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Nomadic breeders Snowy Owls (*Bubo scandiacus*) do not use stopovers to sample the summer environment

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Whereas most migratory animals, such as many birds of prey, return to the same breeding area each summer, nomadic breeders search over large distances to locate breeding areas that vary greatly in location from year to year. Nomadic breeders are assumed to extensively sample patch quality before selecting a summer settlement site (e.g. breeding site) with a high abundance of prey. In addition, patch selection during migration might vary, with immature birds sampling the summer environment for the first time. Here, we examined the migratory movements of a nomadic breeder, the Snowy Owl, to determine whether there are differences in phenology among age and sex classes, and where stopovers occur along their migratory journey. Each owl ($n = 24$) was equipped with a GPS-GSM transmitter during the overwintering period in the USA and Canada from 2014 to 2018. Movement patterns followed a two-process Poisson distribution, allowing us to separate stopovers from directional flights (i.e. migration). Adults completed migration earlier than immatures, with no difference in number of stopovers or time spent at each stopover. Snowy Owls had a higher probability of having a stopover at the beginning of their migration than at the end. Moreover, stopovers occurred primarily on frozen waterbodies more suitable for foraging or roosting outside of the summer range. We conclude that Snowy Owls use stopovers primarily to build up reserves or to rest during migration and they can potentially select appropriate summer settlement sites via short overflights without extensive sampling of patches during lengthy stopovers.

Keywords: Arctic, biologging, GPS-GSM, migration phenology, Strigidae.

Migration phenology plays an important role in linking events across the annual cycle, eventually scaling to influence population dynamics (Marra *et al*. 2015, Shaw 2016). Most migrant bird species show high philopatry, returning to the same breeding area annually, despite sometimes travelling thousands of kilometres between breeding and non-breeding areas (Steiner & Gaston 2005, Lovette & Fitzpatrick 2016). Other species are nomadic, exhibiting low breeding philopatry and high breeding dispersal with unpredictable and variable movements (Newton 2006, Therrien *et al*. 2014, Robillard *et al*. 2018). For example, some birds move over the landscape seeking out areas where food resources are most abundant to settle (Lack 1954, Dingle & Drake 2007, Newton 2010). Other birds, such as male Arctic shorebirds, can move thousands of kilometres post-migration within the Arctic tundra to search for mates, with stopovers in the breeding range that are correlated with the number of females present (Lanctot *et al*. 1998, Kempenaers & Valcu 2017). Many Arctic

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birds of prey disperse large distances between years to breed where lemming *Lemmus* and *Dicrostonyx* spp. abundance is high (Therrien *et al.* 2014, 2015, Holt *et al.* 2020). However, we have a limited understanding of how these birds assess resource availability to locate regions with high lemming abundance across large landscapes because lemming peaks are typically spatially unpredictable (Krebs *et al.* 2002). Bio-logger advancements provide an opportunity for researchers to monitor movements in more detail and identify migratory routes, stopover sites, and breeding and non-breeding areas (Goldstein *et al.* 1999, Webster *et al.* 2002, Haines *et al.* 2003, López-López & Urios 2010).

Migrating birds can either minimize the number of stopovers taken and travel almost non-stop to their breeding site (i.e. time-minimizers, such as adult male passerines in spring) or travel short distances, stopping and refuelling when necessary (i.e. energy-minimizers, such as immature passerines in autumn; Newton 2010, Zhao *et al.* 2017). Such tactics, however, may not apply to species such as Snowy Owls *Bubo scandiacus*, which do not have a fixed breeding site that is their destination. After reaching the breeding range, Snowy Owls must prospect, apparently nomadically, as they seek out appropriate areas with high food abundance on which to settle (Therrien *et al.* 2014, 2017, Curk *et al.* 2020). Hence, movements within the breeding range may be used primarily to prospect for lemming peaks, as Snowy Owls will only settle to breed in areas of high lemming abundance (Gauthier *et al.* 2013, Therrien *et al.* 2014, Robillard *et al.* 2016). In any year, these peaks are separated by large distances, so owls may assess lemming populations within the breeding range via stopovers to sample prey density interspersed by long-distance movements. Alternatively, if owls are able to sample lemming abundance rapidly, perhaps by hearing lemmings under the snow, locating fox attacks and tracks or observing lemming tracks on the snow, they may not require stopovers to assess local prey abundance.

