

Site fidelity and home range variation during the breeding season of peregrine falcons (*Falco peregrinus*) in Yamal, Russia

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Abstract Many different ecological factors affecting the size, use, and spatial configuration of home ranges have been investigated, yet the chronology of the breeding cycle has been relatively under studied. Here, we studied peregrine falcons (*Falco peregrinus*) to describe variation in home range within and between breeding seasons in the Yamal peninsula, a region of the Russian Arctic with a high breeding density of peregrines. We used satellite telemetry to investigate variation in home range at different stages of the breeding cycle during three breeding seasons (2009–2011). We fitted Argos satellite transmitters to 10 breeding peregrines (nine females and one male) and two male fledglings. All breeding females showed fidelity to the region of the southwestern Yamal peninsula, but they were not necessarily faithful to their specific breeding ranges with 33 % dispersing to new ranges up to 40 km away.

The population of peregrines in our study area was relatively synchronous in their breeding chronology, with clutches initiated in close synchrony in early June despite the birds arriving on their breeding ranges ca. 3 weeks earlier. The average home range size for breeding females was 98 km² (95 % Maximum Convex Polygon). Over the breeding season, the home range area utilized by females increased in the late nestling period and again after the chicks fledged. Expansion of the home range coincided with changes in behavior associated with parental care, resulting in greater activity and more time spent away from the nest area when the female began hunting to provision nestlings and fledglings.

Keywords Arctic tundra · Behavioral response · Breeding cycle · Breeding dispersal · Satellite tracking

Vasily Sokolov and Nicolas Lecomte have contributed equally to this work.

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Introduction

Understanding factors affecting animal movement is fundamental for describing space use by wildlife but also for

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management and conservation. A central concept to illustrate animal movement is the home range, which during the breeding season is the area used by an animal to forage, mate and care for young (Burt 1943; Brown and Orians 1970; Börger et al. 2008). Home range is also a useful measure of the scale at which species operate and is likely influenced by multiple biotic and abiotic factors (Drent and Daan 1980; Mace and Harvey 1983; Adams 2001). Many different ecological factors affecting the size, use and spatial configuration of home ranges have been investigated between species, populations or individuals, such as several habitat-related structures, prey availability and population dynamic parameters of the target population (e.g., Gaines and Johnson 1982; Lurz et al. 2000; Peery 2000; Rutz 2006). However, the chronology of the breeding cycle has received relatively little attention despite being central to the concept of home range, which states a direct link between space use and energy needs required during the breeding stages (but see Beltran et al. 2010).

Since the technological revolution of remote sensing applied to animals, our knowledge about home range has expanded dramatically (Cagnacci et al. 2010). Now, the possibility to use relatively small and light transmitters has reduced the risks of negative impacts on survival or reproduction, allowing researchers to work on rare and/or sensitive species (Barron et al. 2010; but see Murray and Fuller 2000; Peniche et al. 2011). Recorded locations where individuals may occur provide the raw material for home range modelization (Millspaugh and Marzluff 2001; Getz et al. 2007).

In birds, it remains unclear how home range may change during the breeding cycle from egg laying through to post-fledging dispersal of the brood, despite this being a key period of parental care with associated energy trade-offs between parents and offspring. This paucity of knowledge is exacerbated in the Arctic, where remoteness constitutes a challenge for monitoring home ranges. Furthermore, the brief window of opportunity for breeding when food is available and environmental conditions are favorable, means that the Arctic is an interesting region in which to examine the temporal dynamics of home ranges.

In the Arctic, top predators play a crucial role in ecosystem functioning, and their use of breeding habitat can bear information on both their spatial requirements and availability of their prey. The peregrine falcon (*Falco peregrinus*; hereafter peregrine), a generalist bird predator, is known to feed on most of the avian species available in the tundra during the short breeding season (Bradley and Oliphant 1991; Rosenfield et al. 1997; Dawson et al. 2011). If and how home ranges vary over this short window of time remains unclear and studies on the peregrine have not yet answered these questions, since they are relatively few

and based on very different ecosystems and methods as well as sample sizes and length of investigation (e.g., White and Nelson 1991; Jenkins and Benn 1998; Ganusevich et al. 2004; Lapointe et al. 2013).

Here, we describe the home range of this top predator for three consecutive years (2009–2011) in the Yamal peninsula, a region of the Russian Arctic with a high breeding density of peregrines (Quinn and Kokorev 2000; Paskhalny and Golovatin 2009). Specifically, our objectives in this study are (1) to examine the fidelity of individuals to their nest site and breeding range across years, (2) to determine temporal changes in range use within and between years and across individuals and (3) to describe how the size and overlap of home ranges changed during the breeding period. To do so, we have used satellite telemetry to monitor peregrine movement at different stages of the breeding cycle and discussed our findings in relation to the constraints imposed by parental care.

Materials and methods

Study area

Our observations on the *calidus* subspecies of the peregrine from 2009 to 2011 were conducted at the Erkuta river (68°13'N 69°09'E), southwestern Yamal peninsula, Russia. This region is classified as low-shrub tundra zone (low arctic; Walker et al. 2005), a landscape characterized by a treeless mosaic of ponds, lakes and bogs, with numerous patches of willow thicket. Our study area included the Erkuta and Payuta rivers interspersed with small hills (ca. 50 m high) and sand cliffs up to 40 m high along rivers and lake banks, which offer potential nesting sites for peregrines. Where the Erkuta river, and the more southerly Enzor and Baydarata rivers, enter the Kara Sea there is a large expanse of low lying, saline marshes in the Baydaratskaya Bay. This network of rivers, marshes and lowland tundra is a hotspot on the Yamal peninsula for migrating and molting birds (Danilov et al. 1984; Estafyev 1986; Chernichko et al. 1998; Sokolov 2003). See details of the study area in Sokolov et al. (2012). In 2009, we explored a 400 km² survey plot via motorboats on the Erkuta river and its tributaries, together with foot surveys of adjacent tundra regions; we found a total of 12 occupied breeding ranges with 10 active nests. In subsequent years, no systematic survey took place though 9 and 10 breeding ranges were visited opportunistically in 2010 and 2011, respectively. The study area supported a maximum of 3.3 occupied breeding ranges per 100 km², indicating that Erkuta is an important breeding region for the peregrine on the Yamal peninsula (see also Danilov et al. 1984; Paskhalny and Golovatin 2009).

