

RESEARCH ARTICLE



Winter home range fidelity and extraterritorial movements of Arctic fox pairs in the Canadian High Arctic

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ABSTRACT

The sociality of the Arctic fox has been extensively studied during the breeding season, so that its summer territorial and generally monogamous social systems are now well described. A key knowledge gap remains, however, during the winter season, when logistic challenges preclude detailed observation of individuals. We have studied the socio-spatial winter dynamics of Arctic fox pairs to determine: (1) winter fidelity of Arctic fox pair mates to their summer home range; (2) the degree to which extraterritorial movements are simultaneous between pair mates; and (3) spatial proximity between pair mates when they perform simultaneous extraterritorial movements. To meet these objectives, 15 Arctic fox pairs from Bylot Island (Nunavut, Canada) were tracked during at least one winter in 2007–2011, using Argos satellite collars, for a total of 21 pair-years. Arctic foxes were generally faithful to their summer home ranges during winter, but some variation occurred among pairs. The degree of territory fidelity was highly correlated between pair mates. When foxes did extraterritorial movements, they performed excursions that were short in duration and generally not synchronized among pair mates. When pair mates were outside the territory at the same time, they did not travel together and rather foraged independently. We discuss some ecological implications of our findings, and suggest that different patterns may be observed in other Arctic fox populations. If such is the case, replicating our study in other parts of the species range will allow productive hypothesis testing regarding the determinants of Arctic fox winter sociality.

KEYWORDS

Pair bonding; satellite tracking; sociality; space use; territory; *Vulpes lagopus*

ABBREVIATIONS

EM: extraterritorial movement; FI: fidelity index; SI: simultaneity index


Introduction

Many canids are socially monogamous, with groups typically including a dominant mated pair and one or more related but reproductively suppressed subordinates (Kleiman 1977; Asa & Valdespino 1998; Baker et al. 2004). This social system implies long-lasting pair bonds that persist across multiple breeding seasons, extensive overlap between home ranges of the pair mates and cooperation in the care of the young (Geffen & Macdonald 1992; Pauw 2000). Social monogamy may optimize individual fitness by enhancing survival and reproductive success (Ralls et al. 2007). It is, however, still unclear why pair mates in some species associate closely year-round, whereas in others they only meet once a year for breeding (Kappeler 2013). A long-lasting pair bond may have some fitness benefits during the non-breeding season. Those benefits can be related to the importance for individuals of maintaining their well-known territory once acquired (Ralls et al. 2007) or to cooperative territory defence (Dobson et al. 2010). Higher benefits may also be obtained the next breeding season by remaining with a

successful and compatible mate. Annually searching for a new mate can increase predation risk and energy cost while travelling through unfamiliar territory, and also increases the risk of mate incompatibility (Kleiman 1977; Ralls et al. 2007). Investigating the social structure during the non-breeding season is important because in many monogamous species the non-breeding season is far longer than the breeding one and sociality during fall–winter could influence dispersal and mortality (Patterson & Messier 2001), with potential effects on population dynamics.

The degree to which activities are simultaneous between pair mates and the spatial proximity of pair mates are two key variables used to describe social monogamy and infer its costs and benefits (Kleiman 1977; Dietz 1984). The degree of simultaneity depends largely on the strength of the pair bond and the need to coordinate activities such as feeding, breeding, resting and territory defence (Kleiman 1981; Kitchen et al. 2005; Bandeira de Melo et al. 2007). Predator avoidance and parental care promote proximity between pair mates (Kleiman 1977, 1981; Pusey 2005), whereas foraging for small prey promotes separation (Parker & Ruttan 1988; White et al. 2000; Kitchen et al. 2005). Territoriality is a

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 Supplemental data for this article can be accessed [here](#).

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common feature in monogamous mammals (Kleiman 1981). Spatial fidelity incurs repetitive or continuous use of previously occupied space (Kitchen et al. 2000). Continued use of a site by an individual is positively related to the cost of changing territory, to the previous reproductive success, and to the probability of mortality in this habitat (Switzer 1993). Range fidelity offers benefits such as knowledge of foraging areas, dens and breeding opportunities (Kitchen et al. 2000). Spatially faithful individuals can make short-term excursions outside of their home range (EMs) to search for mates, resources or better living conditions (Lidicker & Stenseth 1992; Soulsbury et al. 2011). Those movements are different from dispersal movements, which are one-way movements of individuals away from their home range (Lidicker & Stenseth 1992).

