazeppa, about 40 km SSE of Calgary. These sites were chosen without regard to their history of utilization by owls. We selected sites that were well-spaced, not transected by major highways, predominantly agricultural, and representative of the plains near Calgary. All four sites were rectangular in shape and transected by gravel roads at 1.6- to 3.2-km (1- to 2-mile) intervals. All sites had flat or gently-rolling topography, which facilitated location and observation of owls.

In addition to these four primary study sites, three supplementary sites (Beiseker, immediately N of the Airdrie site; Brant, 10 km S of the Mazeppa site; and Kirkaldy, 30 km SE of the Mazeppa site) were sampled in mid-January of 1985 to determine whether the abundance patterns seen on the primary sites were representative of larger areas.

Road counts were conducted from 5 November 1983 to 28 March 1984 and from 24 October 1984 to 29 March 1985. Routes were 100 km long and were usually driven between 11:00 and 15:00 (range = 09:25–17:10). The same routes were used throughout the study, although snow drifts blocking roads necessitated minor changes (<2 km) during several counts. Visibility was rated as moderate to excellent on 135 of 142 road counts (95%). On seven counts, ice–fog, sleet, or poor lighting made visibility poor on varying proportions of the route.

Two persons (driver and observer) were always present on road counts on the MRL-site, whereas only one person (PK) conducted counts on the other sites. Routes were driven at speeds which allowed scanning of both sides of the road. Stops were made only when owls or owl-like objects were observed with the unaided eye. Only owls that were visible from the road without the aid of binoculars were included in our analyses. Driving speed on the MRL-site averaged 48.5 ± 1.8 km/hr ($\bar{x}$ ± SE, n = 15 counts), but only 36.2 ± 0.9 km/hr (n = 15) on the other three sites. This significant difference ($F_{(1,29)} = 37.15$, $P < 0.01$) is probably attributable to the fact that the MRL-site was sampled by two people.

All owls located were examined with binoculars and 20–45 power spotting scopes to determine age and sex using the size and plumage

TABLE 2. Coefficients of determination (r^2) for regressions of the number of owls reported from Christmas Bird Count localities on measures of effort and visibility.

Locality	Coefficient of determination: Number of parties	Party miles	Party hours	Visibility	Number of years[1]
Calgary, AB	0.08	0.41*	0.14	0.00	24
Edmonton, AB	0.01	0.00	0.01 (−)[2]	0.14 (−)	24
Regina, SK	0.06	0.30*	0.22*	0.15 (−)	24
Saskatoon, SK	0.08	0.12	0.08	0.08 (−)	24
Oak Lake, MB	0.12	0.01	0.03	0.02 (−)	20
Winnipeg, MB	0.03	0.18	0.08	0.14 (−)	21
Des Lacs NWR, ND	0.01 (−)	0.01	0.03 (−)	0.01 (−)	21
Fargo-Moorhead, ND-MN	0.05	0.31*	0.18*	0.05 (−)	23
Grand Forks, ND	0.17	0.25*	0.20*	0.04 (−)	22
Jamestown, ND	0.01 (−)	0.02	0.00	0.10 (−)	20
J. Clark Salyer NWR, ND	0.20*	0.07	0.03	0.01	23

* $P < 0.05$ for regression.
[1] Some data on effort and visibility were missing for some counts so that some regressions were calculated from a smaller number of years.
[2] Indicates a negative regression coefficient.

characters described by Portenko (1972), Josephson (1980), Boxall and Lein (1982b), and Kerlinger and Lein (1986). Although we were conservative in these determinations, we were able to assign ages to 240 of 292 owls sighted (82.2%) and sexes to 268 (91.8%). Sample sizes in age-sex class analyses may be greater than the number of owls seen on road counts because birds seen while we drove to and from the study sites were included in the pooled data used for these analyses.

RESULTS

ABUNDANCE AND DISTRIBUTION OF SNOWY OWLS ON THE NORTHERN GREAT PLAINS

Regression analyses indicated that none of the measures of observer effort and visibility were strong predictors of the number of Snowy Owls seen on a CBC. They accounted for only very small proportions of the variance in the number of owls reported on a count (<35% of the variance in 43 of 44 regressions) (Table 2). Only eight of 44 regressions were significant, although four of 11 regressions for party-miles were significant (Table 2).

