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Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic

Sandra Lai, Joël Bêty and Dominique Berteaux

S. Lai (http://orcid.org/0000-0003-0128-3738), J. Bêty and D. Berteaux (http://orcid.org/0000-0003-2728-5985) (dominique_berteaux@uqar.ca), Canada Research Chair on Northern Biodiversity, Centre for Northern Studies and Quebec Center for Biodiversity Science, Univ. du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC, G5L 3A1, Canada.

Animal movement is a fundamental process shaping ecosystems at multiple levels, from the fate of individuals to global patterns of biodiversity. The spatio-temporal dynamic of food resources is a major driver of animal movement and generates patterns ranging from range residency to migration and nomadism. Arctic tundra predators face a strongly fluctuating environment marked by cyclic microtine populations, high seasonality, and the potential availability of sea ice, which gives access to marine resources in winter. This type of relatively poor and highly variable environment can promote long-distance movements and resource tracking in mobile species. Here, we investigated the winter movements of the arctic fox, a major tundra predator often described as a seasonal migrant or nomad. We used six years of Argos satellite telemetry data collected on 66 adults from Bylot Island (Nunavut, Canada) tracked during the sea ice period. We hypothesized that long-distance movements would be influenced by spatio-temporal changes in resource availability and individual characteristics. Despite strong annual and seasonal changes in resource abundance and distribution, we found that a majority of individuals remained resident, especially those located in an area characterized by highly predictable pulse resources (goose nesting colony) and abundant cached food items (eggs). Foxes compensated terrestrial food shortage by commuting to the sea ice rather than using long-distance tracking or moving completely onto the sea ice for winter. Individual characteristics also influenced movement patterns: age positively influenced the propensity to engage in nomadism, suggesting older foxes may be driven out of their territories. Our results show how these mammalian predators can adjust their movement patterns to favor range residency despite strong spatio-temporal fluctuations in food resources. Understanding the movement responses of predators to prey dynamics helps identifying the scales at which they work, which is a critical aspect of the functioning and connectivity among meta-ecosystems.

Animal movements determine not only the fate of individuals, but also shape population dynamics, ecosystem connectivity and patterns of biodiversity at multiple scales (Jeltsch et al. 2013, Liedvogel et al. 2013). The causes and consequences of animal movement have long been challenging questions in ecology (Nathan et al. 2008), although spatio-temporal resource dynamics are clearly major drivers of movements (Alerstam et al. 2003, Mueller and Fagan 2008, Somveille et al. 2015). Movement patterns belong to three general categories: 1) range residency, where individuals reside in relatively small areas within the species' distribution range; 2) migration, often defined as back and forth, long-distance movements between breeding and non-breeding grounds or between different habitats, and 3) nomadism, or long-distance movements with routes that can vary widely among individuals or seasons (Roshier and Reid 2003, Mueller and Fagan 2008, Avgar et al. 2014). On one side, range residency is generally associated with resources relatively abundant with little spatial variability. On the other side, migration allows the exploitation of spatio-temporally variable resources that change in a predictable manner, while nomadism is expected to arise when resources have an unpredictable distribution in space and time (Andersson 1980, Mueller and Fagan 2008, Jonzén et al. 2011). While a species usually displays a single movement pattern over its range, some variability often occurs between populations or between individuals of a given population (Chan 2001, Austin et al. 2004, Freitas et al. 2009, Mysterud et al. 2011). Individual variation in movement behaviour has been widely documented, but the drivers promoting different strategies are not always completely identified (Chapman et al. 2011).

Individual characteristics such as age and sex can influence movement patterns in combination with environmental factors (Austin et al. 2004, Vasko et al. 2011, Singh et al. 2012). Sex-specific differences can arise from different survival or foraging tactics (Nicholson et al. 1997, Singh et al. 2012) or from different needs of males and females to defend important resources, such as a high-quality territory and nest-hole (Korpimäki 1986, 1987). Residency is usually predicted to be positively related to age, as the remaining number of reproductive events diminishes through time and the costs of changing territory may therefore not be compensated for

(Morris 1982, Switzer 1993). However, older individuals may become unable to defend their territory against conspecifics and may be forced to leave (Way and Timm 2008).

