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Winter Use of a Highly Diverse Suite of Habitats by Irruptive Snowy Owls

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Abstract - *Bubo scandiacus* (Snowy Owl) is an irregular winter visitor in the northeastern US and southeastern Canada, where winter irruptions occur roughly every 4 years with varying intensity. The consecutive winters of 2013–2014 and 2014–2015 saw unusually large irruptions of Snowy Owls across eastern North American states and provinces and the Great Lakes region. We tracked 34 individuals equipped with high spatial- and temporal-resolution GPS–GSM transmitters and obtained data that documented in detail the diverse suite of habitats used by irruptive Snowy Owls overwintering and migrating through the region, from heavily urbanized city centers to open agricultural areas, as well as ice floes drifting on the Great Lakes or concentrating along the shores of the Atlantic Ocean.

Introduction

Winter irruptions are an extreme form of facultative migration characterized by unusual and massive movements of individuals to a given area (Lack 1968; Newton 2006, 2008). This type of migration is mostly observed in species that specialize on pulsed resources (i.e., ephemeral events of resource super-abundance; Ostfeld and Keesing 2000) and is generally thought to be a response to fluctuations in food supply (Newton 2008). Most knowledge of irruptive behaviour is derived from ring recoveries and direct observations (Newton 2008); thus, the ability to explore detailed movements during irruptions is rather limited. Here, by using tracking devices with high spatial and temporal resolution, we explore habitat use of winter irruptive *Bubo scandiacus* L. (Snowy Owl).

The Snowy Owl exhibits a complex and poorly understood suite of migratory behaviors ranging from regular migration to nomadism, as well as winter residency and irruptive movements (reviewed in Holt et al. 2015). However, the largest movements seem to be demographic events that predominantly involve young of the year,

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and appear to follow highly productive breeding seasons, likely tied to fluctuations in lemming populations (Holt et al. 2015, Robillard et al. 2016). Indeed, Snowy Owl numbers can fluctuate dramatically on an annual basis in the southern portion of its range in North America, spreading across southern Canada and the northern US (Kerlinger et al. 1985). Throughout their breeding range of open-tundra habitat, these birds have a narrow, specialized diet almost entirely composed of small mammals (Holt et al. 2015). For that reason, it was long thought that irruptive Snowy Owls moving to southern regions during winter were relying upon similar open habitats (grasslands, pastures, and/or agricultural fields) where small-mammal prey can be found (Kerlinger et al. 1985). However, recent publications suggest that the array of habitats used during winter by Snowy Owls might be wider than previously thought, with adult owls spending extended periods of time out on the sea-ice, along coastal habitats, or in urban environments (reviewed in Holt et al. 2015, Smith et al. 2012, Therrien et al. 2011).

Snowy Owls were seen in historically large numbers in the winter of 2013–2014, and to a somewhat lesser degree in 2014–2015, especially in the northeastern US, southeastern Canada, and the Great Lakes region. Those winter irruptions allowed us to track several individuals in various locations across the southeastern part of the species' range in North America. We documented the diversity and the extent of habitat use by winter irruptive Snowy Owls across a wide geographical region and assessed the actual use of grasslands, pastures, and/or agricultural fields, the species' suspected preferred habitat, in eastern North America.

Field-site Description

We trapped and tracked 22 and 12 Snowy Owls from northeastern and upper midwestern states during winters 2013–2014 and 2014–2015, respectively. Nineteen owls were trapped in inland or coastal habitats, tagged, and released at the capture site. We trapped another 15 owls at airport facilities, which we tagged and relocated (mean distance ± SD = 47 ± 35 km) to various inland or coastal habitats to prevent airstrike hazards.

