J. Field Ornithol., 60(1):20–29

TIME BUDGETS AND ACTIVITY OF WINTERING SNOWY OWLS

PETER C. BOXALL[1] AND M. ROSS LEIN[2]
Division of Ecology (Behavioral Ecology Group)
Department of Biological Sciences
University of Calgary
Calgary Alberta T2N 1N4, Canada

Abstract.—We measured diurnal activity budgets of territorial Snowy Owls (*Nyctea scandiaca*) wintering near Calgary, Alberta. Owls spent 98% of the daylight hours perched, but showed peaks of activity in early morning and late afternoon. Energy budgets were estimated from time budgets, assuming that daylight activity was typical of the 24-h period. Estimates of daily energy expenditure were not correlated with the number of attempted prey captures observed. The rates of prey capture observed during daylight hours failed to meet the estimated energy requirements, suggesting that a disproportionate amount of hunting occurs at night.

PRESUPUESTOS DEL PATRÓN DE ACTIVIDADES DE *NYCTEA SCANDIACA*

Resumen.—Hicimos un presupuesto de las actividades diurnas de búhos (*Nyctea scandiaca*) que pasan el invierno en Calgary, Alberta. Los búhos pasan el 98% de las horas diurnas posados en perchas; mostraron mayor actividad temprano en la mañana y bien entrada la tarde. El presupuesto energético de estas aves fue estimado, asumiendo que las actividades diurnas eran típicas de las 24 horas del día. Estimados de gastos diurnos de energía no se correlacionaron con el número de presas que se observó capturar a estas aves. La captura de presas durante el día no llena los requisitos energéticos de estos búhos, lo que sugiere que la cacería por parte de estas aves debe ser considerable durante las noches.

The Snowy Owl (*Nyctea scandiaca*) breeds in the Arctic (Portenko 1972) and winters regularly in southern Canada and the northern United States (Boxall and Lein 1982a, Gross 1947, Kerlinger et al. 1985). It is commonly believed that the Snowy Owl is active during daylight (e.g., Peterson 1947), although there is little information describing the form and extent of its diurnal activity.

Our studies of wintering Snowy Owls have raised questions about many of the popular conceptions of the winter biology of this species (Boxall and Lein 1982a, 1982b; Kerlinger et al. 1985; Kerlinger and Lein 1986, 1988). In this paper we describe the daylight activity pattern and associated energy budgets of Snowy Owls wintering on the Canadian prairies in southern Alberta.

METHODS

Owls were observed from early December to late February in the winters of 1976–1977 and 1977–1978. The birds were territorial residents (Boxall and Lein 1982a) and were individually recognized by distinctive variation in plumage markings (Boxall and Lein 1982b). The study area

[1] *Current address: Fish and Wildlife Division, Petroleum Plaza, 9945 108 Street, Edmonton Alberta T5K 2G6 Canada.*
[2] *Send reprint requests to M. Ross Lein.*

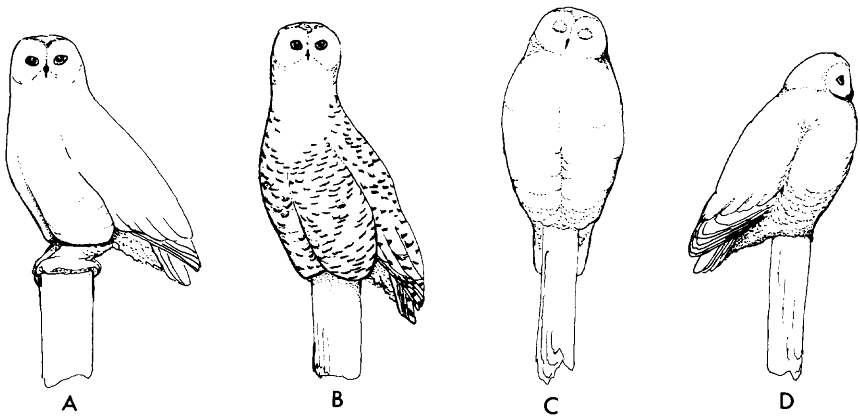

FIGURE 1. Postures of alert (A, B) and resting (C, D) Snowy Owls.

was a 185 km^2 block of agricultural land on the southeastern border of Calgary. The main habitats were stubble fields (37.4%), summer fallow (33.7%), hayfields (12.0%) and pasture (7.7%).