Boreal and arctic predators face a strongly seasonal environment often characterized by cyclic prey populations, a relatively unpredictable resource which typically triggers long-distance movements (Löfgren et al. 1986, Korpimäki and Norrdahl 1991, Poole 1997, Jonzén et al. 2011, Therrien et al. 2014). However, access to an alternative prey when the main cyclic prey becomes rare can allow residency in some populations of nomadic avian predators (Korpimäki 1986, Clulow et al. 2011). Among mammalian arctic predators, the arctic fox *Vulpes lagopus* is often described as a seasonal migrant or nomadic specialist (Chesemore 1968, Fay and Follmann 1982, Barraquand et al. 2014). Although winter migrations and a link between large-scale movements and rodent population crashes have often been suspected in arctic foxes (Wrigley and Hatch 1976, Eberhardt et al. 1982), tests using genetic tools were not entirely conclusive (Meinke et al. 2001, Norén et al. 2011) and these hypotheses have not yet been systematically tested using telemetry. As a facultative migrant neither restricted by movement capacity or complex social structure, the arctic fox is an ideal model species for understanding the factors that may constrain the prevalence of migration and nomadism in terrestrial predators. Arctic foxes rely on food sources that are highly variable in both space and time (Angerbjörn et al. 2004). While they typically specialize on lemmings, *Dicrostonyx* and *Lemmus* spp., they can also rely on other food sources (Elmhagen et al. 2000). Individuals with access to migratory birds in summer can cache many eggs in their den and territory (Careau et al. 2007, Samelius et al. 2007). The consumption of food cached in summer during the following winter and spring has been deduced from analyses of winter fox scats (Bantle and Alisauskas 1998, Gilg 2006) and stable isotope analyses (Samelius et al. 2007). During the cold season, extraterritorial movements to access marine resources on the sea ice, as well as large-scale movements, including loop migrations where the outward and return journeys follow different paths (Dingle and Drake 2007), have been observed (Tarroux et al. 2010, Rioux et al. 2016). The arctic fox in this terrestrial and marine meta-ecosystem thus also represents a good model to test hypotheses about the movements of a predator faced with alternative tactics such as migration, nomadism, and residency.

In a six-year study, we investigated the winter movements of 66 adult arctic foxes tracked during 1–3 years each (97 fox-years) in the Canadian High Arctic. Our use of satellite telemetry to track individuals year-round and over two complete lemming cycles, in a context where some (but not all) foxes also had access to a large nesting goose colony and where marine resources were available on the neighboring sea ice in winter, provided us with a unique opportunity to examine the influence of spatio-temporal resource variation and individual characteristics, such as sex and age, on movement tactics. We hypothesized that the movement tactic used by individuals would be influenced by spatio-temporal changes in resource availability, as well as by individual characteristics. Foxes should remain resident if they can find sufficient food resources to sustain themselves, otherwise they should quit their territory to track the rodent resource or move onto the sea ice habitat. We tested the hypothesis through comparison of our observations with the following predictions:

P_1. Higher densities of the preferred prey, lemmings, should promote residency while lower densities should trigger migration or nomadism.

P_2. Foxes with territories in the goose colony have access to cached eggs and should be less likely to become nomads or migrants during winter than foxes without access to such food. In addition, if they leave their territory during winter, foxes should be more likely to migrate back in spring due to the high spatio-temporal predictability of geese.

P_3. During low lemming years or outside of the goose colony, resident foxes should do more trips to the sea ice to compensate with marine food the scarcity of terrestrial food.

P_4. The propensity to leave the territory should increase with age as old senescent individuals could be excluded from their territories.

Material and methods

Study site

We worked in the south plain of Bylot Island (73°N, 80°W) in the Sirmilik National Park of Canada, Nunavut. The 600-km^2 study area comprises approximately 60 km of coastline and extends 5–15 km inland (see detailed description in Gauthier et al. 2013). Two lemming species are present, the brown lemming *L. trimucronatus*, which shows 3–4 year cycles of abundance, and the collared lemming *D. groendilandicus*, present at low density (Gruyer et al. 2008). Greater snow geese *Chen caerulescens atlantica* arrive in late May to breed in a large but spatially-restricted colony and leave in early September (Gauthier et al. 1996). The goose nesting colony covers approximately 60 km^2 (Supplementary material Appendix 1 Fig. A1), with a mean nest density of 4.17 nests ha^{-1} (Gauthier et al. 2013). Despite some inter-annual fluctuations, the nesting density and reproductive success of geese did not show any temporal trend over the two last decades (Gauthier et al. 2013). The study area is bordered by land-fast ice from late October to late July, giving foxes access to marine carcasses left by polar bears *Ursus maritimus* during winter and to ringed seal *Phoca hispida* pups after mid-March (Smith 1976, Gagnon and Berteaux 2009).