Satellite transmitters and trapping

We used 18 g Argos satellite transmitters (Solar PTT100, Microwave Telemetry Inc., Columbia, MD, USA). The duty cycle for signal transmission was 10 h on/24 off, allowing us to cover most of the daily activities of the birds over the breeding cycle. Argos location data are based on the Doppler effect and location points are of variable quality—classified as location classes (LC). The actual accuracy of location data is difficult to assess but Argos error estimates for different location classes are as follows: LC3 \leq 250 m, LC2 \leq 500 m, LC1 \leq 1,500 m, whereas those at LC0, A, B or Z have no location accuracy (CLS 2014). In this study, we used high-quality Argos LC 2 and 3 signals only.

Over 3 years, the number of high-quality signals was 4,533 from a total of ca. 25,500 signals. The number of positions per bird ranged from 111 to 430, with an average of 3 per day. The total number of days with signals was 1,035 (average \pm SE: 74 ± 5 per bird per year), corresponding to 74 % of the 1,403 days when birds were present in the breeding region.

In 2009, we trapped and deployed Argos satellite transmitters on 10 breeding adults (nine females and a male, which was paired with one of the nine females). In 2010, we also equipped two nestlings of two of the nine females. We used a noose-carpet trap set at the nest site to capture target adults during incubation, while we equipped the chicks prior to fledging when monitoring their nest. Females are typically 15–20 % larger and 40–50 % heavier than males (White et al. 2002), making sexing easy to do in the field. Transmitters were attached with a 5 g harness made of Teflon ribbon stitched at a central ventral rupture point (Kenward et al. 2001). Overall, this represents ca. 2 and 3 % of the body mass of female and male *calidus* peregrines (i.e., ca. 800 and 1,100 g, respectively) and falls within the range recommended to minimize negative effects on the birds (Kenward 2001), but see Barron et al. (2010) and Vandenabeele et al. (2011).

Nesting chronology and success

We divided the breeding period into five stages: pre-laying, incubation, early nestling, late nestling and post-fledging. Pre-laying covered the time period from arrival after spring migration until the start of incubation, which was taken as the period from the penultimate egg until hatching. The nestling period was assumed to last 40 days, with the early nestling stage covering the first 10 days when chicks are still not independent for their thermoregulation and the ‘late nestling’ stage covering the remaining 30 days (White et al. 2002). The post-fledging period was the time from fledging to departure on autumn migration. We back-

calculated first-egg dates by assuming one egg was laid every 48 h, and chicks hatched 33 days after the penultimate egg was laid (Cramp and Simmons 1980). We back-calculated hatching dates from the estimated age of chicks observed during nest monitoring; we estimated the age of chicks during a nest monitoring visit by comparing their development to a photographic chart illustrating the development, at 3-day intervals, of captive-bred chicks of known age.

In 2009, we found three nests of peregrines at the laying stage (one of which failed to hatch), while six other nests already contained full clutches and for four of these nests, we were able to estimate hatching dates and back-calculate laying dates. Thus, we estimated egg-laying dates for seven nests and hatching dates for six nests. In 2010 and 2011, we were able to estimate hatching dates and back-calculate laying dates from the development stage of chicks for three nests in each year.

In 2009, we knew that three nests successfully fledged at least one chick because we observed flying young at the sites, and one nest failed during incubation, probably due to collapse of the sand cliff (as occasionally happens at such sites in this region). Complete nest monitoring was hampered for logistical reasons but in 2010, nests were found at three of the five ranges occupied by satellite tagged females, two of which were known to have fledged chicks, and in 2011, nests were found at three of four occupied ranges, one of which was known to have fledged.

Nest site fidelity

We measured a change of nesting site from 2009 to 2011 by estimating the minimum distance (km) between nest sites from 1 year to the next, derived either from direct geographical positioning of the nest site via handled GPS units (precision = 10 m) or in three cases where nests were not visited, by indirect positioning via Argos locations during the incubation stage of the breeding cycle (we assumed the nest site was the central position of location points). We defined a breeding range as the nest site and surrounding area utilized during the incubation and early nestling period; in subsequent years, females could potentially occupy the same or different nest sites within the same breeding range, or exhibit breeding dispersal to occupy a new breeding range.

Home range area and movements

All statistical analysis was carried out in open-source software R, version 2.12.2 (R Development Core Team 2012). To define the home range of peregrines during the breeding season, we used the adehabitat library (Calenge 2006). In order to maximize the number of locations for

each stage of the breeding cycle, we did not filter the data to eliminate spatial and temporal autocorrelation (De Solla et al. 1999). We quantified the home range area by using the Minimum Convex Polygon (MCP), which is more robust when using unfiltered data (Nilsen et al. 2008) and used 95 % of fixes to define the overall boundaries of peregrine movements (Börger et al. 2008). We then estimated the core area of the home range through fixed-kernel methods (Worton 1989) and calculated 50 % fixed kernels using the least-squares cross-validation procedure to determine the optimal value of the smoothing parameter for a given kernel and sample size (Seaman and Powell 1996; Seaman et al. 1999; Gitzen and Millspaugh 2003). We compared changes in home range size at different stages of the breeding cycle using a general linear mixed model (GLMM) as implemented in the lme4 package (Bates et al. 2013). For this GLMM, we examined residuals to verify that our data met the assumption of linearity and homoscedasticity. We integrated individual identity as a random variable, while using year (2009–2011) and the five individual stages of breeding cycle as fixed factors.