We used the Arctic fox (*Vulpes lagopus*) to study spatial fidelity of pair mates and the degree to which simultaneous activities occur between pair mates during the winter season. Year-round partnership and year-round territoriality are observed in many canids such as the kit fox (*Vulpes macrotis*; Ralls et al. 2007), the swift fox (*Vulpes velox*; Kitchen et al. 2005), the maned wolf (*Chrysocyon brachyurus*; Bandeira de Melo et al. 2007), the coyote (*Canis latrans*; Hennessy et al. 2012) and the grey wolf (*Canis lupus*; Mech & Boitani 2010). Arctic foxes form socially monogamous pairs (Norén et al. 2011) and have been reported to mate for life (Audet et al. 2002). Pairs display a strong territorial behaviour, especially during the denning season (April to August), when the pair mates share an overlapping home range (Eberhardt et al. 1982; Prestrud 1992). However, even during this period, pair mates rarely interact (Garrot et al. 1984). Both actively care for the young at the den (Strand et al. 2000), but the pair bond has been reported to gradually weaken over the course of the summer and to break when the young leave the natal den (Fay & Follmann 1982). Winter movements of Arctic foxes are poorly documented. Some telemetry studies found that Arctic foxes tend to remain close to their denning site during winter (Anthony 1997; Landa et al. 1998), whereas field observations suggested that they show extensive seasonal movements, with a movement towards the coast and onto the sea ice during fall and early winter and a return to the home range at the onset of the next breeding season (Chitty & Chitty 1945; Chesemore 1968; Wrigley & Hatch 1976). Pair mates leaving the territory may remain largely solitary (Fay & Follmann 1982; Audet et al. 2002). During winter, terrestrial resources are scarcer because migratory birds have left (Gauthier et al. 2011). When sea ice is available, it offers additional food resources to Arctic foxes (Smith 1976; Tarroux et al. 2012). Roth (2002) showed that marine food became more important during terrestrial food shortage, accounting for nearly half of the winter protein intake. Sea ice thus offers Arctic foxes the possibility to move to a completely new foraging habitat located outside their

terrestrial home range during winter, which is usually not the case for other canids. The tension between two conflicting forces – on one hand, remaining with the mate and keeping the territory outside of the breeding season; on the other hand, having to search for food resources outside of the home range – may shape the degree of spatial proximity of pairs during winter.

During the summers 2007–2011, we fitted 74 adult Arctic foxes with 91 satellite collars in the Canadian High Arctic to monitor their year-round movements. We analysed the movements of 30 adults forming 21 pair-years to answer three objectives. First, we assessed the degree of fidelity of pair mates to their summer home range during winter and the similarity of this fidelity between pair mates. Considering that marine resources are important during winter and that Arctic foxes can be highly mobile, we expected a low fidelity of Arctic fox pairs to their summer home range. Second, we assessed the degree to which simultaneous EMs occur between pair mates. Because of the solitary nature of Arctic foxes and the benefits derived from maintaining territory defence, we expected a low degree of simultaneous EMs in Arctic fox pair mates. Third, we assessed the spatial proximity between pair mates when they were simultaneously outside of their home range. We expected pair mates to move separately because Arctic foxes are not known to incur benefits from group foraging.

Methods

Study area

We worked in a 600 km² study area located in the southern plain of Bylot Island (73°N, 80°W), which is part of Sirmilik National Park of Canada, Nunavut (Fig. 1). The Arctic fox is the main terrestrial predator of the island. The red fox (*Vulpes vulpes*), a potential predator and a competitor for Arctic fox (Tannerfeldt et al. 2002; Pamperin et al. 2006), is only present in low numbers in the region (Gagnon & Berteaux 2009; Gauthier et al. 2013). Two species of lemmings are present: the brown lemming (*Lemmus trimucronatus*) and the collared lemming (*Dicrostonyx groenlandicus*). Populations of brown lemmings show typical fluctuations of large amplitude with a periodicity of three to four years, whereas populations of collared lemmings show low-amplitude cycles (Gruyer et al. 2008, 2010). The southern plain of the island is the most important breeding site for the greater snow goose (*Chen caerulescens atlantica*) in the Canadian High Arctic (Bêty et al. 2001). Sea ice on the south coast of Bylot Island forms in late October and breaks up in late July (Canadian Ice Service 2013). Inuit traditional knowledge indicates that Arctic foxes in the area forage on the sea ice and hunt seal pups in their birth lairs (Gagnon & Berteaux 2009).

