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SEASONAL MOVEMENTS OF FEMALE SNOWY OWLS BREEDING IN THE WESTERN NORTH AMERICAN ARCTIC

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Abstract.—The Snowy Owl (*Bubo scandiacus*) is a circumpolar raptor that nests in Arctic tundra. Satellite tracking of nesting Snowy Owls in Alaska and eastern Canada has allowed researchers to document the widely nomadic movements of these owls between summer and winter ranges. This study expands that knowledge for Snowy Owls in the western Canadian Arctic. Based on previous studies, we predicted that owls: (1) would not have strong fidelity to specific winter or summer ranges; (2) would travel widely in search of breeding and nonbreeding areas at which they would settle for considerable time (months); (3) would choose areas to settle based on prey concentration; and (4) would use a mix of overwintering strategies, with some staying in Arctic and boreal regions, and some migrating south. Movement patterns of four female owls captured at nesting sites on Herschel Island, Yukon Territory, Canada, supported the first two predictions. The third prediction was partly supported: some sites of summer settlement were located where prey was relatively abundant, whereas other selected sites did not appear to have enough prey for successful nesting. The latter sites may have been the best available in those areas, however. Sites of winter settlement generally overlapped regions with high abundance of snowshoe hares (*Lepus americanus*) or ptarmigan (*Lagopus* spp.), and were located in relatively open alpine, subalpine, or wetland environments, where prey were likely most accessible. Contrary to our last prediction, all four study owls settled in boreal Alaska and the northern Yukon Territory. This pattern contrasts with observations that eastern North American Snowy Owls rarely wintered in the boreal biome. This study highlights the need to better understand the habitat choices and food habits of wintering Snowy Owls in the northern boreal mountains.

Key Words: *Snowy Owl*; Bubo scandiacus; *migration*; *movements*; *North America*; *seasonal habitat*; *wintering*; *Yukon Territory*.

MOVIMIENTOS ESTACIONALES DE HEMBRAS DE *BUBO SCANDIACUS* NIDIFICANTES EN EL OESTE DEL ÁRTICO DE AMÉRICA DEL NORTE

Resumen.—*Bubo scandiacus* es una rapaz circumpolar que nidifica en la tundra ártica. El seguimiento satelital de individuos de *B. scandiacus* nidificantes en Alaska y el este de Canadá ha permitido a los investigadores

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documentar los movimientos ampliamente nómadas de estos búhos entre las áreas de veraneo e invernada. Este estudio completa ese conocimiento para *B. scandiacus* en el oeste del Ártico canadiense. En base a estudios previos, predecimos que los búhos: (1) no presentarían una fidelidad pronunciada hacia áreas específicas de veraneo e invernada; (2) viajarían ampliamente en busca de áreas reproductivas y no reproductivas en las que se establecerían durante un tiempo considerable (meses): (3) elegirían áreas para establecerse basados en la concentración de presas; y (4) utilizarían una mezcla de estrategias de invernada, con algunos individuos permaneciendo en regiones árticas y boreales y otros migrando hacia el sur. Los patrones de movimiento de cuatro hembras de *B. scandiacus* capturadas en lugares de nidificación en la Isla Herschel, Territorio Yukón, Canadá, apoyaron las dos primeras predicciones. La tercera predicción fue apoyada en parte: algunos lugares de establecimiento en verano estuvieron ubicados en zonas donde las presas eran relativamente abundantes, mientras que otros lugares parecieron no tener suficientes presas para una nidificación exitosa. Sin embargo, estos últimos pudieron haber sido los mejores sitios disponibles en esas áreas. Los lugares de invernada generalmente se superpusieron con regiones con una elevada abundancia de *Lepus americanus* y de *Lagopus* spp., y estuvieron ubicados en hábitats alpinos y subalpinos relativamente abiertos y en humedales, donde las presas probablemente fueron más accesibles. Contrariamente a nuestra última predicción, las cuatro hembras estudiadas se establecieron en el norte de Alaska y el norte del Territorio Yukón. Este patrón contrasta con las observaciones de que individuos de *B. scandiacus* de América del Norte raramente invernan en el bioma boreal. Este estudio destaca la necesidad de conocer mejor la selección de hábitat y los hábitos alimentarios de individuos de *B. scandiacus* invernando en el norte de las Montañas Boreales.

[Traducción del equipo editorial]

The Snowy Owl (*Bubo scandiacus*) is a circumpolar species that is known as a food specialist during the breeding season, when it eats almost exclusively small mammals such as lemmings (*Dicrostonyx* and *Lemmus* spp.; reviewed by Holt et al. 2015). It is an irruptive species (Hagen 1969, Newton 2006, 2008, Robillard et al. 2016) that fluctuates widely in density among years at local and regional geographical scales, largely in response to variation in prey abundance (Holt et al. 2015). Individual Snowy Owls are known to breed in widely spaced localities in different years (Fuller et al. 2003, Therrien et al. 2014a), and can have a very high reproductive output during peaks in lemming abundance (Gilg et al. 2006, Therrien et al. 2014b). Large-scale movements likely contribute to low levels of genetic differentiation across the owl's circumpolar range (Marthinsen et al. 2009).