The limited empirical data suggest that Snowy Owls do not migrate in groups, but many individuals seem to use similar migratory paths, following coastlines, river valleys and mountain ridgelines as they move from non-breeding areas to breeding areas (Holt *et al.* 2020). Owls time their spring migration with the retreating snow line, moving on average just north of the snow line (Curk *et al.* 2020). Therrien *et al.* (2015) equipped nine breeding adult female Snowy Owls with satellite transmitters and found that stopovers during pre-breeding movements in the breeding range occurred where snow depth was shallow. Snowy Owls typically nest in areas with snow-free ground (allowing nest construction) and the reported zigzagging movements made by owls while moving within the breeding range may allow owls to assess gradients of lemming density and whether it is high enough to entice them settle or breed (Therrien *et al.* 2014, 2015).

Phenology, including the seasonal timing of departure and arrival from the non-breeding to breeding areas, may be influenced by individual attributes such as age and sex. Kerlinger and Lein (1986) found that adult female owls, which are larger and socially dominant over males, wintered the farthest north, whereas the most subordinate age–sex class (immature males) wintered the farthest south. Hence, socially dominant individuals, i.e. adult females in this case, are predicted to arrive sooner in the breeding range because they may have a shorter distance to travel from their non-breeding areas. Similarly, the body size hypothesis (Cristol *et al.* 1999) predicts that females will leave the non-breeding range earlier than males and reach the breeding range earlier because their larger body size allows them to tolerate cold climates at high latitudes better than males. There is probably incentive to arrive in the breeding range as early as possible to secure and defend the best quality sites against conspecifics (Cristol *et al.* 1999, Morbey & Ydenberg 2001). Socially dominant and larger individuals with greater fat stores are also more likely to initiate or continue migration with fewer or shorter stopovers than are birds in poorer physical condition (Sandberg & Moore 1996, Sandberg 2003).

The complexity of movements by Snowy Owls travelling between their breeding and non-breeding range led us to define several terms. The summer range (i.e. breeding range; Holt *et al.* 2020) was the area north of the treeline where Snowy Owls are confirmed breeders (see the grey-shaded area in Fig. 1). The consistent, directional movement northward from the wintering area (i.e. non-breeding) to the boundary of the summer range was called migration or migratory movement. Within the summer range, movements (often less directional and more nomadic) were called summer range movement which ended at a 'summer