The owls used many types of perches, including knolls and hilltops, utility poles, power transmission towers, trees, and fenceposts. Most perches gave the birds excellent views of the surrounding area and were not sheltered from the wind. Objects used as perches ranged from 1.5 m (fenceposts) to 30 m (towers) in height. Fenceposts and utility poles were the most commonly-used perches.

Owls were observed from an automobile parked 100–300 m away for periods lasting 1–6 h. Durations of activities were measured with a stopwatch. Over the two winters, 138 h of time budget data were collected on 15 individual owls. For analysis, daylight (0800–1800) was divided into five 2-h periods. To control for minor differences in observation time among these periods (range of 23.5 to 31.0 h/period), we present our results as proportions of time, or as rates per hour.

Behavioral categories recorded were:

Alert: Birds perched in an upright position, scanning their surroundings actively (Figs. 1A, B). Such birds were apparently hunting or watching for territorial intruders.

Resting: Perched birds that were sleeping or dozing, with the head retracted and eyes closed (Figs. 1C, D).

Preening: All forms of comfort movements including the manipulation of feathers with bills, scratching with feet, rousing and stretching.

Flight.

Other: Activities not corresponding to any of the above, including feeding and intra- and interspecific interactions.

We distinguished alert owls from resting ones by counting the number of times an owl turned its head in 1 min. After preliminary observations of hunting and resting owls, we chose a value of six head-turns per minute as the lower limit for an alert owl. Counts were made every 5 min, and also when the activity of the bird was uncertain. Cases in which an owl was obviously peering intently at prey items of conspecifics without turning its head were also recorded as alert.

We collected activity data for only the daylight hours (0800–1800), 41.7% of a 24-h period. Attempts to observe owls after sunset, using an image-intensifying telescope, were unsuccessful because of the difficulty of relocating birds after they moved. Therefore, in order to calculate a daily energy budget, we have assumed that the daylight time budget is representative of the 24-h time budget. This assumption is almost certainly invalid, as discussed below, but serves to provide a first approximation for exploratory purposes.

Daily energy expenditures (*DEE*) were estimated using the equation:

$$DEE = (A_a \times C_a) + (A_r \times C_r) + (A_p \times C_p) + (A_f \times C_f) + (A_o \times C_o) \quad (1)$$

where A_a, A_r, A_p, A_f and A_o represent the amounts of time spent alert, resting, preening, flying and in other activity, respectively, and C_a, C_r, C_p, C_f and C_o represent the energetic costs per unit time of these behavioral categories.

The existence metabolism (*EM*) of Snowy Owls in kJ/day was estimated using the equation from Gessaman (1972):

$$EM = 802.56 - 23.82T_a \quad (2)$$

where T_a is ambient temperature. The estimated costs of activities, expressed as multiples of existence metabolism, are: alert = 1.3 × *EM*; resting = 1.0 × *EM*; preening = 1.7 × *EM*; flight = 14.0 × *EM*; other = 1.7 × *EM*. These estimates are derived from King (1974), except for the flight value, which was derived from Tucker's (1974) equation 12 using 1.802 kg as the mean weight of male and female Snowy Owls (Snyder and Wiley 1976). The energetic costs that we use agree with estimates for similar activities of other species (see King 1974, Tarboton 1978).

We have used existence metabolism, as opposed to basal metabolism, in our estimates in order to incorporate the effects of ambient temperature. The use of existence metabolism, although somewhat controversial (King 1974), has been found to produce reasonably accurate estimates (<10% error) of daily energy expenditure when two conditions are met (Weathers et al. 1984). First, T_a must be an accurate measure of the thermal environment of the bird. Although we have no direct evidence on this point, there was no correlation between activity pattern and either T_a or wind speed (see below), suggesting that Snowy Owls make few behavioral adjustments in order to seek particularly favorable microclimates. Second, the activity of wild birds must not differ markedly from that of the captive birds on which the metabolic measurements were made. The owls that we observed spent almost all their time perched and inactive (see below) and thus differences in activity levels from those of confined Snowy Owls in the arctic (Gessaman 1972, Shields 1969) are probably small.