Outside of the breeding season, Snowy Owls are able to broaden their prey base and successfully hunt a wide range of prey, including waterfowl, other raptors, gallinaceous birds, small and medium-sized rodents, and lagomorphs (Holt et al. 2015). A few studies tracked breeding individuals outside the breeding season in North America (e.g., Fuller et al. 2003 in Alaska, and Therrien et al. 2011, 2014a in the eastern Canadian Arctic), and found that individual owls spent the nonbreeding season on Arctic tundra, on the sea ice (apparently feeding mainly on waterfowl and alcids), or in mainly grassland or agricultural habitats near the coast or south of the boreal biome. Within a season, owls may choose a mix of these broad landscape types, but often travel long distances between sites at which they may settle for weeks or months (Therrien et al. 2011, 2014a). Our limited knowledge of parallel behaviors of Snowy Owls in the western North American Arctic indicates that they can survive on sea ice, but mainly on Arctic tundra and in the northern boreal mountains (Fuller et al. 2003). Owls also travel long distances between sites of concentrated use at these northern latitudes, often into the Siberian Arctic, but have not been tracked migrating south of the boreal and temperate forests (Fuller et al. 2003).

We sought to expand knowledge of the seasonal movements and habitat uses of breeding adult Snowy Owls by tracking owls from a nesting population in the western Canadian Arctic, located east of the previous study at Point Barrow, Alaska (Fuller et al. 2003) and west of previous studies in the eastern Canadian Arctic (Therrien et al. 2011, 2014a). Based on the findings of previous studies (Holt et al. 2015, Therrien et al. 2014a, 2014b, 2015a, 2015b), we predicted that owls: (1) would not have strong fidelity to specific winter or summer ranges; (2) would travel widely in search of breeding and nonbreeding areas at which they would settle for considerable time (months); and, (3) would choose areas to settle based on relatively high concentrations of prey. Given that the major observed difference between Alaskan and eastern Canadian studies was the extent of winter movements to temperate latitudes, we also predicted (4) mixed overwintering strategies in western Canadian breeders, with some owls staying in the Arctic and northern boreal regions, and others migrating farther south.

METHODS

In the summers of 2007, 2008, and 2009, we monitored Snowy Owl breeding success and diet, and assessed prey abundance, over a 40-km^2 portion of Herschel Island, Yukon Territory, Canada (69°35.33′N, 139°05.33′W). The landscape comprised gently rolling tundra hills and river valleys, with the vegetation classified as erect dwarf-shrub tundra in the moist to dry tundra types (CAVM Team 2003). Snowy Owls regularly nest on the island (Johnson and Herter 1989).

Snowy Owl Monitoring on Herschel Island. In summer (late May–July), we traversed the focal 40-km^2 portion of Herschel Island on a weekly basis to locate Snowy Owls and their nests. Breeding status was determined by observing behavior of pairs or other signs at the nest site). To minimize any potential for nest desertion through disturbance, breeding stage, and success were monitored weekly using a spotting scope to determine the number of eggs and young.

Satellite Tracking. Using a remotely triggered bow net, we captured four adult female Snowy Owls on their nests during 22–29 June 2008. We captured the owls when their eggs were hatching or they had at least one hatched young. No adults abandoned their nest following capture. We marked birds with 30-g satellite transmitters (PTT-100; Microwave Telemetry Inc., Columbia, MD U.S.A.) attached with backpack harnesses made of Teflon ribbon (Bally Ribbon Mills, Bally, PA U.S.A.; Steenhof et al. 2006, Therrien et al. 2012). Tracking Snowy Owls for up to 3 yr with this technique suggested no effect of the transmitter on the owls' subsequent survival or reproduction (Therrien et al. 2012).

We programmed the transmitters to transmit for 5 hr and then turn off for 125 hr from initial instrumentation through the first winter (February 2009), transmit for 5 hr and turn off for 49 hr during the first spring and summer months, and cycle for 4 hr on and 142 hr off for the remaining battery life. We received locations of marked owls on a regular basis via the Argos system (Collect Localisation Satellites 2011). Each location was assigned to a class (0, 1, 2, 3, A, B, or Z) according to its estimated precision. The estimated accuracy of location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1000 m, <1000 m, <350 m, and <150 m, respectively. Location classes 0, A, B, and Z were considered to be of poorer accuracy, and we excluded those locations from our analyses.

We averaged the retained locations of marked owls on a daily basis. We defined summer and winter settlement dates as the midpoints between two successive location dates when movements were <5 km (Ganusevich et al. 2004, Therrien et al. 2012), with summer settlement periods defined as occurring only after 1 April. Similarly, we defined departure from wintering and summering sites as the first time a given owl was located >5 km away from the centroid of its settlement-site locations after 1 March or 1 July, respectively (Therrien et al. 2014a). Although somewhat arbitrary, we based the 5-km movement threshold on the scale of movements previously observed in Snowy Owls (Ganusevich et al. 2004, Therrien et al. 2012). The specific date thresholds allowed us to compute daily movement rates for both spring and autumn, even though some owls only settled for a few days before moving and finally resettling again, and other owls kept moving throughout summer and/or winter.

We calculated daily travel distances (i.e., the distance between successive daily-average locations divided by the number of days separating them) and the approximate overall extent of movements (100% minimum convex polygon) between settlement and departure dates. We inferred general habitat occupancy in winter settlement areas by overlaying location clusters on vegetation formations represented in the Circumpolar Boreal Vegetation Map (Jorgenson 2015).

