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ORIGINAL PAPER

Northern nomads: ability for extensive movements in adult arctic foxes

Arnaud Tarroux · Dominique Berteaux · Joël Bêty

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Abstract In July 2008 we outfitted reproductively active adult arctic foxes with satellite tracking collars on Bylot Island, Nunavut, Canada and recorded their movements over a complete annual cycle. We present the tracking data from two individuals, one female and one male, who traveled extensively from February to July 2009, covering minimum distances of 4,599 and 2,193 km, respectively. We recorded high and sustained travel rates on both land and sea ice that reached 90 km/day for the female and 88 km/day for the male. Our data confirm that arctic foxes can move extensively and demonstrate sustained travel rates that are 1.5 times those previously measured for the species. Our study is the first presenting detailed year-round satellite tracking of adult arctic foxes and has implications for our understanding of navigational abilities, foraging ecology, trophic interactions with lemming populations, and genetic population structure of arctic foxes.

Keywords *Alopex* · Argos satellite tracking · Bylot Island · Dispersal · *Vulpes lagopus* · Sea ice

Introduction

Long distance movements of canids are often linked to key features of their ecology such as foraging (Frame et al. 2004) or dispersal (Wabakken et al. 2007), which can ultimately influence population structure. The arctic fox (*Vulpes lagopus* L.) is a small carnivore (ca. 3–5 kg; Audet et al. 2002) recognized as a key predator in the arctic terrestrial ecosystem (Angerbjörn et al. 1999; Bêty et al. 2002). Space use patterns are still poorly understood in this species, although they have stimulated the interest of ecologists for several decades (e.g. Macpherson 1968; Northcott 1975). By furthering our understanding of arctic fox movements, we can increase our comprehension of other aspects of their ecology. At the individual level, movement ability can directly influence dispersal (Tannerfeldt and Angerbjörn 1996), as well as foraging capacity in other habitats, such as sea ice, during periods of local inland food shortage (Roth 2002; Pamperin et al. 2008). At the population level, movements directly influence gene flow among populations (Dalén et al. 2005). At the ecosystem level, movements of arctic fox may influence the population dynamics of their main prey (Krebs et al. 2002), for example, through large-scale synchronization of lemming cycles.

Arctic foxes are expected to be more mobile than other canids, due to notable fluctuations in resource levels that are characteristic of the low-productivity arctic ecosystems (Frafjord and Prestrud 1992; Fuglei et al. 2003). Although their summer home ranges are relatively small (Eide et al. 2004), individuals are capable of remarkably extensive winter travel (i.e., >1,000 km); evidence of these movements was collected several decades ago through recovery of tagged individuals, particularly in Alaska and Canada (Chesemore 1968a; Macpherson 1968; Northcott 1975; Eberhardt and Hanson 1978; Eberhardt et al. 1983). Recently, a study based on satellite telemetry showed that, during juvenile dispersal, young foxes in Alaska traveled up to 2,700 km on sea ice over 5 months (Pamperin et al.

A. Tarroux (✉) · D. Berteaux (✉) · J. Bêty
Chaire de recherche du Canada en conservation des écosystèmes nordiques et Centre d'études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada
e-mail: arnaud.tarroux@gmail.com

D. Berteaux
e-mail: Dominique_berteaux@uqar.qc.ca

2008). Furthermore, the existence of large-scale winter migrations has been reported in Canada and in Russia (Chesemore 1968a; Wrigley and Hatch 1976), although it was never clearly demonstrated if it was true migration (involving a return) or massive dispersal. Winter nomadic movements, which are sporadic movements of individuals outside their normal home range, have sometimes been considered rare in this species (Audet et al. 2002), especially in certain areas of its range like in Fennoscandia (Strand et al. 2000). However, in most of the species range, winter movements have received relatively little attention (but see Pamperin et al. 2008). More information is therefore needed to know the frequency of occurrence of such displacements throughout the annual cycle.

We present results from an ongoing study on population dynamics, resource use, and movements in a population of arctic foxes from the Eastern Canadian Arctic. In June–July 2008, we outfitted twelve adult arctic foxes with Argos satellite collars to monitor their year-round movements. Among these twelve individuals, two showed extensive, large-scale movements whose analysis gives new insights about the travel capacity of this species. Here, we describe the movements of these two individuals and discuss their implications for other questions on the ecology of arctic foxes.

