RESEARCH ARTICLE

Landscape cover type, not social dominance, is associated with the winter movement patterns of Snowy Owls in temperate areas

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ABSTRACT

Migrating animals occur along a continuum from species that spend the nonbreeding season at a fixed location to species that are nomadic during the nonbreeding season, essentially continuously moving. Such variation is likely driven by the economics of territoriality or heterogeneity in the environment. The Snowy Owl (*Bubo scandiacus*) is known for its complex seasonal movements, and thus an excellent model to test these ideas, as many individuals travel unpredictably along irregular routes during both the breeding and nonbreeding seasons. Two possible explanations for this large variation in the propensity to move are (1) dominance hierarchies in which dominant individuals (adult females in this case) monopolize some key, consistent resources, and move less than subdominants; and (2) habitat heterogeneity in which individuals foraging in rich and less heterogenic environments are less mobile. We analyzed fine-scale telemetry data (global positioning system [GPS]/global system for mobile communication [GSM]) from 50 Snowy Owls tagged in eastern and central North America from 2013 to 2019, comparing space use during the winter period according to sex and age, and to land cover attributes. We used variograms to classify individuals as nomadic (58%) or range-resident (42%), and found that nomadic owls had ten times larger wintering areas than range-resident owls. The frequency of nomadism was similar in socially-dominant adult females, immatures, and males. However, nomadism increased from west to east, and north to south, and was positively associated with the use of water and negatively associated with croplands. We conclude that many individual Snowy Owls in Eastern North America are nomadic during the nonbreeding season and that movement patterns during this time are driven primarily by extrinsic factors, specifically heterogeneity in habitat and prey availability, as opposed to intrinsic factors associated with spacing behavior, such as age and sex.

Keywords: body condition, *Bubo scandiacus*, Global positioning system/Global system for mobile communication, land cover composition, movement pattern, nonbreeding, wintering areas

LAY SUMMARY

- Global positioning system (GPS)/Global system for mobile communication (GSM) transmitters were used to document two movement behaviors, range-residency, and nomadism in wintering Snowy Owls.
- Social dominance plays little role in determining the distribution of wintering owls in temperate areas.
- Mobility increased west to east, and north to south, and was more common along with bodies of water than in croplands.

Le type de couvert du paysage, et non la dominance sociale, est associé aux patrons de déplacement hivernal de *Bubo scandiacus* dans les zones tempérées

RÉSUMÉ

Les animaux migrateurs suivent un continuum allant d'espèces qui passent la période internuptiale à un endroit fixe aux espèces qui sont nomades pendant la période internuptiale, étant essentiellement continuellement en mouvement. Cette variation semble due à l'économie de la territorialité et l'hétérogénéité de l'environnement. *Bubo scandiacus* est connu pour ses mouvement saisonniers complexes, et constitue donc un excellent modèle pour tester ces idées, car de nombreux individus se déplacent de manière imprévisible le long de routes irrégulières tant au cours de la saison de

reproduction que durant la période internuptiale. Deux explications possibles de cette grande variation de la propension à se déplacer sont (1) les hiérarchies de dominance dans lesquelles les individus dominants (femelles adultes dans ce cas-ci) monopolisent certaines ressources clés stables et se déplacent plus que les sous-dominants; et (2) l'hétérogénéité de l'habitat dans lequel les individus en quête alimentaire dans les environnements riches et moins hétérogènes sont moins mobiles. Nous avons analysé les données télémétriques à fine échelle (Global positioning system [GPS]/Global system for mobile communication [GSM]) de 50 individus de *B. scandiacus* marqués dans l'est et le centre de l'Amérique du Nord de 2013 à 2019, en comparant l'utilisation spatiale au cours de la période hivernale selon le sexe et l'âge, et les caractéristiques de la couverture terrestre. Nous avons utilisé des variogrammes pour classer les individus comme nomades (58 %) ou résidents (42 %), et nous avons trouvé que les individus nomades avaient des aires d'hivernage dix fois plus grandes que les individus résidents. La fréquence du nomadisme était similaire chez les femelles adultes socialement dominantes, les individus immatures et les mâles. Toutefois, le nomadisme augmentait de l'ouest vers l'est, et du nord au sud, et était positivement associé à l'utilisation de l'eau et négativement associé aux champs cultivés. Nous concluons que plusieurs individus de *B. scandiacus* de l'est de l'Amérique du Nord sont nomades au cours de la période internuptiale et que les patrons de déplacement pendant cette période sont principalement déterminés par des facteurs extrinsèques, en particulier l'hétérogénéité dans la disponibilité de l'habitat et des proies, comparativement aux facteurs intrinsèques associés au comportement d'espacement tels que l'âge et le sexe.

*Mots-clés***: condition corporelle, *Bubo scandiacus*, Global positioning system/Global system for mobile communication, composition de la couverture terrestre, patron de mouvement, non reproducteur, aires d'hivernage

INTRODUCTION

In migratory animals, movement patterns during the nonbreeding period can be important predictors of net daily energy gain and, consequently, overwinter survival and future investment in reproductive success (Marra et al. 1998, Harrison et al. 2011). Indeed, there is increasing awareness of the importance of the nonbreeding season to individual fitness and population dynamics, partly due to the miniaturization of tracking equipment that allows researchers to monitor animals year-round (Newton 2008, McKinnon et al. 2013, Kays et al. 2015). Whereas many species settle and defend winter territories, presumably to maximize daily energy intake through monopolization of predictable resources, other species can be nomadic during the nonbreeding period, ranging across continents in search of food (Lack 1968, Newton 2008). The complex and irregular movements of such individuals usually reflect fluctuating resources and opportunistic foraging (Dean 2004). Many nomadic animals are diet specialists, relying on resources that are spatially and temporally heterogeneous, and so select specific habitats or move in response to changing environmental conditions (Runge and Tulloch 2017).