We used the distance and movement information to infer that breeding likely occurred during summer 2009 when the locations fulfilled the following three criteria (Therrien et al. 2012). First, the length of time between settlement and departure dates had to be at least 46 d, which was the minimum length of time previously observed in radio-tracked birds for which a nesting attempt (i.e., eggs or young observed) was confirmed on the ground (Therrien et al. 2012). Second, the mean daily movements had to be within 1 SD of the mean daily movements of known breeders (0.67 ± 0.32 [SD] km per day, $n = 19$). Third, summer home-range size needed to be within one standard deviation of the mean size observed in known breeding birds (18.2 ± 15.2 [SD] km^2, $n = 19$). We performed spatial analyses using ArcGIS 10.2 (Envi-

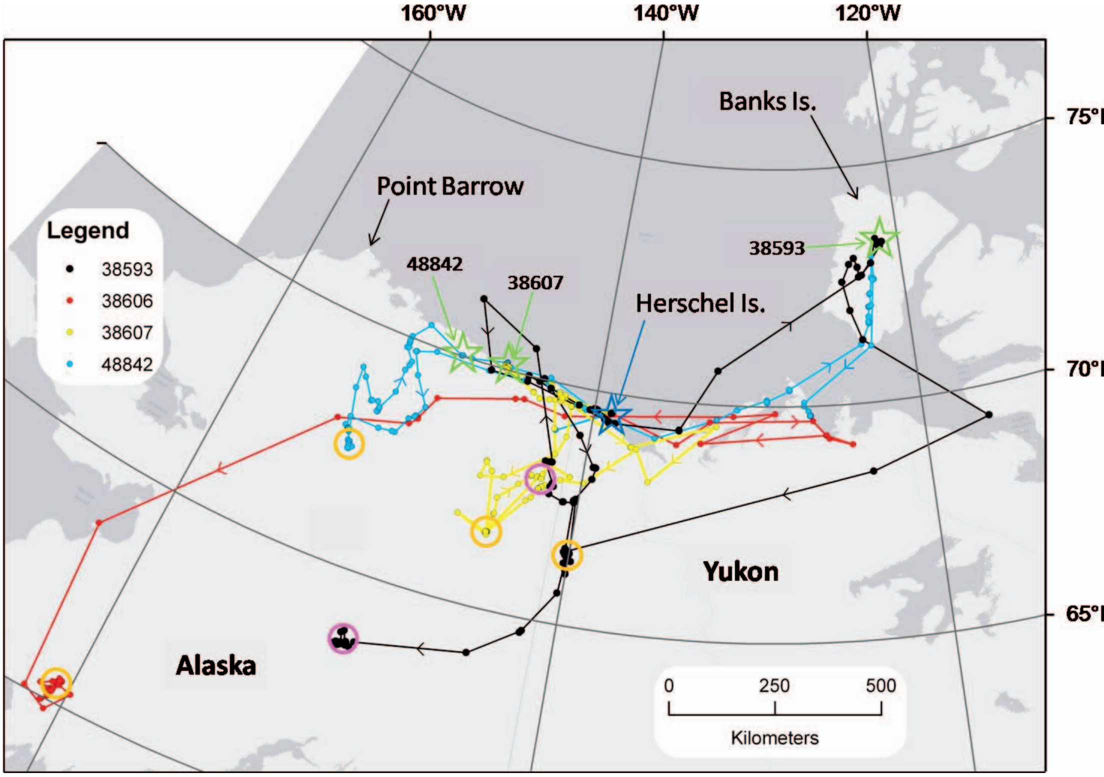

Figure 1. Locations of four adult female Snowy Owls tracked from Herschel Island, Yukon Territory, Canada, between July 2008 and May 2010. Settlement sites are marked with stars in summer (2008 = blue, 2009 = green) and circles in winter (2008–2009 = orange, 2009–2010 = pink), and direction of travel = arrows.

ronmental Systems Research Institute, Inc., Redlands, CA U.S.A.) with the Geospatial Modelling Environment (Version 0.7.3.0; Beyer 2012).

Prey Abundance. We linked settlement areas (breeding and winter) with ground studies of prey abundance from biologists and trappers working concurrently in the same landscapes, assuming that other studies of Snowy Owl diets (Holt et al. 2015, Therrien et al. 2015a) pertained to regions visited by the owls in our study. On Herschel Island, Krebs et al. (2011) used mark-recapture techniques to estimate the absolute abundance of small rodents (*Lemmus, Dicrostonyx,* and *Microtus* spp.) during the spring and summer breeding season for owls. On northern Banks Island ~790 km northeast of Herschel Island (Fig. 1), Parks Canada (2008) estimated the relative abundance of lemmings based on summer counts of nests constructed the previous winter (Duchesne et al. 2011, Reid et al. 2013), which serves as a good index of lemming abundance in spring (Krebs et al. 2012). In wintering areas, we relied on qualitative estimates of the relative abundance of prey (snowshoe hares and ptarmigan) provided by local biologists (e.g., from the U.S. Fish and Wildlife Service) and trappers, and the regional summary of studies focused on snowshoe hare population dynamics reported in Krebs et al. (2013).

Diet. We assessed Snowy Owl summer diet on Herschel Island based on pellets collected at perch and nest sites from 2007 to 2009. We analyzed pellets to determine the identity of prey by using a reference key (Banfield 1974) and voucher specimens, and we determined the number of individual rodent prey from the minimum number of jaws or skulls found in each pellet.

RESULTS

Breeding and Diet. Over three summers on Herschel Island, we observed approximately 80 individual Snowy Owls, but none breeding in 2007, six breeding pairs and fewer than 10 nonbreeding

Table 1. Summary of spring (late May or early June) small rodent (*Dicrostonyx, Lemmus, and Microtus* spp.) densities sampled on three trapping grids in upland and alluvial-fan landscapes on Herschel Island, Yukon Territory, Canada, (data from Krebs et al. 2011).

