

Wiebe, K. L., M. T. Bidwell, and R. A. McCabe. 2023. Snowy Owls in central North America have regular migration and high philopatry to wintering sites though not always to home ranges. *Avian Conservation and Ecology* 18(2):14. <https://doi.org/10.5751/ACE-02528-180214>
Copyright © 2023 by the author(s). Published here under license by the Resilience Alliance. Open Access. CC-BY 4.0

Research Paper

Snowy Owls in central North America have regular migration and high philopatry to wintering sites though not always to home ranges

Karen L. Wiebe¹ , Mark T. Bidwell²  and Rebecca A. McCabe³ 

¹University of Saskatchewan, ²Environment and Climate Change Canada, ³Acopian Center for Conservation Learning, Hawk Mountain Sanctuary

ABSTRACT. Understanding the threats faced by a bird species requires a knowledge of their movements throughout the annual cycle and, for migratory species, the degree of connectivity between breeding and wintering sites. We studied the philopatry of Snowy Owls (*Bubo scandiacus*) tagged in central North America to their wintering sites on the Canadian prairies. The tracking of 16 owls over a period spanning six winters revealed consistent and predictable north-south migration trajectories, in contrast to populations farther to the west and east. Individuals were strongly philopatric to the central prairie region, but at a finer spatial scale, winter home ranges did not always overlap between successive years. Both sexes showed periods of nomadic searching for prey over a similar spatial scale, but males tended to settle closer to previous home ranges on average (88 km) than females (149 km). We hypothesize that the socially dominant females are better able to monopolize the spatially unpredictable hotspots of small mammal prey whereas males rely more on familiarity with a previous home range when settling. The population of Snowy Owls in central North America thus shows greater connectivity to wintering sites than do Snowy Owls documented elsewhere, probably related to the relatively high abundance and predictability of small mammal prey on the prairies. Maintaining prairie habitat on a large spatial scale that supports small rodents will be crucial to maintaining populations of Snowy Owls in the central part of the continent.

Les Harfangs des neiges du centre de l'Amérique du Nord ont une migration régulière et une philopatrie élevée aux sites d'hivernage, mais pas toujours aux domaines vitaux

RÉSUMÉ. Pour comprendre les menaces qui pèsent sur une espèce d'oiseau, il faut connaître ses déplacements tout au long du cycle annuel et, pour les espèces migratrices, le degré de connectivité entre les sites de nidification et d'hivernage. Nous avons étudié la philopatrie de Harfangs des neiges (*Bubo scandiacus*) marqués dans le centre de l'Amérique du Nord vers leurs sites d'hivernage dans les Prairies canadiennes. Le suivi de 16 harfangs sur une période de six hivers a révélé des trajectoires de migration nord-sud régulières et prévisibles, contrairement aux populations situées plus à l'ouest et à l'est. Les individus étaient très philopatriques à la région centrale des prairies, mais à une échelle spatiale plus fine, les domaines vitaux hivernaux ne se chevauchaient pas toujours d'une année à l'autre. Les deux sexes ont eu des périodes de recherche nomade de proies sur une échelle spatiale similaire, mais en général, les mâles ont eu tendance à s'installer plus près de leurs domaines vitaux antérieurs (88 km) que les femelles (149 km). Nous émettons l'hypothèse que les femelles, dominantes socialement, sont plus aptes à monopoliser les sites d'abondance spatialement imprévisibles de proies de petits mammifères, tandis que les mâles comptent davantage sur la familiarité avec un domaine vital antérieur lorsqu'ils s'installent. La population de Harfangs des neiges du centre de l'Amérique du Nord présente donc une plus grande connectivité avec les sites d'hivernage que les harfangs examinés ailleurs, ce qui s'explique probablement par l'abondance relativement élevée et à la prévisibilité des petits mammifères dans les prairies. Le maintien de l'habitat de prairies, à une échelle spatiale suffisamment grande pour abriter des petits rongeurs, sera crucial pour le maintien des populations de Harfangs des neiges dans la partie centrale du continent.

Key Words: *Bubo scandiacus*; movements; nomadism; overwintering; philopatry; territory

INTRODUCTION

Regular migration, a seasonal, repeatable, and predictable movement, occurs in many bird species and is associated with strong connectivity between established breeding and wintering sites (Newton 2010). Long-distance migrants often show lifelong philopatry to a wintering site or small territory where they are resident after fall migration (Robertson and Cooke 1999, Remsen 2001, Holmes and Sherry 1992) but several species move unpredictably, or "nomadically" during the winter season without settling (Teitelbaum and Mueller 2019). Nomadism in the non-breeding season appears to be driven by low predictability of food sources in time or space (Andersson 1980, Newton 2006, Lindberg et al. 2007). For example, species like Emberizidae finches, that

depend on conifer seeds or raptors that rely on mobile prey, are often characterized by extensive movements in the non-breeding season that result in low philopatry to wintering areas (Förschler et al. 2006, Benkman and Young 2020, Dawson 2020).

Even within species characterized by long-distance movements in winter, there may be individual variation in the pattern of movement and settlement that is little understood. A few recent studies have focused on how factors such as age, sex, body condition, or environmental conditions may affect winter residency within or between populations. Opper et al. (2009) found that intraspecific variation in the duration of winter residency for King Eiders (*Somateria spectabilis*) was influenced more by traits

of the individual bird than by the coverage of sea ice in its environment. In wintering Eurasian Siskins (*Carduelis spinus*), resident individuals which settled at rich food patches were socially dominant and in better body condition compared to transients with nomadic behavior (Senar et al. 1992).

Here, our goal was to study the degree of philopatry to wintering range in the Snowy Owl (*Bubo scandiacus*), a top predator which breeds in the circumpolar Arctic and which is designated as vulnerable by the IUCN (IUCN 2020). Snowy Owls are well known for long-distance movements during their annual cycle (Potapov and Sale 2012, Brown et al. 2021). In summer, they specialize on lemming prey and travel widely in the high Arctic to search for hotspots of these rodents which vary cyclically on the tundra landscape (Holt et al. 2015). As a result, Snowy Owls show very low breeding philopatry (Fuller et al. 2003, Therrien et al. 2014). In the eastern Arctic of North America, the average breeding dispersal distance for female Snowy Owls was 710 km which was farther than between their wintering locations (Robillard et al. 2018). Because effective conservation strategies for migratory species should incorporate information about the regularity of habitat use during both the summer and winter periods (Norris et al. 2004, Webster and Marra 2005), we were interested in the degree to which individual Snowy Owls returned to wintering sites on the Canadian prairies.

Many aspects of what directs large scale movements of Snowy Owls in winter remain a mystery, but several studies using satellite and GPS transmitters are starting to fill in the picture. Most (74%) of breeding female Snowy Owls tagged on Bylot Island, Nunavut, in the eastern Canadian Arctic remained in the Arctic during winter, moving along the marine coastlines and around polynyas in the sea ice while preying mainly on seabirds. The average distance between wintering areas of these 21 female owls in the east was 389 km (Robillard et al. 2018). In contrast, eight female Snowy Owls that were tagged in the far western Arctic of the Yukon (Doyle et al. 2017) and Alaska (Fuller et al. 2003), moved inland during winter to settle in Arctic terrestrial montane boreal biomes. In Fennoscandia, Snowy Owls tagged while breeding in northern Norway remained in the Arctic during winter, often migrating eastwards to Russia, while foraging both out on the sea ice but also moving inland to feed on Willow Ptarmigan (*Lagopus lagopus*; Øien et al. 2018). Hence, different populations of Snowy Owls across the circumpolar Arctic migrate in different directions, traverse variable distances, and overwinter in different habitat types with different types of prey.