We computed all locations using the PBSmapping package (Schnute et al. 2008) and plotted the distance moved by individuals from the nest (excluding three nests where the exact location was not directly determined via GPS). We used the frequency of locations <500 and >2,000 m from the nest as a proxy measure of time spent ‘near’ and ‘far’ from the nest in relation to stage of the breeding cycle. We used 500 m as a cut-off value as it fits with the accuracy classes used (i.e., LC2 and LC3). Presence/absence near or far from the nest was recorded as a binary response in a GLMM, with breeding stage and year as fixed factors, and individual identity as a random factor. To compare the time spent near or far from the nest for individuals in a given breeding pair, we used a Generalized Linear Model (GLM) with breeding stage and sex as predictor variables.

We examined spatial and temporal autocorrelation in our dataset to examine activity at different stages of the breeding cycle and to identify any diurnal patterns of activity (Boyce et al. 2010). The distance moved by peregrines between sequential location points was positively correlated with interval duration ($R^2 = 0.09$). We obtained residual values from a linear regression of time interval and distance between sequential locations to provide a measure of movement activity. We compared movement activity at different stages of the breeding cycle using a GLMM, with individual identity as a random variable, and year and stage of breeding cycle as fixed factors. To identify diurnal activity patterns during the late nestling and post-fledging stages, we filtered our data to include only sequential locations with a temporal interval of <1 h and then examined the distance moved between locations each hour over a 24 h period.

Results

Nest site fidelity

Over the period 2009–2011, the mean nearest neighbor distance between nest sites in occupied ranges was 6.3 km (range 3.1–15.0 km). In 2010–2011, the mean date of arrival to the Erkuta study area was 18 May (range 10–29 May) and in 2009–2011, the mean date of departure on autumn migration was 15 September (range 28 August–28 September), while the average duration of stay in 2010–2011 was 117 days (Online Resource 1). Breeding peregrines exhibited relative synchrony in their nesting cycle (mean 07 June, SE \pm 0.6 days), with estimated laying dates in 2009–2011 spanning the period of 29 May to 10 June ($N = 18$; Online Resource 2).

In 2010, five females were tracked back to the breeding region, while the remaining five transmitters (including the PTT deployed on the male) stopped working after the birds left the Yamal region. Two of the five returning females exhibited breeding dispersal to new nesting ranges (i.e., 90,875 and 90,877). One female, which experienced a nesting failure in 2009, moved 40 km eastwards along the Erkuta river and apparently bred there in 2010. Though successful in 2009, the second female moved from the 2009 nest location on a lake bank to a river cliff site, 12 km away; this was a known breeding site for peregrines and was occupied by a pair in 2009, though no eggs were seen in the nest scrape (either failed at egg stage or did not lay).

In 2011, four females returned to breed and three occupied the same ranges as the previous year with a mean nest site shift of 0.3 km (range 0.0–1.0 km), while another moved 1.3 km to nest in an adjacent breeding range (Fig. 1). Over 2 years, 67 % (six of nine) of females exhibited fidelity to the breeding range they used in the previous year.

Home range area

Over 3 years, the mean home range size for female peregrines was 102.7 km² SE \pm 13.3 km² (95 % MCP; median 103.5 km², range 20.7–221.6 km²) over the whole breeding season, while the single male occupied a comparable home range of just 19.7 km² (Fig. 2; Online Resource 3). There was no significant difference in mean home range size across years (GLMM, $t = 0.38$, $P = 0.71$), but there was a significant difference with stage of the breeding cycle. While home range size did not differ among pre-laying, incubation and early nestling period (average 9.8 km²; $t = -0.25$, $P = 0.80$), in the late nestling period, female home range increased to reach an average size of 35.1 km² ($t = 2.50$, $P = 0.02$). After the chicks fledged, home ranges tripled in size, reaching an average area of 106.8 km² ($t = 7.29$, $P < 0.001$; Fig. 2).