Broad Landscape Type	Small Rodent Density (#/ha)		
	2007	2008	2009
Upland dwarf shrub/ graminoid tundra	4.9	6.5	3.2
Upland dwarf shrub/ graminoid tundra	4.6	2.0	4.7
Alluvial fan willow/ graminoid meadow	12.4	18.9	2.8

owls in 2008, and fewer than 10 nonbreeding individuals in 2009.

Of the six breeding attempts monitored in 2008, five failed. Two of the nests failed early, prior to determination of clutch size. Four pairs of owls had clutches averaging 5.8 ± 0.96 eggs, but only one was successful (i.e., fledged at least one young), producing two fledglings. At the remaining nests, older nestlings apparently ate their younger siblings (feet of dead nestlings were found in nest) before they too died (intact carcasses of remaining nestlings found in nest). Causes of the high mortality were unclear, but a lack of cached prey around nests suggested possible starvation. Summer 2008 was unusually hot and dry, so heat and thirst also may have contributed to the mortalities.

Small rodents did not show synchronous irruptive population dynamics across species on Herschel Island during the study (Table 1; Krebs et al. 2011). In upland tundra, the most common habitat in the owl nesting territories, the densities of small rodents were similar among years (2007–2009; Table 1). In spring 2008, coincident with the onset of Snowy Owl nesting, rodent densities were noticeably higher than in other years only on the lowland alluvial fan (Table 1), where brown lemmings (*Lemmus trimucronatus*) predominated. The owl nest closest to the alluvial fan was the only nest that successfully fledged young in 2008. In 2009, rodent densities on the alluvial fan declined (Table 1), few owls visited the island, and there was no breeding.

Owls nesting in 2008 fed on all three of the primary small rodent species in similar proportions (Table 2), based on the pellets collected. Conversely, in nonbreeding years (2007 and 2009), the owls consumed substantially higher proportions of brown lemmings and fewer collared lemmings (*Dicrostonyx groenlandicus*) and tundra voles (*Microtus oeconomus*).

In spring 2009, two marked owls prospected on Banks Island, and one of these owls apparently nested in the uplands between the Thomsen and Bernard Rivers (nesting inferred based on the pattern of GPS locations; Therrien et al. 2014a). The estimated density of lemming winter nests in the upper Thomsen River valley was 3.11 nests/ha in 2009, which was intermediate between the highest (6.60) and lowest (0.20) nest densities recorded during 1999–2011 (Reid et al. 2013). Applying the regression in Krebs et al. (2012) yields an absolute abundance of 1.42 lemmings per ha, which was noticeably less than the densities found coincident

Table 2. Summer diet of Snowy Owls based on pellets collected in May and June (2007–2009) at perch sites and nests on Herschel Island, Yukon Territory, Canada.

Prey Taxon	Number of Individuals (% of Annual Total)					
	2007 ($n = 44$ pellets)		2008 ($n = 43$ pellets)		2009 ($n = 29$ pellets)	
Mammals						
Lemmus trimucronatus (brown lemming)	147	(82)	51	(37)	111	(86)
Dicrostonyx groenlandicus (collared lemming)	23	(13)	51	(37)	11	(9)
Microtus oeconomus (tundra vole)	9	(5)	29	(21)	7	(5)
Mustela nivalis (least weasel)	0	(0)	1	(1)	0	(0)
Unknown small mammal	0	(0)	1	(1)	0	(0)
Birds						
Anatidae	0	(0)	1	(1)	0	(0)
Charadriiformes	1	(1)	2	(1)	0	(0)
Bubo scandiacus (Snowy Owl)	0	(0)	1	(1)	0	(0)
Total Number of Prey Items	**180**		**137**		**129**	

Table 3. Seasonal movement durations (d), travel distances (km), and settlement dates for four Snowy Owls marked on Herschel Island, Yukon Territory, Canada, in summer 2008.

	OWL IDENTIFICATION			
SEASONAL MOVEMENT ATTRIBUTES	38593	38606	38607	48842
Summer 2008				
Date of marking	29 Jun	22 Jun	26 Jun	22 Jun
Number of sample days	1	7	9	7
Distance per day (mean ± SD)	-[a]	0.2 ± 0.1	0.9 ± 1.2	0.2 ± 0.2
Home range (km^2)	-[a]	2.0	4.2	1.6
Breeding attempt confirmed	yes	yes	yes	yes
Breeding attempt successful	no	yes	no	no
Autumn 2008				
Onset of movements	6 Jul	21 Aug	12 Aug	29 Aug
Total distance traveled	791	3480	805	872
Duration of movements	107	95	95	85
Mean distance travelled per day	7.4	36.6	8.4	10.3
Winter 2008–2009				
Settlement date	27 Oct	24 Nov	15 Nov	22 Nov
Duration of winter settlement	101	-[b]	132	126
Spring 2009				
Onset of movements	27 Mar	-	26 Mar	27 Mar
Total distance traveled	2088	-	595	687
Duration of movements	64	-	41	56
Mean distance traveled per day	32.6		14.5	12.3
Summer 2009				
Settlement date	30 May	-	6 May	22 May
Number of sample days	25	-	36	3
Distance per day (mean ± SD)	1.0 ± 1.30	-	0.5 ± 0.52	0.2 ± 0.08
Home range (km^2)	28.7	-	32.2	6.23
Duration of settlement	85	-	98	7
Breeding attempt inferred	yes	-	yes	no
Autumn 2009				
Onset of movements	23 Aug	-	12 Aug	5 Aug
Total distance traveled	2521	-	1742	645
Duration of movements	156	-	155	93
Winter 2009–2010 settlement date	26 Jan	-	14 Jan	-[c]
Linear distance traveled:				
Summer 2008 to winter 2008–2009	348	1491	405	623
Summer 2008 to summer 2009	744	-	264	376
Winter 2008–2009 to summer 2009	1036	-	391	319
Winter 2008–2009 to winter 2009–2010	1577	-	169	-

