Diet of Snowy Owls Wintering in West-Central Montana, with Comparisons to Other North American Studies

Authors: Detienne, Jennifer C., Holt, Denver, Seidensticker, Mathew T., and Pitz, Tim

Source: Journal of Raptor Research, 42(3) : 172-179

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-07-41.1

J. Raptor Res. 42(3):172–179

DIET OF SNOWY OWLS WINTERING IN WEST-CENTRAL MONTANA, WITH COMPARISONS TO OTHER NORTH AMERICAN STUDIES

JENNIFER C. DETIENNE, DENVER HOLT[1] AND MATHEW T. SEIDENSTICKER
Owl Research Institute, P.O. Box 39, Charlo, MT 59824 U.S.A.

TIM PITZ
Raptor View Research Institute, P.O. Box 4323, Missoula, MT U.S.A.

ABSTRACT.—During an irruption of Snowy Owls (*Bubo scandiaca*) into western Montana in the winter of 2005–2006, we collected dietary data from 42 to 48 owls from three sites. We recorded 5400 prey from 1313 pellets, pellet fragments, and prey remains. Voles represented >90% of the prey from each site. Montane voles (*Microtus montanus*) dominated at two sites and meadow voles (*M. pennsylvanicus*) dominated at the third site. Few other prey species were eaten. Food-niche breadth was 1.14, 1.41, 1.92, and dietary evenness was 0.377, 0.398, 0.584 for the three Montana sites. We compared these data to those from six other North American studies reporting 1208 prey items collectively. A random sample of 100 pellets yielded a mean dry mass of 19 g, and a mean length × width of 82 mm × 30 mm, and the number of prey per pellet averaged 5 (SD ± 2). Mean body mass of voles eaten by the owls was 30 g. During the following winter (2006–2007), only three Snowy Owls were found in the same study areas.

KEY WORDS: *Snowy Owl*; Bubo scandiaca; Microtus; *diet*; *Montana*; *pellet*; *prey*; *voles.*

DIETA DE *BUBO SCANDIACA* EN EL PERÍODO DE INVERNADA EN EL CENTRO OESTE DE MONTANA CON COMPARACIONES CON OTROS ESTUDIOS DE NORTE AMÉRICA

RESUMEN.—Durante una irrupción de *Bubo scandiaca* en el oeste de Montana en el invierno de 2005–2006, colectamos datos de dieta de 42 a 48 individuos en tres sitios. Registramos 5400 presas provenientes de 1313 egagrópilas completas o fragmentadas y de restos de presas. Los roedores del género *Microtus* representaron >90% de las presas en cada sitio. *M. montanus* dominó en dos sitios y *M. pennsylvanicus* dominó en el tercer sitio. Otras pocas especies de presas fueron consumidas. La amplitud del nicho alimenticio fue 1.14, 1.41, 1.92, y la equitatividad de las presas en la dieta fue 0.377, 0.398, 0.584 para los tres sitios de Montana. Comparamos estos datos con aquellos de otros seis sitios de estudio de América del Norte que en conjunto registraron 1208 presas. Una muestra al azar de 100 egagrópilas arrojó un peso seco promedio de 19 g y un largo × ancho promedio de 82 mm × 30 mm, y el número de presas por egagrópila promedió 5 (DE ± 2). El peso corporal promedio de los roedores comidos por las lechuzas fue de 30 g. Durante el invierno siguiente (2006–2007), sólo tres individuos de *B. scandiaca* fueron hallados en las mismas áreas de estudio.
[Traducción del equipo editorial]

The Snowy Owl (*Bubo scandiaca*) is a northern circumpolar species that breeds in the Arctic tundra and most often migrates to more southerly latitudes in winter (Cramp 1985, Holt et al. 1999). In North America, Snowy Owls migrate and winter regularly in southern Canada and the northern portion of the United States, primarily the northern Great Plains region (Taverner 1934, Bent 1938, Godfrey 1979, Kerlinger et al. 1985, Parmelee 1992). While some owls apparently remain on the breeding grounds for the winter, many migrate south for reasons largely unknown, but likely related to food availability (Bent 1938, Cramp 1985, Parmelee 1992, Patterson 2007). Recently, satellite tracking data has revealed some variation in the traditionally accepted north-to-south migration (Fuller et al. 2003). Small numbers of Snowy Owls are found wintering in Montana on a regular basis, but irruptions in the western regions of Canada and the United States are uncommon (Hanson 1971, Fuller et al. 2003, Patterson 2007, Holt and Zetterberg in press).