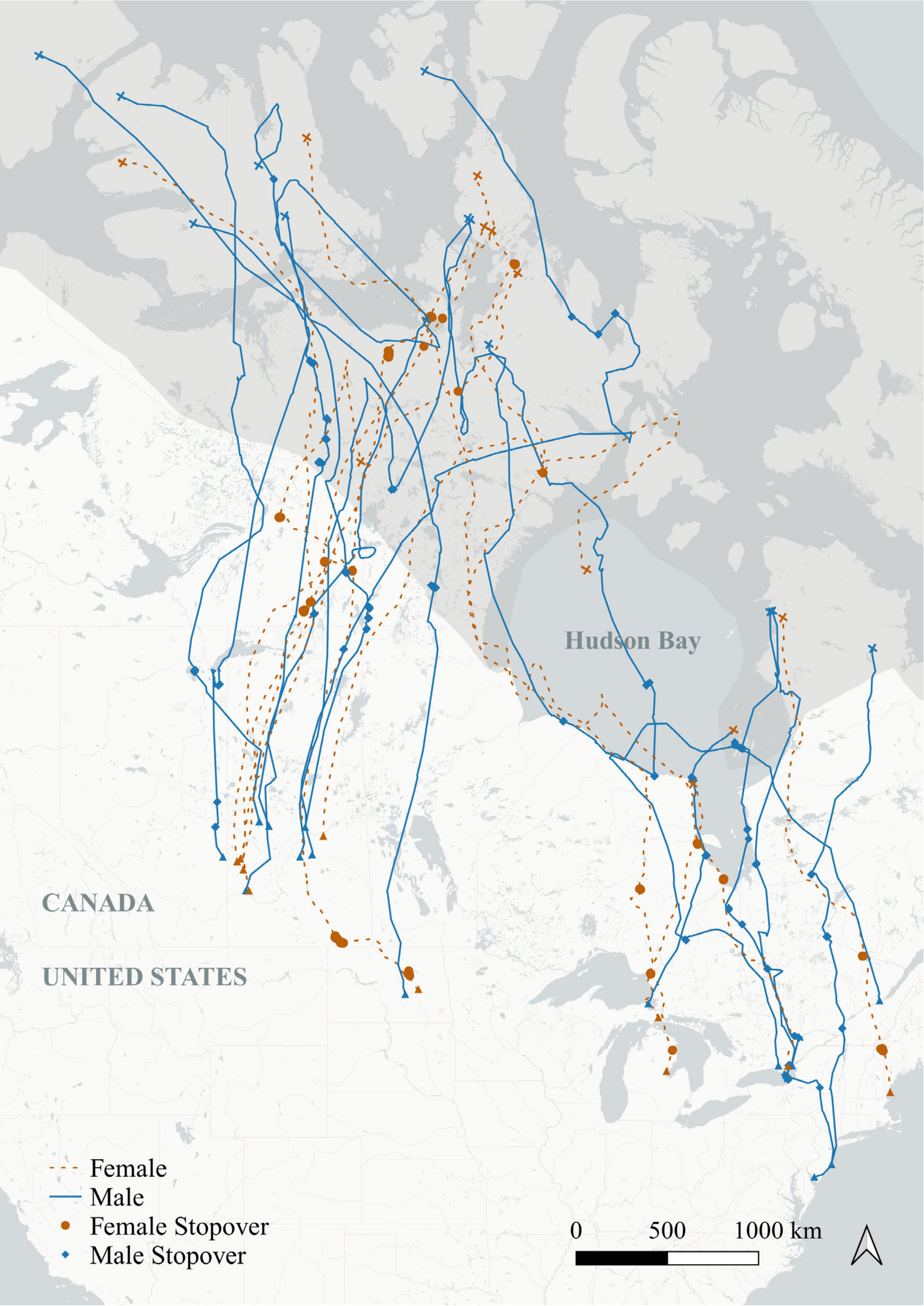

Figure 1. Migration and summer range movements of 24 Snowy Owls ($n = 19$ adults and $n = 5$ immatures) equipped with GPS-GSM transmitters in the USA and Canada in 2014–2018. Dashed lines represent females ($n = 10$; age classes pooled) and solid lines represent males ($n = 14$; age classes pooled). Stopovers, where an individual travelled < 17 km in at least 48 h, are displayed as circles (female) and diamonds (male) along each owl's migratory route. Arrows represent departure from wintering areas (i.e. start of migration) and crosses represent summer settlement sites. The shaded grey area in the north outlines the summer range (i.e. breeding range) in North America

settlement site' where owls either nested or resided during the summer months. Stopovers could occur anywhere along this route. Those occurring anywhere south of the summer range were called 'migration stopovers' and probably had the function of resting and refuelling. Stops within the summer range were called 'summer stopovers' and may have had the additional function of prospecting prey density, although we could not distinguish the function(s) of these stopovers. The entire journey travelled from wintering sites to summer settlement sites (i.e. migratory movements and summer range movements) was referred to as spring migration.

In this study, we examined the spring migration and stopovers of Snowy Owls using GPS-GSM tracking data comparing phenology and patterns among age and sex classes. If social dominance, as described above, and age influences movement, we predict that adults will depart the winter area earlier and will enter the summer range earlier than immatures because immatures will be in worse condition, and will have more migratory stopovers to refuel along the way and migrate more slowly than adults. In addition, because immatures do not breed in their first year, and may have lower body condition and be less experienced in assessing prey abundance (i.e. prospecting), they will also have more stopovers within the summer range compared with adults before settling. Finally, if the body size hypothesis influences migration phenology in Snowy Owls, then females should arrive earlier at their summer settlement sites than males.

METHODS

Capture and GPS-GSM

We trapped and equipped Snowy Owls with GPS-GSM transmitters in November–February from 2014 to 2018 in the USA and Canada. For the present analyses, we selected 1 year of data per individual (i.e. no repeated samples) with complete spring migration data from a larger dataset of Snowy Owls equipped with GPS-GSM transmitters. Owls were trapped using lure animals in either bal-chatri traps or bow nets (Bloom *et al.* 2007). We used plumage characteristics to assess sex and age for each individual (Seidensticker *et al.* 2011, Solheim 2012). Age classes were defined as immatures (< 12 months old) or adults (> 12 months old). We affixed to each owl a ~ 40-g (1.5–3% of the bird's total body mass) solar-powered GPS-GSM wildlife telemetry transmitter (Cellular Tracking Technologies, Rio Grande, NJ, USA; or Ecotone Telemetry, Gdynia, Poland), fitted with a backpack harness using low-friction Teflon ribbon (Steenhof *et al.* 2006). Transmitters recorded GPS locations (± 3 m) at various intervals during the year (i.e. 30–60 min for owls tagged in the USA and 6 h for owls tagged in Canada) and downloaded data via the GSM cellular phone network (i.e. daily or weekly depending on whether birds were south of cell tower range). We subsampled these data every 6 h so that there were data recordings with similar time intervals for all individuals to ensure uniform accuracy during the migratory period. Each GPS-GSM unit transmitted data when within cellular range, recording latitude, longitude, date and time. Four owls were trapped in the Midwestern USA, three near Lake Ontario, three along the mid-Atlantic coast, two in the New England region of the USA and 12 in Saskatchewan, Canada.