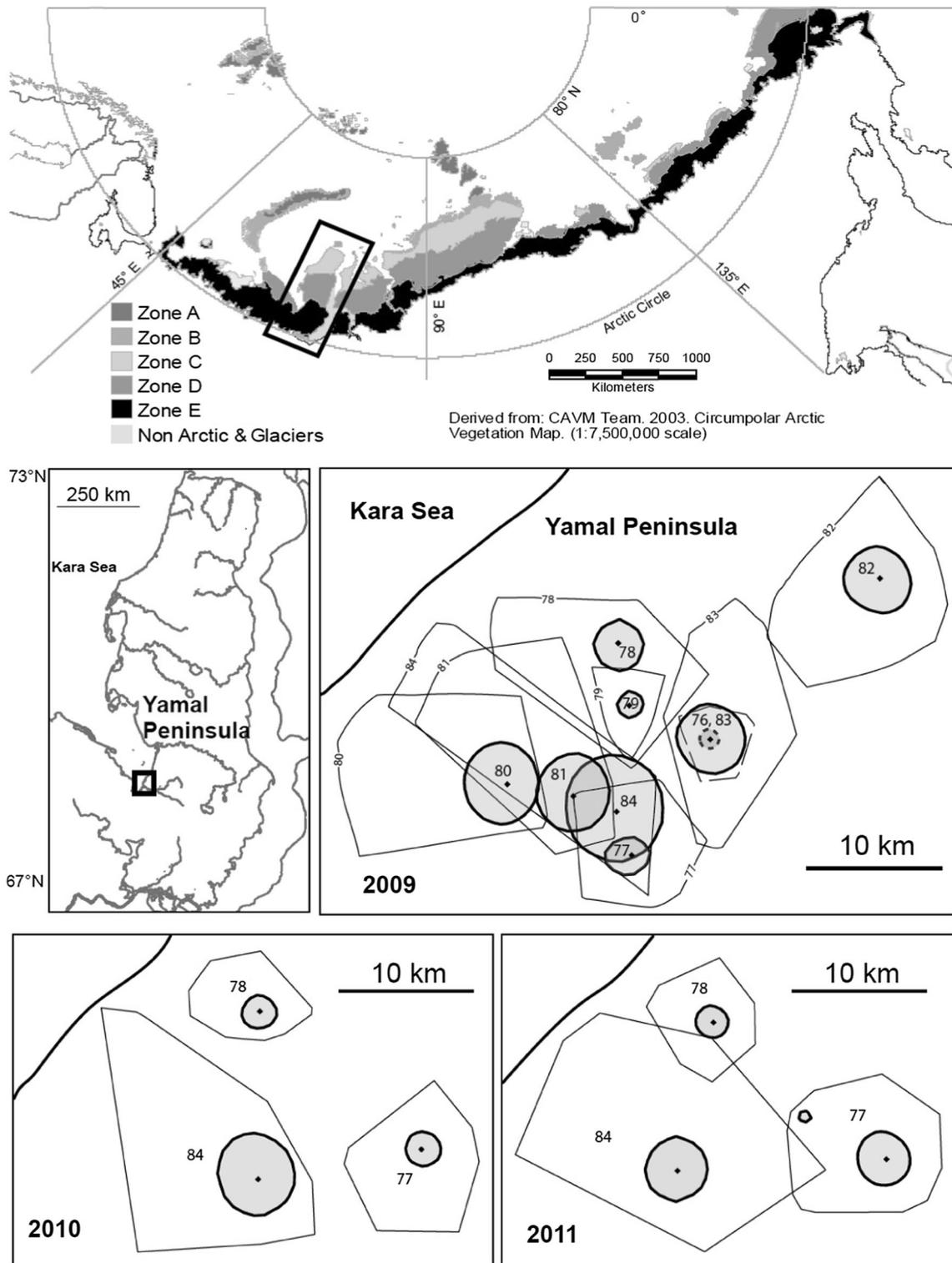


Fig. 1 Map of the study area with the home ranges of eight females (77–84) and one male (76) in 2009–2011. Home range of male 76 is shown with *dashed outline*. Home ranges are estimated with 95 % MCP and *filled polygons* represent 50 % kernel of all location points

The home range of the only tagged male was larger during the incubation period than female ranges, but was smaller at all other stages of the breeding cycle and was completely included within the home range of its mate

(Fig. 1 and Online Resource 3). The change in home range size with stage of the breeding cycle was similar for the male compared to its mate, apart from post-fledging period when it did not exhibit a large increase in range area

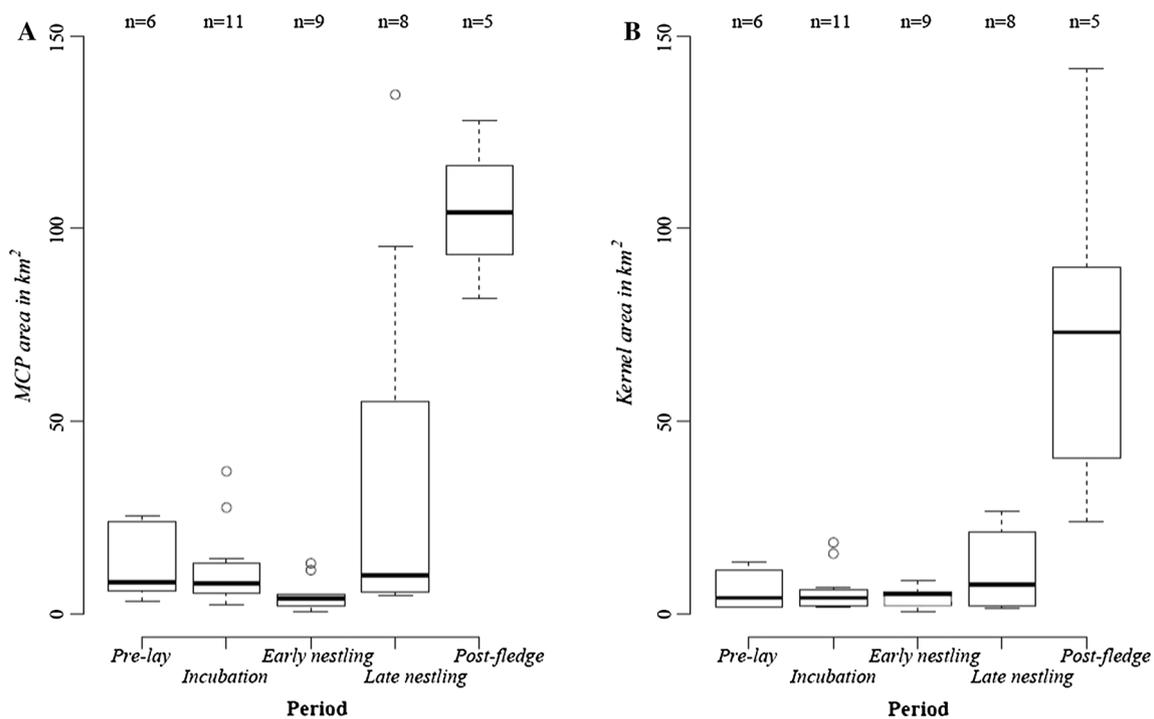


Fig. 2 Female home range area (km²) at different stages of the breeding cycle, 2009–2011. **a** 95 % MCP; **b** 50 % Kernel. Horizontal line shows the median. Bottom and top boxes show the 25th and 75th percentiles, respectively. Vertical dashed lines show interquartile

(Online Resource 3 and 4). Both tagged chicks covered an area of 13 and 66 km² around their nests after fledging, compared with 114 and 132 km² for their respective parents over the same period, and they left the Yamal peninsula on autumn migration 2 days before their parents.

Movements

The maximum linear distance females were recorded from their nest site in the pre-lay, incubation, early nestling, late nestling and post-fledging periods was 10.8, 18.6, 8.2, 22.7 and 34.9 km, respectively. The corresponding distances for the male (excluding the pre-lay stage) were 5.1, 5.8, 4.1 and 6.4 km. Females spent significantly less time far (>2,000 m) from their nests in the early nestling stage ($z = -7.01$, $P < 0.01$) and significantly more time far from their nests during the pre-lay ($z = 1.96$, $P < 0.05$) and post-fledging stages ($z = 14.45$, $P < 0.01$), while they spent significantly less time near (<500 m) their nests over the same stages, respectively ($z = -1.94$, $P < 0.05$; $z = -5.94$, $P < 0.01$; Fig. 3).