The highest density of Snowy Owls overwintering regularly south of the Arctic treeline is on the prairie grasslands of central North America (Kerlinger et al. 1985), but aside from a few band recoveries, information about winter philopatry to this region is lacking. Here, we assessed philopatry at three spatial scales. At the largest (coarsest) continental scale, we predicted that Snowy Owls wintering on the prairies of central North America would be more philopatric than owls wintering along coastlines in eastern North America. This is because the main prey on the prairies, rodents such as deer mice (*Peromyscus maniculatus*) or voles in the genus *Microtus*, characteristic of cropland and grazed pastures (Boxall and Lein 1982), are relatively stable compared to lemmings in the Arctic. At temperate latitudes, most rodents

do not show cyclic "boom-and-bust" cycles as in the Arctic (Hansson and Henttonen 1985) and deer mice rarely cycle, although local densities may vary annually (Galindo and Krebs 1987, Sullivan et al. 2004, Chang and Wiebe 2018a). In contrast, owls wintering along eastern coastlines often subsist on waterfowl or large seabirds; these are patchy prey which are mobile and sporadic in occurrence according to the location of polynyas in the sea ice (Gilchrist and Robertson 2000, Robertson and Gilchrist 2003).

At a medium (regional) spatial scale, within the central prairie region, individuals vary in the degree to which they settle on a stable home range versus move nomadically over hundreds of kilometers during the winter period (Chang and Wiebe 2018b, McCabe et al. 2021). Therefore, we were interested in whether the traveling path of a Snowy Owl during the overwintering winter period overlapped from one year to the next. Finally, at the smallest spatial scale (local), we were interested in whether areas that the owls settled in for a period of time, i.e., home ranges, overlapped between consecutive winters. At all scales, we were interested in behavioral differences between the sexes because previous studies have either followed only females or have not analyzed sexual differences in philopatry. Snowy owls have reversed sexual dimorphism, with males weighing 25–30% less than females on the Canadian prairies (Kerlinger and Lein 1988, Chang and Wiebe 2016). Because the larger females are socially dominant to males (Boxall and Lein 1982), we predicted that females would be more faithful to familiar wintering ranges than males. We have addressed factors affecting home range size elsewhere (Chang and Wiebe 2018b), so we focus here on the extent of spatial overlap of home ranges and of movement tracks of owls between successive winters.

METHODS

Study site and field methods

On the prairies of south-central Saskatchewan, Snowy Owls begin to arrive from their breeding grounds in the Arctic around mid-November and many start to settle on winter home ranges in December. Most migrate north by early April (Brown et al. 2021), depending somewhat on the rate of snowmelt (Curk et al. 2020). Although densities of owls vary somewhat from year to year, the prairie population is not considered "irruptive" because relatively high numbers are present every winter (Kerlinger et al. 1985). The landscape is flat, or gently rolling, with less than 20% of the original short- and mixed-grass native prairie remaining (Samson and Knopf 1994). Today, agricultural lands predominate and include pasture (rangeland), as well as cropland growing mainly canola, pulses, and grains. Agricultural land is gridded in square miles forming mosaic-like rectangular blocks of different species of crop cover usually between 0.64–2.56 km². Winters are cold in south-central Saskatchewan, with frequent sustained temperatures below - 20 °C and some days as low as - 40 °C. Snow depth is variable but may persist from late October to early April. The main prey of Snowy Owls wintering in the prairies is small rodents (76–91% of individual items, Boxall and Lein 1982); 90–99% of items (Detienne et al. 2008) but alternate prey such as Grey Partridge (*Perdix perdix*) and Rock Dove (*Columba livia*) are also hunted.

To monitor the movements of owls, we trapped adults (after second year [ASY]) starting in December, using bal-chattris or a remotely-triggered bow nets, in central Saskatchewan between 2015–2017 and in 2021. Owls were trapped roughly as far north as Saskatoon (52°7' N, 106° 40' W) and as far south as Kyle (50° 49' N, 108° 02' W). We deployed GPS/GSM transmitters (Ecotone Telemetry, model Saker H, 25 g) which recorded locations that were accurate to 20 m every 6 hours. The transmitters were attached using a harness of Teflon ribbon (0.25 inch tubular tape, Bally Ribbon Mills Inc., USA) so the units weighed < 3% of the owl's body mass. Survival analyses indicate no increased mortality by the use of such tags (Heggøy et al. 2017) or reduction in reproductive success (Therrien et al. 2012). Because the transmitters relied on cell phone towers, we could not determine the status (dead vs. alive) of any owl that remained in the high Arctic all winter. Of the 27 owls originally tagged, 16 returned to the prairies in at least one subsequent year, allowing us to calculate philopatry. Some owls returned for more than one successive year: two males and three females with three winters; one female with four winters; two males with five; and three males and one female with six winters. Thus, we had 56 owl-winters based on nine female and seven male owls.

Measures of philopatry

Because the timing of migration varied among individuals and years, we defined the winter period for each owl-winter by examining the individual's tracking data for the full annual cycle. An owl was said to have arrived on the wintering grounds the first time its flight path from the Arctic changed from a unidirectional southward trajectory and turned at a $\geq 90^\circ$ angle within the prairie biome. Similarly, its winter period ended when the flight path began to move in a unidirectional north trajectory out of the prairie biome.

During this winter period, we considered philopatry at three spatial scales: continental, regional, and local. At the continental scale, we considered philopatry during winter to the central prairie biome. At the regional scale, we characterized residency by estimating each owl's occurrence distribution (OD; Fleming et al. 2016) during the entire winter; ODs quantify where an animal may have traveled during the observation period given the data. Thus, an owl's OD included the area of any home range(s) plus the area of nomadic flight paths between them over the entire winter period. At the local scale, previous work showed that Snowy Owls in Saskatchewan often alternated between a period of residency on a local home range and a period of linear, nomadic movement before settling on a different local home range (Chang and Wiebe 2018b). Here, we defined periods of residency on local home ranges as when the owl remained in a restricted area, moving daily back and forth across a central point on the landscape for a time span of at least one week. This gave a minimum cluster of 28 GPS fixes (7 days of 4 fixes per day) and usually more (Appendix Table 1) to model home ranges.

Of the 16 owls that returned in at least one subsequent year and for which we could determine philopatry at the continental scale, 12 owls' transmitters provided data that were suitable for reliable estimation of home ranges or ODs at the local scale.