[a] Too few locations.
[b] Transmitter stopped during winter 2008–2009.
[c] Transmitter stopped prior to winter settlement 2009.

with owl nesting on Herschel Island (Table 1). The low lemming density may have resulted in only one of the two tagged female owls apparently breeding. We lack information on the density of small rodents near the mouth of the Canning River, Alaska, where another marked owl settled and apparently bred in summer 2009 (inferred from telemetry movement patterns).

Seasonal Movements and Habitats. Autumn departure dates from Herschel Island averaged 10 August in 2008, but ranged widely from 6 July to 29 August (Table 3). All four birds initially moved onto the mainland and occupied tundra habitats north of tree line, well west into Alaska and east into the Northwest Territories (Fig. 1). All eventually moved into the boreal biome and settled for the winter in widely dispersed landscapes south and southwest of Herschel Island. Winter settlement dates averaged 14 November ± 12 d and travel times averaged 96 ± 9 d (Table 3). Total autumn travel distances varied widely, averaging 1487 ± 1329 km. Linear distances from the breeding site on Herschel Island to initial winter settlement sites ranged from 348–1491 km and averaged 717 ± 530 km (Table 3, Fig 1).

All tracked owls occupied primarily non-forested winter ranges. Environments used included alpine dwarf scrub, meadows, and coniferous woodlands and scrub in the northern Ogilvie Mountains (Miner River drainage) in the Yukon Territory and on the south side of the Brooks Range (upper Koyukuk River drainage) in north-central Alaska; wet coniferous woodlands and scrub in the Yukon River Flats National Wildlife Refuge (Black River drainage) in eastern Alaska; and alpine dwarf scrub and meadows, tall and low scrub, and mires in the ranges east of the Kuskokwim River mouth in southwest Alaska. One owl (PTT ID 38593) was located on marine ice in the Beaufort Sea for 8 d (Table 3, Fig. 1). The signals from owl 38606 indicated that she (or the PPT) had ceased moving by 21 February 2009, before she undertook any spring movements; the fate of this owl is unknown.

In spring 2009, the three remaining owls departed their widely dispersed winter settlement areas almost synchronously on 26–27 March, and all moved north to the Arctic tundra landscapes along the Beaufort Sea coast. Owl 38607 settled in northern Alaska near the mouth of the Canning River. Owl 38593 travelled much farther east into the mainland Northwest Territories and then across the eastern Beaufort Sea (then largely frozen) to Banks Island. Owl 48842 settled briefly (<7 d) a few times on the North Slope, then kept moving slowly east from May through July, before finally moving onto Banks Island in late July. These spring movements took 54 ± 12 d, and covered 1123 ± 836 km. The straight line distance between late spring settlement sites and winter settlement areas averaged 582 ± 395 km. Over the 2 yr, (2008–2009), the autumn movements of owls (117 ± 32 d, $n = 6$ trips) tended to be longer than spring movements (54 ± 12 d, $n = 3$).

Based on prolonged settlement periods in summer, limited daily movements, and their home-range sizes, we inferred that two of the three owls (PTT ID 38607 and 38593) probably nested in 2009. The third owl (PTT ID 48842) never settled for more than 7 d, so we inferred that she did not attempt to nest even though her summer range was located near owl 38593 on Banks Island (Fig. 1). Although none of the owls used the nesting areas on Herschel Island in both 2008 and 2009, two moved east along the Yukon North Slope and may have visited their previous nesting area while prospecting. Breeding dispersal distances for the two presumed breeders in 2009, measured as the straight line distances between their 2008 breeding sites on Herschel Island and 2009 summer settlement sites, were 264 and 744 km (Table 3).

In late summer 2009, the three owls left their summer settlement areas on 13 August ± 9 d and travelled for 135 ± 36 d before settling for the winter. Owl 38607 revisited her previous wintering area in the Yukon River Flats National Wildlife Refuge, but stayed for only approximately 20 d before moving again and settling 169 km farther northeast in the Coleen River drainage, in an area of alpine dwarf scrub and meadows, and coniferous woodlands and scrub (Fig. 1). Owl 38593 also revisited her previous wintering area in the north Ogilvie Mountains, but after approximately 12 d continued southwest to a different wintering area in the Alaska Range near Mt. Denali, in an area of alpine dwarf scrub and meadows, and subalpine woodlands and scrub. Owl 48842 reached the mouth of the Horton River, Northwest Territories, in early November, but then ceased transmitting.

The two owls with consecutive winter data both revisited their previous winter areas, but in 2009 ultimately settled in different areas separated by distances of 169 km and 1577 km from their previous wintering areas. These owls' settlement dates also averaged substantially later in winter 2009/2010 (20 January) than in winter 2008/2009 (15 November). This large difference in dates may indicate yearly differences in time required to locate high densities of prey, or it may simply be an artifact of the small sample size.

