The White-winged Crossbill consumes conifer seeds, with spruce ranking highest in North America (Gabrielson, U.S. Dept. Agric. Bull. 1249, 1924; Bent, U.S. Natl. Mus. Bull. 237, 1968) and in Europe (Pulliainen, Am. Zool. Fenn. 8:326–329, 1971, Am. Zool. Fenn. 9:28–31, 1972). Newton (1970; Finches, Taplinger, New York, 1973) and Ulfstrand (pp. 780–794 *in* Proc. XIII Int. Ornithol. Congr., 1963) considered it essentially a tamarack seed eater.

Coniferous tree cone production is cyclic with very high crop years occurring in different places in different years (Svärdson, Br. Birds 50:314–343, 1957). Our observations and specimens of White-winged Crossbills examined suggest that tamarack seeds were sufficiently abundant in southeastern Manitoba during the winter of 1975–76 to promote settling by dispersing birds. Also, tamarack cones and hence probably seeds were fed on by Red Crossbills (in small numbers in the area in 1975–76), Common Redpolls (*Carduelis flammea*), Black-capped Chickadees (*Parus atricapillus*), Sharp-tailed Grouse (*Pedioecetes phasianellus*) and Gray Jays (*Perisoreus canadensis*) during the invasion period. Bent (U.S. Natl. Mus. Bull. 162, 1932; U.S. Natl. Mus. Bull. 191, 1946; U.S. Natl. Mus. Bull. 237, 1968) reports that of these species only Red Crossbills are known to feed regularly on tamarack seeds and Sharp-tailed Grouse occasionally feed on these seeds.

We did not obtain evidence of breeding by White-winged Crossbills during our study. None of the specimens examined was in breeding condition (Table 1). We last saw White-winged Crossbills on 10 April 1976, despite continued work by Collins in the area until late June. A gradual increase in body fat from November through March (Table 1) suggests a build up prior to movement in spring. Newton (1970) reports a similar situation in the Red Crossbill in Europe.

We thank Ian Newton, Henri Ouellet and Harrison B. Tordoff for commenting on the manuscript. The field work in 1975–76 was funded by grants to Sealy from the Manitoba Department of Renewable Resources and Transportation Services and the Northern Studies Committee of the University of Manitoba.—SPENCER G. SEALY, DONALD A. SEXTON AND K. MICHAEL COLLINS, *Dept. Zool., Univ. Manitoba, Winnipeg, Manitoba R3T 2N2 Canada.* (Present addresses: [DAS] *Ducks Unlimited [Canada], Box 776, Dauphin, Manitoba R7N 3B3;* [KMC] *96 Noble Ave., Red Deer, Alberta T4P 2H5.*) *Accepted 2 Jan. 1979.*

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Winter hunting behavior of a Snowy Owl in Michigan.—The Snowy Owl (*Nyctea scandiaca*) has been frequently studied on its breeding grounds (e.g., Pitelka et al., Ecol. Monogr. 25:85–117, 1955a; Pitelka et al., Condor 57:3–18, 1955b; Sutton and Parmelee, Condor 58:273–282, 1956; Watson, Ibis 99:419–462, 1957; Parmelee, Beaver (summer):30–41, 1972; Taylor, Living Bird 12:137–154, 1973) and the literature abounds with diet analyses of this species (e.g., Keith, Wilson Bull. 75:276–277, 1963; Catling, Ont. Field Biol. 27:41–45, 1973; Allan, Jack Pine Warbler 55:42, 1977). Winter studies have been confined to censuses, the periodicity of invasions, food habits and territoriality (Keith, Can. Field-Nat. 74:106–112, 1960; Can. Field-Nat. 78:17–24, 1964; Quilliam, Ont. Field Biol. 19:1–8, 1965). I found no extensive reported examination of hunting behavior of the Snowy Owl in winter.

Study area and methods.—The study area was in slightly rolling terrain consisting of agricultural land (planted mostly to hay, with some rye and corn) with several small cherry orchards and scattered woodlots. The area included eastern Green Lake and western Blair townships in Grand Traverse County, in northwestern lower Michigan. Sunrise and sunset occurred at 07:35 and 18:01 EDST, respectively, on the first day of observations and at 06:39 and 18:44 on the last.

I studied 1 Snowy Owl, recognizable by distinctive plumage, between 11 February and 19 March 1978 for 143 h, including 8 daylong observations (½ h before sunrise to ½ h after sunset). Observations, made from a parked car with 7 × 35 binoculars and a 20–45× scope, were spread evenly throughout the day under varying cloud cover, precipitation and temperature (−29–7°C). An attempt was made to keep the number of observation hours per week equal.