Statistical analysis

Traditional methods for calculating home ranges, maximum convex polygons, and kernel density estimates assume independent fixes but most GPS-tracking datasets are autocorrelated so such modeling techniques result in area estimates that are negatively biased (Noonan et al. 2019). Hence, we estimated home ranges by computing autocorrelated kernel density estimates (AKDE) which directly model the autocorrelation of the dataset, using the continuous-time movement modeling (ctmm) version 1.1.1 package (Fleming and Calabrese 2017) for Program R version 4.2.2 (R Core Team 2022). In each year it was monitored, an owl used ≥ 1 discrete home range (s) for a period of at least one week; for each of these we computed a suite of movement models and used the Akaike Information Criterion (AICc) to select the best-supported model, optimizing the smoothing bandwidth of the kernel density estimate based on the selected model (Fleming and Calabrese 2017). Our suite of movement models included the IID process, which is the model assumed by conventional range estimators in which both positions and velocities are uncorrelated; the OU process which models correlated positions but uncorrelated velocities; the OUF process with both correlated positions and velocities (Calabrese et al. 2021); and the OUF process which is a special case of OUF where the two autocorrelation timescales cannot be distinguished. We fit isotropic and anisotropic versions of these models, which correspond to circular and elliptical covariances respectively. Using the best-supported model for each home range, we created AKDEs and calculated their 95% contours (Appendix Table 1). For each owl, we estimated the percent overlap between its joint home ranges (consisting of ≥ 1 discrete home range) in year x with those in year $x + 1$. We also estimated the proximity of home range(s) in year x to any range(s) in year $x + 1$ by calculating the distance between centroids of the ranges. If the owl used more than one home range in a year such that there were multiple distance estimates to range(s) in the subsequent year, we averaged the distances.

For the ODs, we used a 99% CI to obtain an area (a probability distribution) that encompassed all the movement tracks of an owl during its overwintering period. These distributions used a Dynamic Brownian Bridge Movement model (Kranstauber et al. 2012) which provide a confidence region of area of usage based on the actual movement pathways. Such models provide more accurate estimates of space use than conventional kernel or minimum convex polygons which can severely overestimate the area of use of an animal with a complex movement track (Silva et al. 2020). We calculated percent overlap between these ODs between year x and year $x + 1$ for each owl-year using the coefficient of areal correspondence (Minnick 1964), by dividing the area of overlap of the two ODs (numerator) by their total summed areas (denominator; code in Appendix 2).

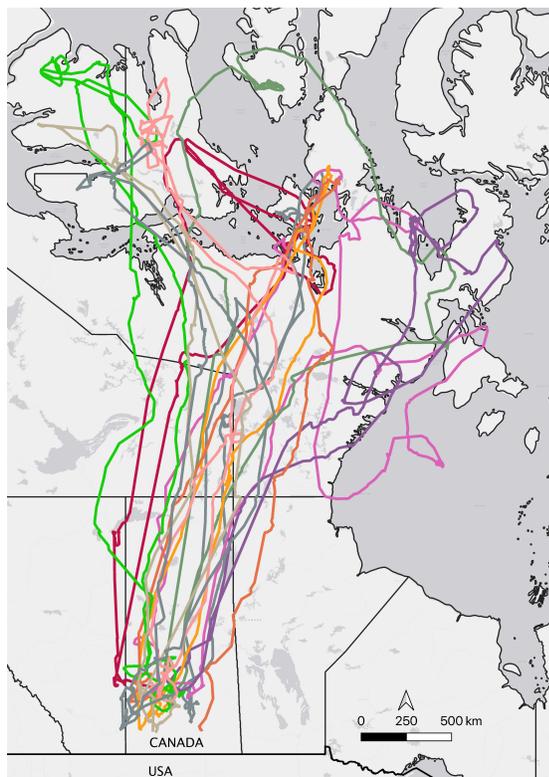
To quantify the extent that owls moved during the winter period, we calculated two variables. As a measure of the geographic space an owl covered during its winter travels we calculated the maximum linear distance ("span") between two GPS fixes. Because the tracks of owls sometimes looped back on themselves during the winter period, we also calculated the total distance flown by the owl along its flight path which included any short

movements while on home ranges and any flights between them. To test for an effect of sex on these two variables and on distances between the centroids of successive home ranges between years and the amount of overlap of ODs between years, we entered sex as a fixed factor in a Linear Mixed Model (LMM) with Owl ID as a random factor to account for individuals that provided more than one year of data. The frequency of each sex with overlapping home ranges vs. non-overlapping ranges was assessed with Chi-square test. LMMs and Chi-square tests were run in SPSS v. 28 with alpha set at 0.05. Means are reported with standard errors.

RESULTS

At a largest (continental) scale, all 16 owls (nine females and seven males) that were tagged in central Saskatchewan and which returned to winter south of the Arctic tree line (where the transmitters were detectable by cell phone towers) were philopatric to the central prairie region. Both males and females remained north of the United States border and did not drift east or west out of the provinces of Alberta or Saskatchewan (Fig. 1). A visual inspection of migration tracks for individual owls indicated greater philopatry to a wintering region than to a breeding region in the high Arctic (Fig. 2).

Fig. 1. Annual movements of adult Snowy Owls (*Bubo scandiacus*) to and from their wintering areas on the Canadian prairies showing linkage to the prairie biome within the population at the continental scale. To avoid clutter, only the first year of tracking an individual is depicted here, with different colors showing one year of movement for each of 12 owls.



The duration of wintering periods of owls ranged from 79 to 163 days (128 ± 3.5 , $n = 40$ owl-winters) and spanned the period from 1 November to 18 April. The maximum linear geographic span between fixes during these winter periods averaged 156.1 ± 20.3 km for the five females and 201.2 ± 17.1 km for the seven males; the longest span over the landscape was that of a male which roamed across 467 km during the winter of 2019–2020. There was extensive overlap between the sexes in the 95% confidence intervals around the maximum spans (LMM: $F_{1,6.45} = 1.43$, $P = 0.27$). The total flight paths of owls during winter averaged 1053 ± 81.7 km for males and 805.0 ± 79.1 km for females with the longest flight path recorded as 1931 km, for a male. The 95% confidence intervals for mean lengths of flight paths overlapped between the sexes (LMM: $F_{1,10.1} = 2.40$, $P = 0.15$).

Most (72.2%) of ODs overlapped somewhat between consecutive owl-winters ($n = 36$) but the proportion of overlap was rather small (Fig. 3). For males it averaged $6.34\% \pm 1.2$ and for females $4.25\% \pm 2.0$ and the amount of overlap was considerable for the 95% confidence intervals between the sexes (LMM: $F_{1,8.85} = 0.63$, $P = 0.44$).

Owls had between 1–4 home ranges during a winter period, settling for durations between 7–121 days within these areas (Fig. 4; Appendix 1). Home ranges averaged 162 ± 47 km² for males ($n = 76$ home ranges for seven males) and 94.3 ± 36 km² for females ($n = 39$ home ranges for five females). More males (6 of 7, 86%) than females (1 of 5, 20%) had some overlap of home ranges between successive winters (Chi-square test: $X^2 = 5.18$, $P = 0.023$). When overlap occurred, the proportion of the ranges that overlapped was 21% for the female and was also $21\% \pm 16$ (range 5–49%) for the six males. However, with only one female showing overlap, it was impossible to test for a difference between the sexes. At this finest spatial scale, the average distance between centroids of home ranges in one year and those in the following year was shorter for males (88 ± 14 km) than for females (149 ± 20 km; LMM: $F_{1,8.4} = 5.77$, $P = 0.041$). Thus, successive home ranges of males were closer to each other and were more likely to overlap than were those of females.