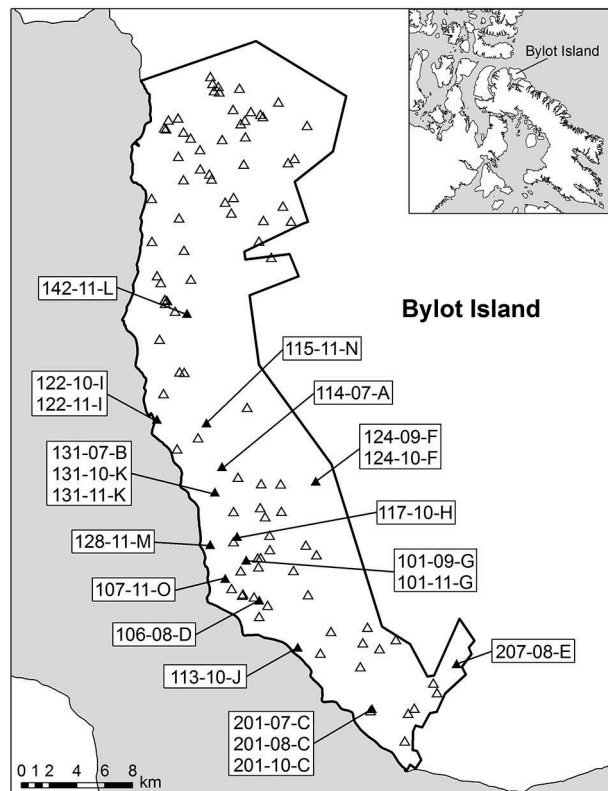


Figure 1. Arctic fox study area (black contour) on Bylot Island, Nunavut, Canada. Fox dens are represented with triangles, with filled triangles indicating dens occupied by fox pairs followed during the study. Identification of numbered dens is as follows: den identification-last two digits of year-fox pair identification.

Captures and satellite tracking

The Bylot Island Arctic fox population has been monitored opportunistically since 1993 and systematically since 2003. Every summer, all known dens (ca. 100) are visited to assess presence of young and adults. We captured adults using padded foot traps (model Softcatch # 1, Oneida Victor). When needed, we anaesthetized animals using a combination of Medetomidine (0.05 ml kg^{-1}) and Ketamine (0.03 ml kg^{-1}). Atipemazole (0.05 ml kg^{-1}) was used as an antidote to the anaesthetic before releasing individuals at their capture site. We marked individuals using a unique combination of coloured and numbered ear tags (Rototags, Dalton Supplies). Since 2007, we have been fitting individuals with collars bearing Argos Platform Transmitter Terminals (Model Kiwisat 202, Sirtrack). Collars weighed 2.6–3.5% of body mass and we used three different collar settings. The collars transmitted for a three- to four-hour period (13:00–17:00 UTC, corresponding to 07:00–11:00 local time) daily or every two days (Table 1), with a repetition rate of 60 seconds for all collars. We therefore obtained locations only during the morning, potentially generating sampling bias, considering that fox activity can vary throughout the 24-hour cycle (Eberhardt et al. 1982; Cypher 2003). This should not, however, affect our comparisons within and between pair mates since all individuals were

Table 1. Description of the Argos Platform Terminal Transmitter settings for 40 collars fitted on 30 adult Arctic foxes tracked during winter (2007–2011) in the Canadian High Arctic (for two individuals, the same collars transmitted in both 2007 and 2008, giving a total of 42 fox-years).

Collar setting	Description	Number of collars fitted				
		2007	2008	2009	2010	2011
Setting I	Every day (13:00–17:00 UTC) from 1 June to 15 August and every second day (13:00–17:00 UTC) from 16 August to 31 May	6	4			
Setting II	Every day (14:00–17:00 UTC) from 15 October–15 May and every second day (14:00–17:00 UTC) from 16 May–14 October			2	5	5
Setting III	Every day (14:00–17:00 UTC) year-round			2	7	9

sampled in a similar way. Data were recovered through the Argos System. We used data from May 2007 to April 2012.

In this study, we defined the winter season as the period between sea-ice formation (25 October) and end of the mating period (30 April), whereas we considered the summer season to start with the beginning of pup rearing (1 May) and end with juvenile dispersal (1 October) (Audet et al. 2002). We selected for analyses 30 Arctic foxes forming 15 pairs, for a total of 21 pair-years. Mated pairs were confirmed by visual field observations or pictures taken at dens (Silent Image and RapidFire Professional, Reconyx) and were monitored for ≥ 2 –6 months during winter (see monitoring length in Supplementary Table S1).