For each observation period I recorded time, weather conditions and all behavior of the owl. Movements were mapped and pellets collected weekly at all perches and loafing sites. Pellets regurgitated as I watched were collected the same day. All pellets were air-dried for 2 weeks then weighed to the nearest 0.01 g. Meadow vole (*Microtus pennsylvanicus*) skeletons were sexed using pelvic characters defined by Guilday (J. Mamm. 32:216–217, 1951) and Dunmire (J. Mamm. 36:356–361, 1955). Specimens of prey species were also captured with snap-traps in the same area.

Weekly snow depth measurements were taken by inserting a meter stick at 10 sample sites (5 in frequent strike areas of the owl, 5 in randomly selected areas) scattered throughout the owl's hunting range. The measurement for each site was the average of 3 measurements made at 2 m intervals.

Winter hunting range.—The winter hunting range was drawn by plotting all observations of the owl on a map and connecting the peripheral locations. Area was measured using the cross-section paper method. The range was roughly oval, with a 1.3 km long axis and an area of 0.8 km^2. Keith (1960, 1964) noted a range of about 1.2 km^2 in Manitoba and 0.5–2.5 km^2 in Wisconsin. Keith (1964) reported that territories were defended against both wild and captive conspecifics.

The size of the winter hunting range was smaller than summer breeding territories, which ranged in size from 1.3–5.2 km^2 on Baffin Island (Watson 1957) and 5.2–10.4 km^2 at Point Barrow, Alaska (Pitelka et al. 1955a). Summer territories must be of a sufficient size to provide food resources adequate to support not only 2 adults, but several growing young as well, while the winter hunting range is used by only 1 individual.

Activity periods.—Three major activity periods were recognized: hunting, loafing and observing. When hunting the owl was acutely responsive to every movement and sound and made frequent assessment movements of the head, bobbing and swaying while staring at a particular location. No preening occurred during hunting.

Loafing was characterized by inactivity and inconspicuousness and consisted of extensive periods of preening and sleeping. The same activities and sounds that would have elicited an immediate response during a hunting period brought no visible response. Loafing usually occurred on the ground next to a fence post, stump or clump of tall weeds, and less commonly on the lee side of a snowbank or next to the center post on a t-bar utility pole. Periods of observing contained behavior common to both hunting and loafing.

Activity periods were easily recognizable by abrupt changes of behavior. Commencement and termination of a loafing period was indicated by a flight to or from the loafing site. Periods of early morning hunting frequently ended with several successful strikes, although if unsuccessful, the transition from hunting to observing was less well defined, but invariably occurred by midmorning.

Mean durations of hunting, loafing and observing periods were 73 min (N = 31), 166 min (N = 15) and 123 min (N = 18), respectively. Hunting times represent minimums since the owl undoubtedly hunted, prior to and after my observation times, when there was too little light for me to see. During a full moon on 21 February the owl was observed hunting 1.5 h after sunset. Long loafing periods (5–7.5 h) occurred twice during very heavy snow falls and twice after the owl had just fed on 3 voles. The shortest observing periods occurred after successful morning hunts, just before the owl began loafing.

The owl's daily behavior appeared to follow a fairly regular routine. The earliest and latest portions of the day were occupied with hunting. A midday loafing period ($\chi^2 = 16.41$, df = 2, $P < 0.005$) followed the early hunting period and preceded the evening hunt.

Approximately one third of each day was spent in each of the 3 general types of behavior. Hunting consumed 30.7% of the daylight hours. This contrasts markedly with the amount of time needed for food-getting during the summer. During 10 observations by Watson (1957) of a male Snowy Owl hunting in July the owl "never failed to catch a lemming after 5 minutes continuous hunting." The owl spent 34.5% and 34.8% of the day loafing and observing, respectively.

The amount of time spent flying was relatively brief. The number of flights per day during daylong observations ranged from 13–57 ($\bar{x} = 27.5$) and covered a total of from 2.7–11.0 km per day ($\bar{x} = 5.1$). The calculations included flights during strikes, as well as between hunting perches and loafing sites. No significant correlation was found between the frequency of the owl's flights and the daily low temperatures. Prey availability and hunting success would appear to be more influential factors.

Hunting methods.—Three hunting methods were employed by the Snowy Owl: still-hunting, ground-hunting and coursing. During still-hunting the owl scanned the surrounding area from a commanding perch on, in decreasing order of frequency: utility poles, fence posts and the tops of hillocks. The owl perched in a tree 5 times ($\bar{x}$ duration = 10 min; range = 3–31 min). One successful strike was launched from a tree.