DISCUSSION

At the large continental scale, wintering Snowy Owls in central North America were highly philopatric to the central prairie region whereas at the smallest spatial scale, home ranges of an individual owl did not always overlap between successive years. Because all owls in our study were initially tagged as adults, we cannot rule out the possibility that yearlings are the age class which shows large-scale, cross-continental dispersal movements between their first and second winters. However, once an adult Snowy Owl winters on the prairies, it appears to return there in a regular, annual migration to the same biome. There were no annual gaps in our detection of individuals across time, suggesting that an owl which is migratory maintains that overwintering strategy through its lifetime; however, a larger sample is needed to determine whether individuals in central North America ever alternate between remaining in the high Arctic all year versus migrating southward. Philopatry to an overwintering latitude would be consistent with Therrien et al. (2011) and Robillard et al. (2018) who documented that only two of 21 female Snowy Owls tagged in the eastern Arctic switched to wintering on the prairies in the subsequent year.

Fig. 2. Example of migratory tracks of a female owl (left panel) and of a male (right panel) with six successive years of data showing strong winter philopatry at the continental scale to the central prairie region. Breeding philopatry in the high Arctic is comparably much weaker.

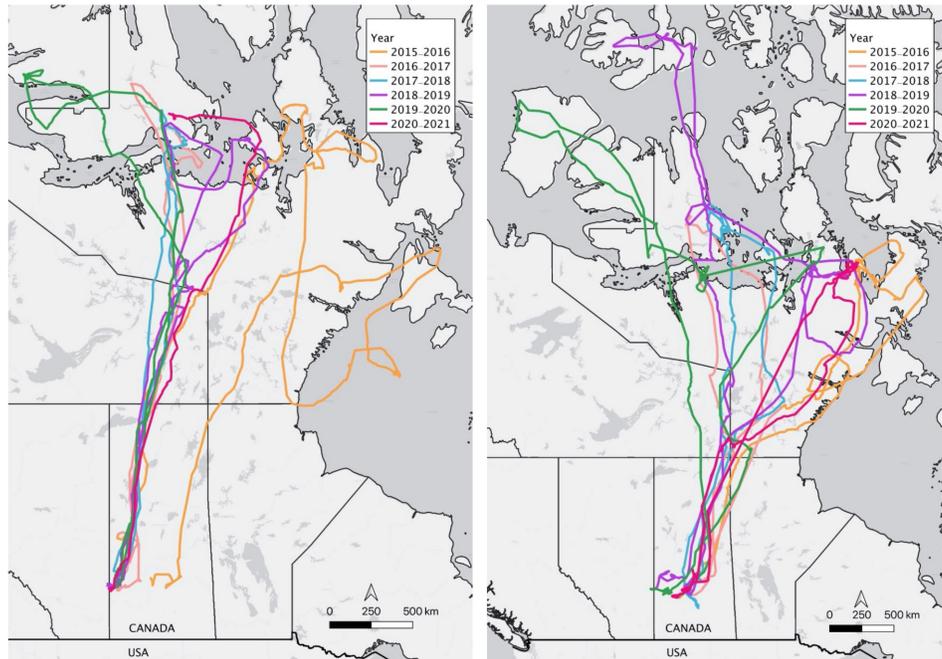
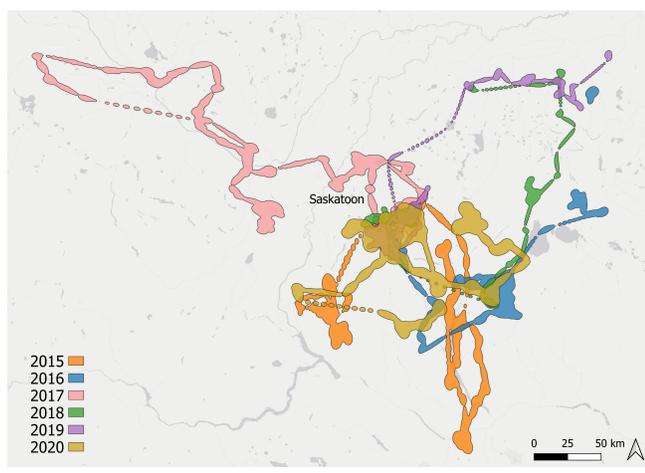


Fig. 3. Example of Occurrence Distributions of a male owl tracked during six consecutive winters in Saskatchewan.



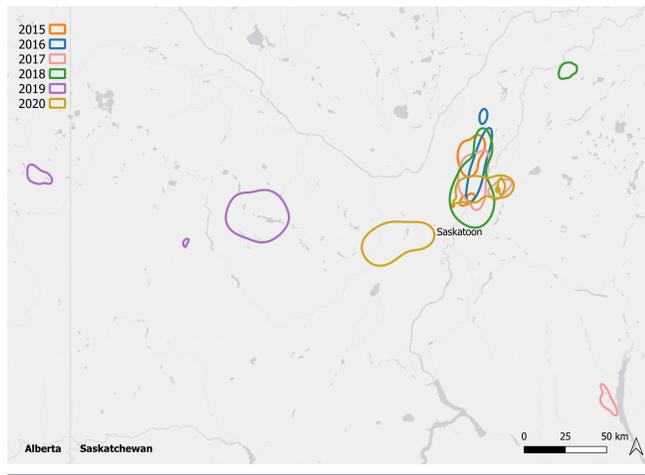
In eastern North America, female Snowy Owls were also consistent in the general habitat type they used between winters, most returning to either inland (terrestrial) biomes versus to marine coastlines (Robillard et al. 2018). At this large geographical scale, perhaps it is most profitable for an individual owl to return to the same overwintering biome in order to take advantage of learned hunting skills needed to specialize on a certain prey type (e.g., small mammals versus seabirds). Although Snowy Owls overwintering on the prairies in the current study were quite philopatric to a winter region, they showed much

greater breeding dispersal in the Arctic, consistent with other populations breeding to the east, in Nunavut (Therrien et al. 2014). The owls in Fennoscandia which move east and west within the Arctic during winter (Øien et al. 2018) probably also experience a similar type of biome each year.

After migrating to the central prairies, most male and female Snowy Owls alternated periods of nomadic wandering with periods of residency on one or more home ranges. We could not quantify prey abundance over this vast spatial scale, but it is reasonable to assume that such winter movements are linked to searching for prey hotspots on the landscape and that owls leave a home range when prey are depleted below a certain threshold. A previous study found that the distance moved between successive home ranges within a year did not differ between the sexes (Chang and Wiebe 2018b). Similarly, the results of the current study indicate that males and females covered a similar-sized spatial area and flew similar total distances while searching for prey during their winter periods. Although the movement tracks of an individual (the OD) usually crossed over a place where it had traveled the previous winter, the total movement path did not overlap closely between years. Thus, Snowy Owls did not follow a memorized or systematic traveling route during nomadic searches for prey on the prairie landscape. We are unaware of another bird species that alternates periods of nomadic wandering with residency on a defended home range during the non-breeding period.