In order to have a suitable level of accuracy for the analyses, we only kept positions with a Location Class 3, 2 or 1, corresponding respectively to positioning errors having a 68% probability of being $< 250 \text{ m}$, $< 500 \text{ m}$, and $< 1500 \text{ m}$ (CLS 2011). We removed all positions with a Location Class 0, A, B or Z, corresponding to large ($> 1500 \text{ m}$) or unquantifiable positioning errors (CLS 2011). Using coordinates projected in the Universal Transverse Mercator, North American Datum 83 system, we filtered Argos data through R 3.0.1 software (R Core Team 2013) in order to exclude locations resulting in unrealistic speed and distance values ($> 7 \text{ km h}^{-1}$ cruising speed, with possible 12-minute acceleration bouts of 10 km h^{-1} ; see S1 File in Christin et al. 2015). We previously evaluated Argos telemetry accuracy on Bylot Island and reported some of the lowest published errors for this system (Christin et al. 2015), likely on account of increased satellite coverage at high latitudes.

Home range fidelity of pair mates

A preliminary analysis based on an Utilization Distribution Overlap Index (Fieberg & Kochanny

2005) showed that the summer home range of males and females overlapped by $82\% \pm 13\%$ (mean \pm standard deviation), therefore we combined male and female locations to obtain the pair's summer home range. We estimated home ranges using the fixed kernel method with a 90% isopleth (Seaman & Powell 1996; Borger et al. 2006) using the *adehabitatHR* library in R (Calenge 2006). We selected the 90% isopleth to represent the full range of the pairs while excluding exploratory movements (Borger et al. 2006). To decrease data temporal autocorrelation when estimating home ranges, we kept one location per day of tracking, based on the smallest location error. Using the 12 pairs with the highest number of locations during the summer period ($n > 77$ locations per individual), we plotted the summer home range size of the pairs with respect to the number of locations. Locations were randomly added in increments of five until all locations of a pair were assessed, and the process was repeated 99 times for each pair (Harris et al. 1990). Kernel estimates reached an asymptote at 44 ± 10 locations on average. All pairs used in this study have a number of locations higher than 44. When calculating fixed kernels, we chose the smoothing parameter by first allowing R to allocate specific smoothing parameters to each pair using the reference bandwidth (h_{ref}) in *adehabitatHR*. We then ran a second analysis in which we manually calculated a global smoothing factor as the median smoothing parameter (0.656) from the first analysis (Dahl & Willebrand 2005). We used the h_{ref} method because it is suitable for central place foragers showing unimodal utilization distribution (Bowman 1985; Worton 1989; Hemson et al. 2005), such as the Arctic fox in summer.

We created an FI to estimate the winter fidelity of each member of the pair relative to the pair's summer home range:

$$FI = \frac{\text{Number of locations inside the summer home range during winter}}{\text{Number of locations during winter}} \times 100 \quad (1)$$

Individuals always remaining in their summer home range during the winter have an FI of 100, whereas individuals never using their summer home range during winter have an FI of 0. We calculated FI for each pair mate.

To complement our analysis of the winter fidelity of fox pairs to their summer home range, we also compared the size of each pair's summer home range to their winter home range after removing locations outside Bylot Island (hereafter the 'terrestrial winter home range'). In addition, as each member of the pair may move independently during winter, we also estimated the winter ranging area of each fox separately using all of their winter locations (on land and on the

sea ice) with the specific smoothing parameters allocated by h_{ref} for each individual.

Extraterritorial movements and spatial proximity of pair mates

EMs could be considered as all movements beyond the boundary of the summer home range. However, to take positioning errors into account and avoid confusions between EM and seasonal changes in position or size of home ranges, we identified EM as all movements ≥ 2 km from the summer home range boundary followed by a return. This 2 km distance represents approximately 30% of a home range diameter and is consistent with the threshold used by Nicholson et al. (2007) to study EM in swift foxes. A movement ≥ 2 km from the summer home range boundary not followed by a return was identified as a dispersal movement (permanent departure) and not considered in the analysis of EMs. When pair mates were both outside their home range during an EM for a given collar transmission period, we considered that they did a simultaneous EM for that day. We created an SI to estimate the tendency of pair mates to perform simultaneous EM:

$$SI = \frac{\text{Number of days with simultaneous EM of pair mates}}{\text{Number of days with EM of at least one pair mate}} \times 100 \quad (2)$$

Pair mates always doing simultaneous EMs have an SI of 100, whereas pair mates never doing simultaneous EMs have an SI of 0. For each pair, we used for analysis data obtained during the period over which both pair mates were tracked. When an adult dispersed, we considered dispersal to break the pair bond and therefore only analysed locations obtained before dispersal. The daily or bi-daily duty cycle of the collars may have caused us to miss some short-term EMs, but we likely detected most of the longest excursions, which were also the most relevant in terms of pair bonding. When we observed a simultaneous EM and both pair mates were located within an hour, we measured spatial proximity between pair mates by calculating the Euclidian distance between pair mate locations.