Data collection and analyses

We defined the departure date from the wintering area as the first point of consistent northern movement that occurred for more than 3 days after 1 March (Robillard *et al.* 2018). Following Therrien *et al.* (2012), birds were considered to reach their summer settlement site when they were stationary within a home-range of < 43 km^2 for 2 weeks, and therefore the first point when they entered the home-range was considered the arrival date (i.e. end of summer range movements). Some owls displayed nomadic behaviour and did not settle within a home-range (i.e. may have been continuously prospecting throughout the summer), and therefore we defined the arrival date as the first date when they did not subsequently move > 140 km from that point in 2 weeks (i.e. subsequent movement is < 20 km/day from the end point). We focused on movements within the first 2 weeks of entering the summer settlement site because some breeders may subsequently fail and then resume wide-ranging summer movements.

Stopovers were classified as a period during which an individual travelled < 17 km (half the average minimum daily distance travelled; $n = 24$) for at least 48 h, with no continuous northern movement, and excluding the 48 h before the arrival date on the summer settlement. To examine the robustness of the 17-km cut-off, we fitted a two-process Poisson distribution to the daily distance travelled, under the assumption that the short-distance process would represent stopovers and the long-distance process would represent directional movement (i.e. migration; Sibly *et al.* 1990). The intersection of the two processes can be considered the cut-off between directional movements and stopovers (Supporting Information Fig. S1). Stopover sites were identified using the calculated daily distance travelled by each Snowy Owl as well as using their mapped trajectory to exclude sections where there was short (< 17 km in 48 h or more) but continuous movement in a northern direction. We used QGIS 3.8.3 (QGIS Development Team 2009) with GRASS 7.6.1 (2009) to examine the trajectory of all the Snowy Owls for each period where they travelled < 17 km in 48 h to ensure that owls were stationary during this time.

We calculated the average daily distance travelled (total distance travelled divided by the number of days migrating) for each individual and grouped them into weekly periods, classified as 7-day periods starting from the departure date from the wintering area. These distances were separated into the migratory period (i.e. prior to arrival in summer range) and distances travelled in the summer range. We also calculated the average departure and arrival dates for each age and sex class. We mapped all migratory paths and stopovers in QGIS and used Geospatial Modeling Environment 0.7.4 (Beyer 2012) and R 3.5.2 (R Core Team 2018) to calculate the total distance travelled. Finally, we used Google Earth to classify stopover points (using the centroid of all locations within each stopover), and two random, paired points from the entire track within either 50 or 500 km of the stopover, as water body (marine or freshwater), open landscape (usually prairie or tundra) or forest. Stopover centroids that fell within 500 m of shorelines of oceans and lakes were considered part of water bodies. The 50-km scale was chosen to represent the stopover scale as being roughly the diameter of a stopover circle and the 500-km scale was chosen to represent the migration scale as being approximately the average distance between stopovers. We only considered lakes > 1 km. To examine the use of waterbodies, we provided anecdotal information on the timing of stopovers relative to ice breakup. Ice breakup timing was obtained from the Canadian Ice Service (CIS 2020). The absence of systematic data on ice breakup across the Canadian North prevented us from systematically examining the relationship between ice breakup and stopovers.

Statistical analyses

To compare the number of stopovers and the time spent at each stopover site (response variables) between adult and immature birds (predictor variables), we used a generalized linear model (GLM). We used separate GLMs to examine departure and arrival date of spring migration (response variables) between sexes (predictor variables) and to compare duration of spring migration and daily distance travelled (response variables) between sex and age classes (predictor variables). We performed a mixed linear model fit by REML with the lme4 and lmerTest packages in R 3.5.2 as well as a *t*-test using Satterthwaite's method to calculate the probability of a stopover changing throughout migration. We used one-tailed tests to compare immatures with adults, as we had strong *a priori* expectation that immatures would travel slower and arrive later than adults, but we used two-tailed tests for other comparisons because we had no strong *a priori* expectations. We used a Fisher exact test to compare stopover habitat to paired non-stopover habitat. Values reported in the results are means ± standard error, and an α level of 0.05 was used for all statistical tests.