Still-hunting was used most often (92.5%) and averaged 99 min in duration (range = 67–252 min; N = 21). Twenty-five successful strikes were observed during 35 h of still-hunting, for 0.7 successes per h of effort. Still-hunting minimizes energy expenditure because a large area can be monitored from a single high perch and thus seemed to be the most appropriate during the winter.

Ground-hunting (6.8%) involved walking and/or hopping on the surface and breaking through the snow either with the talons or the beak. The owl pulled vigorously at the ground vegetation exposed by the lunges, tearing open surface runways of voles. Mice under snow are thought to be located by ear by Great Gray Owls (*Strix nebulosa*) (Law, Blue Jay 18:14–16, 1960; Godfrey, Can. Field-Nat. 81:99–101, 1967) and are audible through 25–30 cm of snow to other winter predators such as the red fox (*Vulpes vulpes*) (Kirk, Snow, William Morrow, New York, N.Y., 1977).

Ground-hunting averaged 19 min in duration (range = 7–41; N = 8). One successful strike occurred 9 min after ground-hunting began. This single success, during 152 min of ground-hunting, gave a rate of 0.4 successes per h of effort. No ground-hunting was observed prior to 10:00, further suggesting its secondary importance to still-hunting.

Coursing is a low, search flight over the ground that allows the hunting of a large area with few high perches. According to Watson (1957) systematic quartering over the ground was a common hunting method of breeding owls in the summer. Coursing was observed only twice during this study (0.7% of all hunting time) and was limited to the snow-free areas of the road right-of-way and a barnyard. The 2 search flights lasted 5 and 11 min.

Once, after staring intently at some potential prey, the owl made a low pass over the spot, landing on a nearby stump for a closer examination. After 4 min the owl took flight and hovered for 2 sec over the site before returning to the original perch. Hovering is common during summer (Watson 1957).

Small mammals were usually carried in the talons to a perch for consumption. Occasionally, when the owl landed in the snow during a strike or captured prey while ground-hunting, the prey were consumed on the ground. The owl fed on the remains of a rabbit (*Sylvilagus floridanus*) while on the ground.

Post-capture treatment of prey by the owl appeared to reflect degree of satiation. On 2

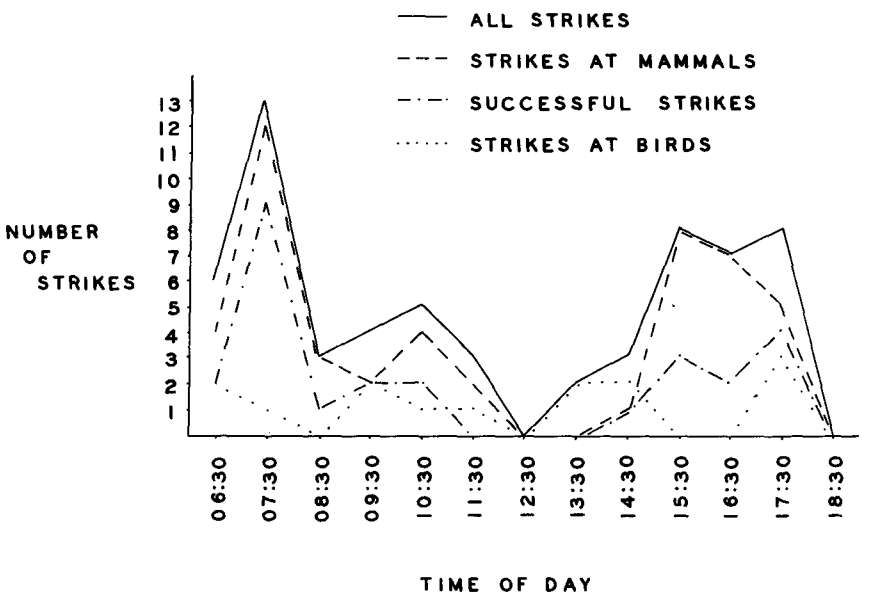

FIG. 1. Number of strikes relative to time of day. Each time block represents 10–11 h of observation.

occasions, when 3 voles were consumed during 1 hunting period, the first voles were totally consumed with 4 quick swallows. Once, the second vole was swallowed immediately, and in the other case held in the talons and mantled before being swallowed whole. The third vole was dismembered and eaten piece by piece. After 1 such bout the owl repeatedly stuck its bill in the snow.