Capture and satellite tracking data

All known dens (ca 100) were visited at least twice during summer, once in early May and once in late June. Dens showing signs of activity (digging, hairs, tracks, prey remains, presence of adults or pups) in May were monitored until the end of July using infrared automatic color cameras. Pictures from cameras and visual observations performed at selected dens in June and July during at least three 12-h sessions were used to determine the identity of adults using the dens and the presence of pups. We captured adults between May and August, as described in Tarroux et al. (2010). We determined their sex upon capture. We estimated their age from pictures of dentition (front and sides) taken during captures, based on a tooth wear notation system calibrated with the dentitions of foxes which age was known from tooth cementum layer counts (Chevallier et al unpubl.). Mean (± SD) estimated age was 3.4 ± 1.7 years (Supplementary material Appendix 2 Table A1). From 2007 to 2012, we fit 85 adults with 107 collars equipped with Argos Platform Transmitter Terminals (PTT, with temperature sensor; 95g–115g; < 5% of body mass). We used for analyses only foxes which held territories during the summer preceding the recorded winter movement and for which we had the complete winter track, starting 25 October (when sea ice is formed) and ending at least 16 April but up to 31 May, depending on individuals (mid-April to late-May corresponds to the birth season). This resulted in 66 individuals (38 females and 28 males) tracked from 1–3 years, for a total of 97 fox-years. The PTT transmitted daily or every two days for a 3- to 4-h period (13:00–17:00 UTC, corresponding to 07:00–11:00 local time) with a repetition rate of 60 s. Duty cycles of the PTT varied slightly between years and collars (details in Supplementary material Appendix 2 Table A1). Argos locations were filtered using a speed filter (see S1 File in Christin et al. 2015) implemented in R 3.1.0. (<www.r-project.org>). First, we kept only positions with a location class of LC 3, 2 and 1, respectively corresponding to positioning errors having a 68% probability of being < 250 m, < 500 m, and < 1500 m (CLS 2011). Locations were then projected in the Universal Transverse Mercator, North American Datum 83 system, and any location requiring unrealistic speed values from the previous one ($>$ 7 km h^{-1} cruising speed, with possible 12-min acceleration bouts of 10 km h^{-1}) was removed. We set speed values from data obtained from GPS collars in the same fox population (Christin et al. 2015). We kept for analyses one location per transmission period, based on the smallest location error, in order to reduce spatial autocorrelation in further analyses. We mapped locations using ArcMap 9.3 (ESRI).

Categorization of extraterritorial movements and movement tactics

Since arctic foxes can repeatedly use the same den across years (Angerbjörn et al. 2004) and may keep their breeding territory after the summer (Rioux et al. 2016), we used the summer home range as reference against which to compare winter movements. An animal's home range is usually described as the area with a defined probability of occurrence of the individual during a specified time period (Kernohan et al. 2001). For territorial species, such as canids, the territory is an area of exclusive use by the territory holders and is maintained through several behaviours, such as active defence, scent marking and territorial calls (Kleiman 1977, 2011). Although we cannot confirm the exact area of exclusive use within a home range from telemetry data only, we hereafter refer to a fox's home range estimated from satellite-tracking data as a 'territory', for ease of interpretation. We used locations from 1 June to 30 September to delineate territories, using the fixed kernel method at the 90% isopleth. We used a constant smoothing parameter *h* (0.8) for all individuals corresponding to the rounded mean of the smoothing parameters estimated by the reference method (h_{ref}) for each individual territory (Costello 2010). We plotted territory size against an incremental number of locations added randomly to estimate the sample size after which additional locations resulted in a minimal increase in range size (Harris et al. 1990). Using 18 ranges with > 110 locations, we found that range size reached 90% of its maximum value by 22 locations on average. All individuals used in this study had a number of locations higher than this threshold. The mean (± SD) number of locations used for territory calculation was 76 ± 28 (median = 67). Kernels were estimated with the *adehabitatHR* library in R.