In many animals, competitive ability plays a role in how individuals use the landscape. Dominant individuals defend better quality habitats with more resources compared to subordinates, sometimes termed the "ideal despotic distribution" (Fretwell and Lucas 1970, Morse 1974, Gauthreaux 1978). For example, male American Redstarts (*Setophaga ruticilla*) monopolized the higher quality habitats with more food during winter and displaced subordinates (i.e. females and hatch-year males) (Marra 2000). In some birds, home range size is inversely related to prey abundance presumably because ample food can be obtained within a small area (Zabel et al. 1995, Pfeiffer and Meyburg 2015, Kouba et al. 2017). Thus, individuals that

do not move large distances are usually those in the most favorable habitat (Kouba et al. 2017) and are socially dominant (i.e. older, larger birds of the dominant sex). Hence, by comparing space use among sex and age classes of birds in the nonbreeding season, we can make inferences about the quality or density of food in the habitats they occupy (Lynch et al. 1985, Marra and Holmes 2001). In raptors with reversed sexual size dimorphism, larger adult females are often socially dominant over males and immatures, and the pattern of females occupying the higher quality habitats and/or moving less has been reported in a few species (Kerlinger and Lein 1986, Ardia and Bildstein 1997, Littlefield and Johnson 2005, Chang and Wiebe 2018a).

The Snowy Owl (*Bubo scandiacus*) shows a diversity of movements during its annual cycle, often traveling thousands of kilometers (Holt et al. 2020). Whereas some individuals appear to be fairly stationary on bounded home ranges during winter (Boxall and Lein 1982, Chang and Wiebe 2018b), other owls undergo highly variable and unpredictable long-distance movements (Therrien et al. 2014, Robillard et al. 2018). Thus, Snowy Owls show a range of wintering movement patterns with some remaining residents on winter home ranges but others moving nomadically for months. Previous studies have examined movements in relation landscape composition of Snowy Owls that winter primarily above the tree-line (Fuller et al. 2003, Therrien et al. 2014, Doyle et al. 2017), or in the Canadian Prairies (Chang and Wiebe 2018a, 2018b). Individuals wintering in the marine environment, on pack ice, had average home ranges three times larger than individuals wintering in the terrestrial environment, primarily the North American Prairies, perhaps reflecting stable and dense prey resources on the prairies (Robillard et al. 2018). However, little is known about factors that may affect the movements and habitat use of Snowy Owls in the southern part of their winter range where irruptions occur.

The unpredictable movements of Snowy Owls over long distances during the annual cycle is likely an adaptation allowing them to seek out habitats to meet their food intake requirements (200–400 g of prey per day for captive owls; Gessaman 1972, Boxall and Lein 1989) and evolved in response to fluctuating prey abundance on the breeding grounds (Krebs et al. 2002, Gilg et al. 2006, Therrien et al. 2014). On the Canadian Prairies, wintering owls spent more time in habitats with high prey availability than in resource-poor habitats (Chang and Wiebe 2018a). Furthermore, on the prairies, home ranges of male owls averaged 25% larger than those of females, although non-significantly so, consistent with females occupying the areas with a higher quality food source (Chang and Wiebe 2018b). Home range size of these owls was inversely related to body condition suggesting that individuals in poorer quality habitats required larger home ranges (Chang and Wiebe 2018b). The relatively low site fidelity reported in Snowy Owls for some individuals suggests that there is little advantage associated with familiarity or memory of a particular region and that there are advantages to searching widely for prey hotspots (Therrien et al. 2014, Robillard et al. 2018, Holt et al. 2020).

Our objectives for this study were to assess whether social dominance (i.e. age and sex) or environmental factors influence how Snowy Owls distribute on the landscape. If dominance and competitive exclusion, as described above operate among owls during the nonbreeding season, we expect females and adults to have smaller wintering areas and to move less than males and immatures. If the distribution of owls is explained primarily by environmental factors, such as the spatial heterogeneity of the landscape (i.e. access to food resources via land cover composition), then we expect owls that move less and have smaller wintering areas will be those in less developed regions and in homogeneous landscapes compared to owls in landscapes that are more altered by humans and fragmented by structures such as roads, towns, and buildings. Finally, we tested whether age and sex classes differ in body condition at the time of capture, expecting that females and adults might be in better condition than males and immatures, and individuals in lower body condition will move more and have larger wintering areas.

METHODS

Study Area and Data Collection

We studied wintering Snowy Owls in central (Great Lakes and the Prairies) and eastern (Atlantic Coast) United States and Canada from 2013 to 2019. Geographic regions were distinguished by the North American Bird Conservation Initiative (NABCI) Bird Conservation Regions (BCRs) (Bird Studies Canada and NABCI 2014). Due to small sample sizes for certain BCRs (i.e. Atlantic Northern Forest; *n* = 1),