Several studies have been published on the feeding habits of breeding Snowy Owls in Europe and North America (see Mikkola 1983, Cramp 1985, Par-

[1] Email address: owlmontana@charlo.net

melee 1992, Holt et al. 1999, for reviews). Other researchers have also investigated their winter diet in North America (see Boxall and Lein 1982, Parmelee 1992, for reviews). Few studies, however, have comprised samples sizes >100 prey items, and none >314 prey items (Gross 1944, Catling 1973, Allan 1977, Campbell and MacColl 1978, Chamberlin 1980, Boxall and Lein 1982, Patterson 2007). We here present diet data from pellets we collected during the 2005–2006 irruption of Snowy Owls into west-central Montana. Our objectives were to (1) describe the trophic niche of wintering Snowy Owls from western Montana sites, and (2) compare our results with those of other North American studies that reported the diet of wintering Snowy Owls.

STUDY AREA

We located between 42 and 48 individual Snowy Owls that wintered in the Mission and Flathead Valleys of west-central Montana in 2005–2006. The owls were concentrated at three sites: 31–35 individuals were seen roosting in a 2.6-km^2 fallow potato field near Polson (47°40′N, 114°09′W); six individuals roosted in a 2.6-km^2 area outside Ronan (47°29′N, 114°10′W), along a border of grassland and fallow fields; and 5–7 individuals roosted within a 13-km^2 site consisting primarily of farmlands, conservation lands, and recent housing developments near Somers (48°06′N, 114°11′W). The Polson and Ronan sites were 16 km apart, and the Somers site was 96 km north of Polson.

METHODS

We collected whole pellets, pellet fragments, and prey remains from the three roosting sites on a weekly basis from December 2005 through April 2006. Pellets were collected while some owls were present, after they departed for evening foraging, before they settled for daily roosting, and after the owls began to migrate from the study area. Pellets and prey remains were identified as specific to Snowy Owls based on observations of the owls roosting on the ground at their daily roost sites, evidence of Snowy Owl feathers, and buff-colored feces. Pellets were sorted by site and air-dried. Complete pellets were recorded as such. Because whole pellets were very long, some broke into two or three pieces after falling to the ground. These pieces were collected and counted as one pellet if they were obviously part of a whole, placed carefully in the collecting bag, and then realigned in the laboratory. Other pellets were too fragmented or crushed to tabulate, and thus were combined as a fragment mass. Pellets were then air-dried on screens for a minimum of 48 hr prior to measurement and dissection.

Other raptors occurred in the same area; however, we excluded Short-eared Owl (*Asio flammeus*), Northern Harrier (*Circus cyaneus*), Rough-legged Hawk (*Buteo lagopus*), and Red-tailed Hawk (*Buteo jamaicensis*) pellets by roost site selection, pellet size, and direct observation. Great Horned Owls (*Bubo virginianus*) produce pellets similar in size to Snowy Owl pellets and two pairs were located roosting and hunting in the vicinity of the Snowy Owls' roost area at the Polson site. One of the pairs of Great Horned Owls roosted during the day in a barn at the Polson site where they deposited their pellets. The other pair roosted in a grove of trees >3 km from the Snowy Owls' roosting area at the Polson site, and deposited their pellets there. In our experience, most owls cast their pellets at their roost sites before hunting, thereby significantly decreasing the chance of accidental collection of Great Horned Owl pellets.

We randomly selected a sample of 100 Snowy Owl pellets to weigh, measure, and dissect to determine pellet mass, length, width, species, and number of prey per pellet. The random sample was chosen by selecting the first 100 pellets that were laid out on drying screens. Pellet mass was measured using a 30-g Pesola spring scale. Length and width measurements (to the nearest mm) were taken from the longest and widest portions of each pellet using a Mitutoyo dial-faced caliper. We dissected the pellets to obtain skulls and upper palates containing teeth necessary for identifying avian and mammalian prey. For each of these measurements, we calculated the range, mean, sample standard deviation, and 99% confidence intervals.