Methods

Study area

We worked in the southern plain of Bylot Island (73°N, 80°W), which is part of Sirmilik National Park, Nunavut, Canada. A small region of the island offers suitable denning habitats for arctic foxes (Szor et al. 2008). The rest of the island is mainly comprised of a large barrier glacier. Foxes prey mostly on lemmings and migratory birds, primarily nesting snow geese (*Chen caerulescens atlantica*) (Careau et al. 2008). Local Inuit traditional ecological knowledge suggests that sea ice surrounds Bylot Island from late October to late July and that some arctic foxes forage on the sea ice when it is present (Gagnon and Berteaux 2009).

Capture and satellite tracking

We captured 12 adult foxes in June–July 2008 using padded foot traps (model Softcatch # 1, Oneida Victor Ltd, USA). We anesthetized the animals using a combination of medetomidine (0.05 ml/kg) and ketamine (0.03 ml/kg) and fitted them with 95-g collars bearing Argos Platform Transmitter Terminals (PTT), Model Kiwisat 202, Sirtrack Ltd, New Zealand. We then used atipemazole (0.05 ml/kg) as an antidote to the anesthetic before releasing individuals at their capture site. Between 1 June to 15 August, positions were recorded daily for one 4-h period (4 h on, 20 h off); during 15 August to 31 May, positions were recorded every second day for one 4-h period (4 h on, 44 h off). Repetition rate was set to 60 s, and we recovered data through the Argos System (CLS 2008).

During the following year, only two (a 3.3 kg female and a 4.0 kg male) of the 12 adults fitted with a PTT showed extensive movements. All the other foxes remained within 100 km of Bylot Island, and their movements do not fit the subject of this paper. The female was first captured and ear-tagged as an adult on May 26, 2007, but was recaptured and then collared on July 4, 2008; the male was first captured and collared on June 19, 2008. They both reproduced successfully in 2008 in two different dens, raising litters of at least eleven (for the female) and nine (for the male) pups.

Data processing and analyses

We used a geographical information system (GIS; ESRI ArcGIS version 9.3) to project locations in the Canada Albers Equal-Area Conic system, which is adapted to projections at large scale and oriented mainly on an east–west axis (Harvey 2008). We first removed all positions with a location class (LC) 0, A, B, or Z, corresponding to large ($>$1,500 m) or unquantifiable positioning errors. Therefore, we kept only LC 3, 2 and 1 positions, typically corresponding to errors of $<$150, $<$350, and $<$1,000 m, respectively (CLS 2008). We considered this level of precision to be suitable to analyze such large-scale movements. Then, using projected coordinates, we filtered Argos data through Microsoft Access/Visual Basic recursive routines in order to exclude all locations resulting in unrealistic speed values ($>$20 km/h for more than 10 min). Finally, we kept one location per day from 1 June to 15 August and one location every second day from 15 August to 31 May. Due to occasional gaps in the data set, the average interval between successive locations was 24.6 ± 0.4 h SE from 1 June to 15 August and 49.7 ± 0.9 h SE from 15 August to 31 May. We used $n_\mathrm{f} = 212$ locations for the female (21% LC3, 39% LC2, and 40% LC1) and $n_\mathrm{m} = 217$ locations for the male (21% LC3, 35% LC2, and 44% LC1). We used the GIS to map filtered locations and the Hawth's Analysis Tools extension (Beyer 2004) to derive tracks from these locations.

We defined the center of the 2008 summer home range as the barycenter of all filtered locations collected between July 17, 2008 and August 15, 2008. We calculated average travel rates (km/day) assuming straight-line movements between locations. To compare our results to those from other studies, we used the Hawth's Analysis Tools extension to calculate 100% minimum convex polygons (MCP) as estimates of the surface potentially covered annually by arctic foxes. We also calculated the daily distance covered (km/day), averaged by month, to compare movement characteristics between seasons.

Results

Foxes revealed complex and heterogeneous movement patterns through their annual cycle (Fig. 1). The female had the most extensive movements and traveled up to 600 km away from the center of her 2008 summer home range (Fig. 1). The male had less extensive movements but still travelled as far as 486 km away from the center of his 2008 summer home range. The total annual distance covered by the female was at least 4,919 and 2,597 km for the male. However, both individuals had higher movement rates from February to July 2009 (Fig. 2): during that 5.5-month period, the female covered 4,599 km (93.5% of the total annual distance) while the male covered 2,193 km (84.4% of the total annual distance). The annual 100% MCPs were 305,481 and 171,280 km^2 for the female and male, respectively.