we grouped geographic regions (see Appendix Figure 3) and analyzed three regions: the Prairies region, the Great Lakes region, and the Atlantic Coast region. Human population density is highest along the Atlantic Coast region, intermediate in the Great Lakes region, and the lowest in the Prairies (Bhaduri et al. 2007); owls along the Atlantic Coast are often associated with coastal foraging on waterfowl while those in the Prairies are often associated with grassland foraging on small mammals (Therrien et al. 2017, Holt et al. 2020). Owls were trapped using lure animals (e.g., Rock Pigeon [*Columba livia*], European Starling [*Sturnus vulgaris*], house mouse [*Mus musculus*], gerbil [*Meriones unguiculatus*], Russian hamster [*Phodupus sungorus*]) in either bal-chatri traps or bow nets (Bloom et al. 2007). We used plumage characteristics to assess sex and categorize age as an adult versus immature (first year) (Seidensticker et al. 2011, Solheim 2012). Within each sex, body mass was not correlated with structural size (wing chord) so we used body mass itself as an index of condition (nutrient reserves) of the owls. Two owls with incomplete data were removed from the body mass analysis. We equipped each owl with ~40 g solar-powered GPS/GSM transmitters (Cellular Tracking Technologies, Rio Grande, NJ, USA), fitted with a backpack harness of 10 mm tubular Teflon (Steenhof et al. 2006), which weighed <3% of the owls' total body mass ($\bar{x}$ = 1,885 ± 38 g). Transmitters recorded one GPS location between 30–60 min intervals during the wintering period, and downloaded the data via GSM cellular phone network.

We analyzed the movements of individuals that had >28 days of data, and were captured before March 1, to ensure a representative picture of their winter movements prior to the initiation of spring migration (Therrien et al. 2014). We assumed the wintering period ended once an individual began moving northward systematically with no reverse migration or stopovers longer than three days, and we examined individual movement maps to apply these criteria and truncate the data. Thus, the duration of monitoring ranged from 28.5 days to 146 days ($\bar{x}$ = 70.2 days), with the earliest tracking date starting on 24 November and the latest end tracking date ending on 4 May. The number of recorded locations ranged from 680 to 4,497 ($\bar{x}$ = 1,895 fixes) per individual.

Winter Behavior and Occurrence Distributions

We used two methods to classify winter behavior and to measure space use in Snowy Owls. We first categorized winter behavior as either (1) range-resident (i.e. birds that exhibited bounded overwintering home ranges [Calabrese et al. 2016]) or (2) nomadic (i.e. birds that moved with no fixed spatial or temporal pattern [Newton 2010] and which did not have a bounded home range). To do so, we imported GPS data in R 3.5.2 (R Core Team 2018) using the *ctmm* package (Calabrese et al. 2016), following the

methods of Fleming et al. (2014). For each individual, we visually inspected the empirical variograms (spatial statistics) to determine the asymptotic behavior of the semivariance function over time. An asymptote in the variogram suggests movements are restricted in space (i.e. the bird is resident on a home range) whereas a lack of asymptote means that the data are not appropriate for a home range analysis because the individual is continually shifting its range (Calabrese et al. 2016) (see Appendix Figure 4). The variograms also determine which continuous-time stochastic model is appropriate for the data by accounting for autocorrelation and variable sampling intervals. The best-suited models are determined by maximum likelihood as ranked by Akaike Information Criteria values and the two best fitting models include either the Ornstein–Uhlenbeck, or the Ornstein–Uhlenbeck motion with foraging and correlated velocities (Fleming et al. 2014, Calabrese et al. 2016). Prior to model selection, we removed outliers based on speed or distance from the center (>100 km) that was not biologically possible for the species using the outlie function in *ctmm*.

Our second method of classifying winter behavior of all 50 owls (nomadic and range-resident) was to use continuous-time movement models in the *ctmm* package to estimate an individual's 95% occurrence distribution. The occurrence distribution uses locations and the location error to interpolate where the animal was located over distribution of times during the sampling period (Horne et al. 2007, Calabrese et al. 2016, Fleming et al. 2016), and allows for model selection prior to the analysis for best fit of the data to the model. This method which uses the Brownian Bridge Density Estimator via time-series Kriging for autocorrelated telemetry data (Calabrese et al. 2016) allows the analysis of land cover composition based on where the animal was located during the study period. In comparison, home range analysis extrapolates where an animal will travel over a long period of time if similar movement behaviors persist (Fleming et al. 2016). We used the default parameters in the *ctmm* package (Fleming and Calabrese 2015) and exported the occurrence distributions as shapefiles in ArcGIS 10.5.1 (Earth Systems Research Institute, Inc., Redlands, CA) and calculated the total area (km^2) of the occurrence distribution for each individual using the *Calculate Geometry* tool in ArcGIS.

In the only other study that used telemetry to report sex-specific range sizes of Snowy Owls in winter, Chang and Wiebe (2018b) found an average size of 54.4 ± 22.2 km^2 for males (*n* = 12) and 31.9 ± 21.6 km^2 for females (*n* = 11). Therefore, a sample of 15 individuals per group should be sufficient to detect this magnitude of difference between the sexes with a statistical power of 0.8. With 50 individuals in our study, we should have sufficient statistical power to detect relatively small differences in wintering areas

between land cover types and movement patterns when the sexes and ages are pooled. However, dividing our sample by sex and movement pattern would only allow us to detect large effect sizes, e.g. nomadic: 15 females and 14 males; range-resident: 10 females and 11 males.

Land Cover Composition
We obtained 30-m resolution land cover data for North America (Canada 2010 and USA 2011) from the North American Land Change Monitoring System (NALCMS) (Homer et al. 2017) and quantified percent land cover composition in each owl's occurrence distribution (hereafter "winter/wintering area") by overlaying occurrence distribution shapefiles with NALCMS data in ArcGIS 10.5.1. We categorized land cover types as follows: (1) forest (including evergreen, deciduous, and mixed forest); (2) shrubland/grassland, (3) wetland, (4) cropland, (5) barren lands (areas characterized by bare rock, gravel, sand, silt, or clay with little or no green vegetation), (6) urban (areas that contain ≥ 30% of constructed materials for human activities including cities, towns, transportation), and (7) water (permanent water bodies).