Snowy Owls were present on the northern Great Plains in all winters from 1961–1984. Within the area shown in Figure 1 there was a latitudinal gradient in owl abundance (mean number of owls per year for a locality vs. latitude, $r = 0.676$, $n = 33$ localities, $P < 0.01$; percentage of years reporting owls for a locality vs. latitude, $r = 0.757$, $n = 33$ localities, $P < 0.01$). CBCs in Canada, with the exception of Oak Lake, Manitoba, averaged >2.25 owls per year and reported owls in >75% of all years (Table 1). In contrast, only three count localities in North Dakota, three in South Dakota, and one in Montana averaged >1.0 owl per year, and none averaged >2.0 owls per year. Of 26 count localities from the United States only nine reported owls in >50% of all years.

The abundance of Snowy Owls did not fluctuate synchronously throughout the northern Great Plains during the 24-year period, as indicated by a paucity of significant correlations among the number of owls reported from various CBC localities. Only three of 55 pair-wise correlations were significant (Edmonton and Calgary, Alberta, $r = 0.506$, $P < 0.05$; Oak Lake, Manitoba, and Saskatoon, Saskatchewan, $r = 0.508$, $P < 0.05$; Des Lacs National Wildlife Refuge (NWR) and J. Clark Salyer NWR, North Dakota, $r = 0.566$, $P < 0.01$). The number of significant correlation coefficients is nearly identical to the number which would be expected by chance (2.75) with 55 analyses.

A year-by-year examination of CBCs also shows that the abundance of owls is apparently patchy in both time and space. In one year the number of owls reported from a CBC site may be large, whereas at a locality 100 km away the number may be small. Similarly, the number at one locality may be large in one year and small the next. For example, in 1979 the Regina CBC reported 24 owls (the highest number reported by any count during the study period) while four

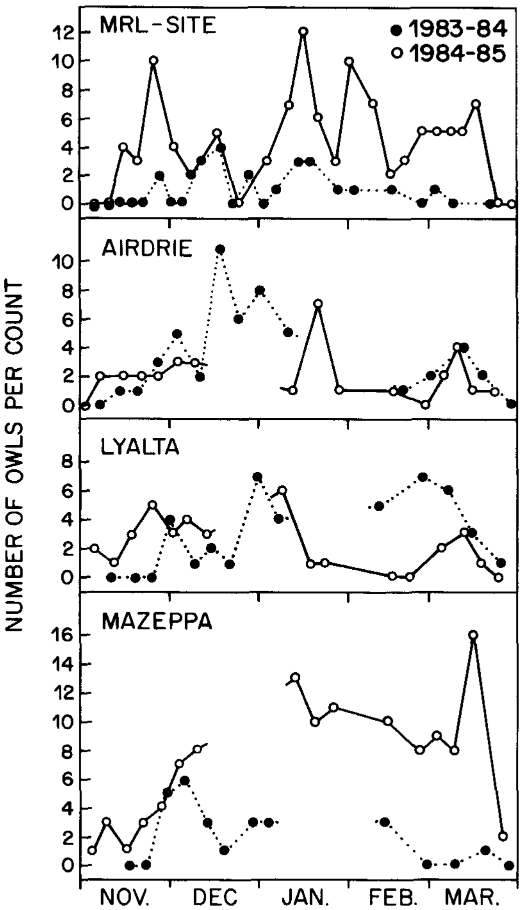

FIGURE 2. Abundance of Snowy Owls on four study sites near Calgary, Alberta during the winters of 1983–1984 and 1984–1985.

of five other Canadian localities reported below average numbers. In 1980 the Winnipeg CBC reported 23 owls, whereas most (four of five) other Canadian stations reported fewer owls than average. These are extreme examples, but, along with many others, they suggest that Snowy Owls are not homogeneous in dispersion within a year, or among years, on the Great Plains. The dispersion of owls south of the Canadian border is less patchy because most localities report one or no owls per year.

