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Authors	Doyle, Susan;Cabot, David;Griffin, Larry;Kane, Adam;Colhoun, Kendrew;Redmond, Courtney;Walsh, Alyn;McMahon, Barry J.
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University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Home range of a long-distance migrant, the Greenland Barnacle Goose *Branta leucopsis*, throughout the annual cycle

Susan Doyle¹, David Cabot², Larry Griffin³, Adam Kane⁴, Kendrew Colhoun⁵, Courtney Redmond¹, Alyn Walsh⁷, and Barry J McMahon¹

¹UCD School of Agriculture and Food Science, University College Dublin, Ireland.

²School of Biological, Earth and Environmental Sciences, University College Cork, Ireland.

³ECO-LG Limited, Dumfriesshire, UK.

⁴UCD School of Biology and Environmental Science, University College Dublin, Ireland.

⁵KRC Ecological Ltd., Bryansford, Down, BT33 0PZ, UK.

⁶Department of Housing, Local Government and Heritage, National Parks and Wildlife Service, Wexford Wildfowl Reserve, North Slobland, Wexford, Ireland.

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Corresponding author: Barry McMahon (barry.mcmahon@ucd.ie)

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Summary

Capsule

Home range area and foraging distance of the Greenland Barnacle Goose *Branta leucopsis*, a long-distance migrant, was calculated and activity patterns described.

Aims

To understand Barnacle Goose space use throughout the annual cycle to inform effective wildlife management and conservation planning.

Methods

Overall (80-99% utilisation distribution; UD) and core (50% UD) home range was mapped from satellite telemetry data using a Brownian bridge kernel method to determine patterns of space use. Maximum and core foraging distance was then estimated from the 80-99% UD and 50% UD respectively. Finally, daily activity patterns including the location of roosts and foraging sites in the landscape were described, along with variability in home range among seasons and between males and females, and spatial and temporal repeatability.

Results

Overall home range area was approximately 14 km² in winter, 9.5 km² in spring, 7 km² in the nesting period, 43 km² in the post-nesting period and 48 km² in autumn. However, the core area used by the birds within this overall area was substantially smaller: mean core home range area was approximately 1.5 km² in winter, 1 km² in spring, 2 km² in the nesting period, 7 km² in the post-nesting period and 12 km² in autumn. Maximum foraging distance was approximately 7 km in winter, 5 km in spring, 3.5 km in the nesting

period, 15.5km in the post-nesting period and 32.5km in autumn. Core foraging distance was approximately 5.5km in winter, 3km in spring, 1km in the nesting period, 8.5km in the post-nesting period and 19.5km in autumn.

Conclusion

Although our study focuses on the movements of Barnacle Geese, such data can be used to inform a range of pure and applied ornithological issues, including resource partitioning, human-wildlife conflicts and the dissemination of zoonotic disease.

Introduction

Home range, foraging distance and activity patterns have been well studied in waterfowl, prompted in part in recent times by the exponential growth of many northern-breeding goose and swan species, and their shift from foraging in natural habitats to agricultural habitats (Fox & Abraham 2017, Fox & Leafloor 2018). Studies show that space use in waterfowl is influenced by a range of internal factors such as rearing conditions and age (Avé *et al.* 2017), local external factors such as sward height (Durant *et al.* 2004) and landscape factors such as the positioning of waterbodies and boundary features (Jensen *et al.* 2017). In addition, home range area and foraging distance have been comprehensively quantified for some waterfowl species (e.g. Giroux & Patterson 1995, Bengtsson *et al.* 2014). These and similar studies provide useful data for conservation plans, conflict resolution and, where relevant, hunting management. For example, knowledge of space use patterns can be used to predict spatial distribution in relation to protected areas (Thornton *et al.* 2021), assess probability of occurrence (Jensen *et al.* 2017) and guide crop damage prevention measures (Giroux & Patterson 1995).

The Greenland population of Barnacle Goose *Branta leucopsis* winters in north-west Ireland and Scotland, and summers in north-east Greenland, staging in north-west Iceland during spring migration and in south-east Iceland during autumn (Jensen *et al.* 2018; Figure 1). In recent years, a new and rapidly growing breeding population derived from the Greenland population has also emerged in south-east Iceland. Overall Greenland/Iceland population numbers have increased substantially since a critical low in the 1950s (Mitchell & Hall 2020) and conflicts with agricultural interests now occur in some areas of the wintering and staging grounds where Barnacle Geese

forage on arable crops and pasture, necessitating detailed conservation and management strategies (Mason *et al.* 2017, Tombre *et al.* 2019). However, despite these management challenges, comparatively little is known about the home range and foraging distance of the Greenland population: although population dynamics have been studied in depth at key wintering sites (e.g. Cabot & West 1973, Trinder 2014) and migratory movements have been well described (e.g. de Boer *et al.* 2014, Shariatinajafabadi *et al.* 2014, Kölzsch *et al.* 2015, Shariati *et al.* 2017, Doyle *et al.* 2020, 2021), no study to our knowledge has quantified the home range area or foraging distance of the Greenland population throughout the annual cycle. Furthermore, Barnacle Geese spend a large proportion of the annual cycle in offshore or remote Arctic sites, where access for study is limited. A number of manned Arctic expeditions to breeding sites in Greenland were undertaken between the 1950s and 1980s to investigate breeding dynamics (including Hall 1962, Marris & Webbe 1969, Ferns & Green 1975, Meltofte 1975, Hardy 1979, Cabot *et al.* 1984, 1988, Madsen *et al.* 1984), but estimation of home range and foraging distance across the extensive summering range was beyond the scope of these studies. Hence, following Johnson's (1980) hierarchical framework of habitat selection, the 'first order' selection of Greenland Barnacle Geese (i.e. their geographic range in Greenland, Iceland and the British Isles) is well documented in the literature, as described above. However, the 'second order' selection (i.e. home range of social groups within the geographic range) has not been formally described for this population, nor has the 'third order' selection (i.e. habitat components within the home range) been described from this holistic perspective.