The remaining pellets and fragments were placed in a solution of Clorox® bleach and water for 30 min to dissolve and separate bone and fur. Timing was critical to ensure skulls were removed from the wash before the teeth fell out. This technique was similar to the sodium hydroxide technique used by others (see Marti 1987).

Skulls and palates containing teeth were identified to species by dental traits outlined in Foresman (2001a) and previously identified specimens housed at our lab. Vole skulls that were missing the second molar were categorized as *Microtus* spp. based upon remaining dentition and skull characteristics. Bird skulls were identified to species when corresponding feathers were found at the same site and then recorded as one prey item. Bird feathers were identified to species using local field guides, specimen collections, and personal experience.

We used a *G*-test to analyze the frequency of occurrence of prey at each of the three pellet collection sites. We also used a *G*-test on the pooled prey data from all three sites for an overview of Snowy Owl diet in Montana. Analysis consisted of prey we identified to species only. In order to meet the assumptions of the *G*-test, we eliminated prey categories with fewer than five individuals (Fowler and Cohen 1990). We also eliminated the *Microtus* spp. category because only two species of *Microtus* occur in the area (*M. montanus* and *M. pennsylvanicus*).

Diversity indices were used to compare the diet of Montana Snowy Owls with those of other North American Snowy Owls. We used only those studies that reported a minimum of 100 prey items identified to species. Only prey items identified to species were included in these calculations because higher resolution of categories is thought to yield greater niche breadths (Marti 1987). Food-niche breadth (FNB) was determined using the antilog of the Shannon-Weaver index, where:

$$H' = -\Sigma p_i \log p_i$$

and p_i represents the proportion of each species in the sample (Shannon and Weaver 1949, Marti 1987). We followed Marti's (1987) definition of trophic diversity, where a broad FNB represents a large number of prey species with a relatively equal distribution and a narrow FNB represents few species or an unequal distribution of species.

Dietary evenness (DIEV) values were calculated using Alatalo's (1981) modification of Hill's (1973) equation where:

$$F = (N_2 - 1)/(N_1 - 1)$$

where N_1 is the antilog of the Shannon-Weaver index (H') and N_2 is the reciprocal of Simpson's index ($1/D$; see Marti 1987). Evenness values range from zero to one, where a value of one indicates a uniform representation of prey proportions in the diet (Marti 1987).

We used a Spearman Rank Correlation (Fowler and Cohen 1990) on our data and the data from six other North American studies to examine whether FNB and DIEV values were influenced by the number of prey items (i.e., sample size). We did this to determine if broader FNB values correlated with increased sample sizes.

Mean biomass estimates for *Microtus* voles were determined from two snap-trap lines run approximately 3.5 km from the Ronan site and 3 km from the Polson site. These lines have been run for 14 consecutive years. The trap lines were run during the first week of February 2006. One hundred traps were spaced approximately 3 m apart and checked daily for five consecutive nights, yielding 500 trap-nights/line. We believe this was an accurate measure of biomass because (1) the trap lines were run during the time owls were present near the site, (2) multiple age classes of voles were captured in the traps, thus representing the natural variation in body mass, and (3) Snowy Owls swallow small mammalian prey whole, thus allowing appropriate comparisons of trapped and consumed small mammals.

We calculated the estimated biomass consumed by Snowy Owls based on the mean mass of voles and an estimate of mass for adult northern pocket gophers (*Thomomys talpoides*) from Foresman (2001b). *Peromyscus* mice and shrews (*Sorex* spp.) were also caught on the trap lines, but we have not included their biomasses because only two *Peromyscus* and no *Sorex* species were found in pellets. We did not include avian biomass estimates because only 11 birds were eaten and most were only partially consumed. However, we do report a range of the relative mass of large avian prey.