Because we lacked a continuous record of temperatures on our study area, we calculated monthly energy budgets using mean monthly temperatures from meteorological summaries for the Calgary International Airport, 20 km N of the study area. Numerous temperature readings taken on the study area showed close agreement with the airport data, with a maximum difference of 2–3 C. Such differences would produce minimal errors in calculations of energy budgets and can therefore be ignored. Calgary's winter climate is humid continental (Powell 1978) and is dominated by Arctic air masses. Warm periods with strong westerly winds ("chinooks"), resulting from the inflow of Pacific air masses, are common but of short duration (Longley 1972). The mean January temperature is approximately −10 C and the mean annual snowfall is approximately 150 cm (Longley 1972). During the winters of our study, Calgary experienced temperatures as low as −37 C and sustained winds as high as 70 km/h (data from Monthly Meteorological Summaries, Atmospheric Environment Service, Calgary).

For purposes of illustration we convert daily energy requirements into equivalent numbers of deer mice (*Peromyscus maniculatus*) or meadow voles (*Microtus pennsylvanicus*), the major prey of Snowy Owls on our study area (Boxall and Lein 1982b). To make this conversion we used average body weights of 25 g for *Peromyscus* and 38 g for *Microtus* (derived from fall samples collected in the Calgary area), energetic values of 6.74 kJ/g for *Peromyscus* and 5.95 kJ/g for *Microtus* (Fleharty et al. 1973), and an assimilation efficiency of 77% for Snowy Owls (Gessaman 1972). A higher caloric value for *Peromyscus* relative to *Microtus* has been supported by other studies (e.g., Bergeron 1976).

RESULTS

Snowy Owls exhibited diurnal variation in activity (Fig. 2). In 1977–1978 owls spent more time alert or flying during the early morning (0800–1000) and late afternoon (1600–1800) than at other times. These activity maxima were separated by a period of inactivity (resting) from 1000–1600. Significant differences among the 2-h time periods were found for the alert, resting and flying categories in 1977–1978 (ANOVA, $P < 0.05$). The amount of time spent in these behavioral categories did not differ significantly among the three time periods in the middle of the day (1000–1600), but activity in these periods differed significantly from that in the early morning and late afternoon time periods (Student-Neumann-Keuls multiple range tests, $P < 0.05$).

This bimodal activity pattern was not as apparent in 1976–1977 (Fig. 2). Although the mean percentages of time spent in various activities did not differ significantly among time periods (ANOVA, all $P > 0.05$), they showed a trend similar to the pattern observed in 1977–1978.

Perch-changes, indicative of hunting activity (Boxall and Lein 1982b), were more frequent in early morning and late afternoon than during the middle of the day (Fig. 3A). Actual attempts to capture prey showed a pronounced peak in late afternoon (1600–1800) (Fig. 3B). In addition,