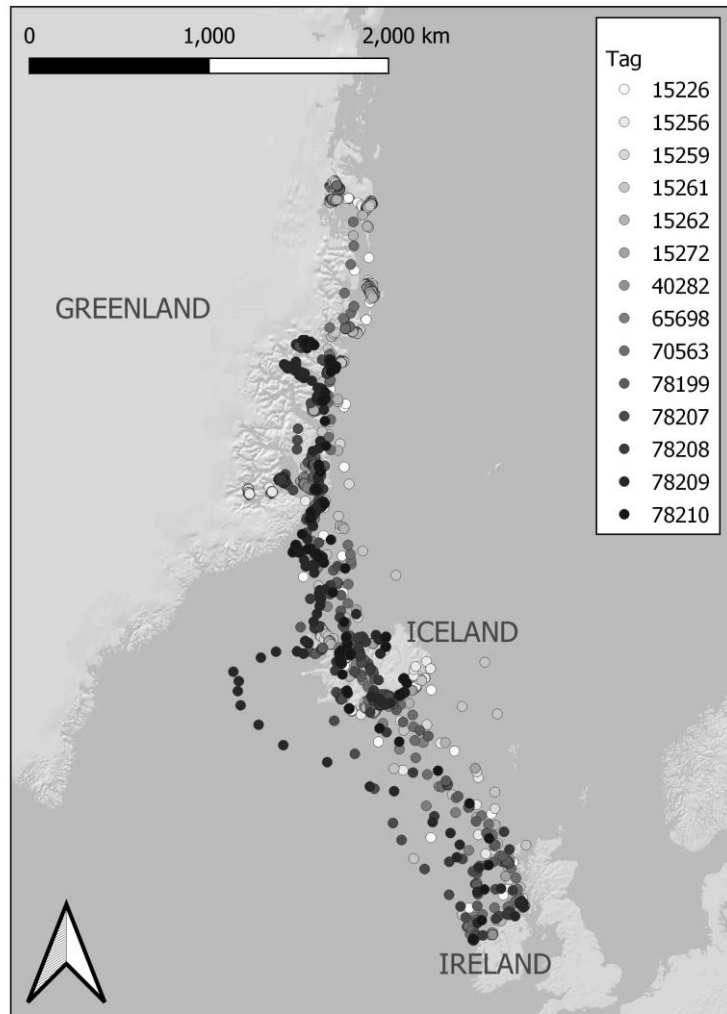


Figure 1 Fixes from tagged Barnacle Geese across their range throughout the study.

The aim of this study was to map and quantify the home range of Greenland Barnacle Geese throughout the annual cycle ('second order' selection) and use this information to quantify foraging distance and describe activity patterns ('third order' selection). Home range was estimated from satellite telemetry data using a Brownian bridge kernel method, which is an extension of the traditional kernel method that can show how intensely birds use different areas. It is based on the path travelled between successive fixes and accounts for temporal autocorrelation inherent in telemetry time series (Horne *et al.* 2007). Activity patterns included a description of roost and foraging sites in a landscape context, and a description of daily movements. It also included an

assessment of variation in home range area among seasons (larger home ranges could be expected in winter and autumn, when resources are less abundant) and between males and females (high similarity could be expected during the non-breeding season, because pairs associate throughout winter, but divergence could be expected during nesting, when the female is restricted to the nest; Black *et al.* 1996). Finally, it included an assessment of spatial repeatability in home range location and temporal repeatability in arrival/departure dates. Our results provide useful data to underpin conservation management of this species, especially where its range overlaps with agricultural interests and areas vulnerable to environmental change.

Materials and Methods

Transmitter tag deployment

Barnacle Geese were captured for tag deployment using cannon nets at their wintering grounds in Ireland. A total of 28 tags were deployed between 2008 and 2019 at three sites: $n = 5$ (2008), $n = 2$ (2009) and $n = 2$ (2010) on the Inishkea Islands; $n = 8$ (2018) and $n = 5$ (2019) on the Inishowen Peninsula; and $n = 6$ (2019) in Lissadell. To avoid tagging both birds of a pair, only males or only females were tagged during each capture session. Tags from 2008-2010 were 30-45g GPS-ARGOS platform transmitter terminals (Microwave Telemetry Inc, Columbia, MD) with an elastic body harness attachment. Tags from 2018-2019 were ~15g nanoFix® GEO+RF (Pathtrack Ltd, Otley, UK) on a neck collar attachment. Both tag types were solar powered, but the interval time between fixes varied to optimise battery capacity: tags from 2008-2010 collected a geographical coordinate fix at 2 hour intervals and transmitted data via the Argos system almost daily, while tags from 2018-2019 collected a fix at 6 hour intervals and transmitted these data via ultra-high frequency radio to mobile base stations

positioned at known winter foraging sites. Data was collected from deployment (including night time) until the tag no longer transmitted data.

Behaviour monitoring

To ensure that the transmitter tag did not affect ordinary behaviour of the birds, a matched cohort study was conducted following one capture event in November 2019. Behavioural time budgets of three cohorts were assessed: (1) birds carrying a transmitter and leg ring, (2) birds wearing a leg ring only or (3) unmarked birds. Individuals from each cohort were observed for a session of 300s during which the number of seconds engaged in foraging, walking and vigilance behaviour was recorded using a stopwatch. The summed time engaged in each behaviour was compared using an analysis of variance test (other behaviours were also recorded, but were too sporadic to statistically analyse). No difference was found in foraging time (analysis of variance, $F[2, 6] = 0.59$, $P = 0.59$), vigilance time ($F[2, 5] = 0.77$, $P = 0.51$) or walking time ($F[2, 6] = 0.02$, $P = 0.98$). During this behavioural monitoring, no excessive preening of the neck, pecking at or around the collar, or excessive head shaking was observed. The proportion of time engaged in all observed behaviours is provided in Supplementary Material 1.

Home range

Data were retrieved from 18 of the 28 tags, and multiple years of data were available for some birds, providing a total of 29 annual trajectories, which comprised a time series of fixes (latitude and longitude) with a corresponding date and time. Within each annual trajectory, data were subdivided into seasonal trajectories according to whether the bird was present at its main wintering grounds, spring staging grounds, summering

grounds or autumn staging grounds home range. Here, home range was defined as the area occupied by the bird during its normal activities of foraging and breeding (Burt 1943): the main winter or summering grounds were the areas in which birds engaged in overwintering or breeding and post-breeding activities, including moult, whilst the spring and autumn staging grounds were the areas where birds spent an extended period of time refuelling during migration between wintering and summering grounds, as defined by Warnock (2010). Fixes from migratory journeys (long-distance flights over sea and land) and migratory stopovers (areas birds rest and feed during migratory journeys, as defined by Warnock, 2010) were excluded. The final analysis included 24 winter trajectories (from 17 birds), 15 spring trajectories (from 12 birds), 16 summer trajectories (from 13 birds) and 12 autumn trajectories (from 10 birds). It was noted from the data that some individuals settled in a nesting locale within the home range in May and June, but then moved to a new post-nesting locale in late June or July. Other individuals remained in the same locale throughout the summer (these may have been non-breeding birds). If trajectories between the nesting and post-nesting period were distinguishable ($n = 8$), then home range was estimated separately to provide further resolution.