We did not compare mean biomass of prey from the other studies for several reasons. First, mass was not always known for prey species at the specific study site. Second, there are general uncertainties about mass reported from museum specimens. Third, biomass estimates are often calculated based upon the adult age class; therefore, they are inaccurate if other age classes are consumed. Finally, the estimates usually measure whole prey carcasses, which may only be partially consumed when the prey size is medium to large (Holt 1993, 1994, Holt et al. 2001). For example, the mass of Ring-necked Pheasants (*Phasianus colchicus*) found as prey in our study was ca. 900 g; however, the owls only ate the breast muscles and small portions of the biceps and triceps. Therefore, for a valid estimate of biomass eaten, one would need to know the mass of the individual muscles consumed and subtract that from the total mass.

RESULTS

Snowy Owl Pellet Mass and Size. Snowy Owl pellet mass ranged from 7 to 33 g (mean = 19 ± 6 [SD] g, 99% C.I. = 2, $N = 100$ randomly selected pellets). Pellet length ranged from 42 to 151 mm

Table 1. Diet of Snowy Owls based upon 1313 pellets, pellet fragments, and prey remains collected from three sites in west-central Montana (Polson, Ronan, and Somers) during the winter of 2005–2006.

Species	Polson No. (%)	Ronan No. (%)	Somers No. (%)	Total No. (%)
Mammals				
Microtus montanus	4048 (84.1)	349 (81.2)	17 (11.0)	4414 (81.7)
Microtus pennsylvanicus	98 (2.0)	19 (4.4)	115 (74.7)	232 (4.3)
Unidentified *Microtus* spp.	656 (13.6)	53 (12.3)	8 (5.2)	717 (13.3)
Microtus subtotal	4802 (99.7)	421 (97.9)	140 (90.9)	5363 (99.3)
Thomomys talpoides	7 (tr[a])	2 (tr)	13 (18.4)	22 (tr)
Peromyscus maniculatis	2 (tr)	0 (–)	0 (–)	2 (tr)
Mustela spp.	1 (tr)	0 (–)	0 (–)	1 (tr)
Unidentified mammal	0 (–)	0 (–)	1 (tr)	1 (tr)
Mammal subtotal	4812 (99.9)	423 (98.4)	154 (100)	5389 (99.8)
Birds				
Circus cyaneus	0 (–)	3 (tr)	0 (–)	3 (tr)
Perdix perdix	1 (tr)	2 (tr)	0 (–)	3 (tr)
Phasianus colchicus	0 (–)	2 (tr)	0 (–)	2 (tr)
Larus delawarensis	1 (tr)	0 (–)	0 (–)	1 (tr)
Unidentified raptor	1 (tr)	0 (–)	0 (–)	1 (tr)
Unidentified passerine	1 (tr)	0 (–)	0 (–)	1 (tr)
Bird subtotal	4 (tr)	7 (tr)	0 (–)	11 (tr)
TOTAL	4816	430	154	5400

[a] tr = trace (<1.0%)

(mean = 82 ± 22 mm, 99% C.I. = 6, $N = 100$) and width ranged from 21 to 42 mm (mean = 30 ± 3 mm, 99% C.I. = 1, $N = 100$). The number of prey items per pellet ranged from 1 to 11 (mean = 5 ± 2, 99% C.I. = 1, $N = 100$).

Snowy Owl Diet in Montana. We recorded 5400 prey items from 1313 whole pellets, miscellaneous pellet fragments, and a few prey remains collected at three sites. Voles were clearly the most numerous prey eaten at each site, representing 99.7% at Polson; 97.9% at Ronan; and 90.9% at Somers (Table 1). Of the voles identified to species, montane voles (*M. montanus*) represented 84.1% and 81.2% of the prey from Polson and Ronan, respectively (Table 1). In constrast, Meadow voles (*M. pennsylvanicus*) represented 74.7% and montane voles only 11% of the prey from Somers (Table 1). Prey species proportions were highly significantly different at each site: Polson ($G_{adj} = 8092.4$, df = 2, $P < 0.001$); Ronan ($G_{adj} = 360$, df = 1, $P < 0.001$); and Somers ($G_{adj} = 129.1$, df = 2, $P < 0.001$).