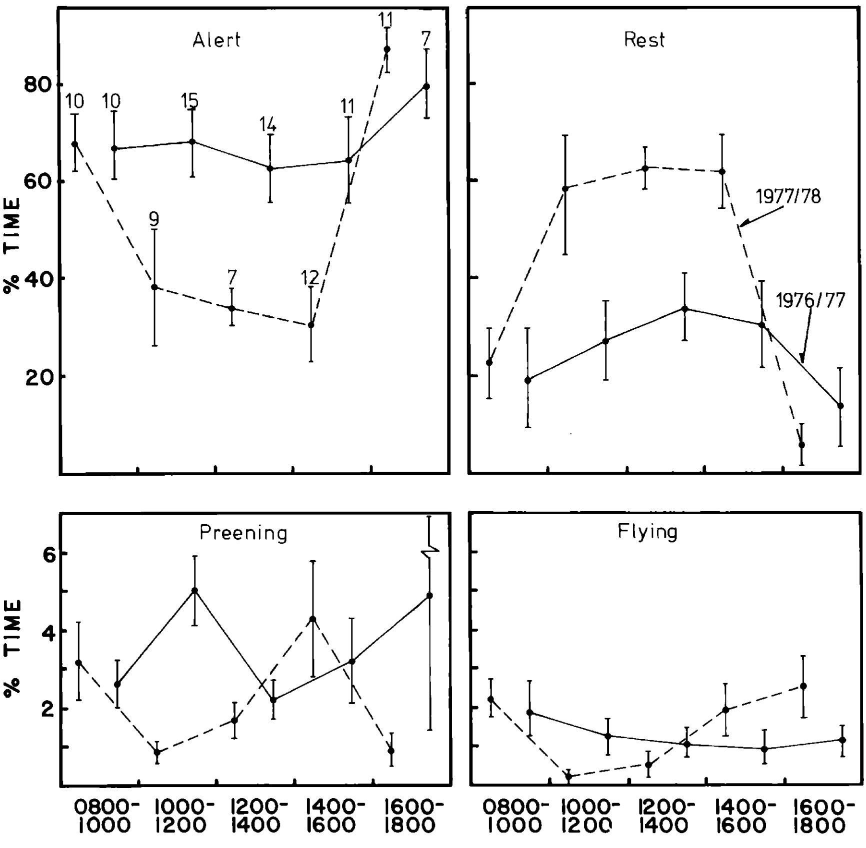

FIGURE 2. The proportions of time spent by Snowy Owls in four activities during different periods of the day in the winters of 1976–1977 (solid lines) and 1977–1978 (dashed lines). Vertical bars are standard errors of the means; numbers above the bars represent the number of hours of observation. Values for the two winters are slightly offset for ease of presentation.

perch height was significantly higher between 1600 and 1800 than at other times of the day (Table 1); high perches are used more often than low perches for hunting (Boxall and Lein 1982b).

Because of the diurnal activity rhythm, we analyzed activity data for each 2-h period separately. No significant correlations were found between the amount of time spent in any of the activities in any time period and either temperature or wind velocity. Using average values for each 2-h period and correcting for unequal samples, we estimated overall time budgets of owls during daylight hours for both winters (Table 2). Owls spent 98% of the daylight hours perched. Owls were alert more often than resting. This was more pronounced in 1976–1977 than 1977–1978,

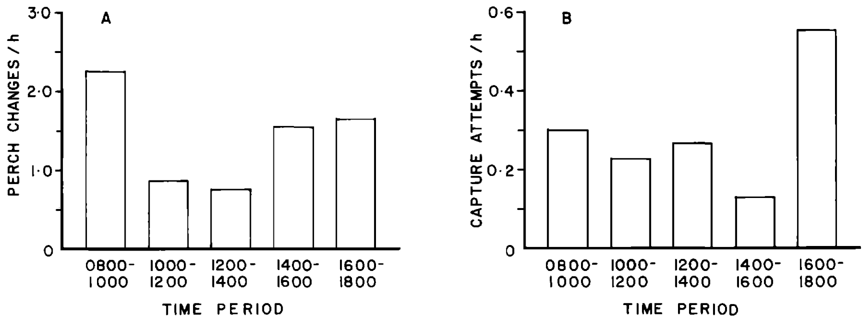

FIGURE 3. Rates of perch changes and prey-capture attempts by Snowy Owls at different times of day. A. The number of perch changes per hour (n = 184). B. The number of prey-capture attempts per hour (n = 36). Data for both winters combined.

although time budgets did not differ significantly between years (Table 2).

Using the overall time budget (Table 2), equations 1 and 2, and the grand mean of the daily mean temperatures in each winter, we estimated that the average daylight (0800–1800) energy costs were 511.2 kJ and 590.0 kJ for 1976–1977 and 1977–1978, respectively. The higher energy costs in 1977–1978 resulted from lower ambient temperatures. If the time budget data in Table 2 are representative of the entire 24-h period, these values become 1227.0 kJ/day for 1976–1977 and 1415.9 kJ/day for 1977–1978. Converting these figures to numbers of prey individuals, we estimate that Snowy Owls needed to eat about 9.5 *Peromyscus* (236 g) or about seven *Microtus* (268 g) per day in 1976–1977 in order to meet their energy requirements. Because of colder ambient temperatures in 1977–1978, food requirements rose to about 11 *Peromyscus* (273 g) or about 8 *Microtus* (309 g) per day. On a monthly basis (Table 3) there was no correlation between the number of attempted prey captures and the number of prey needed to meet energy needs (Spearman rank correlations, $r_s = -0.10$, $P = 0.44$).