To compare data from PTTs with different duty cycles, we subsampled winter locations to one every second day. To examine movement types out of the territory, we extracted all extraterritorial movements, defined as ≥ one location > 2 km away from the limit of the territory. This 2 km distance represents approximately half the average radius of a territory and also extends beyond the largest class of Argos errors (up to 1500 m). For each extraterritorial movement, we calculated the duration (number of consecutive days with no location in the territory), the minimum distance travelled (sum of straight-line distances between successive locations) and the maximum distance to the territory (largest straight-line distance between a location and the nearest territory boundary). Extraterritorial movements without a return to the territory before the next reproductive season were identified as nomadic movements (Fig. 1A). Extraterritorial movements reaching the sea ice and followed by a return to the territory were identified as excursions. We plotted the duration of excursions (n = 509) against the minimum distance travelled during each trip to perform a piecewise regression (Crawley 2007) and we identified a breakpoint at 38 days (Supplementary material Appendix 3 Fig. A3). We classified excursions lasting < 38 days as commuting trips (short-term and short-distance round-trip journeys, Hofer and East 1993), while the remaining were categorized as loop migrations (long-term and long-distance movements). In addition to these differences in duration and distances, movements categorized as loop migrations all reached areas beyond the neighboring land-fast ice of Navy Board Inlet and Eclipse Sound (Fig. 1B), while commuting trips were largely restricted to this area (Fig. 1D). This further confirmed that this breakpoint identified two distinct types of movements. Based on the three movement types identified (nomadic movements, commuting trips, loop migrations) and using the entire winter track of foxes, we classified movement tactics into three categories: 1) resident – foxes remained in their territories with possible commuting trips, 2) migrant – foxes left for a least one loop migration and returned to their territory, 3) nomad – foxes left and did not return to their territory before 31 May or died while undertaking a nomadic movement. Foxes were considered on 31 May to be alive (PTT moving or fox seen alive), dead (PTT not moving and low temperatures from sensor) or of unknown status (PTT failure and fox not resighted).

Resource variables

We assessed lemming availability by estimating density of brown and collared lemmings in July of each year via