Nine prey species were identified from the three sites (Table 1). When all sites were combined, there was a highly significant difference among proportions of prey species consumed ($G_{adj} = 8133$, df = 2, $P < 0.001$). Northern pocket gophers represented 18.4% of the prey at Somers, but <1% at the other sites; however, sample sizes were too small for meaningful statistical comparisons (Table 1). Several other small mammal species were represented in small numbers, as were a few bird species, but their contributions to the diet were numerically negligible (Table 1). Unusual or large prey included Ring-billed Gull (*Larus delawarensis*), Northern Harrier (*Circus cyaneus*), and a larger unidentified raptor skull that appeared to be a Rough-legged Hawk (*Buteo lagopus*).

We calculated FNB and DIEV for the three Montana sites. Food-niche breadth values among the three Montana sites ranged from 1.14 (Polson) to 1.92 (Somers; Table 2). Dietary evenness was lowest in Polson (0.377) and highest in Somers (0.584; Table 2). Food-niche breadth and DIEV were similar between the Polson and Ronan sites, but yielded higher values from the Somers site, indicating a slightly broader FNB, and a slight increase in the equality (DIEV) of prey for Somers. Overall, however, the FNB and DIEV values indicated a narrow trophic structure for this study.

Voles from our Polson and Ronan trap lines had body masses ranging from 23–42 g (mean = 29.9 ± 4.9, $N = 23$). We believe it is reasonable to assume

Table 2. Food-niche breadth (FNB) and dietary evenness (DIEV) of Snowy Owls from three Montana sites (Polson, Ronan, and Somers). Only prey identified to species ($N = 4680$) were used in these calculations.

NUMBER OF PREY	FNB	DIEV	LOCATION
4158	1.14	0.377	Polson
377	1.41	0.398	Ronan
145	1.92	0.584	Somers

that voles from Somers probably had similar mass. By multiplying this value times 5223 voles eaten, we estimated that the owls ate at least 156.7 kg of voles. We calculated that the owls ate nearly 2 kg of northern pocket gophers, based on an adult mass estimate of 90 g (Foresman 2001b). Based on the remains of the three largest bird species, Snowy Owls ate avian prey weighing up to 1000 g.

Comparison with Other North American Studies. Summation of the prey data from our study and six other North American studies yielded 6623 prey remains, of which 5888 were used for trophic calculations (see methods and Table 3). Fourteen species of mammals, 43 species of birds, and one mussel (*Mytilus edulis*) composed the wide variety of prey consumed by wintering Snowy Owls from New England, Michigan, and Montana (United States), and Alberta, British Columbia, and Ontario (Canada). Campbell and MacColl's (1978) study in British Columbia reported exclusively avian prey, while Chamberlin's (1980) study in Michigan and Catling's (1973) study in Ontario reported exclusively mammalian prey. The remaining four studies reported a mixture of avian, mammalian, and aquatic prey.

Food-niche breadth (FNB) values ranged from 1.28 to 13.85 (Table 3). The narrowest FNBs occurred in Montana, Ontario, and Michigan (Table 3). In Montana, >99% of prey were *Microtus* voles (montane and meadow voles); in Ontario, 90.4% of prey were meadow voles (Catling 1973); and in Michigan, 85.9% were meadow voles (Chamberlin 1980). The broadest food-niche breadth occurred in Gross's (1944) New England study of Snowy Owl stomach contents, where 26 species were represented (Table 3). Seven mammalian species constituted 51.5% and 18 avian species constituted 47.8% of the owls' diets, with one mussel documented. Campbell and MacColl's (1978) study in British Columbia also had a broad food-niche breadth: the prey comprised 22 avian species (Table 3), of which three species of grebes and eight species of ducks made up 81.1% of the owls' diet. Evenness calculations ranged from 0.428 to 0.647. The lowest value was from Montana and the highest value was from Alberta (Table 3).

Although sample size can influence diversity and evenness values (Marti 1987), Spearman correlations revealed no relationships between the number of prey items and FNB values ($r_s = -0.607$, $P > 0.05$) and the number of prey items and DIEV values ($r_s = -0.393$, $P > 0.05$), thus indicating that sample size did not influence our FNB or DIEV results.

DISCUSSION

The Snowy Owls in our study wintered in farmland and wildlife management areas dominated by relatively flat, open grasslands and crops. This is

Table 3. Food-niche breadth (FNB) and dietary evenness (DIEV) of Snowy Owls from seven North American studies reporting 100 or more prey items, representing 5888 prey. Only prey identified to species were used in the calculations.