TABLE 1. Numbers of observations of territorial Snowy Owls perched at various heights at different times of day. Data for both winters combined.

Time period	Perch height (m)[a]					Total
	0	1–2	2–5	5–10	>10	
0800–1000	8	36	13	8	7	72
1000–1200	7	22	5	10	4	48
1200–1400	16	21	12	15	8	72
1400–1600	13	17	20	11	5	66
1600–1800	1	3	11	7	3	25

[a] Perch height differs significantly with time period (G-test, $P < 0.005$); differences among rows 1–4 is not significant ($P > 0.10$); difference between combined rows 1–4 and row 5 is significant ($P < 0.01$).

TABLE 2. Diurnal time budget of wintering Snowy Owls during two winters near Calgary, Alberta.

Year	% Daylight hours spent in activity					Observation time (h)
	Alert	Rest	Preening	Flight	Other	
1976/1977	65.6	25.8	4.8	1.2	2.6	58
1977/1978	55.0	39.6	2.1	1.5	1.8	69
Both years[a]	59.9	33.2	3.3	1.3	2.2	127

[a] Differences between years are not significant (G-test, $P > 0.05$).

DISCUSSION

Wintering Snowy Owls in southern Alberta appear to be most active around sunrise and sunset. The bimodal distribution of time spent flying and alert (Fig. 2), and the temporal distributions of perch-changes (Fig. 3A), attempts at prey capture (Fig. 3B), and use of higher perches (Table 1), support this suggestion. These findings confirm anecdotal reports of crepuscular peaks of activity for wintering Snowy Owls (e.g., Höhn 1973, Weir 1973, Young 1973).

Some parallels can be drawn between the activity patterns of Snowy Owls and those of their principal prey, *Peromyscus, Microtus,* and Gray Partridges (*Perdix perdix*) (Boxall and Lein 1982b). *Peromyscus* are essentially nocturnal, although some diurnal activity occurs during winter (Hamilton 1937). Their winter activity pattern consists of a major period of activity early in the evening, starting at sunset and lasting one or two hours, and another late in the night, at about 0300 (Falls 1968). *Microtus* shift from a nocturnal or crepuscular activity patterns in summer to a more diurnal emphasis during winter (Madison 1985). However, activity peaks are of greater amplitude near sunrise and sunset (Hamilton 1937). Westerskov (1966) found that Gray Partridges forage throughout the day in winter, but most intensively in the late afternoon. The pronounced activity of Snowy Owls at sunset and the few hours before coincides with activity maxima of all three prey species. Other raptors utilizing these prey species show similar activity patterns (Craighead and Craighead 1956).

The activity cycle of wintering Snowy Owls may be similar to that exhibited during the breeding season. Shields (1969) found that, in early summer (continuous daylight) near Barrow, Alaska, owls were relatively active throughout the 24-h period. However, there were minor peaks in activity from 0500–0700, and particularly from 1600–1800. Later in the year, when the days became shorter, Shields found that captive owls were most active at sunset and for several hours following darkness. Shields argued that these patterns apparently were related to the activity periods of lemmings, the major prey of owls in the area.

Gessaman (1972), using metabolic measurements on captive birds, estimated that the food requirements of a free-living Snowy Owl in winter

TABLE 3. Mean monthly temperatures and corresponding daily energy requirements, and rates of hunting during daylight hours, for Snowy Owls wintering near Calgary, Alberta. Energetic requirements calculated using monthly time budgets and existence requirements.

Month	Mean temperature (°C)	Energetic requirements (no. of prey/day)		No. of hunting attempts/h
		Microtus	*Peromyscus*	
Jan 1977	−7.7	8.0	10.7	0.45
Feb 1977	2.2	5.9	8.0	0.28
Dec 1977	−13.0	8.9	11.9	0.31
Jan 1978	−14.9	8.9	12.0	0.28
Feb 1978	−10.9	8.6	11.6	0.50

at Barrow, Alaska, would vary between 240–400 g of lemmings per day, depending on temperature. Our calculated requirements (236–309 g of mice per day) agree closely with these figures, as well as with other estimates (Watson 1957).