Biologists or trappers visited seven of the eight winter settlement areas, and reported a regional peak in hare and ptarmigan numbers in all of the visited landscapes. These patterns are reinforced by years of peak hare densities in regions fairly close to wintering sites as reported by Krebs et al. (2013): 2008–2009 (Tetlin Wildlife Refuge) and 2006–2009 (Delta Junction) for owl 38607 in the Yukon River Flats (winter 2008/2009) and Coleen River drainage (winter 2009/2010); and 2009/2010 (Denali National Park) for owl 38593 in the Alaska Range (winter 2009/2010).

Discussion

The study results supported two of our four predictions, indicating that western North American Snowy Owls do not exhibit strong interannual site fidelity to their summer and winter settlement areas, and that they travel widely in search of breeding and wintering areas. These patterns match the results of other tracking studies of Snowy Owls nesting in northern Alaska (Fuller et al. 2003) and the eastern Canadian Arctic (Therrien et al. 2014a). This species appears to be strongly nomadic, travelling widely in spring and autumn in search of suitable breeding and wintering sites, and only rarely using the same sites for long periods in successive years (Holt et al. 2015). Indicative of these movements, mean breeding dispersal distance in our study (461 km) was large and comparable to that of Snowy Owls in eastern Canada (725 km; Therrien et al. 2014a) and on the north slope of Alaska (1088 km; Fuller et al. 2003). Some of the owls in our study did pass through or close to areas in which they had settled the previous year, but then moved on. Like other researchers, we interpret these long-distance movements to be prospecting searches for suitable breeding and wintering areas with high prey abundance (Therrien et al. 2014a). These observations are based on comparisons from relatively few years; however, they do not preclude the possibility that over a longer period some of these long-lived owls become familiar with the large region they traverse and eventually settle in areas well-known to them.

Our results partly support our third prediction that settlement sites would have high seasonal abundances of prey. For breeding sites, this prediction depends on the spatial variability in absolute density of small rodent prey across the large expanses of tundra over which the nomadic owls prospect in spring (Therrien et al. 2015a). For example, Snowy Owls breed in Greenland when lemming densities exceed approximately two lemmings/ha (Gilg et al. 2006). Knowledge of how rodent populations vary across this region is lacking. We must instead rely on abundance data from a few sites where we can compare years when no owls bred to those when owls attempted to breed. In spring and summer, the Snowy Owls on Herschel Island fed primarily on lemmings, consistent with other studies (Holt et al. 2015), but the abundance of lemmings was apparently insufficient to support successful breeding in most pairs. This pattern suggests that Snowy Owls select from among the best available options they encounter while prospecting, and sometimes attempt breeding in areas with moderate prey abundance. The mean clutch size of 5.75 eggs in 2008 was within the range observed in this species when prey is limited, but below the maximum attainable (7–11 eggs) when prey is abundant (Holt et al. 2015).

Snowy Owls have a fairly short period in late winter and early spring to find a breeding area with abundant small rodents. During much of this time the tundra is snow-covered, which may hinder the owls' ability to judge prey abundance, in particular lemming densities under the snow (Therrien et al. 2015b). Nevertheless, across all three North American studies that have satellite-tracked individual owls (Fuller et al. 2003, Therrien et al. 2014a, this study), 16 of 17 (94%) females attempted to breed in successive years, though not always successfully. In some mainland regions covered by these owls, lemmings may remain at low densities for many years and do not always follow cyclic dynamics with peaks every 3 or 4 yr (Krebs et al. 1995, 2002, 2011), though lemmings do vary substantially in density on Banks Island (Maher 1967, Reid et al. 2013). The nomadic strategy in spring appears to be adaptive by increasing the chances that a female will encounter a region with a male and a sufficient density of accessible prey to breed. Overall, the western Canadian Arctic (and perhaps the Alaska North Slope) may be a challenging region for this species, because irruptive high densities of lemmings appear less frequent than in other regions (Therrien et al. 2014b). Further investigation of the Snowy Owl's breeding-site selection is warranted, however, and our study results should be interpreted with caution owing to small sample size and the lack of information on prey density and accessibility in areas where the owls did not settle.

Our results indicate that owls wintered in open habitats with relatively high abundances of boreal species, such as snowshoe hares and ptarmigan, on which Snowy Owls are known to prey (Potapov and Sale 2012, Holt et al. 2015). The locations of such sites vary through time as the nonsynchronous pattern in hare cycles spreads across the northwest boreal region (Krebs et al. 2013), sometimes coincident with high abundances in ptarmigan (Boutin et al. 1995). Owls would have to search annually to find these regions. Shorter travel times in spring probably reflect the necessity to choose a breeding site before it is too late to complete a nesting cycle in the short arctic summer, whereas extended travel times in autumn and early winter probably reflect the relative difficulty in northern boreal areas of finding suitable open environments with good prey abundance during fall and especially winter. The difficulty is likely a consequence of snowshoe hares fluctuating widely in population density across years and preferring thick cover (Hodges 2000), and Willow Ptarmigan (*Lagopus lagopus*) moving from summer to winter areas over long distances and with considerable variability in timing (Hannon et al. 1998).

Sea ice and associated open water (polynyas) were not prominent wintering environments for the study owls, in contrast to the behavior of owls in the eastern Canadian Arctic (Robertson and Gilchrist 2003, Therrien et al. 2011). Further work is required to establish whether prey densities and concentrations on sea ice (i.e., sea ducks and alcids) in the Beaufort and Chukchi Seas are lower than those in Baffin Bay, Davis Strait, and Hudson Bay. Alternatively, the small sample size of satellite-marked owls in the western Arctic might have been insufficient to accurately portray the species' overall use of the marine environment in winter.