Methods

Generally, we located target owls during the day, but because Snowy Owls are primarily nocturnal in winter, most successful trapping occurred near or after dark. We trapped owls using either bow nets or bal-chatri traps (Bloom et al. 2007) with live bait (e.g., *Columba livia* Gmelin [Rock Pigeon], *Sturnus vulgaris* L. [European Starling], *Mus musculus* L. [House Mouse] or *Rattus norvegicus* Berkenhout [Norway Rat]). We used plumage characteristics given in Josephson (1980), Seidensticker et al. (2011), and Solheim (2012) to assess age (i.e., juvenile [first-year] vs. non-juvenile) and sex for each trapped owl. We fitted each owl with a ~45-g solar-powered GPS–GSM transmitter (Cellular Tracking Technologies, Rio Grande, NJ), which weighed <3% total body mass. All transmitters were fitted with a backpack harness made of 10-mm tubular Teflon (following the model of Steenhof et al. 2006). Studies of Snowy Owls wearing similar transmitters in this fashion have reported no effect on survival or breeding success (Therrien et al. 2012). The GPS–GSM transmitters can record data as frequently as every 30 sec, but we generally programmed those used in our study to record locations (± 1m accuracy) every 30 min, and to send the data via GSM cell-phone network every 3–7 days. The units recorded date, time, latitude, and longitude for each location. Units could be reprogrammed (e.g., to modify the duty cycle) after deployment, and were capable of storing ~100,000 GPS locations when out of cell range.

Analyses

We drew 100-m and 4000-m–radius areas for each location received from the units, from which we assessed the proportions of land cover according to 6 classes (barren, developed, forested, grassland/pasture/agricultural, open water, and wetland) using the 30-m resolution National Land-Cover Database (NCLD) 2011 images (Homer et al. 2015). We choose the 100-m and 4000-m radii because they (1) encompass more than 65% and 98%, respectively, of the average half-hour distance traveled by Snowy Owls during winter, (2) fit well with the precision of the NLCD, and (3) represent a local and regional scale, respectively, considering the accuracy of the transmitters. There is no 30-m resolution land-cover database map for Canada; thus, we limited our analyses to locations within the US. We computed the proportion of each habitat surrounding each location and averaged them daily for each individual. We assessed the inter-individual variance in habitat use with a random-effect model using habitat (grasslands/pasture/agricultural), sex, and year as fixed effects and individual and day as random effects. We then calculated proportions of the different habitats used for each bird over a complete winter for graphical purposes. We performed spatial analyses using ArcGIS software 10.2 (Environmental Systems Research Institute Inc., Redlands, CA) with the Geospatial Modelling Environment (Version 0.7.3.0; Beyer 2012). We performed statistical analyses using the lme4 package (Bates et al. 2015) in R software (3.2.4) Statistical Environment (R Core Team 2015).

Results

We tracked 22 individual Snowy Owls (14 males, 8 females) from 17 December 2013 to 24 April 2014, and 17 individuals (12 new [5 males, 7 females] and 5 from the previous year) from 19 November 2014 to 3 May 2015. During the first winter, all tracked birds were juveniles, hatched during the previous summer (2013), whereas those tracked during the second winter were all non-juvenile owls. Transmitter performance was generally strong, although some of the units deployed first experienced battery-recharge issues, which were subsequently resolved with software and hardware updates. Over the 2 winters of tracking, we received more than 85,000 locations (average = 2505 locations per bird per winter, with an average of 38 ± 22 days of identified locations per individual per winter).

Individual owls used a very diverse suite of habitats over the 2 winters. The proportion of daily locations over grassland/pasture/agricultural areas, the suspected preferred habitat, varied among owls, years, and radii (Table 1, Figs. 1, 2) but comprised only one third (35%) and a little over half (58%) of the habitat used during winter 2013–2014 and 2014–2015, respectively, for the 100-m radius. When using a 4000-m radius, those proportions fell to 32% and 42%, respectively. In addition to grassland/pasture/agricultural areas, wintering Snowy Owls were often located over bodies of water (between 22% and 31% of locations according to winter season and radius), primarily the Great Lakes and the Atlantic Ocean. Offshore daily locations were on average (± SD) 3.0 ± 3.3 km away from the nearest coast line. Although classified as open water by NLCD, such locations were a mix of frozen and open surfaces. Indeed, almost all Great Lakes locations represented lake ice. Moreover, owls extensively used developed lands such as suburbs and even cities (e.g., Baltimore, MD; Manhattan, NY), especially during the first winter.

Finally, not only did we observe a relatively high diversity of habitat use among individuals, we also noted that shifts in habitat use could occur within individuals over consecutive winters. As an example among the owls that we tracked during the 2 years, Millcreek spent most of the 2013–2014 winter on the Great Lakes' ice floes, but then spent the 2014–2015 winter exclusively over grassland/pasture/agricultural and developed habitats. Those observations were limited to a very small number of individuals, but still demonstrate diverse habitat use at the individual level in this species.