The lack of correlation, on a monthly basis, between the number of prey-capture attempts and the calculated food requirements is perhaps not surprising. Such a correlation would require that the owls were adjusting their hunting behavior according to their short-term energy requirements. Instead, we believe that the owls probably are maximizing their food intake. Any food obtained that is "surplus" to the short-term energy requirements would be stored as fat reserves, which may be extensive in wintering Snowy Owls (Kerlinger and Lein 1988).

Evidence for extensive nocturnal activity comes from the lack of agreement between the numbers of prey-capture attempts during daylight and daily energy expenditure (Table 3). The discrepancy is too large to be explained by the inaccuracy of our estimate of daily energy expenditure, which agrees with estimates of other workers. The most likely explanation is that the birds were doing a considerable amount of hunting between 1800 and 0800. The measured rates of prey-capture attempts (0.28–0.5/h, Table 3) would result in only 1.6–2.9 prey captures per 10-h day at a success rate of 58% (Boxall and Lein 1982b). The same hunting rates and success rates would result in 3.9–7.0 prey captures in a 24-h period. These latter figures are closer to, but still lower than, our estimates of the numbers of mice required to satisfy daily energy requirements (Table 3). The rates of both prey-capture attempts and successful hunts may be higher during darkness than those we measured because of the nocturnal habits of *Peromyscus,* the most frequent prey of Snowy Owls on our study area (Boxall and Lein 1982b) and because the owls may be more successful under cover of darkness. This would further reduce the noted discrepancy. In addition, capture of large prey items such as Gray Partridges or white-tailed jack rabbits (*Lepus townsendii*) (Boxall and Lein 1982b), although infrequent, would reduce the total number of prey captures required to meet energy requirements.

We found no indication that owls either were starving or adjusting their behavior in response to the low temperatures and strong winds on our study area. This is not surprising because Snowy Owls appear well adapted to survive under the harshest winter conditions. Some owls apparently overwinter in the arctic, as far north as 82°N on Ellesmere Island (Gessaman 1972, Manning et al. 1956, Sutton 1932). Their thermal conductance is the lowest recorded for any animal except the Adelie Penguin (*Pygoscelis adeliae*); the insulation of their plumage is equivalent to the highest value reported for arctic mammals; their standard metabolic rate is lower than that of other avian species of comparable body weight; and they can survive at ambient temperatures below the lowest recorded in the Northern Hemisphere (Gessaman 1972). Snowy Owls possess a thermoneutral zone (the range of temperatures where neither physical nor chemical mechanisms for controlling heat production need be employed) between 2.5 and 18.5 C (Gessaman 1972). During this study, temperatures consistently below 2.5 C were encountered only in the winter of 1977–1978. The owls decreased their activity slightly during this winter, but this change was insignificant compared to the adjustments in activity that other avian species must make to survive cold winter temperatures (e.g., Black-capped Chickadee, *Parus atricapillus* [Chaplin 1974]; Canada Goose, *Branta canadensis* [Raveling et al. 1972]).

ACKNOWLEDGMENTS

We thank C. C. Mamo and G. M. Webber for their assistance in the field. C. C. Mamo also drew the illustrations for Figure 1. J. A. Gessaman and P. Kerlinger made numerous valuable comments on earlier versions of the manuscript. This study was supported by grants from the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service, and the University of Calgary.

LITERATURE CITED

BERGERON, J. M. 1976. Caloric values of small mammals of southeastern Quebec. Acta Theriol. 21:157–163.

BOXALL, P. C., AND M. R. LEIN. 1982a. Territoriality and habitat selection of female Snowy Owls (*Nyctea scandiaca*) in winter. Can. J. Zool. 60:2344–2350.

———, AND ———. 1982b. Feeding ecology of Snowy Owls (*Nyctea scandiaca*) wintering in southern Alberta. Arctic 35:282–290.

CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. J. Comp. Physiol. 89:321–330.

CRAIGHEAD, J. J., AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Wildlife Management Institute, Washington, D.C.

FALLS, J. B. 1968. Activity. Pp. 543–570, *in* J. A. King, ed. Biology of *Peromyscus* (Rodentia). Am. Soc. Mammal., Spec. Publ. No. 2.