Movements of both individuals were restricted to the vicinity of their 2008 summer home ranges until February (female) or March 2009 (male; Fig. 1). The female later returned to Bylot Island on two occasions, April 22 and May 26, 2009, but did not return to her previous summer

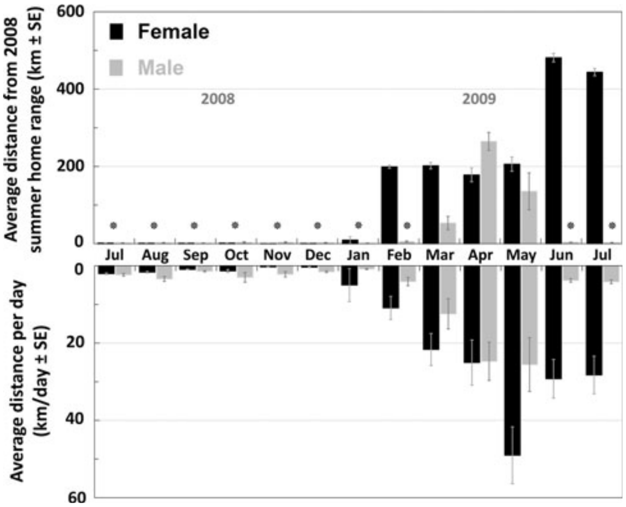

Fig. 2 Monthly average (±SE) distances from previous summer home ranges (*upper panel*) and monthly average (±SE) travel rates (*lower panel*) for two adult arctic foxes tracked using satellite telemetry in the Eastern Canadian Arctic, July 2008–July 2009. In the *upper panel*, all distance values <10 km are considered to be very close to the previous year's home range and are indicated by a *asterisk* (*)