Home ranges where owls settled often did not overlap between one year and the next. However, contrary to our prediction, males were more philopatric to previous areas of settlement than females. Namely, a greater proportion of males than females

Fig. 4. Example of home range polygons (95% CI) of a male owl tracked during six consecutive winters in Saskatchewan.



settled on a range that overlapped (at least partially) with one that they had used the previous winter and the average distance between the centroids of annual home ranges was shorter for males compared to females. Although small rodents on the prairies in winter do not show predictable cycles, population densities at a certain location can vary by a factor of 4 or 5 between successive years (Mihok et al. 1985, Chang and Wiebe 2018a). Thus, prey hotspots for owls on the prairies may shift on the landscape over distances of 100 km or more. Another reason why a home range at a certain location may not retain its quality for owls is that farmers on the prairie rotate most crop fields annually. For example, a particular area may lose its attractiveness for owls if much of the preferred hunting habitat, legume fields, are converted to canola fields which tend to be avoided by Snowy Owls (Chang and Wiebe 2018a).

Settlement patterns at the fine spatial scale of home ranges are consistent with the hypothesis that females, which are socially dominant to males (Kerlinger and Lein 1986), are more likely to monopolize prey hotspots that shift annually and which may be some distance from former home ranges. If the richest areas of prey become monopolized by females, males may be likely to “make the best of a bad situation” by returning to a former home range where their familiarity with the landscape structure would aid in hunting success (Lundberg 1979, Greenwood and Harvey 1982, Merkle et al. 2014) and perhaps compensate for somewhat lower prey densities. The fat reserves and body condition of overwintering males were less than that of females (Chang and Wiebe 2016) but both sexes usually maintained a winter body mass above the starvation threshold so males seem to be able to meet energy requirements even if they are excluded from areas of peak prey.

In other regions of North America, the sample size of Snowy Owls tracked over multiple years is small but none of the four females tagged in Alaska (Fuller et al. 2003) or the four females in the Yukon (Doyle et al. 2017) migrated in a regular north-south

direction to settle south of the subarctic boreal region. These owls in western North America did not use the same home range in two successive winters, although some briefly visited locations from the previous winter. Based on two females, the average distance separating wintering home ranges in subsequent years was 873 km (Doyle et al. 2017), considerably longer than the 149 km for females in our study. In eastern North America, the average distance between centroids of wintering home ranges of 21 females in successive years was 389 km and the average overlap between successive home ranges was 29% (Robillard et al. 2018). However, the different methodology used to calculate home range size for the eastern owls resulted in estimates an order of magnitude larger than in our study, so quantitative comparisons of home range overlap between populations are difficult based on existing data. However, Snowy Owls on the central prairies of North America were more philopatric to a home range on a fine scale than were owls from either the west or the eastern parts of the continent.

The strong connectivity of a breeding population of Snowy Owls in the central Arctic to a particular wintering area on the central prairies may make it vulnerable to changes in land use, or to changes in climatic regimes that reduce access to small mammals over a large part of the central prairie region. For example, shifts in winter climate that affect the depth or density of snow could alter the density of small mammals wintering beneath protective snow cover (Bilodeau et al. 2013) or the ability of owls to hunt them (Chamberlain 1980). Changes to grassland vegetation as a result of fire, haying, or cropping practices also affect the density of mice and voles (Lafond et al. 2020). On a fine spatial scale, Snowy Owls, especially females, may be able to mitigate annual fluctuations in prey by tracking, and settling, at prey hotspots within the prairie biome although the ability to assess prey numbers may be negatively affected by deep snow cover (Therrien et al. 2015). Long-term information on the abundance and predictability of small rodents of the central prairie region, and the extent to which they are affected by changing winter climate, will be needed to model Snowy Owl numbers in central North America in relation to climate change.

Acknowledgments:

This research was made possible with assistance in Snowy Owl trapping from M. Stoffel and D. Zazelenchuk and we are indebted to their patience and perseverance in the field. We thank Chris Fleming for helpful discussions about continuous-time movement modeling. Snowy Owls were trapped under banding permit numbers 10736 and 10737. The study was funded by a Natural Sciences and Engineering Research Council of Canada to K. Wiebe (Discovery Grant 203177) and by a grant from the Kenneth M. Molson Foundation. This is Hawk Mountain Sanctuary contribution to conservation science number 391.