Trajectories were analysed in the R language and environment for statistical computing (R Core Team 2021). For every fix_i in the trajectory, the following values were calculated using the *adehabitatLT* package (Calenge 2006): the incremental change on the x and y plane between fix_i and fix_{i+1} ; the distance (metres) between fix_i and fix_{i+1} ; the angle (absolute and regular) between fix_i and fix_{i+1} and; the time (seconds) between fix_i and fix_{i+1} . Home range was then estimated with these values using a Brownian bridge kernel method via the *adehabitatHR* package (Calenge

2006). Firstly, the utilisation distribution (UD; the probability density that a bird will be at a given location on the plane) was estimated from the trajectory time series. Secondly, the home range of a bird was estimated as the minimum area of the utilisation distribution in which the probability of bird occurrence equalled a chosen value. The chosen values in our model were the 80-99% UD (to distinguish overall home range area) and the 50% UD (to distinguish the core home range area). The 80-99% value varied for individual birds depending on the proportion of extreme outlier fixes excluded. Extreme outlier fixes were identified by iteratively calculating the minimum convex polygon area with varying percentages of the fixes farthest from the centroid excluded (0-50%, in increments of 5%). The resulting polygon areas were plotted against the corresponding percentages and the turn of the asymptote was taken to be the value above which fixes could be considered extreme outliers. The Brownian motion variance smoothing parameter (σ^1) was calculated for each bird by a subjective visual assessment of a plot of its maximum likelihood estimation to find the optimum value, following Horne *et al.* (2007), and the telemetry error smoothing parameter (σ^2) was set at 27m, based on imprecision tests of fixes by the tags prior to deployment. Imprecision was tested for two tags: the tags were placed in an outdoor location and allowed to collect 3 fixes over 6 hours, then the distance between the generated fixes and the true location on the ground was measured and averaged across both tags.

Foraging distance

Following the delineation of home range, foraging distance was calculated for each period of the annual cycle. During winter and spring, roosts were identified as the 25% UD area(s) with accumulations of fixes during lowest light levels. During summer

nesting, nest territories were identified as the 25% UD during the nesting period (end of May to start of July). Following this, maximum and core foraging distance during winter ($n = 24$), spring ($n = 15$) and nesting ($n = 8$) were taken as the longest distance between a roost/nest centroid and the edge of the 80-99% UD and 50% UD respectively. During summer post-nesting ($n = 8$), or for the whole summer in the case of indistinguishable nesting-post-nesting periods birds ($n = 8$), and during autumn ($n = 12$), maximum and core foraging distance was taken as the longest distance transecting the 80-99% UD and 50% UD respectively. This is because there is 24 hour daylight at the summering grounds, therefore roosting and favoured foraging sites can no longer be distinguished, and birds tended to roost and forage in the same area during autumn.

Activity patterns

Activity patterns of birds within their home range were inferred by overlaying home range maps with their associated timestamped fixes on aerial (and where available land-use) maps. From this, the location of roosts in the landscape was described with reference to habitat and major landscape features such as waterbodies, along with the relative location of foraging sites. The timing and sequence of daily movements around roost and foraging sites was also described.

The influence of season and sex on home range area, and their interaction, was tested using an analysis of variance test (winter $n = 17$, spring $n = 15$, summer $n = 16$ and autumn $n = 12$). The study overall included 7 females and 11 males. To account for potential sampling bias, deployment location was included as a blocking factor in this model.

Multiple years of data were available for just three individuals to assess spatial and temporal repeatability. For spatial repeatability, we overlaid successive years of home range maps and calculated the percentage overlap in core (50% UD) area. For temporal repeatability, we compared the arrival and departure dates to/from home ranges in successive years and considered those within 48 hours as high repeatability.

Results

Home range

During winter, tagged Barnacle Goose home ranges in north-west Ireland were located on the Inishowen Peninsula, Mullet Peninsula and Sligo. Individuals arrived at their winter home range between 4 October and 22 November and departed between 13 March and 23 April. Mean overall home range area (80-99% UD) was 13.78km² with a core area (50% UD) of 1.53km² (Figure 2).