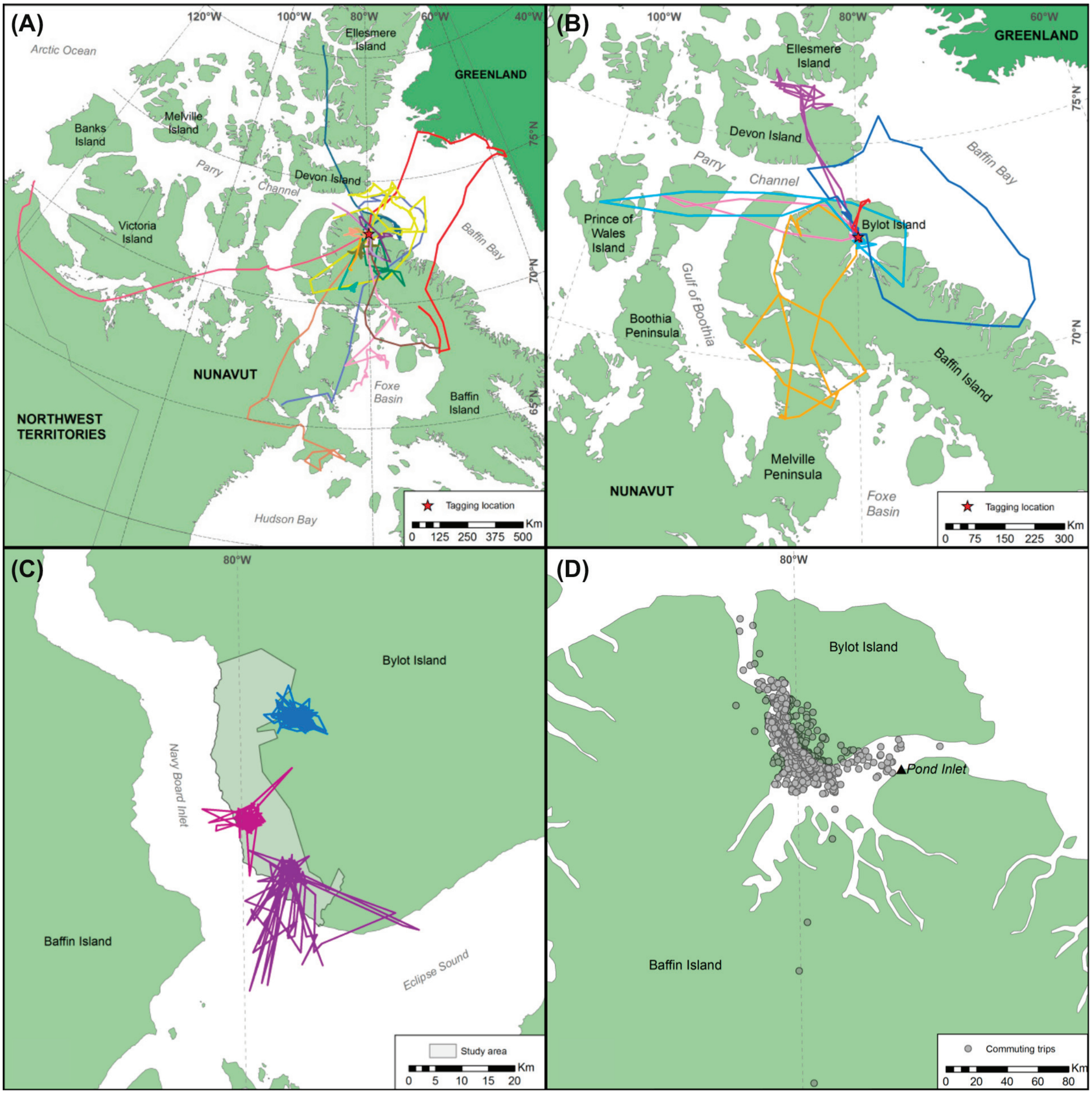

Figure 1. Filtered tracks (A to C) and point locations (D) of adult arctic foxes from Bylot Island equipped with Argos PTT during six winters (25 October 2007 to 31 May 2013). Tracks display (A) nomadic movements (n = 18), (B) loop migrations (n = 6) and (C) examples of complete winter tracks (n = 3) showing range residency and commuting trips to the sea ice, while point locations (D) depict the total area covered by all commuting trips (n = 503).

capture–mark–recapture methods, using live-trapping data from two 11-ha grids located in the northern part of the study area (see Gauthier et al. 2013 for details). Since no trapping occurred during winter, we considered winter densities as the average between those estimated during the previous and next summers. Our 2007–2013 study period covers two lemming cycles, with lemming densities peaking in summers 2008 and 2011 (Fig. 2). We recorded the contour of the goose colony with a helicopter and GPS every year in late June. Using stable isotopes, Tarroux et al. (2012) showed that the use of this food source (especially eggs) by foxes was marginal beyond an estimated distance of 6.2 km from the edge of the colony. To allow the influence of the colony to decrease as the distance to its edge increased until it became irrelevant after a certain threshold, we used two distance-dependent decay functions, one exponential and one Gaussian. Both are often used to model the effects of habitat edges or human features on wildlife species (Ries et al. 2004, Nielsen et al. 2009, Aue et al. 2012, Takahata et al. 2014). The exponential decay function was of the form $e^{-\alpha x}$, while the Gaussian decay function was $e^{-(\alpha x)^2}$, with α representing the decay constant and x the distance of the center of a fox territory from the closest edge of the colony (km). Both functions were set to decrease to a decay score of 0.05 at 6.2 km, meaning that a fox had almost no access to the colony after this distance. Decay scores ranged from 1 to 0, with scores of 1 inside the colony and scores nearing 0 at large distances. As shown in the Supplementary material

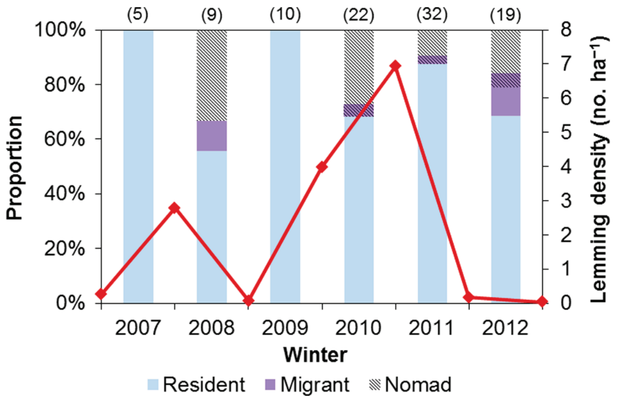

Figure 2. Proportion of movement tactics used by adult arctic foxes during the sea ice season (25 October to 31 May) on Bylot Island, Nunavut, Canada during six years covering two lemming cycles. Numbers on top of bars indicate the number of individuals followed each year. The red line shows the density index of lemmings.

Appendix 1 Fig. A2, the exponential decay function decreases more rapidly than the Gaussian decay function.

Statistical analyses

We compared parameters of the three movement types (nomadic movements, commuting trips, loop migrations) using Student's t or Wilcoxon signed-rank tests, depending on data normality. As migrants and nomads were few, we combined both groups in subsequent analyses. We used a randomisation χ^2-test with 1000 randomisations to assess if the proportion of residents versus migrants/nomads varied between winters. We compared the risk of winter mortality between residents and migrants/nomads using a mixed Cox proportional hazards analysis with year and fox identity as random effects. We used a right-censored design with time-at-risk based on the time (days) since the start of the winter period (25 October).