Statistical Analyses
We used generalized linear models (GLMs) to test if the size of the wintering area (response variable) was associated with age and sex category and with the type of wintering behavior (nomadism versus range-resident). Another GLM was used to see whether the size of the wintering area was affected by where the owl wintered (i.e. the three "region" categories). We subsequently used separate GLMs for each sex to test for effects of age, wintering behavior, and date of capture on body mass (the response variable) and in a different set of models to examine whether wintering behavior (binary response variable) was related to body mass and age. To address our prediction that owls will have smaller wintering areas and move less in regions affected by human development, we used two Fisher's exact tests: one to compare nomadic versus range-resident owls outside versus inside of the irruptive zone (i.e. south of the normal winter range ~41°N; Holt et al. 2020), and second to compare nomadic versus range-resident owls west versus east of the Great Lakes (i.e. east of Lake Erie and Lake Ontario). To examine various effects on the winter behavior (binary response variable) we used three GLMs with a binomial link, one to model potential effects of wintering latitude or longitude, a second to test the effects of sex, age, or region, and a third to look at the effects of the proportion of land cover types within wintering areas. Before running the latter model, we performed log-transformations on the 6 land cover classes since data were highly skewed for 6 out of the 7 land cover classes (excluding cropland as it was normally distributed). We performed all statistical analyses in R software (3.5.2).

TABLE 1. Size of the wintering areas (km²) of Snowy Owls in the USA and Canada based on occurrence distribution (see Methods).

	Mean	Standard error	n
Adults			
Females	80	27	11
Males	110	42	11
Adults pooled	105	30	22
Immatures			
Females	115	61	14
Males	190	55	14
Immatures pooled	155	45	28
Winter behavior			
Range-resident	19	5	21
Nomadic	206	38	29
Region			
Prairies	75	28	16
Great Lakes	201	61	17
Atlantic Coast	102	31	17

TABLE 2. Results of two generalized linear mixed models on winter behavior (i.e. nomadic versus range-resident) of Snowy Owls in the USA and Canada. The first model examines the effects of age, sex, and region and the second model examines the effects of land cover types on winter behavior. SE = standard error.

Explanatory variables	Estimate	SE	z value	P-value
Model 1				
Intercept	−1.85	0.82	−2.26	0.02
SexMale	−7.97e−2	0.63	−0.13	0.90
AgeImmature	0.54	0.63	0.85	0.40
RegionGreatLakes	1.48	0.81	1.82	0.07
RegionPrairies	2.11	0.84	2.52	0.01
Model 2				
LandCoverForest	−1.39e−2	1.02e−2	−1.37	0.18
LandCoverShrubland/Grassland	−2.80e−3	5.19e−3	−0.54	0.59
LandCoverWetland	3.42e−3	4.76e−3	0.72	0.48
LandCoverCropland	1.00e−2	1.22e−3	8.20	<0.001
LandCoverBarrenLands	1.19e−3	1.03e−2	0.12	0.91
LandCoverUrban	1.14e−3	3.19e−3	0.36	0.72
LandCoverWater	6.64e−4	1.64e−3	0.41	0.69

RESULTS

Effects of Age, Sex, Mass and Region on Wintering Areas

Of the 50 owls in our study, 22 were adults (11 females and 11 males) and 28 immatures (first-winter owls; 14 females and 14 males) with 42% exhibiting range-residency and 58% showing nomadism during the wintering period. On average, adult females had the smallest wintering areas, followed by adult males, immature females, and immature males (Table 1), however the size of wintering area was not affected by age or sex class (GLM: $F = 1.23$, df = 2 and 47, $P = 0.30$). As expected, the average wintering area for range-resident owls was significantly smaller than that of nomadic owls (GLM: $F = 17.53$, df = 1 and 48, $P < 0.0001$; Table 1). Owls from the Prairies had the smallest wintering areas, followed by owls from the Atlantic Coast, and Great Lakes (Table 1); however, the size of wintering area was not affected by region (GLM: $F = 2.37$, df = 2 and 47, $P = 0.10$).

Adult female Snowy Owls ($n = 11$) weighed on average 2,130 ± 37 g, immature females ($n = 13$) averaged 2,117 ± 49, adult males ($n = 11$) averaged 1,638 ± 34 g, and immature males ($n = 13$) averaged 1,706 ± 33 g. The mass of female Snowy Owls was not associated with age class (GLM: $F = 0.02$, df = 1 and 20, $P = 0.88$), wintering behavior ($F = 1.55$, df = 1 and 20, $P = 0.23$) or date of capture ($F = 0.64$, df = 1 and 20, $P = 0.43$). The mass of male Snowy Owls was also not associated with age class (GLM: $F = 2.73$, df = 1 and 20, $P = 0.10$, wintering behavior ($F = 0.22$, df = 1 and 20, $P = 0.64$), or date of capture ($F = 1.05$, df = 1 and 20, $P = 0.32$). The type of wintering behavior (range-resident versus nomadic) was not related to body mass (females: odds ratio = 1.0, $\chi^2 = 1.71$, df = 1 and 22, $P = 0.19$; males: odds ratio: 1.0, $\chi^2 = 0.18$, df = 1 and 22, $P = 0.66$) or age (females: odds ratio = 3.10, $\chi^2 = 1.64$, df = 1 and 21, $P = 0.20$; males: odds ratio = 0.82, $\chi^2 = 0.05$, df = 1 and 21, $P = 0.81$).