Movement activity of female peregrines was significantly greater in the late nestling ($t = 2.44$, $P < 0.05$) and post-fledging periods ($t = 7.74$, $P < 0.01$) than at other stages of the breeding cycle. During the late nestling and post-fledging stages, the diurnal activity pattern of female peregrines indicated that most movements took place in

range of the data and open circles represent outliers. N = the number of breeding stages that were tracked for eight females in 2009, five in 2010 and four in 2011 (no birds were tracked during pre-lay stage in 2009)

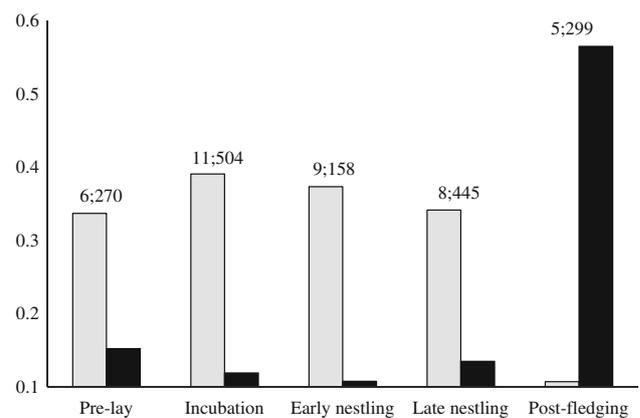


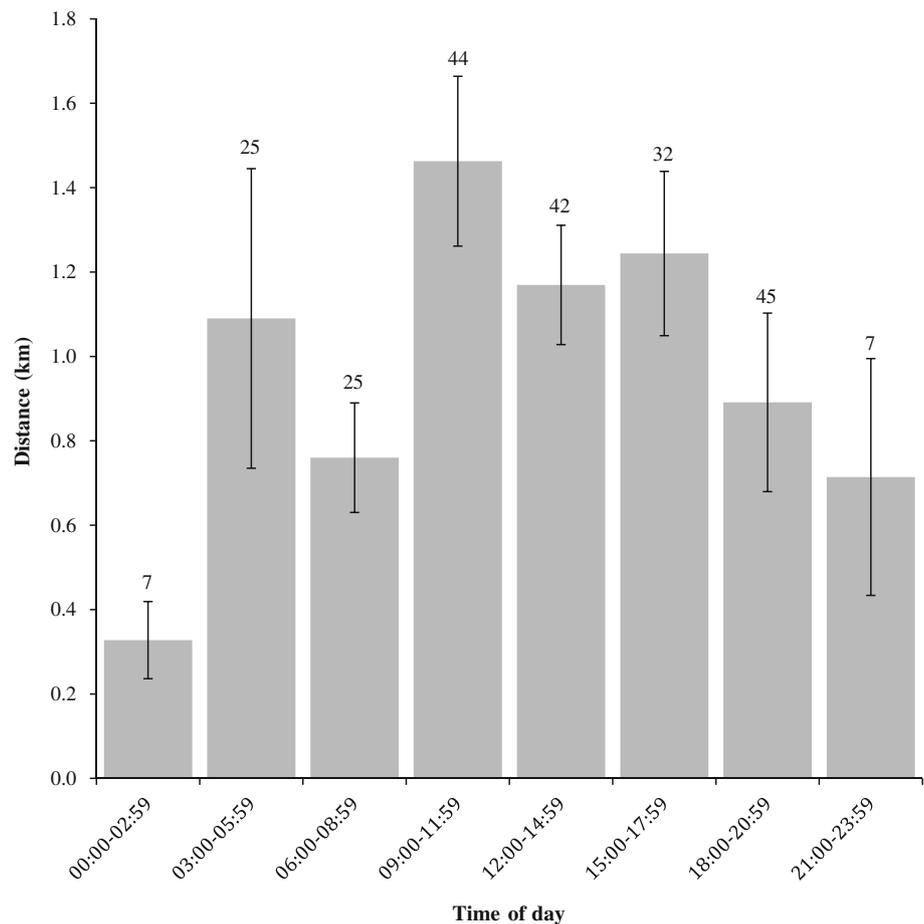
Fig. 3 Chronology of breeding events and movements of peregrines (*Falco peregrinus*) 2009–2011. Gray columns represent proportion of locations close (<500 m) to the nest and black columns the proportion of locations far (>2,000) from the nest at different stages of the breeding cycle (N = number of birds; number of locations)

late morning, while the least activity took place in the period around midnight (Fig. 4).

Home range dynamics after nest failure

Although based on a single individual, the pattern of home range dynamics after nest failure is worth documenting as there is no other known publication of satellite tracking of

Fig. 4 Diurnal movement activity of female peregrines (*Falco peregrinus*) during the late nestling and post-fledging stages of the breeding cycle, 2009–2011. Error bars show SE, and value above bars represent the number of movements initiated in each 3-h block



the ranging behavior of peregrines whose breeding attempt failed at the egg stage. For the female that failed in its breeding attempt, from the date of PTT deployment (12 June) until the 19 June, all locations were received from the vicinity of the nest site and movements were within an area of 3 km² around the nest site (Fig. 5). Following nest failure, the female moved over a vast area of ca. 2,185 km², but within this large range the bird occupied four discreet temporary settlement areas (TSAs; Fig. 5; Online Resource 5).

Discussion

Home range fidelity and breeding chronology

Females exhibited fidelity to the breeding region by returning to our study area in Yamal to breed in subsequent years. However, at a finer spatial scale, they were not necessarily faithful to their specific breeding ranges; we found that 33 % of returning females switched breeding ranges between years. A study using recapture data for a non-migratory population in Scotland found that 9 % of

females switched ranges from 1 year to the next ($N = 66$), though some breeding dispersal movements may have gone undetected (Mearns and Newton 1984). Nevertheless, breeding dispersal was slight, with the maximum distance moved being 40 km along the same river system. Birds that exhibited breeding range fidelity displayed similar home ranges in terms of size and shape from 1 year to the next, suggesting stability of resources across years and/or territorial interactions.