We used an information-theoretic approach to identify which predictor variables influenced the propensity of individuals to become a nomad or migrant (P_1, P_2 and P_4). We removed from the analyses eight fox-years (five individuals) for which age was unknown. Using GLMMs with binomial family and logit link, and fox identity as a random effect, we built candidate models including the two resource covariates (lemming density and distance decay to the goose colony), the two individual covariates (age and sex), and two-way interactions between the covariates. We checked collinearity among predictor variables prior to statistical analyses, using correlations, scatterplots and boxplots. We conducted model selection using Akaike's information criterion corrected for small sample size (AIC_c) and AIC_c weights (Burnham and Anderson 2002), considering models with $\Delta AIC_c < 2$ as having substantial empirical support (Anderson 2008). We used multimodel inference to calculate the unconditional parameter estimates (β_i) and the 95% confidence intervals (CI) for the regression coefficient of each predictor variable. Only variables with a 95% CI around β_i that did not overlap zero were considered to have a significant effect (Burnham and Anderson 2002).

We then studied the commuting behaviour using data from the resident foxes only. We first extracted for each resident the number of commuting trips over the winter. Since tracking periods varied between foxes, we transformed the total number of commuting trips to a monthly frequency (30 days) to allow comparison across individuals. To assess the influence of the environmental and individual covariates on the frequency of commuting trips (P_3), we used linear mixed models with the model structure and procedure described previously. The response variable was square root-transformed to meet the assumptions of normality in its distribution. We performed mixed models with the *lme4* and the *coxme* libraries, and model selection and averaging with the *MuMIn* library in R. Results were similar with both distance decay functions, therefore we discuss the results of model selection for both functions but present the coefficients with the Gaussian decay function only. The results with the exponential decay function are available in the Supplementary material Appendix 4 Table A3–A4.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b56d4> (Lai et al. 2016).

Results

Movement types and movement tactics

From July 2007 to May 2013, we recorded 229 657 Argos locations from 66 individuals (n = 97 fox-years), which were reduced to 142 686 after filtering (62.1% rejection rate, Supplementary material Appendix 2 Table A1). We recorded 14 mortalities (six in the nomad/migrant category, eigth in the resident category) and only two foxes had an unknown fate. Commuting trips (excursions < 38 days) were the most common type of extraterritorial movement during winter (95.5%, n = 503). The frequency of commuting trips per individual ranged from 0 to 2.9 trips per month (mean ± SE = 0.8 ± 0.1). Nomadic movements (3.4%, n = 18) and loop migrations (1.1%, n = 6) were rare. Out of the 66 tracked individuals, 56 performed at least one commuting trip. Fifteen foxes performed nomadic movements, three did loop migrations and an additional three did a loop migration followed by a nomadic movement during the same winter. Duration, maximum distances to the territory and minimum total distances travelled did not differ significantly between males and females, whatever the type of movement (Wilcoxon signed-rank tests, all p > 0.20). Commuting trips were relatively short-termed, lasting on average (± SE) 2.7 ± 0.1 days (n = 503; Supplementary material Appendix 3 Fig. A3). The average duration of commuting trips was 26–28 times shorter than that of loop migrations or nomadic movements, respectively, whereas average minimum distances moved by foxes were 37–48 times shorter in the former case than in the latter one (Table 1). Nomadic movements and loop migrations covered the whole Canadian archipelago and crossed over to Greenland and the Northwest territories of Canada (Fig. 1A–1B), while commuting trips occurred on the land-fast ice of Navy Board Inlet and Eclipse Sound

Table 1. Mean (± SE) duration, minimum distance travelled and maximum distance to the territory for adult arctic foxes making commuting trips, loop migrations and nomadic movements in the Canadian Arctic, 2007–2013.

Type of movement	n	Duration (days)	Min. distance travelled (km)	Max. distance to territory (km)
Commuting trip	503	2.7 ± 0.1	32.3 ± 1.5	11.1 ± 0.6
Loop migration	6	70.2 ± 9.6	1565.4 ± 305.4	449.9 ± 79.1
Nomadic movement	18	75.2 ± 11.6	1214.7 ± 227.9	487.8 ± 112.8

(Fig. 1C–1D). Movement parameters were not significantly different between loop migrations and nomadic movements (Student's t-tests, all $p > 0.29$; Table 1). Since three foxes that undertook a loop migration also dispersed as nomads during the same winter, out of 97 fox-years, 78.3% were classified as resident, 18.6% as nomad and 3.1% as migrant. Residency was always the most prevalent movement tactic in winter (range: 55.5–100%; Fig. 2) but the proportion of residents versus the two other tactics varied between years (randomisation χ^2-test, $p = 0.046$). We tracked 18 individuals over two years and six over three years and thus obtained 30 cases allowing comparison of movement tactics between successive winters. In 66.7% of cases, foxes remained resident, 23.3% switched from resident to nomad and 10% switched between migrant and resident. When nomads or migrants occurred during winter, their mean (± SE) annual mortality rate was 30.1 ± 7.1%, while it was 8.5 ± 5.3% for residents. The Cox regression indicated that the movement tactic was significantly related to survival, with the risk of dying of nomads/migrants being 3.4 times higher that of residents (coefficient = 1.21, SE = 0.59; $p = 0.039$).