Statistical analyses

Because transmission rate varied across collars, with some pair mates sampled daily and others sampled every second day (Table 1), we checked whether SI or FI was affected by sampling effort. Using data subsampling and paired t-tests, we found that retaining only locations obtained every second day for the pairs that had been located daily did not affect FI

($FI_{24\text{ h}} = 74.4 \pm 24.5$; $FI_{48\text{ h}} = 74.4 \pm 24.5$) but decreased slightly SI ($SI_{24\text{ h}} = 15.5 \pm 14.8$; $SI_{48\text{ h}} = 11.8 \pm 14.8$). None of these differences, however, were significant (FI: $t = -0.019$, $p = 0.99$, $df = 41$; SI: $t = 2.07$, $p = 0.07$, $df = 19$) so we report values obtained from the original data sets. To test whether males and females had a similar FI, we used a Pearson's product-moment correlation after normalizing our data using the arcsine square root transformation. To compare the size of the pairs' summer home ranges with the size of the pairs' terrestrial winter home ranges, we used paired t-tests after normalizing our data using the log transformation. We similarly compared the size of summer home ranges with the size of the winter ranging areas of each pair mate.

To assess whether SI was different than expected by chance, we performed the following randomization procedure. For each pair, we first calculated the observed SI. Then, the days with EM for each pair mate were mixed over the tracking period of the pair and a new SI was determined from this random rearrangement of days with EM. This procedure was repeated 999 times for each pair. If the observed SI was significantly different from the mean SI obtained by randomization ($p < 0.05$), the observed SI was considered to be significantly different from the one expected by chance.

To assess the level of spatial proximity of pair mates when they were simultaneously outside of their home range, we compared distances between pair mates when they were both located inside their home range to distances between pair mates during simultaneous EM, using a Student's t-test. Sample sizes were higher inside the home range than outside, so to have the same sample size as distances outside we carried a sampling without replacement of distances inside the home range 10 000 times. We performed the Student's t-test 10 000 times for each pair (once for each sampling without replacement). If 95% of the observed t-values were higher than or equal to the critical t-value, we considered that the mean distance inside the home range was significantly different from the mean distance during simultaneous EM.

We present summary statistics as means \pm standard deviation. We performed all statistical analyses in R 3.0.1.

Results

We obtained 6128 locations (after filtering) for the 42 fox-years, with a mean of 4.7 ± 2.5 locations per day of tracking per individual. During the 2007–2011 study period, nine collars stopped transmitting before 30 April and four females and three males (from five pairs) dispersed during winter (Supplementary Table S1).

Home range fidelity of pair mates

The size of fox pairs' summer home ranges ($34.9 \pm 14.6\text{ km}^2$; range: 16.9–84.2) was not significantly different (paired t-test, $t = 1.07$, $p = 0.298$, $df = 20$) from the size of pairs' terrestrial winter home ranges ($34.2 \pm 20.8\text{ km}^2$; range: 16.9–86.6). In contrast, the winter ranging areas (including locations on land and sea ice) of pair mates were significantly larger than their summer home ranges (paired t-test, $t = -5.97$, $p < 0.001$, $df = 41$) and varied widely from 15.7 to 9615.9 km^2 (median = 102.1 km^2). The mean FI of individuals was $74 \pm 25\%$ (range: 19–100%), indicating that during winter foxes still spent a large proportion of their time in their summer home range. Within a given pair, FI of the male and female were highly correlated ($r = 0.73$, $p < 0.001$, $df = 19$). Only five out of 21 pair-years had a FI $\leq 60\%$ for at least one of the pair mates. In four of them, one or both pair mates dispersed during winter (Fig. 2).

Simultaneous extraterritorial movements between pair mates

We excluded from this analysis one pair tracked in 2008 because the collars of the pair mates were not transmitting the same day so we could not determine simultaneous EM. The mean SI for the remaining 20 pair-years was $15.5 \pm 14.8\%$ (range: 0–58.8%), indicating that pair mates performed rather few simultaneous EMs. EMs were generally of short duration (median = 1 day, mean = 2.0 ± 4.8 days, $n = 652$).