RESULTS

We tracked 24 Snowy Owls, 19 adults (11 males, eight females) and five immatures (three males, two females), from their wintering areas in the USA and Canada to their summer settlement sites in the Canadian Arctic (Fig. 1). Overall, owls departed from wintering areas on $\bar{x} = 10$ April ($n = 24$) and arrived at their summer settlement sites on $\bar{x} = 28$ May ($n = 24$). The average distance travelled (mean ± se) during migration (i.e. including both migratory and summer range movements) was 2804 ± 787 km and the average duration was 47 ± 17 days, including time spent and distance travelled at stopover sites. Several individuals followed landscape features, especially shorelines, and flew towards areas where spring melt was occurring, such as the mouth of Lake Ontario and the Belcher Island polynyas in Hudson Bay

(Fig. 1). Waterfowl concentrate in these areas, such as at the Belcher Islands, where immense concentrations of waterfowl are hunted by owls in spring when the ice is first breaking up (Gilchrist & Robertson 2000). Northeastern Lake Ontario is also known for large numbers of waterfowl during spring breakup (Schummer *et al.* 2008). Nonetheless, individual owls were dispersed across the various flyways, moving north at relatively similar longitudes to their winter departure points, and without evidence of common routes indicative of social migration (Fig. 1).

Departure and arrival dates

We found no difference in the departure date from wintering areas between adults and immatures ($F_{1,22} = 3.92$, $P = 0.06$); however, adults entered the summer range earlier ($F_{1,22} = 4.49$, $P = 0.0002$) and arrived at their summer settlement sites earlier ($F_{1,22} = 8.69$, $P = 0.007$; Fig. 2) compared with immatures. The sexes did not differ in departure date ($F_{1,22} = 0.002$, $P = 0.96$), entering the summer range ($F_{1,22} = -1.18$, $P = 0.25$) or arrival date at the summer settlement site ($F_{1,22} = 1.28$, $P = 0.26$; Fig. 2).

Duration and distance travelled

Adults travelled $\bar{x} =$ 2859 ± 143 km (n = 19), in $\bar{x} =$ 46 ± 3 days, with an average daily distance of 68.4 ± 5.9 km/day. Immatures travelled $\bar{x}$ = 2593 ± 676 km (n = 5) and took $\bar{x}$ = 52 ± 10 days to migrate with an average daily distance of 49.2 ± 7.7 km/day. There was no difference between adults and immatures in daily distance travelled ($F_{1,22} = 3.28$, $P = 0.083$) or in the total distance travelled ($F_{1,22} = 0.23$, $P = 0.63$). Males travelled 2868 ± 201 km (n = 14) and spent 49 ± 4 days migrating with an average daily distance of 63.9 ± 7.0 km/day. Females travelled 2714 ± 299 km (n = 10) for 44 ± 5 days before reaching their summer settlement sites, with an average daily distance travelled of 65.2 ± 7.14 km/day. Overall, there was no significant difference between males and females in total distance travelled ($F_{1,22} = 0.03$,