Factors influencing winter tactics and the frequency of commuting trips

When using the Gaussian decay function, two models explaining the propensity to become a nomad or migrant were within $\Delta AIC_c < 2$ and included distance to the goose colony and age (Table 2, A). When using the exponential decay function, only one model (colony + age) was within $\Delta AIC_c < 2$ (Supplementary material Appendix 4 Table A3, A). This supports our prediction on the effect of the colony (P_2), but does not support our prediction on the influence of lemming density (P_1). According to multi-model averaging, the propensity of a fox to become a nomad or migrant decreased by 70.5% (odds ratio: 0.29; 95% CI [0.08; 0.98]) as the distance of its territory to the goose colony decreased from far to inside the colony (Table 2, B). Age affected the propensity to quit the territory, as expected (P_4): a fox was 1.56 times more likely (95% CI [1.14; 2.19]) to become a nomad or migrant for every additional year of age (Table 2, B). None of the foxes performing loop migrations had a territory inside the goose colony, thus providing no support to the prediction that the highly spatio-temporally predictable goose colony would promote fox migration (P_2).

Regarding the frequency of commuting trips by resident foxes, four models were within $\Delta AIC_c < 2$, irrespective of the distance decay function used. Models included the distance to the goose colony, lemming density, sex, and the interaction between the distance to the goose colony and lemming density (Table 3, A, Supplementary material Appendix 4 Table A4, A). According to multi-model averaging, the frequency of commuting trips decreased with increasing lemming densities, the decline being steeper as foxes were located further away from the goose colony, in accordance with P_3. Depending on the decay function used, the frequency of sea ice excursions for foxes at the periphery of the colony was either intermediate between those inside the colony and those far from it (Gaussian decay function, Fig. 3) or closer to the frequency of foxes far from the colony (exponential decay function, Supplementary material Appendix 4 Fig. A4). Finally, while sex was retained in the best models, with a tendency of males to commute to the sea ice more often than females, the influence of sex was minimal as

Table 2. General linear mixed effect regression models with logit link for the occurrence of nomadism and migration, and fox identity as a random variable, for adult arctic foxes (n = 89 fox–years) studied on Bylot Island, Nunavut, Canada. (A) Variables, number of parameters (k), Akaike's information criterion adjusted for small sample size (AICc), AICc difference (Δ_i), and AICc weight (w_i) for all models up to $\Delta_i < 4$ and the null model. (B) Parameter estimates, unconditional standard errors (SE) and 95% confidence interval for variables of the selected models ($\Delta_i < 2$). The confidence limits with a 95% confidence interval not overlapping 0 are in bold. Variable abbreviations: Age = individual's age in years, Cln = Gaussian distance decay to the goose colony (from 0, far to 1, inside the colony), Lmm = lemming density in no. ha^{-1}.

(A) Model	k	AIC_c	Δ_i	w_i
Age + Cln	4	92.29	0.00	0.21
Age	3	94.16	1.86	0.08
Age + Cln + Lmm	5	94.42	2.13	0.07
Age + Cln + Sex	5	94.49	2.20	0.07
Age + Cln + Age × Cln	5	94.52	2.23	0.07
Age + Cln + Lmm + Age × Lmm	6	96.05	3.75	0.03
Null	2	101.39	9.10	0.00

(B) Parameter	Estimate	SE	Lower limit	Upper limit
Intercept	–2.36	0.80	–3.94	–0.79
Age	0.45	0.17	**0.13**	**0.78**
Cln	–1.22	0.61	**–2.42**	**–0.02**

Table 3. Linear mixed effect regression models with fox identity as a random variable for the monthly frequency of commuting trips, for adult arctic foxes ($n = 68$ fox-years) studied on Bylot Island, Nunavut, Canada. (A) Variables, number of parameters (k), Akaike's information criterion adjusted for small sample size (AIC_c), AIC_c difference (Δ_i), and AIC_c weight (w_i) for all models up to $\Delta_i < 4$ and the null model. (B) Model-averaged parameter estimates, unconditional standard errors (SE) and 95% confidence intervals for variables of the selected models ($\Delta_i < 2$). Confidence limits with a 95% confidence interval not overlapping 0 are in bold. Variable abbreviations: Age = individual's age in years, Cln = Gaussian distance decay to the goose colony (from 0, far to 1, inside the colony), Lmm = lemming density in no. ha^{-1}, Sex (M = males).