Discussion

Tracking several individual Snowy Owls allowed us to quantify their use of many habitat types during the course of 2 winters. Such heterogeneity in habitat use adds to the suite of possible variables (such as the absolute number of individuals, the timing of the irruption, its geographical coverage, and the time between irruptions) to account for in order to fully understand irruptive behavior (e.g., Cottee-Jones et al. 2015; Lack 1968; Newton 2006, 2008).

Despite the diversity of habitat used by winter-irruptive Snowy Owls, the majority of daily locations in both years were in habitats largely modified by human activities, i.e. agricultural and developed lands. Irrespective of radius used in the analysis, >50% of all daily locations were in modified habitats in both winters.

Table 1. Mixed-models summary of the variance for all fixed effects describing the habitat use of Snowy Owls in winters 2013–2014 and 2014–2015. Random-effects variances for Snowy Owl individuals and sampling days were close to 0. The response variable is the proportion of daily positions within a particular habitat. The model used a Poisson distribution.

Factors	χ^2	df	*P*
Intercept	25.77	1	<0.01
Sex	0.01	1	0.99
Habitat	1763.37	5	<0.01
Year	2.66	1	0.10
Radius	8.22	1	<0.01
Habitat × Year	477.19	5	<0.01
Radius × Habitat	225.25	5	<0.01