Our monitored population of peregrines was synchronous in their breeding chronology contrasting markedly with southern resident peregrine populations, which can exhibit a range of more than 2 months in egg-laying dates (Rizzolli et al. 2005). Unlike their southern congeners, tundra-breeding, migratory peregrines have little time to lay a replacement clutch after an initial failure during incubation. Breeding could be synchronized with temporal variation in prey availability (Perrins 1970; Drent 2006), as demonstrated in an Australian peregrine study where peak prey availability coincided with the period after fledgling (Olsen and Georges 1993). Climate change can result in a mismatch of resource availability and demand in breeding birds, e.g., (Thomas et al. 2001), which is particularly

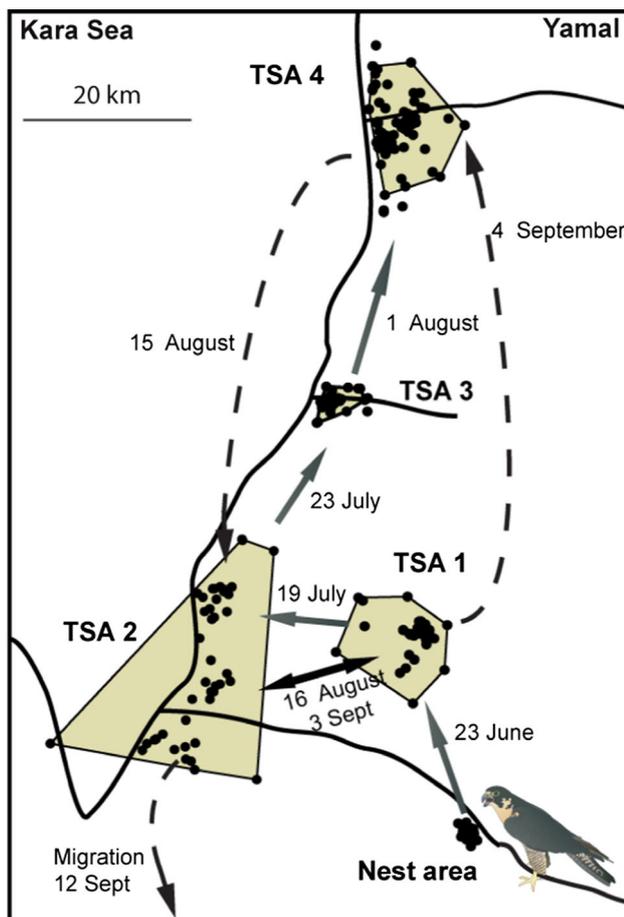


Fig. 5 Movement of a female peregrine (*Falco peregrinus*) following breeding failure, 2009. The 95 % MCP of temporary settlement areas (TSAs) are shown with arrows indicating date and direction of movement between them

critical in the Arctic due to the highly compressed breeding season for birds and the sharp, short-lived peaks in resource availability, e.g., (McKinnon et al. 2012). Future research should focus on understanding the key factors determining the timing of breeding in peregrines, and how they relate to food abundance with regard to a changing arctic climate.

Home range area and movements

Home range areas utilized by female peregrines in this study (mean 98 km²) were substantially smaller than those reported for the same species elsewhere in Arctic Russia by Ganusevich et al. (2004; mean 1,175 km², range 104–1,556 km²), although direct comparison is not appropriate as the former study also incorporated Argos data with lower location accuracy (i.e., LC0 and LC1), which will result in larger range size estimates. The ranges used by peregrines (95 % MCP), were smaller than those used by another large arctic-dwelling raptor, the gyrfalcon (*Falco rusticolus*), in Greenland with a mean 90 % MCP

home range area of 571 km² (range 140–1,197 km²) (Burnham and Newton 2011). This is consistent with the idea that specialist predators like the gyrfalcon require larger home ranges than a generalist like the peregrine (Peery 2000). More recently, GPS satellite telemetry has been used to quantify home ranges of breeding peregrines in southern Québec, Canada (Lapointe et al. 2013), where mean home range size was larger than at Yamal during both the nestling period (mean 83.9 km², range 0.3–392.5 km²) and the post-fledging dependence period in the first month after fledging (mean 201.9 km², range 10.0–811.1 km²). This difference probably reflects greater prey availability in the Arctic, one of the basic driving forces for the evolution of migratory behavior (Alerstam et al. 2003), where the benefits of Arctic breeding include permanent daylight and time limited but abundant resources (Gilg and Yoccoz 2010).

Female peregrines undertake the majority of incubation (Ratcliffe 1993), and this pattern was evident in our study as we only caught one male in the ten birds trapped during incubation. During the latter part of the pre-lay period, and the incubation and early nestling stages, females are mainly provisioned by their mate (Ratcliffe 1993). In the late nestling phase, chicks no longer require thermoregulation by brooding and females then switch to a more active parental care role in hunting prey and provisioning the nestlings. After the chicks leave the nest, they continue to receive parental care and provisioning during the post-fledging dependence period (Sherrod 1983; Mearns 1985).

Home range area can be influenced by temporal changes in parental care behavior (Clutton-Brock 1991). Constraint on movement imposed by the demands of parental care, including the production of eggs in the pre-lay period, and thermoregulation of eggs and chicks in the incubation and early nestling periods corresponds with the small home range area utilized by female peregrines at these stages of the breeding cycle. Expansion of the home range in the late nestling and post-fledging period when females begin to hunt for prey was associated with greater activity and more time spent away from the nest area. In contrast, the one male did not increase its home range area in the later stages of the breeding cycle, but it is not possible to draw any conclusion from this single case.