POPULATION ECOLOGY OF SNOWY OWLS IN SOUTHWESTERN ALBERTA

Snowy Owls were first noted on our Alberta study sites in early to mid-November with the first individuals observed on 13 November 1983 and 2 November 1984 (Fig. 2). Owls were present on all sites by 27 November 1983 and 14 November 1984. After arrival of the first birds, migrants seemed to arrive in "waves" composed of many individuals. At least three apparent waves were noted during the 1983–1984 "autumn" migration: 26–30 November, 14 owls recorded on four sites; 13–18 December, 20 owls; and 28 December to 1 January, 20 owls. The first wave of migrants in 1984–1985 was between 24–27 November when 21 owls were seen on the four sites. Prior to the earliest waves the greatest number of Snowy Owls seen on one site was two in 1983 and four in 1984 (Fig. 2). Although we use the term "wave," we do not imply that the number of owls fluctuated synchronously among all sites. During the waves of 13–18 December 1983 and 24–27 November 1984, the MRL and Airdrie sites accounted for 55% (11 of 20) and 48% (10 of 21) of all owls, respectively.

Female owls were seen earlier than males in both winters. In 1983 the first adult male was observed on 27 November, 2 weeks after the first bird, an adult female. The first adult male seen in 1984 (14 November) was observed 8 days after the first adult female and 12 days after the first immature female. Owls of all age-sex classes had been observed by 30 November 1983 and 14 November 1984 (Table 3).

Although adult females were seen before adult males in both years, adult males sometimes accounted for large percentages of individuals seen in early winter. During the periods 13–18 December 1983 and 28 December 1983 to 1 January 1984, adult males comprised >50% of all owls seen. Adult females accounted for only 10% and 24%, respectively, of the owls seen during these periods. At no time in the early winter of 1984–1985 did adult males account for more than 10% of the owls seen, whereas adult females made up between 28.5% and 60% of the birds seen between 24 November and 17 December 1983 (Table 3).

The exodus of owls from southwestern Alberta in 1984 apparently began during the last week of February. During that week and the first week of March the number of adult females present on the four sites decreased from 10 to three (Table 3). During the same period the number of adult males increased from five to seven. Thus, adult males apparently either stayed in Alberta longer than did adult females or they migrated through later. By the week of 18–24 March 1984, the number of owls had declined to about one-

TABLE 3. The numbers of Snowy Owls of different age-sex classes seen during various periods of two winters on study sites in southwestern Alberta.

Period	Number of owls[1]							Total
	Adult		Immature		Unknown age			
	Female	Male	Female	Male	Female	Male	Unknown	
1983–1984								
26 Nov–30 Nov	1	3	6	2	1	0	1	14
13 Dec–18 Dec	2	11	3	2	1	0	0	19
28 Dec–01 Jan	5	11	3	0	2	0	0	21
12 Jan–26 Feb	10	5	0	0	3	0	0	18
27 Feb–11 Mar	3	7	0	1	2	0	2	15
14 Mar–24 Mar	2	4	0	0	0	0	2	8
1984–1985								
24 Nov–27 Nov	6	1	3	3	3	0	4	20
09 Dec–17 Dec	12	2	3	2	0	0	1	20
03 Jan–13 Jan	21	9	2	1	6	0	6	45
14 Jan–27 Feb	24	9	4	13	4	0	5	59
28 Feb–05 Mar	9	5	1	5	1	0	0	21
12 Mar–18 Mar	5	6	5	8	2	3	3	32

[1] Values represent the maximum number of individuals of an age-sex class seen on each site during one round of samples, pooled over sites.

third the number in midwinter (Fig. 2). In 1985 owls began to leave in large numbers from the last week of February into the first week of March. By the second week of March immatures were present in numbers approximately equal to those of adults. The final large-scale exodus occurred between 15–18 March (25 owls) and 23–25 March (three owls). The largest change in the numbers of owls was on the Mazeppa study site where the number of owls declined from 16 on 16 March to two on 25 March.