Individual owls often used the same broad landscape types in successive winters, perhaps specializing on particular foraging strategies. This pattern was apparent among owls returning to sea ice in the eastern Canadian Arctic (Therrien et al. 2011), grassland/prairie habitats (Therrien et al. 2011, Potapov and Sale 2012), and boreal montane tundra and shrub habitats (Fuller et al. 2003, this study). It may be that owls learn how to effectively forage on a particular prey type (e.g., sea ducks [Robertson and Gilchrist 2003] or ptarmigan/snowshoe hares or small rodents [Boxall and Lein 1982]), and choose to return in winter to the broad environments where these prey can be found, even though the particular sites supporting adequate prey in those landscape types may vary geographically among years.

The study results did not support our fourth prediction, that some owls tagged in the western Arctic would winter in grasslands south of the boreal biome. All of the wintering sites used by owls in our study were in the northern boreal mountains, as was true of the owls studied by Fuller et al. (2003). These results should be interpreted with caution, however, because of the low sample sizes and a potential sex-specific bias; adult female Snowy Owls have been reported to overwinter farther north than males and younger females (Kerlinger and Lein 1986). Further investigation might show that individuals from other breeding sites in the western Arctic, or their fledglings, are among the Snowy Owls reported on the west coast of North America, as far south as the mouth of the Fraser River in British Columbia (Campbell et al. 1990), or on the Great Plains (Holt et al. 2015). Our results are consistent with those of Fuller et al. (2003) and Therrien et al. (2011), however; in all three studies, most or all of the adult females spent the winter at high latitudes in subarctic or Arctic regions. This appears to be the predominant wintering strategy for adult female Snowy Owls in North America.

It is striking, however, that only one of the eastern Canadian owls tracked by Therrien et al. (2014a) wintered in the boreal biome of eastern Newfoundland, whereas all of our owls and those followed by Fuller et al. (2003) wintered in the northern boreal and subarctic mountains of Yukon and Alaska. A probable explanation is that the montane regions include much larger areas of relatively open tundra, scrub, and sparsely forested landscapes than the boreal forests in central and eastern Canada. These open landscapes appear essential for this owl, which is primarily a visual hunter that uses perch-and-scan, and less frequently hover-and-scan, hunting modes (Holt et al. 2015). Likely boreal prey include snowshoe hare and Willow Ptarmigan, which, at high densities, can occupy open country and are common in the boreal regions of western North America (Elton and Nicholson 1942, Hannon et al. 1998, Krebs et al. 2013). To allow for a more rigorous assessment of the threats to this species from the rapidly changing climate and spreading human footprint in the north, we recommend more detailed investigation of the Snowy Owl's diet and fine-scale habitat choices in winter in the Northern Boreal Mountains.

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Literature Cited

Banfield, A.W.F. 1974. Mammals of Canada. University of Toronto Press. Toronto, ON Canada.

Beyer, H.L. 2012. Geospatial modelling environment (Version 0.7.3.0). http://www.spatialecology.com/gme (last accessed 3 May 2016).

Boutin, S., C.J. Krebs, R. Boonstra, M.R.T. Dale, S.J. Hannon, K. Martin, and A.R.E. Sinclair. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74:69–80.

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

Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990. The birds of British Columbia: Vol. 2: nonpasserines. Royal British Columbia Museum, Victoria, BC Canada.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S.D.I. Fish and Wildlife Service, Anchorage, AK U.S.A. http://www.geobotany.uaf.edu/cavm/ (last accessed 3 May 2016).

Duchesne, D., G. Gauthier, and D. Berteaux. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia* 167:967–980.

Elton, C. and M. Nicholson. 1942. The ten-year cycle in numbers of lynx in Canada. *Journal of Animal Ecology* 11:215–244.

Fuller, M., D. Holt, and L. Schueck. 2003. Snowy Owl movements: variation on the migration theme. Pages 359–366 *in* P. Berthold, E. Gwinner, and E. Sonnenschein [Eds.], Avian migration. Springer-Verlag, Berlin, Germany.

Ganusevich, S.A., T.L. Maechtle, W.S. Seegar, M.A. Yates, M.J. McGrady, M. Fuller, L. Schueck, J. Dayton, and C.J. Henny. 2004. Autumn migration and wintering areas of Peregrine Falcons (*Falco peregrinus)* nesting on the Kola Peninsula, northern Russia. *Ibis* 146:291–297.

Gauthier, G. and D. Berteaux. 2011. ArcticWOLVES: Arctic Wildlife Observatories Linking Vulnerable Eco-Systems. Final synthesis report. Centre d'études nordiques, Université Laval, Quebec City, QC Canada.

Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. Functional and numerical responses of four lemming predators in high Arctic Greenland. *Oikos* 113:193–216.

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. *Fauna* (*Oslo*) 22:73–126.

Hannon, S.J., P.K. Eason, and K. Martin. 1998. Willow Ptarmigan (*Lagopus lagopus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NYU.S.A. https://birdsna.org/Species-Account/bna/species/wilpta (last accessed 25 June 2017).

Hodges, K. 2000. The ecology of snowshoe hares in the northern boreal forests. Pages 117–161 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires [Eds.], Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, CO U.S.A.

Holt, D.W., M.D. Larson, N. Smith, D.L. Evans, and D.F. Parmelee. 2015. Snowy Owl (*Bubo scandiacus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/snoowl1 (last accessed 25 June 2017).