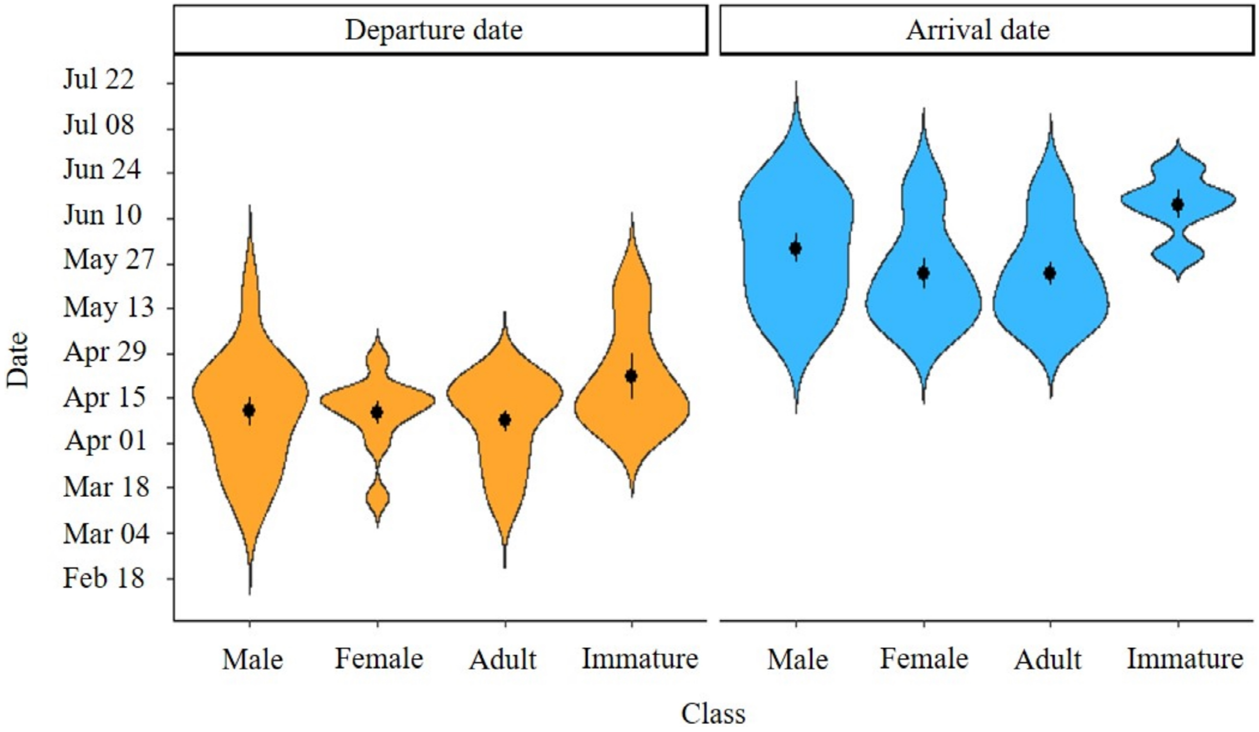

Figure 2. Departure dates from wintering areas and arrival dates at summer settlement sites of Snowy Owls tracked with GPS-GSM in the USA and Canada in 2014–2018. Dots and vertical lines inside violin plots represent averages with standard error. Sex and age classes are pooled: males (n = 14), females (n = 10), adults (n = 19) and immatures (n = 5)

$P = 0.86$) or daily distance travelled ($F_{1,22} = 0.44$, $P = 0.51$).

Stopovers

A two-process Poisson model fit the data better than a one-process model with the two models intersecting at 18.2 km (ΔAIC = 82.0; Fig. S1). South of the summer range, the two models intersected at 17.8 km. Within summer range they intersected at 24.3 km. Adults ($n = 19$) had similar numbers of stopovers (2.5 ± 1.7 stopovers, mean duration: 5.1 ± 3.4 days) compared with immatures (2.2 ± 0.8 stopovers, 6.6 ± 3.2 days, $n = 5$; $F_{1,22} = 0.21$, $P = 0.65$) and a similar duration of stopovers ($F_{1,22} = 0.76$, $P = 0.39$). Males had a similar number of stopovers (2.8 ± 1.7; $n = 14$) compared with females (2.0 ± 1.3; $n = 10$) ($F_{1,22} = 1.69$, $P = 0.20$) and there was no difference in the duration of stopovers between males and females (i.e. males: 5.5 ± 3.5 days, females: 5.2 ± 3.3 days; $F_{1,22} = 0.62$, $P = 0.43$). The probability of a stopover occurring at the beginning of migration was higher compared with at the middle or end ($P = 0.006$, $n = 24$; Fig. 3) and greater outside than within the summer range ($P = 0.001$, $n = 24$). Of the 61 stopovers, only 19 occurred within the summer range (Fig. 1). South of the summer range, 9% of stopovers were in forest, 73% on waterbodies (79% freshwater, 21% saltwater) and 18% in open habitats. Compared with non-stopover habitat, waterbodies were selected (500 km: $P = 0.002$; 50 km: $P = 0.01$) and forests were avoided ($P = 0.006$). Within the summer range, 72% of stopovers were on waterbodies (28% freshwater, 71% saltwater) and 28% in open habitats. Waterbodies ranged from 1 to 900 km^2 in size, averaging 86 km^2 (median = 25 km^2). In some cases, stopovers on waterbodies coincided with ice breakup. For example, one owl stopped at Amherst Island while Lake Ontario was breaking up (30 March–13 April 2015) and subsequently stopped at the Belcher Islands in Hudson Bay (16–31 May 2015) as the local polynya was enlarging with spring melt. Likewise, two other individuals in eastern North America stopped near Lake Superior and Lake Saint-Jean (Québec) in late April and May during ice break-up. In contrast, two owls migrating from the central prairies stopped in March and April at lakes that were still completely frozen over.