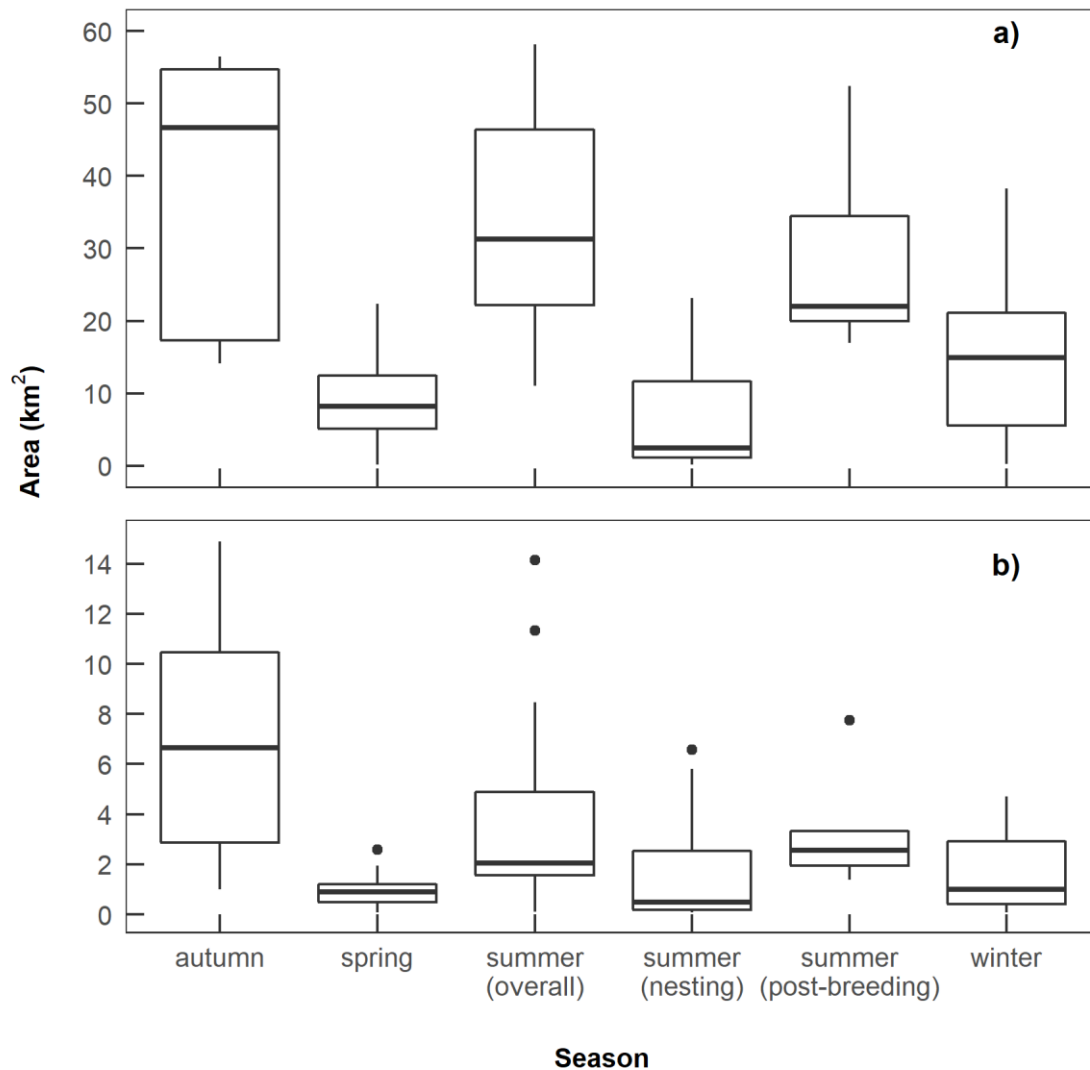


Figure 2 Comparison of the mean area (km²) of Barnacle Goose home range across the autumn staging, spring staging, summering and wintering grounds. Summering is divided into overall (for geese that remained in the same locale throughout the summer), and nesting and post-nesting (for geese that moved locale after nesting). Overall (80-99% utilisation distribution) and core (50% utilisation distribution) home range area are presented.

During spring staging, home ranges in northern Iceland were located in Vatnsdalshólar, Varmahlíð, Eyjafjörður, Svínavatn and Laugarbakki. One individual was also recorded on Dýrafjörður in the Westfjords. Individuals arrived at their spring home range between 10 April and 11 May, and departed between 13 May and 22 May. Mean overall home range area was 9.40km² with a core area of 0.95km².

During the summer, home ranges in Greenland were located in Okselandet, Fønfjord, Jameson Land, Germania Land, Daniel Bruun Land, Ole Rømer Land, Milne Land and Andrée Land. Individuals arrived at their summer home range between 14 May and 29 May, and departed between 8 August and 9 September. For trajectories in which the nesting and post-nesting period were distinguishable ($n = 8$), mean overall home range area was 6.80km^2 during nesting and 42.94km^2 post-nesting, with a core area of 1.90km^2 during nesting and 7.17km^2 post-nesting. For trajectories in which individuals remained in the same locale throughout the summer ($n = 8$), mean overall home range area was 31.73km^2 , with a core area of 3.79km^2 .

Finally, during autumn staging, home ranges in southern Iceland were located in Skeiðarársandur and nearby Kúðafliót, Skaftafell, Skálafell and Reynivellir. Individuals arrived at their autumn home range between 9 September and 1 October, and departed between 3 October and 18 October. Mean overall home range area was 47.99km^2 , with a core area of 12.24km^2 . All individual home range areas are presented in Supplementary Material 2.

Foraging distance

During winter, mean foraging distance was 7.00km (maximum) and 5.66km (core). During spring staging, mean foraging distance was 5.12km (maximum) and 2.79km (core). During summer, for birds in which the nesting and post-nesting period were distinguishable, mean foraging distance during nesting was 3.35km (maximum) and 1.18km (core), while mean foraging distance post-nesting was 15.58km (maximum) and 8.45km (core). For birds that remained in the same locale throughout the summer, mean foraging distance was 31.43km (maximum) and 11.86km (core). Finally, during

autumn staging, mean foraging distance was 32.66km (maximum) and 19.38km (core). All individual foraging distances are presented in Supplementary Material 2.

Activity patterns

In winter in Ireland, home ranges encompassed a roost site and a number of discrete foraging sites in coastal areas with abundant agricultural land. Particular roosts were associated with particular foraging sites and segregation between roost-foraging networks was evident. A low rate of mixing between networks was observed: 18% of tagged birds switched network during the winter (usually permanently). Within their home range, all tagged birds roosted in dark hours on offshore islands and showed strong roost site fidelity. However, within-home range roost switching to other islands 9-10km away was observed in 35% of tagged birds. During daytime, birds visited a number of foraging sites within their home range, with clear evidence of favoured or only occasionally used foraging sites. The occupants of some island roosts commuted to the mainland daily to forage on improved agricultural pasture. On other island roosts, the occupants remained on the island to forage during the day, although daytime commutes to forage on the mainland were occasionally recorded.

In spring in Iceland, Barnacle Goose home ranges were located along inland waterbodies including rivers, deltas, lakes and fjords. Home ranges encompassed a waterbody for roosting (fixes on water/in outwash gravel when light levels are lowest) and adjacent grasslands dominated by agricultural grassland for foraging. As might be expected in long light hours, geese foraged in agricultural fields for the majority of the day, with evidence of favoured foraging fields that were intensively used.

In summer in Greenland, home ranges were generally located along steep inland river valleys, lake shores and islands, or on the edges of inland fjords, and encompassed some surrounding tundra. As might be expected under 24 hour daylight regimes, there was no discrete within-home range pattern of roosting and foraging sites akin to that observed in winter and spring. Accumulations of fixes occurred where geese nested (mostly on lake edges and islands) and during moult, when individuals travelled up and down a river valley or lake edge for consecutive weeks before regaining flight. Some individuals remained in the same locale throughout the breeding and post-nesting/moult period, moving between adjacent valleys within a 10km radius. Others moved a greater distance (20-70km) to new moulting and post-nesting locales in river valleys, estuaries or coastlines, before southward migration proper began.

In autumn in Iceland, home ranges mainly encompassed river deltas, estuaries and outwash sands. Home range was patchy and less well defined compared to other seasons, with no discrete within-home range roosting and foraging sites and no concentrated area of activity overall. Geese remained in gravelly, poor growth areas throughout the day. Often, they spent a number of days in one place, then moved to a new place within the overall home range, without returning to the old place.

After accounting for variation in deployment site, there was a significant synergistic relationship of season and sex with area for overall home range (analysis of variance; $F = 6.348$, $P < 0.001$); variation in home range area among seasons was reduced in males. There was a significant relationship of season and area for core home range (analysis of variance; $F = 5.372$, $P = 0.003$); core range was significantly smaller in winter and spring compared to autumn. Mean overall home range was larger in

females compared to males in winter (18.9km² and 9.4 km² respectively), spring (10.8 km² and 7.8 km²) and autumn (59.1 km² and 32.4 km²), but smaller during summer nesting (3.9km² and 11.6km²) and similar during post-nesting (42.7km² and 43.5km²). Mean core home range was also similar in females and males in winter (2.2 km² and 1.0 km² respectively) and spring (1.0 km² and 0.9 km²), but male range was larger in autumn (9.8 km² and 15.6km²), summer nesting (0.5km² and 4.2km²) and post-nesting (7.8km² and 17.1km²).

Regarding spatial repeatability, there was a mean 71% overlap in the core winter home range used by individuals for which we had multiple seasons of data ($n = 2$), a mean 29% overlap in spring ($n = 3$), a mean 23% overlap in summer ($n = 3$) and a mean overlap of 6% in autumn ($n = 2$). Regarding temporal repeatability, there was one case of an individual arriving at their home range within the same 48 hour period in successive years in winter ($n = 2$), one case in summer ($n = 3$) and one case in autumn ($n = 2$). There were three cases of an individual departing their home range within the same 48 hour period in successive years in spring ($n = 3$), two cases in summer ($n = 3$) and one case in autumn ($n = 2$).