Johnson, S.R. and D.R. Herter. 1989. The birds of the Beaufort Sea. BP Exploration (Alaska) Inc., Anchorage, AK U.S.A.

Jorgenson, T. 2015. The Alaska-Yukon region of the circumboreal vegetation map (CBVM). CAFF Strategy Series Report, Conservation of Arctic Flora and Fauna, Akureyi, Iceland. https://oaarchive.Arctic-council.org/bitstream/handle/11374/1523/EDOCS-2690-v2-ACSAOUS201_Anchorage_2015_Info_doc_5-4_CBMP_CBVM_Map_Alaska_Yukon.pdf?sequence=1&isAllowed=y (last accessed 3 May 2016).

Kerlinger, P. and M.R. Lein. 1986. Differences in winter range among age-sex classes of Snowy Owls *Nyctea scandiaca* in North America. *Ornis Scandinavica* 17:1–7.

Krebs, C.J., F. Bilodeau, D. Reid, G. Gauthier, A.J. Kenney, S. Gilbert, D. Duchesne, and D.J. Wilson. 2012. Are lemming winter nest counts a good index of population density? *Journal of Mammalogy* 93:87–92.

———, R. Boonstra, and A.J. Kenney. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia* 103:481–489.

———, A.J. Kenney, S. Gilbert, K. Danell, A. Angerbjorn, S. Erlinge, R.G. Bromley, C. Shank, and S. Carriere. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. *Canadian Journal of Zoology* 80:1323–1333.

———, K. Kielland, J. Bryant, M. O'Donoghue, F. Doyle, C. McIntyre, D. Difolco, N. Berg, S. Carrier, R.

BOONSTRA, S. BOUTIN, A. KENNEY, D. REID, K. BODONY, J. PUTERA, H.K. TIMM, AND T. BURKE. 2013. Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. *Canadian Journal of Zoology* 91:562–572.

———, D.G. REID, A.J. KENNEY, AND S. GILBERT. 2011. Fluctuations in lemming populations in north Yukon, Canada, 2007–2010. *Canadian Journal of Zoology* 89:297–306.

MAHER, W.J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. *Canadian Field-Naturalist* 81:248–250.

MARTHINSEN, G., L. WENNERBERG, R. SOLHEIM, AND J.T. LIFJELD. 2009. No phylogeographic structure in the circumpolar Snowy Owl (*Bubo scandiacus*). *Conservation Genetics* 10:923–933.

NEWTON, I. 2006. Advances in the study of irruptive migration. *Ardea* 94:433–460.

———. 2008. The migration ecology of birds. Elsevier, London, U.K.

PARKS CANADA. 2008. Lemming winter nest survey: Aulavik National Park. Western Arctic Field Unit, Parks Canada Agency, Inuvik, NT Canada. http://www.pc.gc.ca/eng/pn-np/nt/aulavik/plan/plan8.aspx (last accessed 3 May 2016).

POTAPOV, E. AND R. SALE. 2012. The Snowy Owl. T. and A.D. Poyser, London, U.K.

REID, D.G., D. BERTEAUX, AND K. LAIDRE. 2013. Mammals. Pages 79–141 *in* H. Meltofte [ED.], Arctic biodiversity assessment—status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Arctic Council, Akureyi, Iceland. http://www.Arcticbiodiversity.is/ (last accessed 3 May 2016).

ROBERTSON, G.R. AND H.G. GILCHRIST. 2003. Wintering Snowy Owls feed on sea ducks in the Belcher Islands, Nunavut, Canada. *Journal of Raptor Research* 37:164–166.

ROBILLARD, A., J.F. THERRIEN, G. GAUTHIER, J. BÊTY, AND K.M. CLARK. 2016. Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the Snowy Owl. *Oecologia* 181:423–433.

STEENHOF, K., K.K. BATES, M.R. FULLER, M.N. KOCHERT, J.O. MCKINLEY, AND P.M. LUKACS. 2006. Effects of radio marking on Prairie Falcons: attachment failures provide insights about survival. *Wildlife Society Bulletin* 34:116–126.

THERRIEN, J.-F., G. GAUTHIER, AND J. BÊTY. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. *Journal of Avian Biology* 42:363–369.

———, ———, AND ———. 2012. Survival and reproduction of adult Snowy Owls tracked by satellite. *Journal of Wildlife Management* 76:1562–1567.

———, ———, E. KORPIMÄKI, AND J. BÊTY. 2014b. Predation pressure by avian predators suggests summer limitation of small mammal populations in the Canadian Arctic. *Ecology* 95:56–67.

———, ———, D. PINAUD, AND J. BÊTY. 2014a. Irruptive movements and breeding dispersal of Snowy Owls: a specialized predator exploiting a pulsed resource. *Journal of Avian Biology* 45:536–544.

———, ———, A. ROBILLARD, N. LECOMTE, AND J. BÊTY. 2015a. Écologie de la reproduction du harfang des neiges dans l'Arctique canadien. *Le Naturaliste Canadien* 139:17–23.

———, D. PINAUD, G. GAUTHIER, N. LECOMTE, K.L. BILDSTEIN, AND J. BÊTY. 2015b. Is pre-breeding prospecting behavior affected by snow cover in the irruptive Snowy Owl? A test using state-space modeling and environmental data annotated via Movebank. *Movement Ecology* 3:1. doi: 10.1186/s40462-015-0028-7 (last accessed 25 June 2017).

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