Snowy Owls remained in Alberta until mid- to late March in both years (Fig. 2). Although the last owl was seen on the MRL-site on 2 March 1984, owls were present on the Airdrie, Mazeppa, and Lyalta sites on 18, 19, and 24 March, respectively. Departure dates in 1985 were similar to those in 1984 with owls seen on all sites during the period 17–25 March (11 owls). Owls may have been present after 25 March 1985, but fieldwork was terminated on that date.

The abundance of Snowy Owls during midwinter (29 December 1983 to 11 March 1984; 3 January 1984 to 5 March 1985) varied among sites and between years (Table 4, Fig. 2). The average number of owls per site during the 2 years of observations was 4.06 ± 1.03 ($\bar{x}$ ± SE, n = 8). Two-way analysis of variance revealed significant differences in the number of owls observed among sites ($F_{(3,46)} = 5.32$, $P < 0.01$) and between years ($F_{(1,46)} = 12.88$, $P < 0.01$). Nearly twice as many owls were seen on the four sites in 1984–1985 as in 1983–1984 (1983–1984: 2.84 ± 0.48, n = 25; 1984–1985: 5.03 ± 0.75, n = 29). However, the difference among sites did not always reflect the overall difference between years. For instance, the Lyalta site reported the most owls of any site in 1983–1984 and the lowest number in 1984–1985 (Table 4, Fig. 2). The greatest change in abundance was on the Mazeppa site where owl numbers increased >five times between the first and second year. A four-

TABLE 4. Snowy Owl abundances during midwinter (28 December 1983–11 March 1984; 3 January–5 March 1985) on the four study sites in southwestern Alberta.

Site	Mean number of owls ± SE (number of samples)		
	1983–1984	1984–1985	Both winters combined
MRL-site	1.30 ± 0.34 (10)	5.73 ± 0.94 (11)	3.92 ± 0.70 (21)
Airdrie	4.00 ± 1.23 (5)	2.00 ± 1.03 (6)	2.91 ± 0.81 (11)
Lyalta	5.80 ± 0.58 (5)	1.67 ± 0.92 (6)	3.55 ± 0.85 (11)
Mazeppa	1.80 ± 0.73 (5)	10.17 ± 0.70 (6)	6.37 ± 1.40 (11)

fold increase was obvious between years on the MRL-site.

Adult owls predominated during midwinter in both years, accounting for 71–83% of all owls present during midwinter of 1983–1984 and 56–67% during 1984–1985 (Table 3). In both midwinter periods females outnumbered males. The sex ratio in 1983–1984 appeared to change dramatically in January. Adult males outnumbered adult females early in the month, while adult females outnumbered adult males from mid-January until late February. The numbers of adult males and adult females remained fairly constant for nearly 2 months during the midwinter of 1984–1985 with adult females twice as abundant as adult males (Table 3). A large influx of immature males was evident after mid-January 1985 and these birds outnumbered adult males for the remainder of the month.

DISCUSSION

The evidence from 24 years of CBCs and 2 years of fieldwork confirm that the Snowy Owl is a widespread and regular winter resident on the northern Great Plains. It is important to note that our fieldwork was conducted during a period in which no major irruption of owls was reported from central North America, so we did not conduct our study at a time when owls were overly abundant. Our findings support the suggestions of Boxall and Lein (1982a) and Kerlinger et al. (1985) that the Snowy Owl is a regular winter resident of the northern Great Plains, but are not consistent with Shelford (1945), Gross (1947), or Chitty (1950), who concluded that Snowy Owls left their tundra breeding range most often at intervals of 3 to 4 years, when populations of their lemming prey crashed.

Several factors make the northern Great Plains a suitable wintering area for Snowy Owls. The most important factors are probably the proximity and physiographic similarity of the prairies to the tundra, and the abundance of suitable prey (Boxall and Lein 1982b). Inspection of topographic and vegetation maps of North America shows that the northern Great Plains is the closest area with suitable habitat (Boxall and Lein 1982a) to the breeding range of the species. Most Snowy Owls observed in winter in areas to the east or west of the northern Great Plains are along or near coastlines of oceans or the Great Lakes (Gross 1947; Kerlinger and Lein, unpubl. data). Few owls are reported from forested or mountainous localities, suggesting that these regions may be avoided by owls (Kerlinger and Lein, unpubl. data). The fact that experienced birds (adults) reach the eastern and western areas of North America only infrequently (Kerlinger and Lein 1986) also suggest that habitats in these regions are unsuitable for Snowy Owls and that the migrations of mostly immature birds to these areas are irruptions (sensu Gauthreaux 1982).