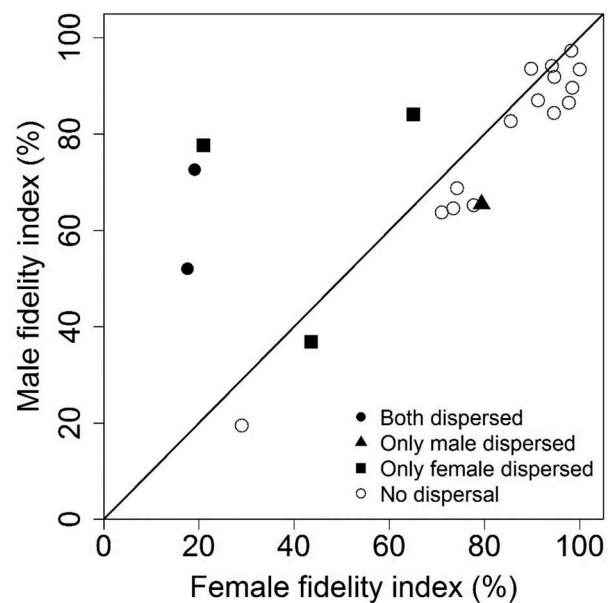


Figure 2. Relationship between the FI of males and females within Arctic fox pairs tracked during winter (2007–2011) in the Canadian High Arctic. Each data point represents a given pair during a given winter. The diagonal indicates a similar FI for both pair mates. Data come from 15 pairs, including one tracked for three years and four tracked for two years (21 pair-years).

and most simultaneous EMs occurred in December–January (Supplementary Fig. S1). We observed no simultaneous EM at all in six out of 20 pair-years. In eight of the 14 pair-years with simultaneous EMs, the observed SI was significantly higher than the mean SI obtained by randomization (Table 2). Overall, these results thus indicate no clear tendency of Arctic fox pair mates to seek or avoid simultaneous EMs.

Spatial proximity of pair mates during extraterritorial movements

We obtained 33.1 ± 24.5 distances per pair-year of pair mates located within one hour while performing simultaneous EMs (range = 6–71, median = 23.5, $n = 14$ pair-years). Pair mates were further apart during simultaneous EMs (18.9 ± 21.4 km) than when inside the boundaries of their summer home range (2.5 ± 0.8 km). The difference was significant in 12 of the 14 pair-years showing simultaneous EMs (Fig. 3).

Discussion

Our study of space use by Arctic fox pairs during winter is, to our knowledge, the first for the species based on a relatively large sample of individuals. It shows that individuals were highly faithful to their summer home range during the winter period, which contrasts with our first prediction. Although we observed that individuals could roam over relatively wide areas when leaving their terrestrial winter home ranges, home range fidelity remained generally high for both pair mates, suggesting interactions between them (Hennessy et al. 2012) and year-round maintenance of the pair bond.

Arctic foxes in our study area therefore display the typical social structure of canids, which consists of a long-lived pair bond, with pair mates that may continue to interact even after the breeding season (Kleiman & Eisenberg 1973; Kleiman 2011). Interestingly, the dispersal of one pair mate, male or female, did not necessarily lead to the dispersal of the other, indicating that either sex may hold and maintain the territory after a mate's departure. Consistent with our two other predictions, we also found a low degree of simultaneous EMs in Arctic fox pair mates, and solitary movements when pair mates were simultaneously outside of their territory, indicating that they appear to behave independently once they leave the territory.

Home range fidelity of pair mates

The patterns of social monogamy and perennial pair bond found in canids, unusual in other mammals, have been hypothesized to represent phylogenetically old traits within the Canidae family (Kleiman & Eisenberg 1973; Dietz 1984). The Arctic fox was the only canid for which it was assumed, based on relatively old reports, that pair mates would separate and leave the breeding grounds to relocate on the coast or the sea ice until the following breeding season (Soper 1944; Wrigley & Hatch 1976; Fay & Follmann 1982). Previous telemetry studies showed conflicting results regarding adult winter movements in Arctic foxes. Lifelong mate and home range fidelity were reported for Arctic foxes living in areas with no access to sea ice, such as Iceland, Sweden and Norway (Tannerfeldt & Angerbjörn 1996; Landa et al. 1998; Strand et al. 2000). In regions with access to the sea ice, such as Alaska (Anthony 1997; Pamperin 2008;

Table 2. Observed SI and mean SI (\pm standard deviation) obtained through randomization for Arctic fox pairs studied by satellite tracking in the Canadian High Arctic. Data are from 14 pairs tracked for one to three years (20 pair-years). EMs were defined as movements ≥ 2 km of the summer home range boundaries. Values of p in boldface indicate statistical significance at the 0.05 level.