Discussion

Home range characteristics

Greenland Barnacle Goose home range was delineated using a Brownian Bridge kernel method and the 80-99% UD and 50% UD were mapped. The 80-99% UD best represented less frequently used foraging sites and the path birds travelled between sites. In contrast, the 50% UD best represented roosting, nesting and favoured foraging sites, and very regularly used flight paths.

Home range area was smallest during winter, spring and nesting, with a mean core area of approximately 1-2km. In comparison, post-nesting and autumn core home range was larger, at approximately 7-12km. Foraging distance broadly followed this pattern. A relatively small home range was expected during nesting, as the female remains on the nest for the majority of her time while the male acts sentinel nearby (Cabot *et al.* 1984, Black *et al.* 2014). However, the small home ranges in winter and spring may be related to food availability. During both winter and spring, home ranges were dominated by agricultural landscapes, compared to natural tundra and outwash landscapes that dominated home range in summer and autumn. Therefore, it is possible that Barnacle Geese exploit agricultural land to maintain a smaller home range in winter and spring, due to the high density and quality of forage material on agricultural pasture (Fox & Abraham 2017). Depletion of food sources during post-nesting and in autumn may force the geese to increase their home range and foraging distance to meet their energy requirements. Indeed, food availability is considered to be one of the primary determinants of home range size in birds (Rolando 2002) and other animals (Duncan *et al.* 2015); for example, Rühmann *et al.* (2019) found that great spotted cuckoos *Clamator glandarius* had larger home ranges where there was significantly lower food availability per unit area. Autumn home range, often in outwash sands and river deltas with comparatively lower food resources, was the largest and most variable, with the longest foraging distance. This reduced food availability coupled with hunting disturbance, which occurs during September-November in Iceland, could plausibly explain our results.

Our study suggests high spatial and temporal repeatability in Barnacle Geese, which was expected, as strong philopatry is well documented among Anserinae (Robertson & Cooke 1999). Although there was only a small sample size of birds with multiple years of data (three individuals), a high percentage of overlap in home range was observed in winter, spring and, to a lesser extent, summer, as the three individuals generally returned to the same foraging, roosting and nesting locations in successive years (Figure 3). There was also evidence of temporal repeatability among years in the arrival and departure dates of these three individuals to their home range in different parts of the annual cycle.

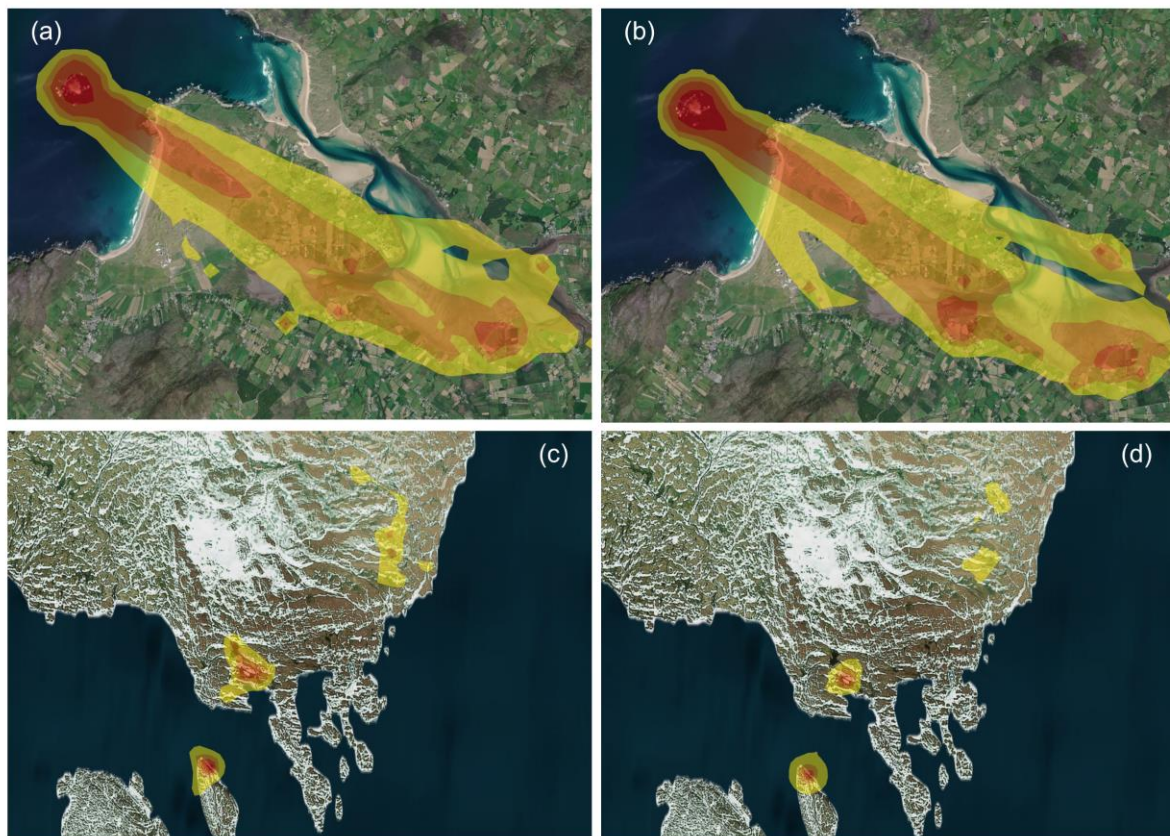


Figure 3 Spatial repeatability in home range among years. Top panel: winter home range of an individual bird in (a) winter 2018-2019 and (b) winter 2019-2020. Bottom panel: summer home range of individual bird in (c) breeding season 2018 and (d) breeding season 2019. Home range is delineated into the 25%, 50%, 75% and 80-99% utilisation distribution (coloured darkest to lightest).

Our study also suggests admixture of the population on the wintering grounds, which is of interest, particularly in light of ongoing avian influenza (Miller 2022) and as non-random mate selection and resource partitioning can ultimately lead to genetic divergence (Ely *et al.* 2017). Although birds were tagged in just three sites in Ireland spanning ~140km, breeding home ranges were located throughout north-east Greenland (Okselandet, Jameson Land, Germania Land, Daniel Bruun Land, Ole Rømer Land, Milne Land, Andrée Land) spanning ~800km. This indicates winter admixture and no non-random association between particular wintering and breeding sites (i.e. birds that socialise in winter do not breed together). None of the birds tagged later in our study (2018-2019) were recorded breeding in Iceland, although their range during autumn staging overlapped with the range of the Iceland-breeding population.