Effects of Sex, Age, Region, and Land Cover Composition on Wintering Behavior

There were 6 nomadic and 2 range-resident owls in the "irruptive" zone south of the normal winter range and 23 nomadic and 19 range-resident owls north of that latitude (i.e. within the normal geographic winter range; Fisher exact test: $P = 0.44$). However, the probability of range-resident owls increased with latitude from south to north (GLM: $t_{48} = 2.18$, $P = 0.03$; Figure 1A). There were 5 nomadic and 12 range-resident owls west of the Great Lakes and 24 nomadic and 9 range-resident owls east of the Great Lakes (Fisher exact test: $P = 0.006$). Moreover, the probability of range-residency increased with longitude from east to west (GLM: $t_{48} = -2.25$, $P = 0.03$; Figure 1B).

Furthermore, the likelihood of nomadism versus range-residency was associated with a geographical region but not age or sex (Table 2). Post-hoc Tukey's test revealed that it was the Atlantic Coast owls that were more likely to be nomadic than owls in the Prairies ($z = -2.50$, $P = 0.03$), whereas the likelihood of nomadism did not differ among the other regions. The model testing the effect of land cover type on wintering behavior revealed that range-residency is more likely to occur as the percent of cropland increases (Table 2, Figure 2). The decision to settle on a range or to keep moving was independent of the other land cover classes (Table 2).

DISCUSSION

Snowy Owls wintering near their southern range limit across North America showed large variation in space use with some individuals remaining resident on ranges of a few square kilometers and others moving nomadically over
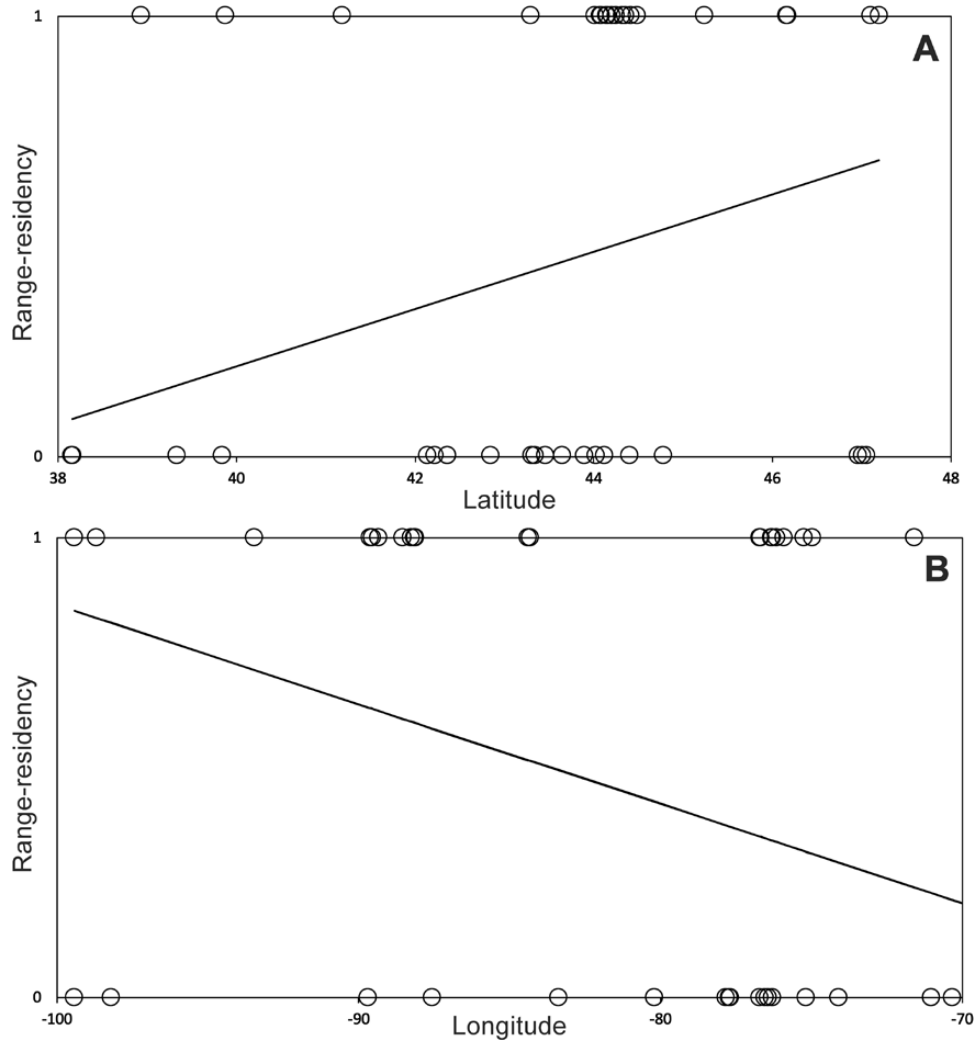
FIGURE 1. Range residency (yes = 1, no = 0; open circles) relative to (**A**) latitude and (**B**) longitude in Snowy Owls wintering near their southern range limit. Probability of range-residency shows the best-fit of regression (line).

hundreds of kilometers. We did not find those traits intrinsic to the birds themselves predicted the extent to which they moved in winter. Instead, movement patterns were associated with longitude, latitude, and land cover types.

Social Dominance does not Affect the Movements of Snowy Owls in Winter

We found no support for the hypothesis that range residency is associated with social dominance. Overall, 42% of owls established a bounded winter range, but the likelihood of doing so did not vary with sex, age, or body mass at capture. Furthermore, female and adult owls did not have smaller wintering areas than other sex and age classes and an individual's traits were not associated with the type of land cover composition so dominant owls did not seem to be competitively excluding others from certain habitats. We suggest that owls in the south

tend to assort themselves according to the Ideal Free Distribution—where the number of individuals that aggregate in various habitat patches is proportional to the number of resources available in each patch (Fretwell and Lucas 1970).