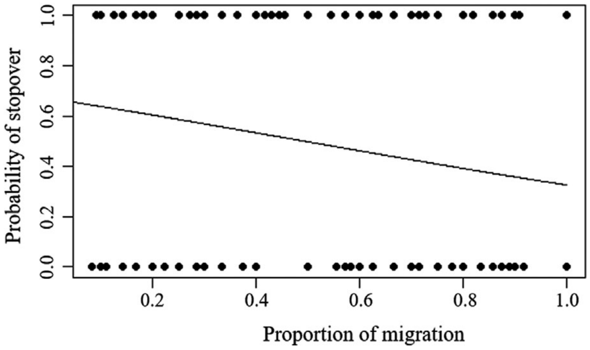

Figure 3. Probability of a stopover occurring at the start, middle or end of spring migration for Snowy Owls ($n = 24$) in the USA and Canada in 2014–2018

DISCUSSION

We tracked the migratory and summer range movements from Snowy Owls wintering near the southern limit of their North American range. Our method for separating stopovers from directed movements, based on the bout-ending criterion of Sibly *et al.* (1990), provides a simpler way to categorize these behaviours during migration compared with previous state-space models with a hidden Markov process (e.g. Therrien *et al.* 2015). The strong fit to a two-process model implied that movements in Snowy Owls were not purely Brownian but could be grouped effectively. Our cut-off of 17 km, based on half the daily distance travelled, is quite similar to the value derived from the more complex modelling technique (18 km; Therrien *et al.* 2015). Indeed, a recent study showed that a simple spatial threshold was often more efficient at predicting migration phenology than more complex models (Soriano-Redondo *et al.* 2020).

Age and sex effects on spring migration

Previous studies have found that social dominance influences the latitudinal distribution of Snowy Owls, with females wintering further north than males (Kerlinger & Lein 1986, Robillard *et al.* 2016); we therefore expected females to have a shorter migration with fewer stopovers. However, despite differences in social dominance and body size between the sexes, males and females did not differ in departure time, number of stopovers or time spent at each stopover. Consistent with our *a priori* hypothesis and with other studies of avian migration (e.g. Yosef *et al.* 2003), adults entered the summer range and arrived earlier on their summer settlement sites compared with immatures. There are probably two different dynamics at work between breeding adults and immatures. Although our sample size of immatures is small ($n = 5$), it is likely that the after-hatch-year owls will not breed during their first summer and do not need to arrive early at summer settlement sites (Gorney & Yom-Tov 1994). Whereas adults have limited time to locate a potential breeding site with high lemming density, immatures do not experience such pressure and are not time-restricted.

The body size hypothesis suggests that females would initiate migration first and arrive on the summer range first due to their larger size and increased tolerance to colder weather (Cristol *et al.* 1999). However, our data do not indicate that female Snowy Owls arrived earlier than males. Perhaps competition for high-quality territories does not drive mating success for female Snowy Owls, and individual traits such as age or experience may be more important drivers of mating success. Furthermore, there is still snow on the ground when Snowy Owls arrive at their summer settlement sites (Taylor 2012), which may reduce their ability to capture prey (Robillard *et al.* 2018), as thick and dense snow cover creates a refuge for lemmings and other small mammals (Therrien *et al.* 2015, Poirier *et al.* 2019). Thus, it may not benefit females to arrive too early if access to resources is limited by persistent snow cover.

Location and function of stopovers

We hypothesized that adult Snowy Owls would start searching and sampling suitable habitats towards the end of their migration as they move across the summer range (Jonzén *et al.* 2011), with more summer stopovers occurring at high latitudes. However, stopovers tended to occur in the first portion of migration (between 43° and 63° latitudes) compared with the end. Stopovers south of the summer range are primarily used by migrating birds to rest and refuel when fat stores are low, and often occur at the beginning of migration (Newton 2006, 2010). Thus, we assumed that early stopovers in migrating Snowy Owls are primarily for fuelling, or to wait for snow melt to progress prior to travelling farther north. The distance between stopovers (e.g. average distance between the first third of stopovers $\bar{x} = 320 \pm 180$ km; Andrea Brown unpubl. data) suggests that Snowy Owls migrating in this region fly in short bouts during the early part of migration. Subsequently, perhaps in response to physiological or environmental cues, they travel with fewer and shorter stops until they reach their summer settlement sites. If Snowy Owls are energy-constrained and are depleting fat stores during migration, refuelling stopovers should occur throughout the migratory period. Counter to this hypothesis, the declining frequency of stopovers along their migration suggests the birds are not depleting energy reserves. It is not known to what extent Snowy Owls take advantage of wind currents while flying long distances, but relatively large birds can save energy by soaring and gliding rather than flapping (Newton 2010, Bildstein 2018), which may help conserve energy.