Conservation and management

One important conservation consideration highlighted by this study is the intense and almost exclusive use of agricultural land prior to breeding. A shift from natural to agricultural land during spring staging was documented by Percival & Percival (1997) in the 1990s and the tagged geese in our study preferentially used agricultural land in spring too. Resources consumed during spring staging provide important pre-breeding reserves for onward migration and capital for breeding investment (Hahn *et al.* 2011). The attraction to agricultural pasture highlights the importance of engagement with stakeholders to manage conflicts (such as that observed on Islay; Scottish Natural Heritage 2020), as loss of late winter and spring foraging resources may result in negative carry-over effects to breeding. Similarly, the growth in the population of overwintering Barnacle Goose in Ireland from 2,800 in 1958 to 16,237 in 2018 (Doyle *et al.* 2018) and the use this species makes of agricultural grassland is likely to cause

conflicts. Therefore the data collected in this study are likely to be part of the discussions regarding this issue. A second important conservation consideration highlighted by this study is that tagged geese foraged in a relatively small area of extensive suitable habitat in winter and spring. Several geese also remained in the same roosting and foraging networks throughout the entire winter season and, for the small number of geese that switched network, the switch was usually permanent. This network fidelity is important to take into account when designing refuges because geese may not use a refuge outside their network, even if it presents suitable and attractive habitat. Hence, it is important to combine these holistic top-down determinants of site selection in the landscape with complementary bottom-up factors, such as management of sward height (Si *et al.* 2011), when designing management prescriptions to attract or deter geese.

The data collected in this study also identifies areas of conservation importance for Greenland Barnacle Geese. It was noted from the data that, after departing Iceland in autumn, 9 of the 11 trajectories for which we had data on autumn migration included an extended stopover on Islay (Scotland) before returning to the winter home range in Ireland. These birds remained on Islay for between 8 and 38 days (average 19 days), but none remained on Islay for the entire winter season, despite the extended stopover. This highlights that a large proportion of the Greenland population mix in Islay each year and thus the international flyway importance of Islay. In addition, most tagged birds settled in or near the Skeiðarársandur outwash plain on the Icelandic south coast during autumn staging, highlighting this as a key site for Barnacle Geese on migration through Iceland.

Finally, the data collected in this study provides insight into the remote breeding range of Greenland Barnacle Geese. Tagged birds in our study extended from Føn fjord (70°N) to Cirkus Kløft (77°N), reflecting the distribution observed during aerial surveys by Boertmann *et al.* (2015) and the expeditions to Greenland between the 1950s and 1980s. Analysis of the trajectories revealed that some individuals settled in a nesting locale within the home range in May and June, but then moved to a new post-nesting locale in late June or July, while other individuals remained in the same locale throughout the summer. This post-nesting redistribution is similar to behaviour observed by Madsen *et al.* (1984). The post-nesting home range was similar in size to the home range of individuals that remained in the one locale throughout the summer, while the nesting home range was smaller, as birds were constrained by nest incubation and defence.

The results of this study are taken from a relatively small sample size (18 individuals) which were tagged in a small number of sites, limiting the robustness of the conclusions that can be drawn regarding fine scale habitat selection. Because the tags must store GPS data while the bird is in the remote Arctic, a limited number of fixes can be collected per day, which also limits the daily resolution of activity patterns. Such tags often do not collect data for more than one year, which limits the opportunity to assess trends in one individual over time. Although the data collected in this study provided useful data for conservation and management, future studies should aim to increase the number of tags deployed and aim to obtain data with improved resolution of the interaction with the Arctic habitats, as this is where the knowledge gap exists.

Conclusion

Our Brownian Bridge model delineated the home ranges of Barnacle Geese throughout the annual cycle in both northern Europe and the high Arctic. From this, foraging distance was calculated and broad activity patterns were described with particular reference to conservation considerations. In addition, our study provided new insights into remote Barnacle Goose summering locations in the high Arctic, as well as identifying key sites of conservation importance during migration. Although our study fundamentally provides data on the movement of Barnacle Geese, this can be used to inform a range of pure and applied ornithological issues including resource partitioning, human-wildlife conflicts and the dissemination of zoonotic disease (e.g. avian influenza).

References

- Avé, M. H., Voslamber, B., Hallmann, C. A. & Stahl, J. 2017. Rearing conditions of greylag geese affect habitat choice throughout life. - *Wildlife Biol.* 2017: 1–8.
- Bengtsson, D., Avril, A., Gunnarsson, G., Elmberg, J., Söderquist, P., Norevik, G., Tolf, C., Safi, K., Fiedler, W., Wikelski, M., Olsen, B. and Waldenström, J. 2014. Movements, home-range size and habitat selection of Mallards during autumn migration. *PLoS One* 9: e100764.
- Black, J. M., Choudhury, S. & Owen, M. 1996. Do Barnacle Geese benefit from lifelong monogamy? In: Black, J. M. and Hulme, M. (eds), *Partnerships in Birds: The Study of Monogamy*. Oxford University Press, in press.
- Black, J. M., Prop, J. & Larsson, K. 2014. *The Barnacle Goose*. T & AD Poyser.
- Boertmann, D., Olsen, K. & Nielsen, R. D. 2015. Geese in Northeast and North Greenland as recorded on aerial surveys in 2008 and 2009. *Dansk Ornitol. Foren. Tidsskr.* 109: 206–217.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24: 346–352.
- Cabot, D. & West, B. 1973. Population dynamics of Barnacle Geese, *Branta leucopsis*, in Ireland. *Proc. R. Ir. Acad. B.* 73: 415–443.
- Cabot, D., Nairn, R., Newton, S. & Viney, M. 1984. *Biological Expedition of Jameson Land Greenland 1984*. Barnacle Books, Dublin.
- Cabot, D., Goodwillie, R. & Viney, M. 1988. *Irish expedition to north-east Greenland 1987*. Barnacle Books, Dublin.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197: 516–519.
- de Boer, R., Bauer, S., van der Jeugd, H. P., Ens, B. J., Griffin, L., Cabot, D., Exo, K.-M., Nolet, B. A. & Kölzsch, A. 2014. Een vergelijking van de voorjaarsstrek van drie populaties Brandganzen met behulp van GPS-satellietzenders. *Limosa* 87: 99–106.
- Doyle, S., Walsh, A., McMahon, B. J. & Tierney, T. D. 2018. Barnacle Geese *Branta leucopsis* in Ireland: results of the 2018 census. *Irish Birds* 11: 23–28.
- Doyle, S., Cabot, D., Walsh, A., Inger, R., Bearhop, S. & McMahon, B. J. 2020. Temperature and precipitation at migratory grounds influence demographic trends of an Arctic-breeding bird. *Glob. Chang. Biol.* 26: 5447–5458.
- Doyle, S., Cabot, D., Griffin, L., Kane, A., Colhoun, K., Bearhop, S. & McMahon, B. J. 2021. Spring and autumn movements of an Arctic bird in relation to temperature and primary production. *J. Avian Biol.* 52: e02830.
- Duncan, C., Nilsen, E. B., Linnell, J. D. C. & Pettorelli, N. 2015. Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora. *Remote Sens. Ecol. Conserv.* 1: 39–50.
- Durant, D., Fritz, H. & Duncan, P. 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. *J. Avian Biol.* 35: 144–152.
- Ely, C. R., Wilson, R. E. & Talbot, S. L. 2017. Genetic structure among greater white-fronted goose populations of the Pacific Flyway. *Ecol. Evol.* 7: 2956–2968.
- Ferns, P. N. & Green, G. H. 1975. Observations of Pink-footed and Barnacle Geese in the Kong Oscar Fjord region of north-east Greenland 1974. *Wildfowl* 26: 131–138.
- Fox, A. D. & Abraham, K. F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. *Ambio* 46: 188–197.
- Fox, A. D. & Leafloor, J. O. 2018. A global audit of the status and trends of Arctic