Although changes in parental care behavior alone can explain the observed variation in female home range size over the breeding cycle, changes in home range size can also be driven by prey abundance and/or dispersion, energy demand, and territoriality of conspecifics e.g., (Hixon 1980; Mace and Harvey 1983; Marzluff et al. 1997; Adams 2001). Lemming and vole (Arvicolinae) numbers were generally low in our study area during 2009–2011 (Sokolova et al. unpublished data). Under such conditions in the Yamal region, breeding peregrines feed almost

exclusively on avian prey, taking a wide range of taxa including passerines, waders, and waterfowl ranging in size from 25 to 1,100 g (e.g., lapland longspur *Calcarius lapponicus* to long-tailed duck *Clangula hyemalis*; Osmolovskaya 1948). We have no data on temporal variation in prey availability in this study but known changes in prey distribution may potentially modify ranging behavior. Many waders and waterfowl move from the tundra to pre-migration feeding and molting areas on the coast (Estafyev 1986; Chernichko et al. 1998), and some females exhibited directional shifts to coastal areas during the post-fledging period (Fig. 1). The female whose nest failed, primarily occupied temporary settlement areas (TSA) in coastal river deltas, indicating the rich prey availability in such areas. Furthermore, released from parental care, the TSA's used by this failed breeding female were situated in coastal areas and of similar size to the home ranges of breeding females in late stages of breeding cycle. Larger home ranges coincided with periods of high energy demand associated with provisioning nestlings and fledglings (Olsen and Tucker 2003) and the need to acquire physiological condition for autumn migration (Newton 2008).

Attendance at the nest area in Yamal was similar to that reported in previous studies of peregrines in the temperate zone of southern Europe (Carlier 1993) and interior Alaska (Palmer et al. 2001), where females spent progressively less time near the nest after the early nestling stage when their chicks were >10 days old. The incubation and early nestling stages were also associated with reduced activity, indicative of low energetic demand during these periods of the nesting cycle (Palmer 1999; Palmer et al. 2001). Female peregrines exhibited a 24-h rhythm of activity, with more activity during the day than at night. Activity rhythms of Arctic birds exhibit marked plasticity and diversity, though certain passerine and wader species have been shown to exhibit a similar 24 h rhythm (Steiger et al. 2013). It is possible that the entrained diurnal rhythm of the peregrine is synchronized with the activity of their prey, thus hunting efficiency and prey availability is highest in the late morning and early evening.

Here, initiation of female hunting behavior in the late nestling period resulted in an enlargement of their home range, which coincided with increasing energy demands, which is closely bound by the short window of the Arctic summer and prey availability. Further monitoring of home range use by peregrines across areas with contrasting prey abundance would help decipher the possible adjustments of this generalist predator to the energetic challenges of breeding in Arctic areas.

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References

- Adams ES (2001) Approaches to the study of territory size and shape. *Annu Rev Ecol Syst* 32:277–303
- Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. *Oikos* 103:247–260
- Barron DG, Brawn JD, Weatherhead PJ (2010) Meta-analysis of transmitter effects on avian behavior and ecology. *Methods Ecol Evol* 1:180–187
- Bates D, Maechler M, Bolker B, Walker S (2013) Fit linear and generalized linear mixed-effects models. <http://lme4r-forgery-project.org/>. Accessed 26 Oct 2013
- Beltran JW, Wunderle JM, Arendt WJ (2010) Changes in home range of breeding and post-breeding male pearly-eyed thrashers in the Luquillo Mountains of Puerto Rico. *Ornitol Neotrop* 21:409–423
- Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650
- Boyce MS, Pitt J, Northrup JM, Morehouse AT, Knopff KH, Cristescu B, Stenhouse GB (2010) Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philos Trans R Soc B* 365:2213–2219
- Bradley M, Oliphant LW (1991) The diet of Peregrine Falcons in Rankin Inlet, Northwest Territories: an unusually high proportion of mammalian prey. *Condor* 93:193–197
- Brown JL, Orians GH (1970) Spacing patterns in mobile animals. *Annu Rev Ecol Syst* 1:239–262
- Burnham KK, Newton I (2011) Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. *Ibis* 153:468–484
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos Trans R Soc B* 365:2157–2162
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- Carlier P (1993) Sex differences in nesting site attendance by peregrine falcons (*Falco peregrinus brookei*). *J Raptor Res* 27:31–34
- Chernichko II, Gromadsky M, Dyadicheva EA, Grinchenko AB (1998) Summer and autumn congestion and migration of waders and on the east coast of Baidaratskaya Bay. *Branta* 1:79–91
- CLS (2014) Argos user's manual 2007–14. <http://www.argos-system.org/manual/>. Accessed 08 April 2014
- Clutton-Brock TH (1991) The evolution of parental care. Monographs in behavior and ecology. Princeton University Press, New Jersey
- Cramp S, Simmons KEL (eds) (1980) The birds of the western Palearctic, vol 2. Oxford University Press, Oxford
- Danilov NN, Ryzhanovskiy VN, Ryabitsev VK (1984) Birds of Yamal. Nauka, Moscow