The usual handling time of prey (i.e., the kill, retrieval of prey to a perch, manipulations of prey for consumption) lasted 1–2 min. However, on 1 occasion I saw the owl sit with a freshly caught vole in its talons for 11 min; it regurgitated a pellet, then immediately swallowed its prey.

Hunting success and prey species.—Twenty-six (41.9%) of 62 strikes were successful. The average strike rate per h was 1.7, of which successful strikes averaged 0.7 per h. Excluding 14 unsuccessful strikes at avian prey, the owl's hunting success of mammalian prey was 54.2%. The morning success rate was 59.2% compared with 47.6% during afternoon.

Based on pellet analysis (N = 51) the meadow vole was the most frequent food item, with 159 individuals comprising 86.0% of all prey represented. Of 244 innominates, 85.2% were sufficiently intact to sex, yielding a ratio of 3 females to 1 male. Catling (1973) and Allan (1977) also found this species to be the most common food item of Snowy Owls wintering in southern Ontario and northwestern lower Michigan, respectively.

Other mammalian remains comprised 19 white-footed mice (*Peromyscus* spp., 10.3%) and 6 short-tailed shrews (*Blarina brevicauda*, 3.2%). *Peromyscus* skulls were too fragmentary to differentiate *P. leucopus* from *P. maniculatus bairdi*, however, only *P. leucopus* was trapped in the area. The owl was once observed feeding on a cottontail rabbit. Fur of this species was found in only 1 pellet.

TABLE 1
MEAN SNOW DEPTH RELATIVE TO TIME OF YEAR

Date	Selected sites of frequent strikes (cm)	Random sites (cm)	All sites (cm)
11–19 Feb.	33.4	57.2	45.3
20–26 Feb.	47.8	62.2	55.0
27 Feb.–5 Mar.	41.4	58.6	50.0
6–12 Mar.	30.4	52.2	41.3
13–19 Mar.	27.6	46.8	37.2

All 14 attacks on birds were unsuccessful. Of the 4 species attacked, the Blue Jay (*Cyanocitta cristata*), Starling (*Sturnus vulgaris*) and Snow Bunting (*Plectrophenax nivalis*) have been listed as prey (Gross 1944, Watson 1957, Allan 1977) although, to my knowledge, the Horned Lark (*Eremophila alpestris*) has not. Birds were attacked throughout the day while in flight, perched in a tree or on the snow.

Prey vulnerability.—Peak hunting activity (highest strikes per h) occurred 1 h after sunrise and 1-2 h before sunset (Fig. 1) parallelling peak activity of meadow voles (Hamilton, Ecology 18:255–263, 1937). Hunting success was 75.0% during the first h after sunrise, compared with 47.2% for the remainder of the day. Hamilton (1937) also showed early morning to be the time of greatest vole movement. Craighead and Craighead (Hawks, Owls and Wildlife, Dover, New York, N.Y., 1956) found vole movement increased vole vulnerability to predation. The Snowy Owl appears to be adapted to hunt during these peaks of vole activity and thus successfully take full advantage of localized abundances of this prey species.

A common sign of vole activity was ventilation holes. Mild, stable temperatures under deep snow allow bacterial decay to continue even during the winter (Pruitt, Sci. Am. 202:61–68, 1960; Kirk 1977). Moving away from areas of greatest concentration of the carbon dioxide generated during decomposition, voles tunnel up through the snow, thus constructing ventilation shafts which aerate the subnivean runways. Examination of the snow surface at the sites of successful strikes revealed that voles were very frequently captured at these holes.

Greatest mean snow depth (55.0 cm) occurred during the third week of February, after which snow cover progressively diminished (Table 1). General thawing began the second week in March and continued through the remainder of the month. During mid-March the tops of hillocks and some of the south- and west-facing slopes were bare of snow. These areas were crisscrossed with vole runways. Throughout the winter voles eat subnivean vegetation leaving greatly reduced cover after the snow melts, thus increasing vulnerability to predation (Craighead and Craighead 1956) and as suggested in Table 1. The snow depth of the areas in which prey were captured averaged significantly less than that of randomly selected sites ($t = 4.2$, $P < 0.025$).

Pellet formation.—Pellet regurgitation was seen on 8 occasions (4 observing, 3 loafing, 1 hunting) between 10:00 and 15:30. Twice the owl was under continual surveillance, from prey capture to pellet casting. The owl required 5 h 38 min and 7 h 11 min for pellet formation. Mean length and weight of 51 pellets were 60.6 mm ± 30.5 and 7.7 g ± 6.3, respectively.

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