- and Northern Hemisphere goose population.
- Giroux, J.-F. & Patterson, I. J. 1995. Daily movements and habitat use by radio-tagged Pink-footed Geese *Anser brachyrhynchus* wintering in northeast Scotland. *Wildfowl* 46: 31–44.
- Hahn, S., Loonen, M. J. J. E. & Klaassen, M. 2011. The reliance on distant resources for egg formation in high Arctic breeding Barnacle Geese *Branta leucopsis*. *J. Avian Biol.* 42: 159–168.
- Hall, A. B. 1962. Goose observations from Scoresby Land, 1962. *Wildfowl Trust Fourteenth*: 94–97.
- Hardy, D. E. 1979. Observations on geese of the Kong Oscars Fjord region of North-east Greenland, 1971. *Dansk Ornithol. Foren. Tidsskr.* 73: 185–189.
- Horne, J. S., Garton, E. O., Krone, S. M. & Lewis, J. S. 2007. Analyzing animal movements using Brownian Bridges. *Ecology* 88: 2354–2363.
- Jensen, G. H., Pellissier, L., Tombre, I. M. & Madsen, J. 2017. Landscape selection by migratory geese: implications for hunting organisation. *Wildlife Biol.* 2017: wlb.00192.
- Jensen, G. H., Madsen, J., Nagy, S. & Lewis, M. 2018. AEWA International Single Species Management Plan for the Barnacle Goose *Branta leucopsis* - Russia/Germany & Netherlands population, East Greenland/Scotland & Ireland population, Svalbard/South-west Scotland population. AEWA Tech. Ser. No. 63
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K.-M., van der Jeugd, H. P. & Nolet, B. A. 2015. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *J. Anim. Ecol.* 84: 272–283.
- Madsen, J., Boertmann, D. & Mortensen, C. E. 1984. The significance of Jameson Land, East Greenland, as a moulting and breeding area for geese: results of censuses 1982–1984. *Dansk Ornithol. Foren. Tidsskr.* 78: 121–131.
- Marris, R. & Webbe, A. H. F. 1969. Observations of Birds in East Greenland, 1966. *Dansk Ornithol. Foren. Tidsskr.* 63: 161–170.
- Mason, T. H. E., Keane, A., Redpath, S. M. & Bunnefeld, N. 2017. The changing environment of conservation conflict: geese and farming in Scotland. *J. Appl. Ecol.* 55: 651–662.
- Meltofte, H. 1975. Ornithological observations in Germania Land, Northeast Greenland, 1975. *Dansk Ornithol. Foren. Tidsskr.* 71: 81–94.
- Miller, B. J. 2022. Why unprecedented bird flu outbreaks sweeping the world are concerning scientists. *Nature* 606: 18–19.
- Mitchell, C. & Hall, C. 2020. Greenland barnacle geese *Branta leucopsis* in Britain and Ireland: results of the international census, spring 2020.
- Percival, A. S. M. & Percival, T. 1997. Feeding ecology of Barnacle Geese on their spring staging grounds in Northern Iceland. *Ecography (Cop.)*. 20: 461–465.
- R Core Team 2021. R: A language and environment for statistical computing.
- Robertson, G. J. and Cooke, F. 1999. Winter philopatry in migratory waterfowl. *Auk* 116: 20–34.
- Rolando, A. 2002. On the ecology of home ranges in birds. *Rev. d'Écologie* 57: 53–73.
- Rühmann, J., Soler, M., Pérez-Contreras, T. & Ibáñez-Álamo, J. D. 2019. Territoriality and variation in home range size through the entire annual range of migratory great spotted cuckoos (*Clamator glandarius*). *Sci. Rep.* 9: 6238.

- Scottish Natural Heritage 2020. Islay sustainable goose management strategy.
- Shariati, M., Skidmore, A. K., Darvishzadeh, R., Exo, K. M., Kölzsch, A., Griffin, L., Stahl, J., Cabot, D. & Toxopeus, A. G. 2017. Expert system for modelling stopover site selection by barnacle geese. *Ecol. Modell.* 359: 398–405.
- Shariatinajafabadi, M., Wang, T., Skidmore, A. K., Toxopeus, A. G., Kölzsch, A., Nolet, B. A., Exo, K.-M., Griffin, L., Stahl, J. & Cabot, D. 2014. Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS One* 9: e108331.
- Si, Y., Skidmore, A. K., Wang, T., de Boer, W. F., Toxopeus, A. G., Schlerf, M., Oudshoorn, M., Zwerver, S., van der Jeugd, H., Exo, K.-M. & Prins, H. H. T. 2011. Distribution of Barnacle Geese *Branta leucopsis* in relation to food resources, distance to roosts, and the location of refuges. *Ardea* 99: 217–226.
- Thornton, M. J., Mitchell, C., Griffin, L. R., Briers, R. A., Minshull, B., Maciver, A. & White, P. J. C. 2021. Multi-scale habitat selection and spatial analysis reveals a mismatch between the wintering distribution of a threatened population of Taiga Bean Geese *Anser fabalis* and its protected area. *Bird Study* 68: 157–173.
- Tombre, I., Brunner, A., D'Hondt, B., Düttmann, H., Enzerink, R., Fox, A., Feige, N., Heldbjerg, H., Herraro, B., Huysentruyt, F., Kostiuschyn, V., Månsson, J., McKenzie, R., Mensink, G., Meyers, E., Midtgaard, L., Nilsson, L., Nolet, B., Petrovych, O., Post, K., Scallan, D., Teräsväinen, M., Uldal, C., Westebring, M. & Høj Jensen, G. 2019. An overview of the management measures for geese in Range States of the European Goose Management Platform.
- Trinder, M. 2014. Status and population viability of Greenland Barnacle Geese on Islay.
- Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. *J. Avian Biol.* 41: 621–626.