Our prediction that owls in lower body condition (i.e. body mass) would move more in winter was not supported. The body mass of owls captured throughout winter from different geographic areas in our study was similar to that reported for owls wintering in Saskatchewan (Chang and Wiebe 2016) and averaged slightly higher than Snowy Owls sampled in early winter in eastern North America and the Canadian Prairies (Curk et al. 2018). Chang and Wiebe (2016) and Curk et al. (2018) reported that body condition was lower in immatures than adults but that body condition generally improved over the wintering period. We found no differences in mass between age classes,
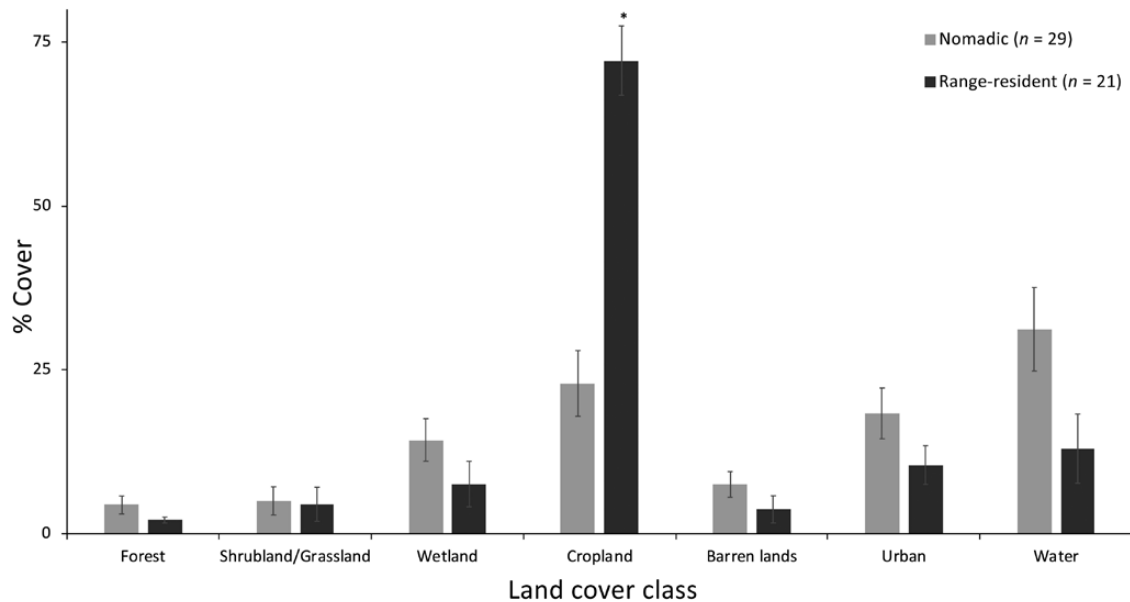
FIGURE 2. Land cover composition within wintering areas of nomadic and range-resident Snowy Owls in USA and Canada, 2013–2019. Mean percent cover and standard error of the 7 land cover types are shown. Asterisk (*) denotes the proportion of cropland as a significant predictor (Table 2) of whether an owl is range-resident or nomadic.

but the immatures we trapped later in winter may have already been able to improve their condition to the level of wintering adults.

Effect of Region and Landscape Characteristics on Winter Movements

The landscape structure on the Prairies is simpler and more homogenous than that of the Atlantic Coast or Great Lakes and Snowy Owls wintering on the Prairies were more likely to be range-resident than those in the other regions farther east. Indeed, nomadism tended to be associated with water or wetland habitats and range residency was strongly associated with cropland. Because aquatic habitats may temporarily freeze during winter, owls preying primarily on waterfowl (e.g., Campbell and MacColl 1978, Robertson and Gilchrist 2003) must follow their prey across the landscape rather than a remaining resident. Brown's (1964) economics model may explain variation in owl range-residency if levels of resources fluctuate. Nomadic birds are believed to respond to resources that fluctuate in both space and time by moving over large distances to find places where food is locally abundant (Dean 2004), as seen in wintering Snow Buntings (*Pletrophenax nivalis*) from southern Canada (McKinnon et al. 2019). Some species such as the Australian Kestrel (*Falco cenchroides*) and Grey-backed Sparrow- Lark (*Eremopterix verticalis*) only cease being range-resident when resource availability is low at the larger landscape scale, moving to exploit better or more plentiful resources elsewhere (Olsen and Olsen 1987,

Dean and Milton 2001, Dean 2004). However, Snail Kites (*Rostrhamus sociabilis*) in Florida had more exploratory movements during times of greater food abundance, suggesting that moving even when food availability is high may change the relative costs-benefits of territoriality and allow individuals to explore potential habitats during times when the risk of starvation is minimal (Bennetts and Kitchens 2000, Bell 2012).

The average home range size (~50 km^2) of both male and female Snowy Owls feeding mainly on small rodents in agricultural fields of Saskatchewan (Chang and Wiebe 2018a) was similar to the wintering areas of the range-resident owls in our study. Apparently, home ranges of this size in croplands support ample prey that may sustain an owl for months so that it does not need to move continuously. In contrast, Robillard et al. (2018) documented wintering areas averaging 71,100 km^2 among owls using coastal or marine habitats in the Arctic. Thus, long-distance movements among wintering owls along coastlines suggest that marine-based prey are dispersed more widely and are highly variable. For example, Snowy Owls have been observed near polynyas (small patches of open water in surface ice) where they attack wintering seabirds such as long-tailed ducks (*Clangula hyemalis*), eiders (*Somateria* spp.), and black guillemots (*Cepphus grylle*) (Gilchrist and Robertson 2000, Robertson and Gilchrist 2003, Therrien et al. 2011). The Atlantic and Great Lakes coasts represent long, linear habitats with few geographic barriers such as mountain ranges. An owl moving along a coastline encounters an almost endlessly unspooling train of

habitat which facilitates long, linear movements in search of food as the water freezes over locally or patchy waterfowl flocks move.