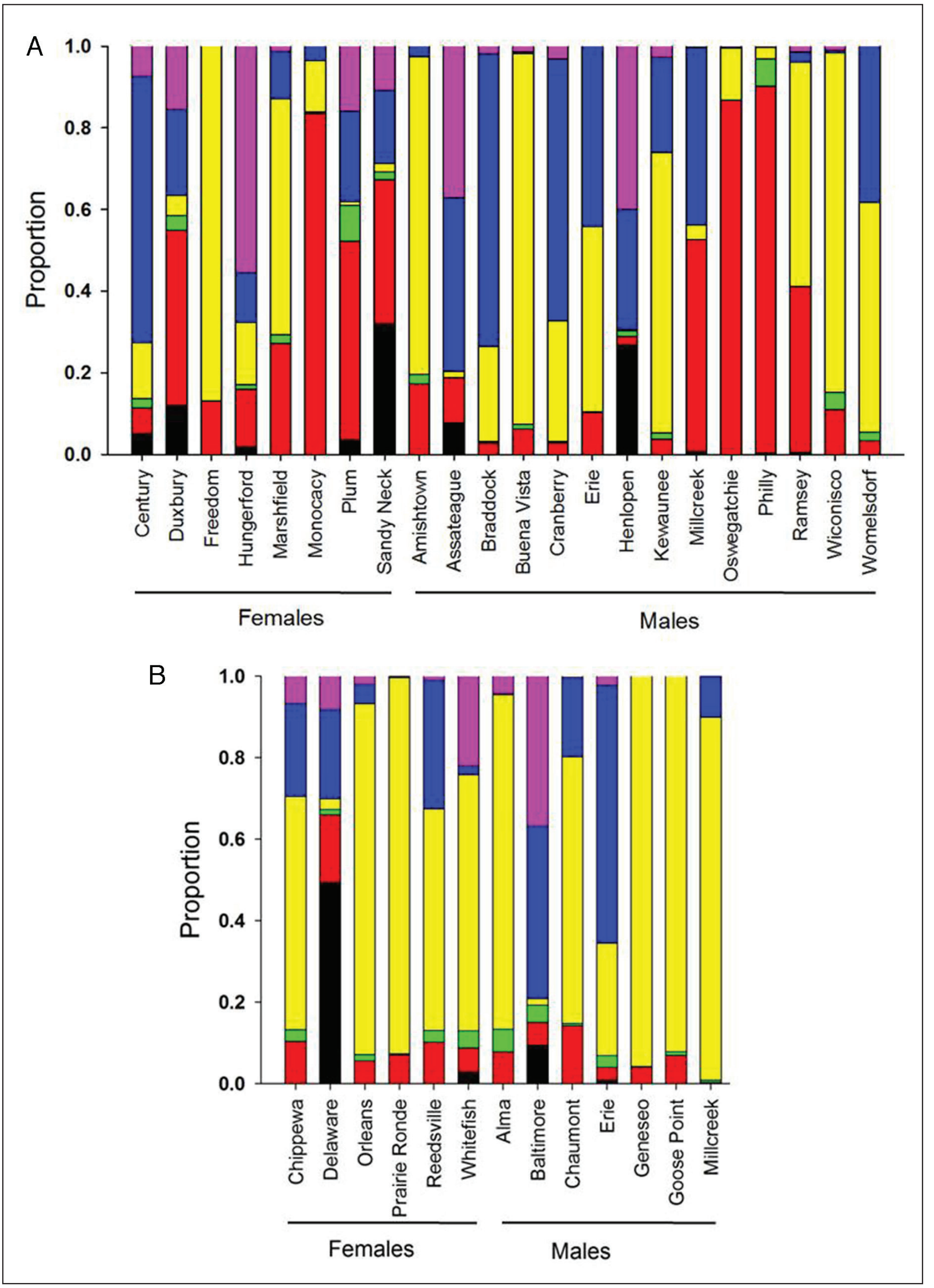

Figure 1. Proportion of each habitat class (black = barren, red = developed, green = forested, yellow = grassland/pasture/agricultural, blue = open water, and pink = wetland) surrounding locations of 34 Snowy Owls tracked during (a) winter 2013–2014 and (b) 2014–2015 in northeastern North America using a 100-m radius.