The age-sex class structure of wintering Snowy Owl populations in southwestern Alberta observed during two winters does not differ greatly from that derived from museum specimens (Kerlinger and Lein 1986). In both data sets, adults outnumbered immatures and adult females outnumbered adult males during midwinter.

Although our sample sizes were small, and therefore should be viewed with caution, we were impressed by the apparent large variation in numbers of owls of different age-sex classes throughout the entire nonbreeding season, and by the protracted arrival of owls in autumn. Influxes of birds from early November to early January along with changing proportions of age-sex classes may indicate either inherent variability in the migratory behavior of these birds or movement of individuals from different populations. The breeding range of Snowy Owls in North America extends from about 57°N to >75°N (AOU 1983), suggesting that the timing of migration might vary with latitude. Birds from farthest north should migrate earliest in autumn, as is the case with other migrants (e.g., Geller and Temple 1983). The logistical problems of identifying the area of origin of wintering owls, and of censusing their populations over large areas, will make it difficult to determine why the timing of migration varies among populations of Snowy Owls and why the proportions of age-sex classes change from week to week.

The difference in the number of owls that we observed between the two winters (more owls in 1984–1985 than in 1983–1984) may not reflect a general difference between years over a larger portion of the Canadian prairies. The 1983 CBCs from seven Canadian localities (Table 1) showed that three localities reported fewer owls (more than one owl less than the mean) than the mean numbers for the entire period (Table 1), two reported numbers within one owl of the mean, and two reported more than one owl above the mean. In 1984 four counts reported numbers below average, two reported numbers within one owl of the mean, and one locality did not report.

DISPERSION PATTERNS OF SNOWY OWLS

The dispersion of owls in southwestern Alberta appears to be a mosaic with patches varying on a scale of several hundred square kilometers. In 1983–1984 owls were more abundant on the two primary sites located north of the Trans-Canada Highway (Airdrie and Lyalta). The situation was reversed in the winter of 1984–1985. Owl numbers on the supplementary road counts conducted in January 1985 were similar to the abundances on the nearest primary study sites. On the Beiseker site, three owls were seen in 100 km, similar to the midwinter mean on the adjacent Airdrie site (Table 4). Eight owls were seen on each of the Brant and Kirkaldy sites, values similar to the mean abundance of owls on the nearby Mazeppa site (Table 4).

During autumn and early winter it seemed that owl abundances were unpredictable on a given site, but by mid-December to early January the numbers became more stable. This may indicate that, early in the winter, the owls are seeking suitable places to spend the nonbreeding season. Boxall and Lein (1982a) demonstrated that female owls became territorial and selected habitat nonrandomly during midwinter on one of our study sites. Because the abundance of owls changed between years on the various sites, habitat selection cannot explain the patchy dispersion pattern that we found. Instead, we suggest that the dispersion of owls is linked to local availability of their primary prey, which are deer mice (*Peromyscus maniculatus*), meadow voles (*Microtus pennsylvanicus*), and Gray Partridge (*Perdix perdix*) in our study area (Boxall and Lein 1982b).

The patchy distribution of Snowy Owls has implications for the techniques used to study these and other predatory birds. We stress the importance of selecting multiple study sites for estimating winter abundances of raptors. Studies in which a single site is sampled can be biased, especially if researchers are attempting to make generalizations about larger geographical areas. If we had sampled owls on only one site, we would not have detected the patchy dispersion and we might have concluded that there was a dramatic change in the numbers of owls present from year to year. Even with samples from multiple sites we are not sure that our data are representative of a larger portion of the Canadian prairies, or even of southwestern Alberta. Most studies of winter raptor populations have examined only a single nonrandomly selected site (see Fuller and Mosher 1981 for a review of the methods). In addition, the use of multiple study sites would result in larger sample sizes and independence of data for analyses regarding habitat selection, home-range size, territoriality, and determination of age-sex class structure of populations.

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