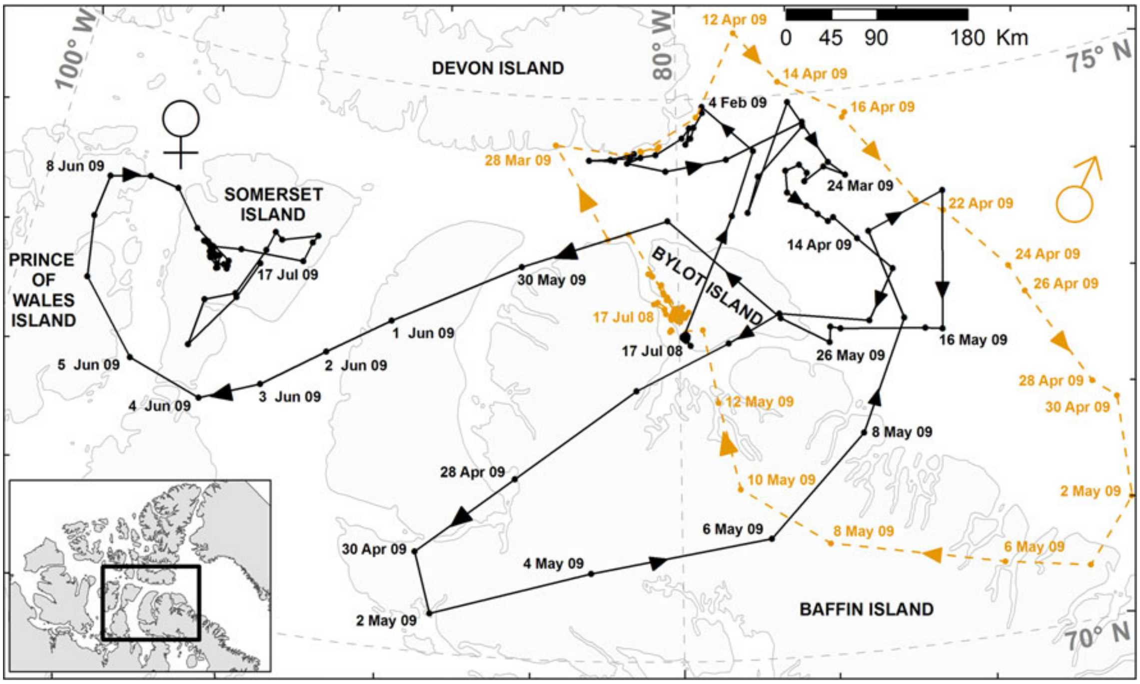

Fig. 1 Locations and estimated straight-line movements of one female (*continuous line*) and one male (*dashed line*) adult arctic fox tracked using satellite telemetry in the Eastern Canadian Arctic from July 17, 2008 to July 17, 2009. Time intervals between successive locations were approximately 24 h (July 17, 2008–August 15, 2008) or 48 h (15 August 2008–17 July 2009). The extreme distance, i.e., distance between the two outermost locations along a given movement path (Frafjord and Prestrud 1992), was 852 km for the female and 675 km for the male. Map projection is Canada Albers Equal-Area Conic, NAD 83

home range and travelled west to eventually settle on Somerset Island (73°N, 96°W) in June 2009, that is >400 km from Bylot. In contrast, the male returned to his previous summer home range in May 2009. Based on analysis of successive locations, we estimated maximum travel rates of 90 km/day for the female and 88 km/day for the male. The track of the female was directional from 28 May to 3 June (average bearing 247° ± 2° SE; Fig. 1). The average distance covered per day was highest from March to May for the male and from February to July 2009 for the female (Fig. 2). This confirms that the female did not establish a restrained home range in summer 2009, as opposed to the male, whose daily distances covered were similar in July of both years. It is noteworthy that despite her departure, the female's mate from 2008 was still present in the research area in June 2009, at the same den where they had raised a litter together on the previous summer. In July 2009, the male that we had tracked for a full year was also confirmed to be in the vicinity of his 2008 den.

Substrate had little influence on travel rate as we observed high rates on both sea ice and tundra. Both foxes were present on sea ice during November 2008 to July 2009, with 42% (female) and 22% (male) of their locations being reported from sea ice locations (Fig. 1). Use of sea ice was associated either with long distance and directional movement bouts (June 2009) or to stays in more restricted areas (April 2009).

Discussion

Our results demonstrate the ability of arctic foxes to cover large distances over very short time periods. The recorded travel rates of 90 km/day are at least 1.5 times greater than those previously reported for this species (24 km/day, Eberhardt and Hanson 1978; maximum rate ever reported: 61 km/day, Pamperin et al. 2008). The female showed average travel rates >61 km/day for 26 days, including nine consecutive days from 28 May to 7 June. The male showed an average travel rate >61 km/day only for 1 day. The average daily travel rate for our marked foxes reached its maximum when local sea ice cover was close to 100%, and ice thickness was >1.2 m (Canadian Ice Service 2009). In the case of the female and during the period when she had the highest travel rates (from 24 April to 8 May and from 28 May to 3 June), this ice was landfast, static ice formed within the archipelago: it is therefore highly unlikely that she was traveling on drifting ice, as has been mentioned earlier (Northcott 1975; Eberhardt et al. 1983; Pamperin et al. 2008). The male was traveling on the pack ice of Baffin Bay, where ice southward movements can reach 13 km/day (15 cm/s) in winter and early spring (Tang et al. 2004). However, the fastest travel rates were recorded on land for the male, from May 6–8, 2009 (Fig. 1).

We assumed straight-line movements between successive locations, and thus negatively biased our estimates of average travel speeds and total distances covered when foxes stayed within the same area for an extended period, e.g., from June to December 2008. However, our calculated values are likely more representative of true speeds and distances traveled when animals were moving directionally over long distances, e.g., from March to June 2009. Yet, we may still have underestimated the traveling capacity of this species. When moving on the pack ice, net travel rates of arctic foxes could thus be even higher when ice and fox move in the same direction and their speeds are thus added (Tang et al. 2004).

Information from resighting of marked individuals had revealed that foxes are capable of traveling up to 2,300 km from their summer home range (Sdobnikov 1940; Macpherson 1968; Garrott and Eberhardt 1987; Samelius 2006). However, associating this information to detailed knowledge regarding travel rates and individual fates (e.g., returning to their previous home range or not) has important implications for our understanding of the ecology of this species. In particular, our results have implications for our understanding of the navigational abilities, foraging ecology, effect on lemming cycles, and genetic population structure of arctic foxes.