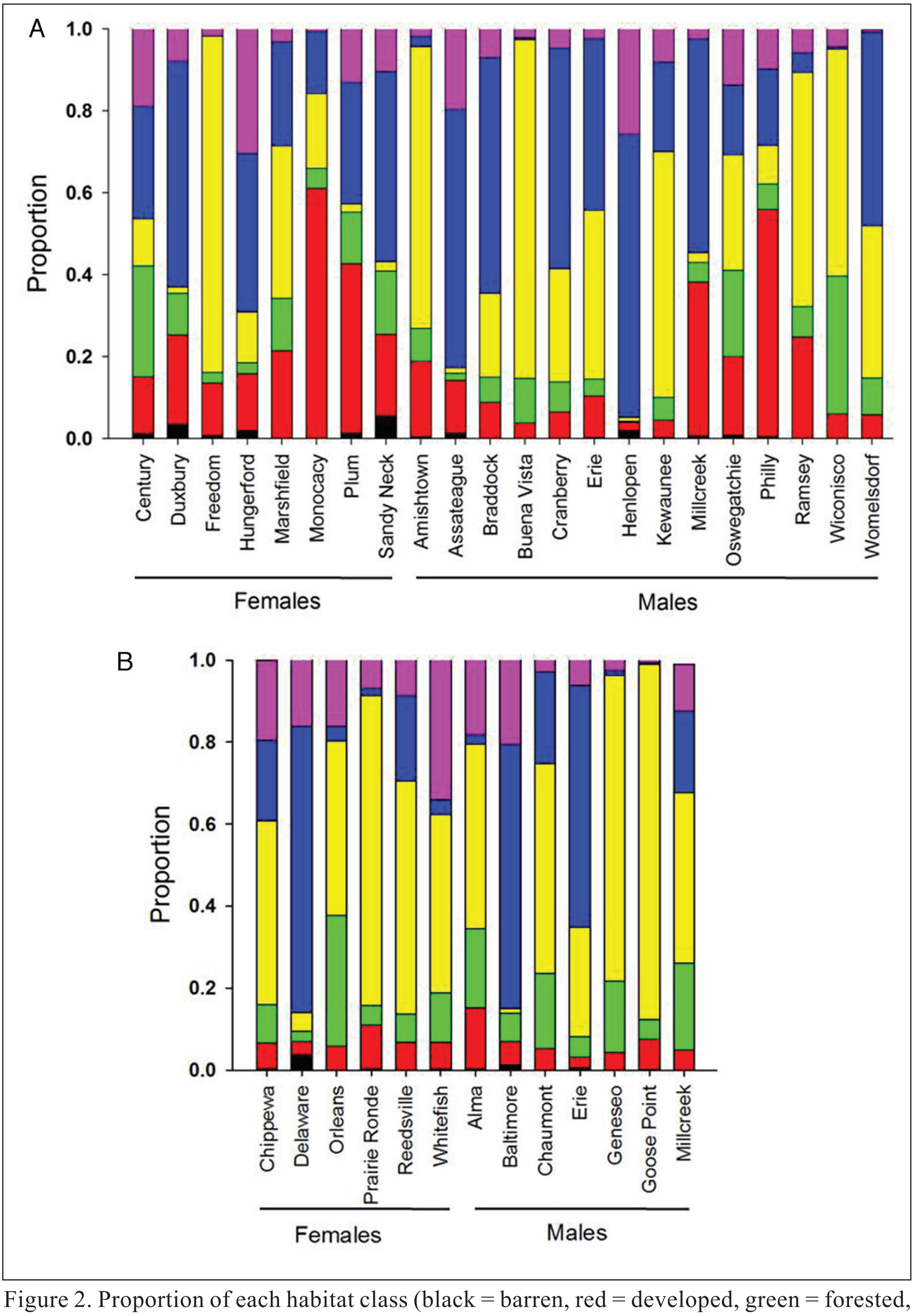

Figure 2. Proportion of each habitat class (black = barren, red = developed, green = forested, yellow = grassland/pasture/agricultural, blue = open water, and pink = wetland) surrounding locations of 34 Snowy Owls tracked during (a) winter 2013–2014 and (b) 2014–2015 in northeastern North America using a 4000-m radius.

Previous studies on habitat use on the plains of Alberta, Canada, found Snowy Owls using agricultural and grassland habitat almost exclusively (>97%; Lein and Webber 1979). In the primarily forested region where the study took place, however, such modified habitats may represent the landscape most closely matching open, treeless Arctic tundra. The reliance on anthropogenic resources may signal some degree of tolerance for human perturbations, and may also reflect age-related tolerance. In the first winter of the study, close to a third of daily owl locations were in developed lands where human perturbations are the highest. Owls tracked during that winter were exclusively juveniles, which may have exhibited greater naiveté and tolerance for human disturbance than more experienced adults. Conversely, during the second winter, when all tracked owls were non-juveniles, half as many locations (14%) were in developed areas. While abundant food sources may be available in agricultural and developed habitats, owls can, however, be exposed to an increased risk of mortality and/or exposure to contaminants in such habitats (Miller et al. 2015).

In addition to our findings for terrestrial habitats, we quantified the degree to which Snowy Owls overwintering and migrating through the northeastern US extensively use open waters of the Atlantic and/or the Great Lakes. A few observations had long suggested that Snowy Owls are able to use offshore waters for hunting, and that they can take a variety of marine or aquatic prey, especially water birds (Holt et al. 2015, Smith 1997). Our results further illustrate that Snowy Owls can travel extensively and/or feed at sea, and that they can switch from a narrow, specialized diet composed of small mammals during the breeding season (Holt et al. 2015), and in some parts of their wintering range (Detienne et al. 2008), to a wider, more opportunistic winter diet. Although the marine element of these top predators had been recently reported in the Arctic (Therrien et al. 2011), our current study shows their significant use of this environment even in the southern parts of their range. This behavior is likely affected by the extent of ice covering the Great Lakes, which varies annually depending on weather patterns (NOAA 2015); however, more research on this issue is needed. Although ice structure over the Great Lakes may modulate owl access to prey concentrations (e.g., as with polynyas with sea-duck gatherings in Arctic waters; Therrien et al. 2011), the use of open waters seems mostly limited to the sea coast. Such coastal zones may be critical in understanding the overwinter strategies of these predators.

By using a wide variety of habitats, the Snowy Owl acts as a predator in several southern ecosystems across their winter range. Indeed, with a large prey-base available across this range, the presence of Snowy Owls might be felt in several food webs. For owls, food availability further increases the possibility of erratic movements during irruptive episodes. The diversity in habitat use exhibited by Snowy Owls may be a mechanism to promote survival, for instance by reducing interspecific competition. Overall, the additional complexity of winter-habitat use exemplified by Snowy Owls creates yet another shortfall (Cottee-Jones et al. 2015) in our ability to predict site fidelity or design conservation strategies for irruptive species, and signals the need for continuing long-term individual-based tracking projects.

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