Year	Pair ID	No. days with simultaneous tracking of both pair mates	No. days with EM of male	No. days with EM of female	No. days with simultaneous EM of male and female	No. days with EM ≥ 1 pair mate	Observed SI	Mean SI	p value
2007	A	95	32	21	11	42	26.2	15.5 ± 4.8	0.04
2007	B	64	20	17	5	32	15.6	17.3 ± 6.0	0.70
2007	C	95	33	27	14	46	30.4	18.6 ± 5.0	0.03
2008	C	37	29	25	20	34	58.8	57.3 ± 5.6	0.53
2008	E	20	14	4	4	14	28.6	19.2 ± 6.6	0.24
2009	F	188	29	10	3	36	8.3	4.1 ± 3.2	0.18
2009	G	174	4	3	0	7	0	NA	NA
2010	C	46	4	13	0	17	0	NA	NA
2010	F	143	32	14	7	39	18.0	7.4 ± 3.7	0.01
2010	H	187	24	4	0	28	0	NA	NA
2010	I	188	19	3	0	22	0	NA	NA
2010	J	133	13	13	4	22	18.2	5.5 ± 4.5	0.03
2010	K	188	11	10	2	19	10.5	2.9 ± 3.7	0.11
2011	G	186	31	27	10	48	20.8	8.4 ± 3.7	0.01
2011	I	120	12	6	0	18	0	NA	NA
2011	K	63	5	0	0	5	0	NA	NA
2011	L	186	24	16	6	34	17.7	5.9 ± 3.8	0.01
2011	M	186	11	19	3	27	11.1	4.0 ± 3.7	0.09
2011	N	112	14	75	13	76	17.1	11.9 ± 2.3	0.03
2011	O	113	40	31	16	55	29.1	18.4 ± 4.2	0.02

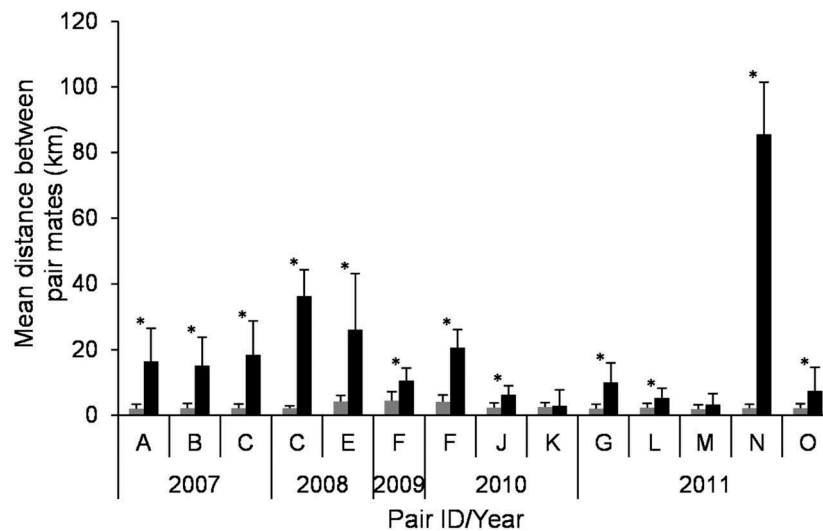


Figure 3. Comparison of the mean (\pm standard deviation) distance between Arctic fox pair mates when they were both inside (grey bars) and outside (black bars) of the boundaries of their summer home range. Each pair is identified by a capital letter. Data come from 12 Arctic fox pairs tracked during winter (2007–2011) in the Canadian High Arctic, including pairs C and F that were tracked for two years each, for a total of 14 pair-years. Distances inside and outside the home range were significantly higher for 12 pair-years (asterisks), and not significantly different for two pair-years, as determined through randomization t-tests.

Lehner 2012) and Svalbard (Frafjord & Prestrud 1992), different residency patterns were observed, with some foxes staying resident and others performing long-distance movements, possibly reflecting the flexibility of the species, but the trend remained unclear on account of the difficulty of relocating the individuals regularly all year or very small sample sizes per year. Possible differences in seasonal home range fidelity and pair bonding across Arctic fox populations may reflect local ecological conditions. Individuals from populations inhabiting inland areas where the sea ice is accessible but further away than for our coastal population may be more prone to leave their mate and territory to move onto the sea ice for the winter, as short EMs would then be too costly. Tracking other populations inhabiting sea-ice areas would be needed to resolve this question.