Most stopovers above and below the summer range occurred on or near waterbodies (presumably largely covered in ice). Such waterbodies are not suitable nesting habitat, so these stopovers were probably not used for prospecting but rather for resting or refuelling. Waterbodies that are breaking up during stopovers have the potential to concentrate waterfowl prey which could use gaps in the ice as they migrate north, a habitat preferred by owls wintering in the Arctic (Therrien *et al.* 2011). Stopovers on waterbodies that were still frozen may provide good visibility when scanning for prey and good camouflage against the still-white ice. Recent work showed that Snowy Owls closely followed the receding snow line (Curk *et al.* 2020) and we suggest the presence of ice on lakes and oceans may be an attractive feature correlated with the timing of snowmelt that may persist on the landscape a few weeks after snow cover has disappeared.

The infrequent use of stopovers in the summer range by adults suggests that the owls do not need long stationary periods to detect lemming hotspots when looking for a place to nest or settle. The single owl that did have a series of summer stopovers had not stopped south of the summer range, and eventually bred on Victoria Island in the Arctic archipelago. Apparently, Snowy Owls can search for signs of lemmings during continuous and slower flights or by frequent short stops of < 48 h, which are indistinguishable in our data from 'movement'. Further research is necessary to determine exactly what cues are used by owls when deciding where to nest.

Future research on Snowy Owl migration should focus on how movements are linked across the entire annual cycle and how, and why, it may vary among years. Prey availability varies temporally and spatially on both the prairie wintering grounds (Chang & Wiebe 2018) and in the summer range (Robillard *et al.* 2016, Ehrich *et al.* 2020) and may trigger large-scale nomadic movements (Therrien *et al.* 2014, Robillard *et al.* 2018). Moreover, Snowy Owl irruptions occur every 3–5 years, causing increased densities of immature owls in southern wintering areas (Robillard *et al.* 2016). During irruption years, there is an increased abundance of prey on the breeding grounds, which leads to a larger population size and, as a result, more Snowy Owls move further south away from their summer grounds when the Arctic landscape presumably can no longer support their numbers (Robillard *et al.* 2016, Santonja *et al.* 2019). Furthermore, additional analyses should include separating the various functions of stopovers (i.e. refuelling and resting stopovers vs. prospecting stopovers). We suspect that stopovers in the winter range would be solely for the purpose of resting and refuelling, whereas in the potential breeding area, the function of a stopover could be for resting, refuelling or prospecting. We hope that our simplified statistical approach used to parse stopovers from periods of travel will be applied to other species, especially those with differential migration or complex nomadic movements to examine the location, frequency and function of any stopovers. Conservation and management efforts can use such information to identify key areas along the migration route which are important for Snowy Owls and other Arctic breeding species.

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AUTHOR CONTRIBUTION

Andrea Brown: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing-original draft (lead); Writing-review & editing (lead). **Rebecca A McCabe:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Methodology (supporting); Supervision (supporting); Writing-original draft (lead); Writing-review & editing (lead). **JF Therrien:** Formal analysis (supporting); Methodology (supporting); Writing-review & editing (equal). **Karen Wiebe:** Funding acquisition (supporting); Methodology (supporting); Writing-review & editing (equal). **Scott Weidensaul:** Funding acquisition (supporting); Methodology (supporting); Writing-review & editing (supporting). **David Brinker:** Funding acquisition (supporting). **Gilles Gauthier:** Methodology (supporting); Writing-review & editing (equal). **Kyle Elliott:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (supporting); Methodology (supporting); Supervision (lead); Writing-original draft (supporting); Writing-review & editing (supporting).

Data Availability Statement

The data used in this study are available on Movebank (movebank.org, study names 'Project SNOWstorm: Snowy Owl Movements' and 'Snowy Owl from Saskatchewan [Wiebe]').

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Logarithm (base 10) of frequency decreases with daily distance travelled by Snowy Owls ($n = 24$) during spring migration in the USA and Canada in 2014–2018. A two-process Poisson model is shown, whereby log frequency is the sum of two Poisson models: a short-distance model (stopover; light grey dotted line) and long-distance model (migration; black dotted line).