LITERATURE CITED

- Andersson, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. *Journal of Animal Ecology* 49:175-184. <https://doi.org/10.2307/4282>
- Benkman, C. W., and M. A. Young. 2020. Red Crossbill (*Loxia curvirostra*) in S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.redcro.01>
- Bilodeau, F., D. Reid, G. Gauthier, C. J. Krebs, D. Berteaux, and A. J. Kenney. 2013. Demographic response of tundra small mammals to a snow fencing experiment. *Oikos* 122:1167-1176. <https://doi.org/10.1111/j.1600-0706.2012.00220.x>
- Boxall, P. C., and M. R. Lein. 1982. Feeding ecology of Snowy Owls (*Nyctea scandiaca*) wintering in southern Alberta. *Arctic* 35:282-290. <https://doi.org/10.14430/arctic2326>
- Brown, A., R. A. McCabe, J-F. Therrien, K. L. Wiebe, S. Weidensaul, D. Brinker, G. Gauthier, and K. H. Elliott. 2021. Nomadic breeders Snowy Owls (*Bubo scandiacus*) do not use stopovers to sample the summer environment. *Ibis* 163 (4):1271-1281. <https://doi.org/10.1111/ibi.12950>
- Calabrese, J. M., C. H. Fleming, M. J. Noonan, and X. Dong. 2021. Ctmweb: A graphical user interface for autocorrelation-informed home range estimation. *Wildlife Society Bulletin* 45:162-169. <https://doi.org/10.1002/wsb.1154>
- Chamberlain, M. L. 1980. Winter hunting behavior of a Snowy Owl in Michigan. *Wilson Bulletin* 92:116-120.
- Chang, A. M., and K. L. Wiebe. 2016. Body condition in Snowy Owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality. *Auk* 133:738-746. <https://doi.org/10.1642/AUK-16-60.1>
- Chang, A. M., and K. L. Wiebe. 2018a. Habitat selection by wintering male and female Snowy Owls on the Canadian prairies in relation to prey abundance and a competitor, the Great Horned Owl. *Journal of Field Ornithology* 89:64-77. <https://doi.org/10.1111/jfo.12244>
- Chang, A. M., and K. L. Wiebe. 2018b. Movement patterns and home ranges of male and female Snowy Owls (*Bubo scandiacus*) wintering on the Canadian prairies. *Canadian Journal of Zoology* 96:545-552. <https://doi.org/10.1139/cjz-2017-0280>
- Curk T., I. Pokrovsky, N. Lecomte, T. Aarvak, D. F. Brinker, K. Burnham, A. Dietz, A. Dixon, A. Franke, G. Gauthier et al. 2020. Arctic avian predators synchronise their spring migration with the northern progression of snowmelt. *Scientific Reports* 10 (1):7220. <https://doi.org/10.1038/s41598-020-63312-0>
- Dawson, A. 2020. Pine Siskin (*Spinus pinus*) in A. F. Poole, editor. *Birds of the world*, Cornell Lab of Ornithology Ithaca, New York, USA. <https://doi.org/10.2173/bow.pinsis.01>
- Detienne, J. C., D. Holt, M. T. Seidensticker, and T. Pitz. 2008. Diet of Snowy Owls wintering in west-central Montana, with comparisons to other North American studies. *Journal of Raptor Research* 42:172-179. <https://doi.org/10.3356/JRR-07-41.1>
- Doyle, F. I., J-F Therrien, D. G. Reid, G. Gauthier, and C. J. Krebs. 2017. Seasonal movements of female Snowy Owls breeding in the western North American Arctic. *Journal of Raptor Research* 51:428-438. <https://doi.org/10.3356/JRR-16-51.1>
- Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2016. Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data. *Ecology* 97:576-582. <https://doi.org/10.1890/15-1607.1>
- Fleming, C. H., and J. M. Calabrese. 2017. A new kernel density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution* 8:571-579. <https://doi.org/10.1111/2041-210X.12673>
- Förschler, M. I., L. Förschler, and U. Dorka. 2006. Population fluctuations of Siskins *Carduelis spinus*, Common Crossbills *Loxia curvirostra*, and Citril Finches *Carduelis citrinella* in relationship to flowering intensity of spruce *Picea abies*. *Ornis Fennica* 83:91-96.
- 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, editors. *Avian migration*. Springer-Verlag, Berlin. https://doi.org/10.1007/978-3-662-05957-9_25
- Galindo, C., and C. J. Krebs. 1987. Population regulation of deer mice: the role of females. *Journal of Animal Ecology* 56:11-23. <https://doi.org/10.2307/4796>
- Gilchrist, H. G., and G. J. Robertson. 2000. Observations of marine mammals wintering at polynyas and ice edges in the Belcher Islands, Nunavut, Canada. *Arctic* 53:61-68. <https://doi.org/10.14430/arctic835>
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21. <https://doi.org/10.1146/annurev.es.13.110182.000245>
- Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67(3):394-402. <https://doi.org/10.1007/BF00384946>
- Heggøy, O., T. Aarvak, I. J. Øien, K.-O. Jacobsen, R. Solheim, D. Zazelenchuk, M. Stoffel, and O. Kleven. 2017. Effects of satellite transmitters on survival in Snowy Owls *Bubo Scandiacus*. *Ornis Norvegica* 40:33-38. <https://doi.org/10.15845/on.v40i0.1309>
- Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. Pages 563-575 in J. M. Hagan III and D. W. Johnstone, editors. *Ecology and conservation of Neotropical migrant land birds*. Smithsonian Institution Press, Washington, USA.
- Holt, D., M. D. Larson, N. Smith, D. Evans, and D. F. Parmelee. 2015. The Snowy Owl (*Bubo scandiacus*) in A. Poole, editor. *The Birds of North America Online*, Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.snoowl1.01>

- IUCN. (2020). The IUCN Red List of Threatened Species. <https://www.iucnredlist.org/>
- 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. <https://doi.org/10.2307/3676745>
- Kerlinger, P., and M. R. Lein. 1988. Causes of mortality, fat condition, and weights of wintering Snowy Owls. *Journal of Field Ornithology* 59:7-12.
- Kerlinger, P., M. R. Lein, and B.J. Sevick. 1985. Distribution and population fluctuations of wintering Snowy Owls (*Nyctea scandiaca*) in North America. *Canadian Journal of Zoology* 63:1829-1834. <https://doi.org/10.1139/z85-273>
- Kranstauber B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* 81(4):738-46. <https://doi.org/10.1111/j.1365-2656.2012.01955.x>
- Lindberg, M. S., D. H. Ward, T. L. Tibbits, and J. Roser. 2007. Winter movement dynamics of black brant. *Journal of Wildlife Management* 71:534-540. <https://doi.org/10.2193/2006-051>
- Lundberg, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. *Oecologia* 41:273-281. <https://doi.org/10.1007/BF00377431>
- Lafond, L. R., E. H. Rave, and K. A. Yurkonis. 2020. Small mammal communities in grasslands at the Grand Forks Air Force Base, North Dakota, USA. *The Prairie Naturalist* 52:11-20.
- McCabe, R. A., J.-F. Therrien, K. L. Wiebe, G. Gauthier, D. Brinker, S. Weidensaul, and K. Elliott. 2021. Landscape cover type, not social dominance, is associated with the winter movement patterns of Snowy Owls in temperate areas. *Ornithology* 138(2):ukaa082. <https://doi.org/10.1093/ornithology/ukaa082>
- Merkle, J. A., D. Fortin, and J. M. Morales. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters* 17:924-931. <https://doi.org/10.1111/ele.12294>
- Mihok, S., B. N. Turner, and S. L. Iverson. 1985. The characterization of vole population dynamics. *Ecological Monographs* 55:399-420. <https://doi.org/10.2307/2937129>
- Minnick, R. F. 1964. A Method for the measurement of areal correspondence. *Papers of the Michigan Academy of Science, Arts, and Letters* XLIX:333-43.
- Newton, I. 2006. Advances in the study of irruptive migration. *Ardea* 94:433-460.
- Newton, I. 2010. Bird migration. Collins, London, UK.
- Noonan, M. J., M. A. Tucker, C. H. Fleming, T. S. Akre, S. C. Alberts, A. H. Ali, J. Altmann, P. C. Antunes, J. L. Belant, D. Beyer et al. 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs* 89:e01344. <https://doi.org/10.1002/ecm.1344>
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B* 271:59-64. <https://doi.org/10.1098/rspb.2003.2569>
- Øien, I. J., T. Aarvak, K.-O. Jacobsen, and R. Solheim. 2018. Satellite telemetry uncovers important wintering areas for Snowy Owls on the Kola Peninsula, Northwestern Russia. *Ornithologia* 42:42-48.
- Oppel, S., A. N. Powell, and D. Dickson. 2009. Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck. *Journal of Animal Ecology* 78:524-531. <https://doi.org/10.1111/j.1365-2656.2008.01513.x>
- Potapov, E., and R. Sale. 2012. The Snowy Owl. T & AD Poyser, Bloomsbury Publishing Plc., London, England.
- R Core Team 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Remsen, J. V. 2001. The true winter range of the Veery (*Catharus fuscescens*): lessons for determining winter ranges of species that winter in the tropics. *Auk* 118:838-848. <https://doi.org/10.1093/auk/118.4.838>
- Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. *Auk* 116:20-34. <https://doi.org/10.2307/4089450>
- Robertson, G. J., 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., G. Gauthier, J.-F. Therrien, and J. Bêty. 2018. Wintering space use and site fidelity in a nomadic species, the Snowy Owl. *Journal of Avian Biology* 49(5):jav-01707. <https://doi.org/10.1111/jav.01707>
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418-421. <https://doi.org/10.2307/1312365>
- Senar, J. S., P. J. K. Burton, and N. B. Metcalfe. 1992. Variation in the nomadic tendency of a winter finch *Carduelis spinus* and its relationship with body condition. *Ornis Scandinavica* 23:63-72. <https://doi.org/10.2307/3676428>
- Silva, I., M. Crane, B. M. Marshall, C. T. Srine. 2020. Reptiles on the wrong track? Moving beyond traditional estimators with dynamic Brownian Bridge Movement models. *Movement Ecology* 8:43 <https://doi.org/10.1186/s40462-020-00229-3>
- SPSS Inc. Released 2022. IBM SPSS Statistics for Windows, Version 28.0. Armonk, New York, USA.
- Sullivan, T. P., D. S. Sullivan, and E. J. Hogue. 2004. Population dynamics of deer mice *Peromyscus maniculatus*, and yellow-pine chipmunks, *Tamias amoenus*, in old field and orchard habitats. *Canadian Field Naturalist* 118:299-308. <https://doi.org/10.22621/cfn.v118i3.7>
- Teitelbaum, C. S., and T. Mueller. 2019. Beyond migration: causes and consequences of nomadic animal movements. *Trends in Ecology and Evolution* 34(6):569-581. <https://doi.org/10.1016/j.tree.2019.02.005>