- Dawson RD, Mossop DH, Boukall B (2011) Prey use and selection in relation to reproduction by Peregrine Falcons breeding along the Yukon River, Canada. *J Raptor Res* 45:27–37
- De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *J Anim Ecol* 68:221–234
- Drent RH (2006) The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. *Ardea* 94:305–322
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Estafeyev AA (1986) Timing of autumn migration and places of Waders concentration in Tundras of European North-East part of USSR. In: Danilov NN et al (eds) Fauna of the vertebrates of the Urals and adjacent territories. UrGU, Sverdlovsk, pp 72–85
- Gaines MS, Johnson ML (1982) Home range size and population dynamics in the Prairie Vole, *Microtus Ochrogaster*. *Oikos* 39:63–70
- Ganusevich SA, Maechtle TL, Seegar WS, Yates MA, McGrady MJ, Fuller M, Schueck L, Dayton J, Henny CJ (2004) Autumn migration and wintering areas of Peregrine Falcons *Falco peregrinus* nesting on the Kola Peninsula, northern Russia. *Ibis* 146:291–297
- Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmsers CC (2007) LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2:e207
- Gilg O, Yoccoz NG (2010) Explaining bird migration. *Science* 327:276–277
- Gitzen RA, Millsaugh JJ (2003) Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildl Soc Bull* 31:823–831
- Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. *Am Nat* 115:510–530
- Jenkins AR, Benn GA (1998) Home range size and habitat requirements of Peregrine Falcons on the Cape Peninsula, South Africa. *J Raptor Res* 32:90–97
- Kenward R (2001) A manual for wildlife radio tagging, 2nd edn. Academic Press, New York
- Kenward RE, Pfeffer RH, Al-Bowardi MA, Fox NC, Riddle KE, Bragin EA, Levin A, Walls SS, Hodder KH (2001) Setting harness sizes and other marking techniques for a falcon with strong sexual dimorphism. *J Field Ornithol* 72:244–257
- Lapointe J, Imbeau L, Tremblay JA, Maisonneuve C, Mazerolle MJ (2013) Habitat use by female peregrine falcons (*Falco peregrinus*) in an agricultural landscape. *Auk* 130:381–391
- Lurz PWW, Garson PJ, Wauters LA (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *J Zool* 251:167–178
- Mace GM, Harvey PH (1983) Energetic constraints on home range size. *Am Nat* 121:120–132
- Marzluff JM, Kimsey BA, Schueck LS, McFadzen ME, Vekasy MS, Bednarz JC (1997) The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. *Condor* 99:567–584
- McKinnon L, Picotin M, Bolduc E, Juillet C, Bety J (2012) Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Can J Zool* 90:961–971
- Mearns R (1985) The hunting ranges of two female peregrines towards the end of a breeding season. *Raptor Res* 19:20–26
- Mearns R, Newton I (1984) Turnover and dispersal in a peregrine *Falco peregrinus* population. *Ibis* 126:347–355
- Millsaugh JJ, Marzluff JM (2001) Radio tracking and animal populations. Academic Press, San Diego, CA
- Murray DL, Fuller MR (2000) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. In: Boitani L, Fuller TK (eds) Research techniques in ethology and animal ecology. Columbia University, New York, pp 15–64
- Newton I (2008) The migration ecology of birds. Academic Press, London
- Nilsen EB, Pedersen S, Linnell JDC (2008) Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecol Res* 23:635–639
- Olsen J, Georges A (1993) Do peregrine fledglings reach independence during peak abundance of their main prey? *J Raptor Res* 27:149–153
- Olsen J, Tucker AD (2003) A brood-size manipulation experiment with Peregrine Falcons, *Falco peregrinus*, near Canberra. *Emu* 103:127–132
- Osmolovskaya VI (1948) The ecology of birds of prey of the Yamal peninsula. *Proc Geogr Inst Acad Sci USSR* 41:5–77
- Palmer AG (1999) Parental care of peregrine falcons in interior Alaska and the effects of low-altitude jet overflights. Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis
- Palmer AG, Nordmeyer DL, Roby DD (2001) Factors influencing nest attendance and time-activity budgets of peregrine falcons in interior Alaska. *Arctic* 54:105–114
- Paskhalny SP, Golovatin MG (2009) The current status of the Peregrine population in Yamal and Lower Ob region. In: Sielicki J, Mizera T (eds) Peregrine Falcon populations—status and perspectives in the 21st century. Life Sciences Press, Warsaw-Poznan, Poland, pp 371–392
- Peery ZM (2000) Factors affecting interspecies variation in home-range size of raptors. *Auk* 117:511–517
- Peniche G, Vaughan-Higgins R, Carter I, Pocknell A, Simpson D, Sainsbury A (2011) Long-term health effects of harness-mounted radio transmitters in red kites (*Milvus milvus*) in England. *Vet Rec* 169:311–316
- Perrins CM (1970) Timing of birds breeding seasons. *Ibis* 112:242–255
- Quinn JL, Kokorev Y (2000) Direct and indirect estimates of Peregrine Falcon population size in northern Eurasia. *Auk* 117:455–464
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ratcliffe D (1993) The peregrine falcon, 2nd edn. Princeton University Press, Princeton, NJ
- Rizzolli F, Sergio F, Marchesi L, Pedrini P (2005) Density, productivity, diet and population status of the Peregrine Falcon *Falco peregrinus* in the Italian Alps. *Bird Study* 52:188–192
- Rosenfield RN, Schneider JW, Papp JM, Seegar WS (1997) Prey of Peregrine Falcons breeding in west Greenland. *Condor* 97:763–770
- Rutz C (2006) Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *Ardea* 94:185–202
- Schnute JT, Boers NM, Haigh R, Couture-Beil A (2008) PBS Mapping 2.57: User's guide. Canadian technical report of fisheries and aquatic sciences, vol 2549
- Seaman D, Powell R (1996) An evaluation of the accuracy of Kernel density estimators for home range analysis. *Ecology* 77:2075–2085
- Seaman D, Millsaugh J, Kernohan B, Brundige G, Raedeke K, Gitzen R (1999) Effects of sample size on kernel home range estimates. *J Wildl Manag* 63:739–747
- Sherrod SK (1983) Behavior of fledgling peregrines. The Peregrine Fund, Ithaca
- Sokolov VA (2003) The bird community of south-western Yamal in fall. Materials about the distribution of birds in the Urals, Priurals and western Siberia, pp 170–175

- Sokolov V, Ehrich D, Yoccoz NG, Sokolov A, Lecomte N (2012) Bird communities of the Arctic shrub tundra of Yamal: habitat specialists and generalists. *PloS One* 7:e50335
- Steiger SS, Valcu M, Spoelstra K, Helm B, Wikelski M, Kempenaers B (2013) When the sun never sets: diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. *Proc R Soc B*. doi:[10.1098/rspb.2013.1016](https://doi.org/10.1098/rspb.2013.1016)
- Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291:2598–2600
- Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2011) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar Biol* 159:1–14
- Walker DA, Raynolds MK, Daniels FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA, Team C (2005) The circumpolar Arctic vegetation map. *J Veg Sci* 16:267–282
- White CM, Nelson RW (1991) Hunting range and strategies in a tundra breeding peregrine and gyrfalcon observed from a helicopter. *J Raptor Res* 25:49–62
- White CM, Clum NJ, Cade TJ, Hunt GW (2002) Peregrine falcon (*Falco peregrinus*). The birds of North America online. Cornell Lab of Ornithology, Ithaca. doi:[10.2173/bna.660](https://doi.org/10.2173/bna.660)
- Worton B (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168