The use of predominate croplands by range-resident owls is in line with the idea that agricultural lands provided the most predictable food during winter, although we were unable to measure the availability of different land cover types and hence could not calculate selection indices. However, Heisler et al. (2013) found the proportion of cropland and the percentage of sand in the soil had the greatest influence on small mammal species composition in the northern Great Plains. Croplands with clay soils were dominated by deer mice (*Peromyscus maniculatus*) whereas the relative abundance of sagebrush voles (*Lemmiscus curtatus*) was greater in areas with higher proportions of grasslands and sandy soils (Heisler et al. 2013). The mosaic of habitat types used by nomadic owls (i.e. wetland, urban, water, etc.), which had larger winter areas, supports the idea that fragmented habitat, and likely the accessibility of prey in each habitat, maybe driving the tendency to move continuously in human-dominated landscapes.

CONCLUSION

In summary, the winter movements of Snowy Owls that we quantified are an important first step in understanding their use of the landscape in the southern portion of their range and are essential for optimizing conservation initiatives over the full annual cycle. We found that the use of landscape was driven by extrinsic rather than intrinsic traits which supports the idea that the evolution of nomadism in some large mammals and in birds such as seabirds, seedeating finches, and some irruptive owls is likely the result of variable food resources (Löfgren et al. 1986, Swenson et al. 1988, Singh et al. 2012, De Grissac et al. 2016). The two types of movement patterns: range-residency versus nomadism suggest that different conservation strategies may be warranted for the two groups. Highly mobile owls using urban and fragmented habitats may be exposed to more risk caused by automobile or aircraft collisions, or higher stress levels associated with human activity and disturbance. The survival rates of owls that are nomadic vs. range-resident and owls wintering in various habitats thus warrants further study.

Future work should consider whether movement patterns and habitat selection vary across years, especially in relation to owl density. During "irruptions" that occur irregularly about every 3–5 years (Newton 2002, Robillard et al. 2016), owl density peaks and may trigger more competition and longer movements by owls in search of prey in coastal environments. Knowing more about the winter movements and survival of these irruptive owls, typically immatures, will tell us how they contribute to population demography.