Attempting to remain with the mate during the winter season has several potential benefits, including the maintenance of a well-known territory once acquired (Ralls et al. 2007) and cooperative territory defence (Dobson et al. 2010). Arctic foxes live in a constraining environment (Fuglei et al. 2004) and store food in summer and fall for retrieval when prey are less abundant (Prestrud 1991; Careau et al. 2007; Careau et al. 2008). This caching behaviour may increase the value of the territory and promote its maintenance year-round. Home range fidelity in winter also directly connects to the mating strategy of individuals. In our study area, multiple paternity and extra-pair paternity are frequent (Carmichael et al. 2006; Cameron et al. 2011), therefore complex interactions within and between fox pairs likely occur in March–April, when females have their unique three-

to-five-day-long oestrus. Higher temporal and spatial resolution of data are needed to test causal hypotheses on this important topic.

Simultaneous extraterritorial movements between pair mates

While Arctic fox pairs remained highly faithful to their summer home range during winter, they often made short-term movements to the sea ice and sometimes inland. Overall, the degree of simultaneous EMs was low. This could result from two strategies that are not mutually exclusive. First, when canids forage primarily on small prey such as rodents, they usually hunt alone and avoid their mate in order to increase foraging efficiency, as reported in the red fox (Pouille et al. 1994), the swift fox (Kitchen et al. 2005), the kit fox (White et al. 2000) and the maned wolf (de Almeida Jácomo et al. 2009). Arctic foxes, as lemming specialists, may also exhibit this solitary foraging behaviour, whether they forage inside or outside their territory, resulting into a low degree of simultaneous EMs. Alternatively, this low degree of simultaneity could reflect a coordination of home range defence, with one mate guarding the territory while the other is foraging outside (Krebs 1982; Davies & Houston 1983). However, EMs of Arctic fox pairs last for only a few days and this short time lapse may not be long enough to lose the territory (Tsukada 1997).

In more than half of the pairs making simultaneous EMs, these were more simultaneous than expected by chance (although the degree of simultaneity remained low). Despite the need to defend the territory year-round, which could prevent long or frequent EMs

(explaining low level of simultaneity), the need to find food outside the territory could be triggered by some environmental conditions shared at the same time by the pair mates (explaining simultaneous EMs). Indeed, simultaneous EMs of pairs peaked in December–January, matching the peak of individual EMs (Supplementary Fig. S1), which could indicate that food is less available in their tundra territory at this time of the year, or that food is more available on the sea ice.

Spatial proximity of pair mates during extraterritorial movements

The distance between pair mates was clearly lower when they were inside the territory than when they were outside, except for two pairs. The distance between both pair mates may depend on the main stimuli leading to EMs. The distance between pair mates outside of the home range may be high during foraging trips triggered by lack of resources inside the home range. An example of a stimulus outside the home range in our study area is a clumped food resource such as a marine mammal carcass, which can attract several foxes from their territory to the same spot on the sea ice (Lai et al. 2015). Pair mates may sometimes detect these hot spots simultaneously and therefore forage in close proximity during an EM. Such circumstances are probably too rare, however, to strongly influence average distance between pair mates when they are out of the territory.

Conclusion

Seasonal movements and solitary winter life are often assumed for Arctic foxes living in sea ice areas (Wrigley & Hatch 1976; Eberhardt et al. 1982; Audet et al. 2002), yet little quantitative information is available to support this. The technological advances in wildlife tracking (e.g., increased precision of location data, miniaturization of tracking devices, remote retrieval of data through satellites) have now overcome the logistic challenges associated with following relatively small mammals over long distances in Arctic winter conditions, providing new knowledge about their movement patterns. These developments, which apply to other species living in remote regions, will allow a better understanding of the ecology of these species and the impact of their movements on ecosystem functioning.

Acknowledgements

We are grateful to all field assistants for their help in the field. We thank Dr Carl Soulsbury and an anonymous reviewer for their comments on an earlier draft. Capture techniques and immobilization procedures were approved by the Université du Québec à Rimouski Animal Care Committee, and field

research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Canada Research Chairs Program; Fonds de la Recherche du Québec (Nature et Technologies); International Polar Year Program; Kenneth M. Molson Foundation; Natural Sciences and Engineering Research Council of Canada; Natural Sciences and Engineering Research Council of Canada - Collaborative Research and Training Experience Program in Northern Environmental Sciences EnviroNorth; Network of Centers of Excellence of Canada ArcticNet; Northern Scientific Training Program (Polar Knowledge Canada); Polar Continental Shelf Program (Natural Resources Canada) and Université du Québec à Rimouski.

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