LOCATION	NO. PREY	% MAMMALS	% *MICROTUS*[a]	% AVIAN	FNB	DIEV	SOURCE
Montana	4680	99.8	99.5	0.2	1.28	0.428	This study
Ontario, Can	314	100.0	90.4	0.0	1.49	0.441	Catling 1973
Alberta, Can	240	93.3	29.9	6.7	3.26	0.647	Boxall and Lein 1982
Br. Col., Can	212	0.0	0.0	100.0	7.73	0.584	Campbell and MacColl 1978
Michigan	185	100.0	85.9	0.0	1.65	0.509	Chamberlin 1980
New England	136	51.5	25.7	47.8	13.85	0.559	Gross 1944
Michigan	121	99.2	66.7	0.8	2.99	0.552	Allan 1977
MEAN					4.61	0.531	
SD					±4.64	±0.078	

[a] % *Microtus* = % of mammals that are *Microtus* spp.

similar to winter habitat selection in Alberta described by Lein and Webber (1979).

Diet and Trophic Structure. Breeding Snowy Owls are generally believed to exhibit a narrow trophic structure (Pitelka et al. 1955, Watson 1957, Petersen and Holt 1999). This is similar to other open-country species of owls such as the Long-eared Owl (*Asio otus*; Marti 1976), Short-eared Owl (Holt 1993), and Barn Owl (*Tyto alba*; Marti 1988). However, wintering populations of Snowy Owls may exploit a broader spectrum of prey, depending on what is locally available, as suggested by Bent (1938), Boxall and Lein (1982), and Mikkola (1983). Although they usually prey upon small mammals, they have been documented taking large birds such as alcids, grebes, geese, ducks, gulls, and medium-sized owls; hares; muskrats; and even fish (Bent 1938, Gross 1944, Keith 1963, Campbell and MacColl 1978, Boxall and Lein 1982, Cramp 1985, Parmelee 1992, D. Holt unpubl. data).

In west-central Montana, the wintering owls we studied consumed almost exclusively *Microtus* voles, which were at a peak in their population fluctuations (D. Holt unpubl. data). Other species of owls in these same areas of west-central Montana are also known to concentrate on voles for food (Holt and Williams 1995, Cromrich et al. 2002, Holt and Bitter 2007) suggesting the area may be important for voles and raptors. In the other North American studies we included for comparison, FNB values were relatively low except in two cases (Table 3); in both these studies, birds were eaten more frequently. One explanation for these differences in FNB may be the diversity and availability of prey. In Montana, we believe the peak population in voles reduced any need for Snowy Owls to seek other food sources. Thus, both extremes in the FNB values support the hypothesis that Snowy Owls exploit locally available prey on their wintering grounds, be it a few very abundant species or a wide diversity of species.

Pellet Size and Mass. Mean pellet size in Montana was similar to that reported in a concurrent study from Washington (80 × 31 mm, $N = 62$; Patterson 2007). Montana pellets were longer than those from Michigan (60 ± 30.5 [SD] mm, $N = 51$; Chamberlin 1980). In Europe, pellets measured 92 × 33 mm ($N = 19$; Hagen 1960) and 66 × 26 mm ($N = 108$; Kennedy 1981, reported in Cramp 1985). A captive Snowy Owl from Finland cast pellets that measured 59 × 30 mm ($N = 20$; Koivusaari 1977, reported in Mikkola 1983). It is likely that pellet dimensions may vary with prey species composition and among regions, and may be related to the number of prey eaten per average meal.

Mean pellet mass in Montana was greater than the 13 g ($N = 16$) reported by Mikkola (1983) for a captive European Snowy Owl, and much heavier than 7.7 g ($N = 51$) reported by Chamberlin (1980) from Michigan. Hagen (1960) reported 4.3 prey per pellet from his winter/breeding study, which was similar to the value in our study.

Based on analysis of pellets, presumably collected from individuals of known sex, Boxall and Lein (1982) suggested that male owls showed more specialization for prey and killed smaller prey than females. We were not able to quantify which sex regurgitated specific pellets because in this study the owls often roosted communally and could not always be confidently identified as a male or female. Regardless of this, the high preponderance of voles in the owls' diet indicated that both sexes were eating predominately the same prey in our study area.