FLEHARTY, E. D., M. E. KRAUSE, AND D. P. STINNETT. 1973. Body composition, energy content and lipid cycles of four species of rodent. J. Mammal. 54:426–438.

GESSAMAN, J. A. 1972. Bioenergetics of the Snowy Owl (*Nyctea scandiaca*). Arct. Alp. Res. 4:223–238.

GROSS, A. O. 1947. Cyclic invasions of the Snowy Owl and the migration of 1945–1946. Auk 64:584–601.

HAMILTON, W. J., JR. 1937. Activity and home range of the field mouse *Microtus pennsylvanicus pennsylvanicus* (Ord.). Ecology 18:255–263.

HÖHN, E. O. 1973. Winter hunting of Snowy Owls in farmland. Can. Field-Nat. 87: 468–469.

KERLINGER, P., AND M. R. LEIN. 1986. Differences in winter range among age-sex classes of Snowy Owls *Nyctea scandiaca* in North America. Ornis Scand. 17:1–7.

———, AND ———. 1988. Causes of mortality, fat condition, and weights of wintering Snowy Owls. J. Field Ornithol. 59:7–12.

———, ———, AND B. J. SEVICK. 1985. Distribution and population fluctuations of wintering Snowy Owls (*Nyctea scandiaca*) in North America. Can. J. Zool. 63:1829–1834.

KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4–79, *in* R. A. Paynter, Jr., ed. Avian energetics. Publ. Nuttall Ornithol. Club, No. 15.

LONGLEY, R. W. 1972. The climate of the Prairie Provinces. Environ. Canada, Atmos. Environ. Serv., Climatol. Stud. No. 13.

MADISON, D. M. 1985. Activity rhythms and spacing. Pp. 373–419, *in* R. H. Tamarin, ed. Biology of New World *Microtus*. Am. Soc. Mammal., Spec. Publ. No. 8.

MANNING, T. H., E. O. HÖHN, AND A. H. MACPHERSON. 1956. The birds of Banks Island. Nat. Mus. Can. Bull. No. 143.

PETERSON, R. T. 1947. A field guide to the birds. Houghton Mifflin Company, Boston, MA.

PORTENKO, L. A. 1972. Die Schnee-Eule. Neue Brehm-Bucherei, Number 454. A. Ziemsen Verlag, Wittenberg.

POWELL, J. M. 1978. Climatic classification of the Prairie Provinces of Canada. Pp. 221–227, *in* K. D. Hage and E. R. Reinelt, eds. Essays on meteorology and climatology: in honour of Richard W. Longley. Univ. Alberta, Studies in Geography, Monogr. 3.

RAVELING, D. G., W. E. CREWS, AND W. D. KLIMSTRA. 1972. Activity patterns of Canada Geese during winter. Wilson Bull. 84:278–295.

SHIELDS, M. 1969. Activity cycles of Snowy Owls at Barrow, Alaska. Murrelet 50:14–16.

SNYDER, N. F. R., AND J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr., No. 20.

SUTTON, G. M. 1932. The birds of Southampton Island. Mem. Carnegie Mus., V. 12, Pt. II, Sect. 2, Pp. 3–267.

TARBOTON, W. R. 1978. Hunting and the energy budget of the Black-shouldered Kite. Condor 80:88–91.

TUCKER, V. A. 1974. Energetics of natural avian flight. Pp. 298–328, *in* R. A. Paynter, Jr., ed. Avian energetics. Publ. Nuttall Ornithol. Club, No. 15.

WATSON, A. 1957. The behaviour, breeding, and food ecology of the Snowy Owl *Nyctea scandiaca*. Ibis 99:419–462.

WEATHERS, W. W., W. A. BUTTEMER, A. M. HAYWORTH, AND K. A. NAGY. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459–472.

WEIR, R. D. 1973. Snowy Owl invasion on Wolfe Island, winter 1971–72. Ont. Field Biol. 27:3–17.

WESTERSKOV, K. 1966. Winter food and feeding habits of the partridge (*Perdix perdix*) in the Canadian prairie. Can. J. Zool. 44:303–322.

YOUNG, C. M. 1973. The Snowy Owl migration of 1971–72 in the Sudbury region of Ontario. Am. Birds 27:11–12.

Received 10 Nov. 1986; accepted 5 Jul. 1988.