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. <https://doi.org/10.1111/j.1600-048X.2011.05330.x>

Therrien, J.-F., G. Gauthier, and J. Bêty. 2012. Survival and reproduction of adult snowy owls tracked by satellite. *Journal of Wildlife Management* 76:1562-1567. <https://doi.org/10.1002/jwmg.414>

Therrien, J.-F., G. Gauthier, D. Pinaud, and J. Bêty. 2014. Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource. *Journal of Avian Biology* 45:536-544. <https://doi.org/10.1111/jav.00426>

Therrien, J.-F., D. Pinaud, G. Gauthier, N. Lecomte, K. L. Bildstein, and J. Bêty. 2015. Is pre-breeding prospecting behaviour affected by snow cover in the irruptive snowy owl? A test using state-space modelling and environmental data annotated via Movebank. *Movement Ecology* 3:1. <https://doi.org/10.1186/s40462-015-0028-7>

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199-209 in R. Greenberg and P. P. Marra, editors. *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, USA.



Appendix Table 1. Summary information for home ranges calculated for five female and seven male wintering Snowy Owls between 2014-2021. An owl had ≥ 1 sequential home ranges each year it was monitored (HR #). Estimated HR area and 95% Confidence Interval (CI) are shown together with the duration the HR was occupied and the number of GPS fixes. The best-supported movement model (based on the Akaike Information Criterion; AICc) used to generate the HR is also shown (see text for explanation of model types and Calabrese et al. (2021)).

Owl ID	Sex	Winter	HR #	Model (AICc)	Area + CI (km ²)	Duration (days)	Fixes (#)
April	F	2015-16	1	OUF-anisotropic	47.3 (16.9-93.2)	11	60
		2015-16	2	OUF-isotropic	143 (37.5-317)	33	87
		2015-16	3	OU-isotropic	112 (70.7-163)	15	55
		2016-17	1	OUF-anisotropic	104 (59.1-160)	7	28
		2016-17	2	OU-anisotropic	49.3 (20.9-89.8)	8	32
		2016-17	3	OUF-anisotropic	17.5 (13.4-22.2)	76	240
Bitey	F	2015-16	1	OUF-anisotropic	168 (87.6-275)	26	161
		2015-16	2	OUF-anisotropic	73.1 (57.2-90.9)	31	124
		2016-17	1	OUF-anisotropic	240 (118-405)	16	65
		2016-17	2	OU-anisotropic	764 (68.7-2280)	8	33
		2016-17	3	OUF-anisotropic	32.9 (25.6-41.1)	76	308
		2017-18	1	OU-anisotropic	68.7 (56.3-82.3)	121	485
		2017-18	2	OUF-anisotropic	137 (92.1-191)	20	82
		2018-19	1	OU-anisotropic	32.9 (23.7-43.6)	19	76
		2018-19	2	OU-anisotropic	95.5 (56.2-145)	19	71
		2018-19	3	OUF-anisotropic	861 (469-1370)	52	211
		2018-19	4	IID-isotropic	81.3 (51.6-118)	7	28
		2019-20	1	OUF-anisotropic	5.27 (4.71-5.87)	102	415
		2019-20	2	OUF-anisotropic	33.8 (23-46.6)	11	43
		2019-20	3	OUF-anisotropic	12.7 (7.99-18.5)	10	39
2020-21	1	OUF-anisotropic	266 (199-342)	188	475		
Hammy	F	2015-16	1	OUF-anisotropic	26.6 (21.4-32.4)	63	351
		2015-16	2	OUF-anisotropic	40.9 (26.8-57.9)	18	77
		2015-16	3	OUF-anisotropic	12.2 (8.32-16.9)	13	50
		2015-16	4	OUF-anisotropic	3.34 (2.25-4.63)	8	35
		2015-16	5	OUF-anisotropic	14.5 (8.8-21.6)	7	28
Jordyn	F	2016-17	1	OUF-anisotropic	8.35 (6.14-10.9)	15	59
		2017-18	1	OUF-anisotropic	46.5 (31.1-64.9)	50	64
		2017-18	2	OUF-anisotropic	37.1 (26.6-49.4)	20	77
Socks	F	2015-16	1	OU-anisotropic	14.4 (11.4-17.7)	64	321
		2015-16	2	OU-anisotropic	16.7 (12.1-22)	19	76
		2016-17	1	OU-isotropic	8.22 (4.08-13.8)	16	49
		2016-17	2	OUF-anisotropic	3.31 (2.88-3.77)	88	359
		2017-18	1	OUF-anisotropic	19.3 (13.6-25.8)	27	91
		2017-18	2	OU-anisotropic	12.9 (8.33-18.6)	17	69