Estimation of Biomass Consumed. The body mass of voles from our trap lines was almost identical to those reported from the same area in 1990 (Blem et al. 1993). Indeed, mean mass for montane and meadow voles were 30 g and 29.1 g, respectively. Furthermore, these weights did not differ statistically from models used to predict vole body mass from crania in Short-eared Owl pellets. Thus, our biomass estimates for voles based upon the number of skulls found in pellets were probably reliable.

Snowy Owls cast approximately one pellet per day in captivity (Mikkola 1983), and we found a mean of 5 prey per pellet; based on these values, we calculated that Snowy Owls in our study consumed at least 150 g of voles per d (or per every pellet cast, regardless of time between pellets). A captive Snowy Owl studied in winter in Montana ate approximately 131 g (range 0–200 g) and 145 g (range 0–298 g) of raw beef heart and mice once per d during two trial periods (Seidensticker 1969), which was similar to our estimates. We realize, however, that this captive did not expend the energy of a wild, free-flying owl. In addition, the captive owl was offered an unlimited supply of food for only 30 min/d, potentially biasing the results. Other winter estimates include 284 g/d of laboratory rats, small birds, caribou, and beef scraps (Gessaman 1972); 320 g/d of laboratory rats and mice (Mikkola 1983); and an estimated 236–268 g/d based on energy budget studies (Boxall and Lein 1989). Breeding male and female

Snowy Owls ate 280 g and 200 g/d, based on observations at a nest (Watson 1957).

ACKNOWLEDGMENTS

We thank Ken Caffrey and the Lake family, for allowing access to their lands. We are grateful to Steve Zetterberg for helping with weekly counts and collecting pellets. Funding was provided by the Flathead Indian Reservation Department of Wildlife Management, Mission Mountain and Missoula Audubon Societies, and Pamela Moriarty. We greatly appreciate the time and valuable comments on this manuscript provided by Cheryl Dykstra, Seppo Salkava, Christer G. Wiklund, and an anonymous referee.

LITERATURE CITED

ALATALO, R.V. 1981. Problems in the measurement of evenness in ecology. *Oikos* 37:199–204.

ALLAN, T.A. 1977. Winter food of the Snowy Owl in northwestern lower Michigan. *Jack-Pine Warbler* 55:42.

BENT, A.C. 1938. Life histories of North American birds of prey, Part II. Dover Publications, New York, NY U.S.A.

BLEM, C.R., L.B. BLEM, J.H. FELIX, AND D.W. HOLT. 1993. Estimation of body mass of voles from crania in Short-eared Owl pellets. *Am. Midl. Nat.* 129:282–287.

BOXALL, P.C. AND M.R. LEIN. 1982. Feeding ecology of Snowy Owls (*Nyctea scandiaca*) wintering in southern Alberta. *Arctic* 35:282–290.

——— AND ———. 1989. Time budgets and activity of wintering Snowy Owls. *J. Field Ornithol.* 60:20–29.

CAMPBELL, R.W. AND M.D. MACCOLL. 1978. Winter foods of Snowy Owls in southwestern British Columbia. *J. Wildl. Manage.* 42:190–192.

CATLING, P.M. 1973. Food of the Snowy Owls wintering in southern Ontario, with particular reference to the Snowy Owl hazards to aircraft. *Ontario Field Biol.* 7:41–45.

CHAMBERLIN, M.L. 1980. Winter hunting behavior of a Snowy Owl in Michigan. *Wilson Bull.* 92:116–120.

CRAMP, S. [ED.]. 1985. The birds of the western palearctic: handbook of the birds of Europe, the Middle East, and north Africa, Vol. 4. Oxford Univ. Press, Cambridge, U.K.

CROMRICH, L.A., D.W. HOLT, AND S.M. LEASURE. 2002. Trophic niche of North American Great Horned Owls. *J. Raptor Res.* 36:58–65.

FORESMAN, K.R. 2001a. Key to the mammals of Montana. Univ. of Montana Press, Missoula, MT U.S.A.

———. 2001b. The wild mammals of Montana. American Society of Mammalogists, Lawrence, KS U.S.A.