Navigational abilities

The existence of homing, and therefore navigational, abilities in arctic foxes has already been questioned (Macpherson 1968; Wrigley and Hatch 1976). The movements of the male show that an adult fox can return to the same den after moving 486 km away without retracing his route; this follows the definition of homing (Caldwell and Nams 2006). Movements of the female also show that foxes possess navigational abilities, allowing them to follow precise bearing over long distances and during several days. The fact that, on two occasions, the female returned to Bylot after having moved several hundreds of kilometers away further supports the hypothesis that foxes can orientate themselves over large areas and long periods of time.

Foraging ecology

In June 2009, the female travelled at high speed for nine consecutive days, while maintaining a very precise bearing, regardless of the substrate she was traveling on (sea ice or land). Our observations fit with those of Wrigley and Hatch (1976) who report arctic foxes in the former USSR "traveling singly for days and nights without stopping". Zollner and Lima (1999) predicted through modeling that an animal searching for resources over long distances would optimize its search by following nearly straight paths, especially when crossing unsuitable habitat and irrespective of the degree of patchiness in resource distribution. Although we have no data on the motivation of the female, her movements fit Zollner and Lima's (1999) predictions and may thus indicate that she was crossing unsuitable habitat with low resource levels. The total minimum distances covered in 1 year by foxes and the corresponding 100% MCPs were comparable to what has been observed in polar bears (*Ursus maritimus*) off the coasts of Greenland and Svalbard (Wiig et al. 2003; Andersen et al. 2008). This confirms that foxes may be capable of following polar bears in winter to scavenge on remains of marine mammals (Chesemore 1968b). Little information is available about movements of polar bears in winter in the Bylot Island area. Nonetheless, experts from the local Inuit community of Pond Inlet have mentioned observations of arctic foxes feeding on carcasses of sea mammals left by polar bears (Gagnon and Berteaux 2009).

Lemming cycles

The arctic fox is considered as an opportunistic specialist, behaving as a generalist predator with a preference for microtine rodents (Elmhagen et al. 2000). Nomadic predators, acting like generalist predators that increase predation pressure when prey is more abundant, can influence prey population cycles by maintaining these cycles through time (Angerbjörn et al. 1999; Gilg et al. 2003) and by synchronizing them through space (Hanski et al. 1991, 2001; Ims and Andreassen 2000; Krebs et al. 2002). During lemming peaks, rapid local increases in numbers of adult foxes (e.g., Gilg et al. 2003) can be explained by fox movements. Lemming abundance was high (peak) on Bylot Island in 2008, but lower in 2009 (G. Gauthier, unpublished data). Whether this could have triggered the movements of the two tracked individuals is unclear to us, especially given the fact that most other individuals remained close to Bylot Island. Because the spatial scale at which these movements can occur determines the scale at which foxes can stabilize and synchronize lemming cycles, Krebs et al. (2002) called for more effort in satellite tracking of mobile predators.

The annual 100% MCPs reported here represented 21.4% (for the female) and 12.0% (for the male) of the Canadian Arctic Archipelago (ca. 1.4 million km^2). Even though individual foxes cannot intensively use their whole polygon area, this shows that they can find high-density populations of lemmings located far away from their territory, and therefore act as synchronizing agents of lemming cycles at large spatial scales. The strength of this synchronizing force should depend, however, on the strength of the numerical response generated by large-scale movements of foxes (Ydenberg 1987). One priority of future satellite telemetry studies should thus be to gather data at the population level to evaluate the proportion of foxes which choose to disperse over a large spatial scale during episodes of local food scarcity. Another priority should be to link prey abundance to fox movements, in order to test the hypothesis that individuals disperse from low-food to high-food locations.

Gene flow among populations

Arctic foxes usually mate in March–April (Audet et al. 2002), which corresponds to the period when we observed large-scale movements (Figs. 1, 2). Such movements probably promote interbreeding between populations and help explain the low genetic differentiation measured among circumpolar populations of foxes connected by sea ice (Dalén et al. 2002, 2005; Geffen et al. 2007). Physical barriers, preventing or impeding movements, can influence the structure of fox populations both at the scale of the whole Arctic region (Geffen et al. 2007) and at a regional scale, within a population (Norén et al. 2009). Future decreases of sea ice extent will undoubtedly lead to a loss of connectivity between islands (Fuglei and Ims 2008) and thus between fox populations.

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