		2017-18	3	IID-anisotropic	5.35 (2.73-8.83)	22	92
		2018-19	1	IID-anisotropic	4.88 (3.44-6.56)	9	38
		2018-19	2	Ouf-isotropic	1.91 (1.25-2.71)	77	37
Berg	M	2014-15	1	OUF-anisotropic	15.7 (11.5-20.5)	18	112
		2014-15	2	OUF-anisotropic	197 (29.4-522)	14	58
		2014-15	3	OU-anisotropic	149 (41.9-322)	19	83
		2014-15	4	OU-anisotropic	123 (32.4-273)	12	47
		2015-16	1	OU-isotropic	22.9 (11.9-37.5)	16	33
		2015-16	2	OUF-anisotropic	184 (112-275)	67	306
		2015-16	3	OUF-anisotropic	9.51 (7.49-11.8)	21	88
Dump	M	2015-16	1	OU-anisotropic	41.2 (25.9-60)	34	156
		2015-16	2	OUF-anisotropic	4.73 (2.89-7.02)	7	28
		2016-17	1	OU-anisotropic	27.7 (15.5-43.4)	38	118
		2016-17	2	IID-anisotropic	5.11 (3.65-6.8)	8	32
		2016-17	3	IID-anisotropic	16.7 (7.32-30)	9	34
		2016-17	4	OUF-anisotropic	6.89 (5.18-8.84)	34	130
		2017-18	1	OUF-isotropic	43.6 (16.9-82.8)	12	41
		2017-18	2	OUF-anisotropic	44.2 (35.5-53.9)	60	229
		2018-19	1	IID-anisotropic	39.3 (35-43.8)	80	312
		2019-20	1	OUF-anisotropic	4.4 (3.91-4.91)	95	361
		2019-20	2	OUF-anisotropic	13.8 (7.15-22.6)	18	69
		2020-21	1	OUF-anisotropic	215 (119-338)	28	111
		2020-21	2	OUF-isotropic	339 (226-475)	72	291
Dundurn	M	2015-16	1	OUF-anisotropic	37.6 (28.8-47.5)	42	168
		2016-17	1	OUF-anisotropic	569 (337-862)	111	398
		2016-17	2	Ouf-isotropic	22.5 (13.2-34.4)	9	33
		2017-18	1	OU-anisotropic	339 (112-688)	12	46
		2017-18	2	IID-isotropic	12.1 (7.73-17.3)	7	28
		2017-18	3	OUF-anisotropic	71.7 (48.7-99.1)	66	259
		2018-19	1	OUF-anisotropic	59.6 (39.8-83.3)	31	118
		2018-19	2	OUF-anisotropic	470 (227-802)	80	282
		2019-20	1	OUF-anisotropic	14.7 (8.01-23.5)	8	30
		2019-20	2	OU-anisotropic	13.3 (10-17.1)	36	136
		2019-20	3	OUF-anisotropic	933 (409-1670)	61	238
		2020-21	1	OUF-anisotropic	614 (289-1060)	66	224
Horse	M	2015-16	1	OUF-anisotropic	43.4 (35.2-52.4)	54	206
		2015-16	2	OUF-anisotropic	266 (135-442)	22	85
		2016-17	1	OUF-anisotropic	299 (152-495)	47	87
		2016-17	2	OU-anisotropic	30.9 (14.7-53.2)	32	81
		2017-18	1	OUF-anisotropic	458 (289-665)	78	216
		2017-18	2	OUF-anisotropic	101 (64.7-145)	25	98
		2017-18	3	OU-anisotropic	91.5 (64.7-123)	11	42
		2018-19	1	OUF-anisotropic	75.8 (54-101)	21	53

		2018-19	2	OUF-anisotropic	957 (541-1490)	70	238
		2019-20	1	OUF-anisotropic	109 (54.8-183)	24	81
		2019-20	2	OUF-isotropic	881 (422-1510)	59	220
		2019-20	3	OUF-anisotropic	9.91 (7.15-13.1)	30	106
		2020-21	1	OUF-anisotropic	768 (348-1350)	57	215
		2020-21	2	OUF-anisotropic	428 (276-614)	57	201
		2020-21	3	IID-anisotropic	31.4 (9.02-67.4)	23	97
Leprec	M	2015-16	1	OUF-anisotropic	43.3 (34.4-53.1)	77	321
		2015-16	2	OU-anisotropic	60.6 (36.6-90.7)	19	72
		2016-17	1	OUF-anisotropic	31.8 (25-39.3)	77	211
Outlook	M	2016-17	1	OU-anisotropic	23.4 (14.7-34.1)	13	52
		2016-17	2	OUF-anisotropic	279 (77.1-610)	24	96
		2016-17	3	OUF-anisotropic	35.8 (28-44.6)	48	194
		2017-18	1	OUF-anisotropic	557 (180-1140)	17	71
		2017-18	2	OUF-anisotropic	78.5 (64.3-94)	90	373
		2017-18	3	OU-anisotropic	181 (107-275)	19	72
		2018-19	1	OUF-anisotropic	64.6 (49.7-81.4)	83	203
		2019-20	1	IID-anisotropic	110 (90.8-131)	23	97
		2019-20	2	OUF-anisotropic	60.5 (48.3-74.1)	34	135
		2020-21	1	OUF-anisotropic	16.5 (11.2-22.9)	64	53
Sover	M	2015-16	1	OUF-anisotropic	61.6 (43.6-82.5)	41	221
		2015-16	2	OU-anisotropic	382 (141-741)	10	39
		2016-17	1	OU-isotropic	13.8 (8.95-19.6)	10	39
		2016-17	2	OUF-anisotropic	35.8 (30.6-41.4)	93	279
		2016-17	3	OUF-anisotropic	16.4 (10.4-23.8)	10	43
		2017-18	1	OUF-isotropic	39.8 (27.4-54.5)	62	87
		2017-18	2	OU-anisotropic	131 (75.7-200)	27	56
		2018-19	1	OUF-anisotropic	68.5 (35.2-113)	63	80
		2018-19	2	Ouf-anisotropic	21.1 (13.1-31)	13	42
		2018-19	3	OUF-anisotropic	12 (6.29-19.6)	9	38
		2019-20	1	OUF-isotropic	122 (31.5-272)	18	24
		2019-20	2	Ouf-isotropic	189 (87-329)	13	34

Appendix 2. R code to compute Coefficient of Areal Correspondence (CAC) with toy examples for overlapping, non-overlapping and perfectly overlapping polygons.

```
library(sf)
library(tidyverse)

# Create sf collections of toy polygons
createSquarePolygons <- function(x, a) { #define function to create square
polygons
  a <- sqrt(a)/2
  return( sf::st_buffer(x, dist = a, nQuadSegs=1, endCapStyle = "SQUARE") )}
overlappingPolygons <- createSquarePolygons(st_as_sf(data.frame(x = c(1,1), y
= c(1,1.5)),coords = c("x", "y")), 1)
nonOverlappingPolygons <- createSquarePolygons(st_as_sf(data.frame(x =
c(1,1), y = c(1,2)),coords = c("x", "y")), 1)
perfectlyOverlappingPolygons <- createSquarePolygons(st_as_sf(data.frame(x =
c(1,1), y = c(1,1)),coords = c("x", "y")), 1)

# Plot toy polygons
plot(overlappingPolygons)
plot(nonOverlappingPolygons)
plot(perfectlyOverlappingPolygons)

# Compute CAC for toy polygons
polygons <- overlappingPolygons #define input polygons
intersect <- polygons %>%
  st_set_precision(1e5) %>%
  st_make_valid() %>%
  st_intersection() %>%
  dplyr::mutate(area=st_area(geometry)) %>%
  select(n.overlaps,area) %>%
  st_drop_geometry
intersect <- rbind(intersect,data.frame(n.overlaps=2,area=0)) #add overlap
row for cases without overlap
intersect <- rbind(intersect,data.frame(n.overlaps=1,area=0)) #add nonoverlap
row for cases with perfect overlap
intersect$overlap[intersect$n.overlap==1] <- "nonoverlaps" #identify
nonoverlaps
intersect$overlap[intersect$n.overlap>1] <- "overlaps" #identify overlaps
intersect_c <-reshape2::dcast(intersect, .~overlap,value.var="area",sum)
#compute sum of overlaps and nonoverlaps
intersect_c$CAC <-
intersect_c$overlaps/(intersect_c$overlaps+intersect_c$nonoverlaps) #compute
CAC
intersect_c$CAC #print CAC
```