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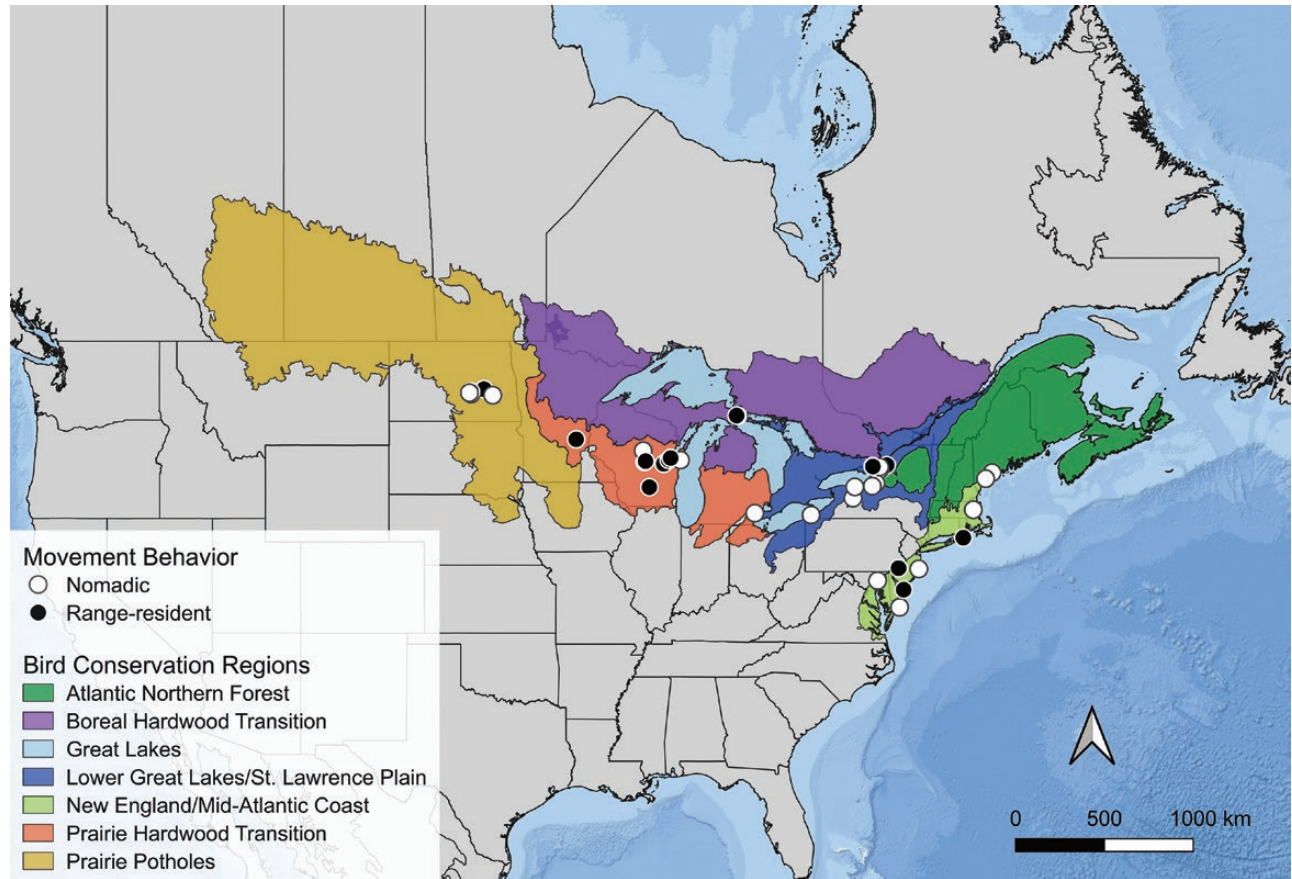
APPENDIX FIGURE 3. Trapping locations (black and white circles) of Snowy Owls (n = 50) in Bird Conservation Regions (BCRs) in USA and Canada. Owls trapped in BCRs Prairie Potholes and Prairie Hardwood Transition were considered to belong to the Prairies (n = 16); and owls trapped in BCRs Boreal Hardwood Transition, Great Lakes, and Lower Great Lakes/St. Lawrence Plains were considered belonging to the Great Lakes (n = 17); and owls trapped in the Atlantic Northern Forest and New England/Mid-Atlantic Coast were considered to belong to the Atlantic Coast (n = 17).
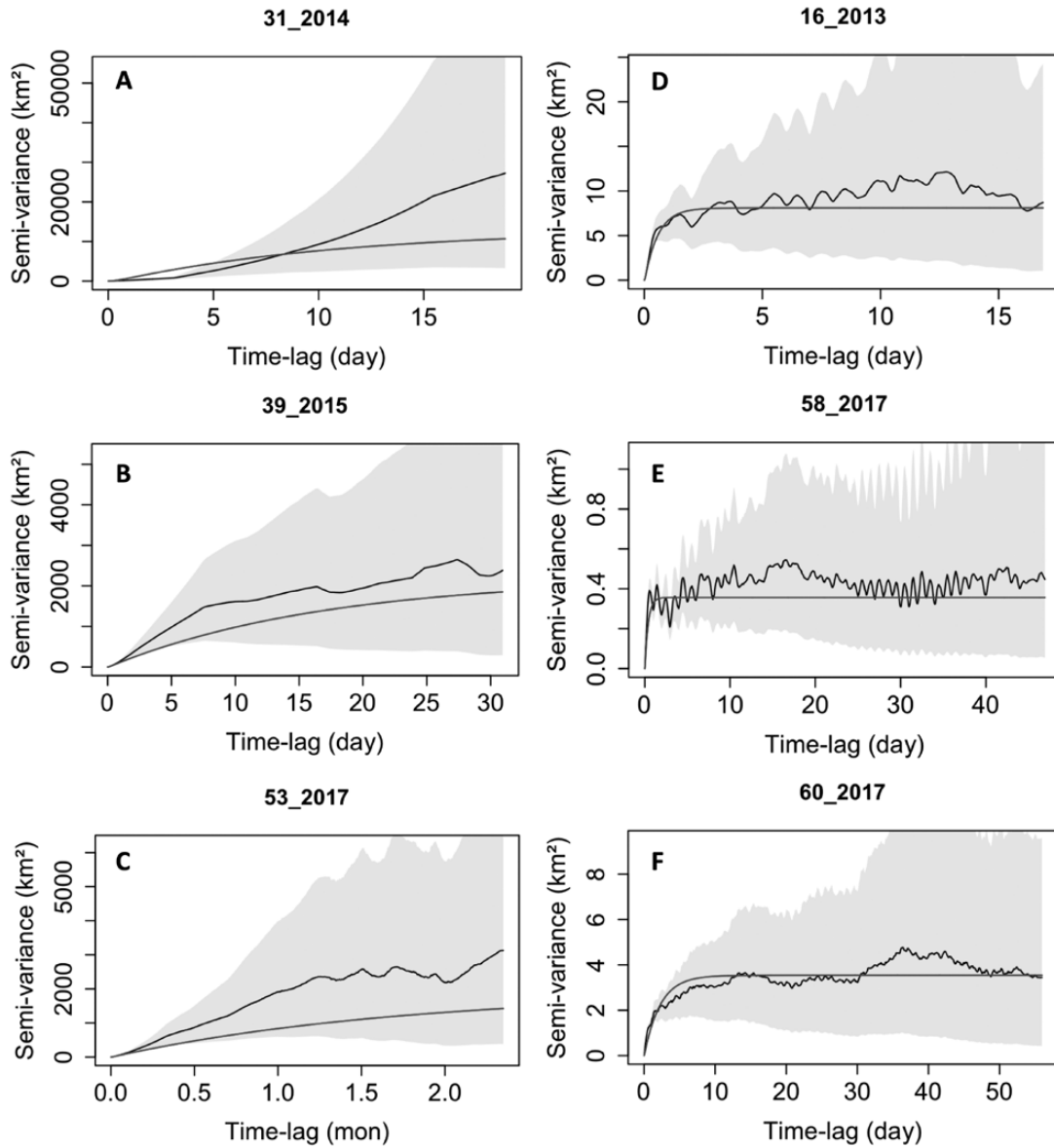
APPENDIX FIGURE 4. Empirical variograms overlaying the statistic of semi-variance function against the time-lag for three nomadic Snowy Owls (A, B, C) and three range-resident Snowy Owls (D, E, F). Individuals showing range-residency display a variogram that eventually reaches an asymptote that is proportional to home range size. Black lines depict semi-variance and grey shading represents ±95% confidence interval, whereas red lines depict the fitted movement model.