Supplementary Material 1

Results of the matched cohort study are presented in Table 1.

Table 1 The mean proportion of time engaged in each behaviour during the matched cohort study for each tag type. Blanks ("-") indicate that this behaviour was not observed by the cohort during the study.

Behaviour	Tag type		
	leg ring only	neck collar transmitter and leg ring	unmarked
attack	0.01	-	0.03
drink	0.11	0.03	0.06
flee	-	0.01	0.01
forage	0.57	0.74	0.70
hiss	-	-	0.01
preen	0.11	0.35	0.17
stand	-	0.01	0.10
stretch	-	-	0.01
vigilance	0.28	0.06	0.07
walk	0.08	0.08	0.08

Supplementary Material 2

Greenland Barnacle Goose home range area and foraging distances throughout the annual cycle are presented in Table 1.

Table 1 The core and overall area of Barnacle Goose home ranges (km²) and the core and maximum foraging distances of Barnacle Geese (km) during each period of the annual cycle (winter, spring, summer and autumn). For nesting birds, nesting (marked *) and post-breeding (marked **) values are provided separately, while for probable non-breeding birds, one value is provided for the whole summer.

	Bird	Year	Core Home Range	Overall Home Range	Core Foraging Distance	Maximum Foraging Distance
winter	15226 (female)	2017-2018	0.3	7.0	6.0	6.1
	15226 (female)	2018-2019	2.7	20.8	9.3	10.6
	15226 (female)	2019-2020	3.3	22.1	9.4	10.1
	15256 (female)	2018-2019	3.0	23.1	9.6	10.8
	15259 (female)	2017-2018	1.3	14.9	3.2	11.0
	15259 (female)	2018-2019	2.9	18.3	9.7	10.8
	15261 (female)	2018-2019	0.9	17.7	6.2	9.5
	15261 (female)	2019-2020	1.3	16.9	9.1	9.8
	15262 (female)	2018-2019	0.4	5.8	0.5	3.3
	15272 (male)	2017-2018	1.3	14.9	10.7	10.9
	16133 (male)	2018-2019	3.7	38.3	12.2	12.4
	40018 (female)	2018-2019	4.7	35.1	11.5	13.1
	40281 (female)	2018-2019	3.3	26.3	13.1	13.2
	40282 (male)	2018-2019	3.1	25.3	11.5	11.7
	65698 (male)	2008-2009	0.5	4.6	3.3	3.6
	65698 (male)	2009-2010	0.9	2.3	1.7	1.7
	78199 (male)	2009-2010	0.3	3.5	0.8	2.3
	78206 (male)	2007-2008	0.4	5.8	1.7	3.4
	78207 (male)	2007-2008	0.1	0.3	0.5	0.9
	78207 (male)	2008-2009	0.6	15.3	1.5	5.4
	78208 (male)	2007-2008	0.1	0.3	0.3	0.4
	78208 (male)	2008-2009	0.4	5.9	0.4	3.1
	78209 (male)	2007-2008	1.0	5.9	3.4	3.7
	78210 (male)	2007-2008	0.1	0.3	0.2	0.4
spring	15226 (female)	2018	0.5	4.9	1.9	3.2
	15226 (female)	2019	0.4	5.3	0.5	4.1
	15256 (female)	2018	1.4	22.4	6.8	9.8
	15256 (female)	2019	2.6	18.8	4.6	6.4
	15259 (female)	2018	0.5	1.9	1.5	1.6
	15261 (female)	2018	0.9	8.2	1.6	2.7
	15261 (female)	2019	0.9	13.6	5.5	11.8
	15262 (female)	2018	1.0	11.3	4.3	4.8
	65698 (male)	2009	0.9	22.0	1.3	17.1
	70563 (male)	2010	1.9	9.1	3.5	3.7
	78199 (male)	2010	0.4	1.2	1.0	1.2

	Bird	Year	Core Home Range	Overall Home Range	Core Foraging Distance	Maximum Foraging Distance
summer	78207 (male)	2008	0.5	5.8	3.7	3.8
	78208 (male)	2008	0.7	5.5	1.9	2.3
	78209 (male)	2008	0.1	0.2	0.2	0.4
	78210 (male)	2008	1.6	10.8	3.5	3.9
	15226 (female)*	2018	0.3	1.3	0.4	0.8
	15226 (female)**	2018	2.0	22.0	7.0	15.1
	15226 (female)*	2019	0.7	3.1	1.5	1.7
	15226 (female)**	2019	18.0	67.3	5.2	14.7
	15256 (female)	2018	2.1	30.7	14.6	18.6
	15259 (female)*	2018	1.4	13.2	0.8	13.2
	15259 (female)**	2018	2.5	20.0	12.6	15.0
	15261 (female)*	2018	0.2	1.8	0.3	1.8
	15261 (female)**	2018	1.4	16.9	1.7	16.1
	15261 (female)*	2019	0.1	0.1	0.2	0.2
	15261 (female)**	2019	15.2	87.4	5.0	20.4
	15262 (female)	2018	4.5	31.9	13.9	16.5
	15272 (male)	2018	0.1	21.4	0.4	42.2
	65698 (male)*	2009	6.6	23.1	1.6	3.4
	65698 (male)**	2009	7.8	34.5	7.4	8.7
	70563 (male)	2010	1.5	11.0	11.9	12.6
	78199 (male)	2010	5.9	46.1	39.6	49.0
	78207 (male)*	2008	5.8	11.1	4.4	4.8
	78207 (male)**	2008	-	-	9.1	14.2
	78208 (male)*	2008	0.1	0.7	0.2	0.8
	78208 (male)**	2008	3.3	52.5	19.5	20.5
	78209 (male)	2008	1.6	22.4	3.4	19.9
	78209 (male)	2009	3.3	36.7	6.0	7.3
	78210 (male)	2008	11.3	53.7	4.9	85.4
autumn	15226 (female)	2018	12.1	45.3	23.7	24.7
	15226 (female)	2019	4.3	52.5	31.3	50.0
	15256 (female)	2018	14.9	56.5	17.0	17.8
	15259 (female)	2018	14.5	55.5	8.6	36.1
	15261 (female)	2018	8.9	68.3	7.1	83.5
	15261 (female)	2019	6.7	54.7	40.7	43.2
	15262 (female)	2018	7.5	81.0	26.4	41.4
	65698 (male)	2009	69.7	69.7	40.2	42.4
	78199 (male)	2010	2.2	14.2	7.9	8.5
	78207 (male)	2008	1.6	14.3	3.2	9.6
	78208 (male)	2008	3.5	17.3	6.9	7.3
	78210 (male)	2008	1.0	46.6	19.4	27.4