FOWLER, J. AND L. COHEN. 1990. Practical statistics for field biology. Open Univ. Press, Buckingham, U.K.

FULLER, M., D.W. HOLT, AND L. SCHUECK. 2003. Snowy Owl movements: variation on the migration theme. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [EDS.], Avian migration. Springer-Verlag, Berlin and Heidelberg, Germany.

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

GODFREY, W.E. 1979. Birds of Canada. National Museum of Canada, Bryant Press Limited, Toronto, Ontario, Canada.

GROSS, A.O. 1944. Food of the Snowy Owl. *Auk* 61:1–18.

HAGEN, L. 1960. The Snowy Owl on Hardangervidda in summer of 1959. *Norw. State Game Res.* 2:3–25.

HANSON, W.C. 1971. The 1966–67 Snowy Owl incursion in southeastern Washington and the Pacific Northwest. *Condor* 73:114–116.

HILL, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.

HOLT, D.W. 1993. Trophic niche of nearctic Short-eared Owls. *Wilson Bull.* 105:497–503.

———. 1994. Effects of Short-eared Owls on Common Tern colony desertion, reproduction, and mortality. *Colon. Waterbirds* 17:1–6.

———, R. BERKLEY, C. DEPPE, P.L. ENRÍQUEZ-ROCHA, P.D. OLSEN, J.P. PETERSEN, J.L. RANGEL-SALAZAR, AND K. WOOD. 1999. Snowy Owl. Pages 194–195 *in* J. del Hoyo, A. Elliott, and J. Sargatal [EDS.], Handbook of the birds of the world, Vol. 5. Lynx Edicions, Barcelona, Spain.

——— AND C. BITTER. 2007. Barred Owl winter diet and pellet dimensions in western Montana. *Northwest. Nat.* 88:7–11.

———, W.D. NORTON, AND E.C. ATKINSON. 2001. Breeding season food habits of Burrowing Owls in south-central Montana. *Intermt. J. Sci.* 7:63–69.

——— AND P.A. WILLIAMS. 1995. Sex of voles eaten by Short-eared Owls. *Northwest. Nat.* 76:145–147.

——— AND S.A. ZETTERBERG. 2008. The 2005 to 2006 Snowy Owl irruption migration to western Montana. *Northwest. Nat.* 89(3).

KEITH, L.B. 1963. A note on Snowy Owl food habits. *Wilson Bull.* 75:276–277.

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

LEIN, M.R. AND G.A. WEBBER. 1979. Habitat selection by wintering Snowy Owls (*Nyctea scandiaca*). *Can. Field-Nat.* 93:176–178.

MARTI, C.D. 1976. Review of prey selection by Long-eared Owls. *Condor* 78:331–336.

———. 1987. Raptor food habits studies. Pages 67–80 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

———. 1988. A long-term study of food niche dynamics in the Common Barn Owl: comparisons within and between populations. *Can. J. Zool.* 66:1803–1812.

MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD U.S.A.

PARMELEE, D.F. 1992. Snowy Owl (*Nyctea scandiaca*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 10. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

PATTERSON, J.M. 2007. An analysis of Snowy Owl (*Bubo scandiacus*) diet during the 2005 to 2006 irruption along the Oregon and Washington coasts. *Northwest. Nat.* 88:12–14.

PETERSEN, J. AND D.W. HOLT. 1999. Observations of the Snowy Owl (*Nyctea scandiaca*) at Barrow, Alaska: a progress report 1992–1998. Department of Wildlife Management, North Slope Borough, Barrow, AK U.S.A.

PITELKA, F.A., P.Q. TOMICH, AND G.W. TREICHEL. 1955. Ecological relations of jaegars and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.* 25:85–117.

SEIDENSTICKER, J.C. 1969. Notes on the food requirements of the Snowy Owl. *Can. Field-Nat.* 83:60.

SHANNON, C.E. AND W. WEAVER. 1949. The mathematical theory of communication. Univ. of Illinois Press, Urbana, IL U.S.A.

TAVERNER, P.A. 1934. Birds of Canada. National Museum of Canada. Bulletin No. 72. J.O. Patenaude, Ottawa, Ontario, Canada.

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

Received 25 July 2007; accepted 7 April 2008