(A) Model	k	AIC_c	Δ_i	w_i
Cln + Lmm + Sex + Cln× Lmm	7	168.89	0.00	0.17
Lmm + Sex	5	170.39	1.49	0.08
Cln + Lmm + Cln× Lmm	6	170.53	1.64	0.08
Lmm	4	170.83	1.94	0.07
Cln + Lmm + Sex + Cln× Lmm + Lmm × Sex	8	171.15	2.26	0.06
Cln + Lmm + Sex + Cln× Lmm + Cln × Sex	8	171.23	2.34	0.05
Age + Cln + Lmm + Sex + Cln × Lmm	8	171.37	2.48	0.05
Lmm + Sex + Lmm × Sex	6	172.11	3.22	0.03
Age + Cln + Lmm + Cln × Lmm	7	172.58	3.69	0.03
Age + Lmm + Sex	6	172.58	3.69	0.03
Cln + Lmm + Sex	6	172.64	3.75	0.03
Age + Lmm	5	172.64	3.75	0.03
Null	3	179.24	10.35	0.00

(B) Parameter	Estimate	SE	Lower limit	Upper limit
Intercept	2.39	0.39	1.63	3.15
Cln	–0.90	0.40	**–1.67**	**–0.13**
Lmm	–0.32	0.14	**–0.59**	**–0.05**
Sex(M)	0.36	0.19	–0.01	0.74
Cln× Lmm	0.31	0.12	**0.06**	**0.55**

the 95% CI of the parameter estimates overlapped zero (Table 3, B).

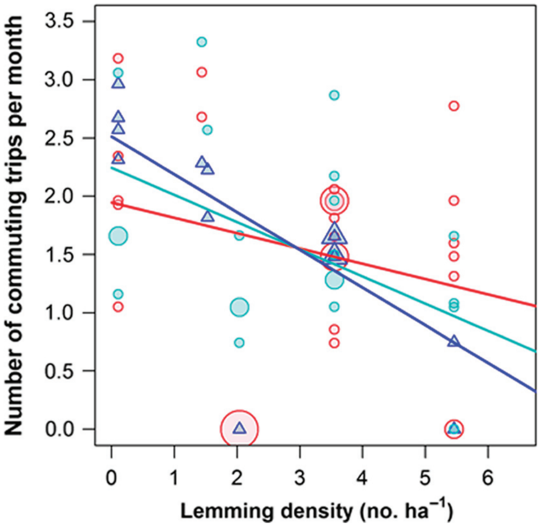

Figure 3. Relationship between winter lemming density and monthly number of commuting trips to the sea ice by resident adult arctic foxes on Bylot Island, Nunavut, Canada. We illustrate the general fit of the model obtained after averaging the best linear mixed models ($\Delta AIC_c < 2$), with regression lines depicting foxes with territories moving away from the goose colony, going from inside (distance = 0 km; red line) to the middle of the periphery (distance = 3.1 km; cyan line) and to far away (distance > 6.2 km; blue line). The number of commuting trips (2√ values) is shown for territories located inside (red circles), within the periphery (cyan circles) and outside (blue triangles) of the goose colony. Size of data points in the plot reflects the number of observations (1 to 4 per point).

Discussion

Through satellite tracking of 66 individuals over six years covering two complete lemming cycles, we found that arctic foxes from the south plain of Bylot Island did use a flexible movement strategy. However, the responses to resource variation were not all in line with our predictions. Though movement tactics involving long-distance movements exist in the study population, they were rare (especially migration), and residency was the main tactic used. The propensity of an individual to become a nomad or migrant during winter did increase for foxes with territories further away from the goose colony. Surprisingly, this was not linked to the abundance of the main prey, lemmings. Lemming density, however, affected the frequency of sea ice trips, which was higher as foxes were further away from the goose colony and increased more markedly as lemming densities decreased for these foxes. These results are in line with studies in birds suggesting that the access to alternative food sources can favor residency over nomadism in predators specializing on cyclic rodents (Korpimäki 1986, Clulow et al. 2011), but the added particularity of our study model was the presence of a food source outside of the territory.

We describe, for the first time in arctic foxes, a pattern of range residency coupled with a commuting system. Commuting trips allowing individuals to keep their territories despite a shortage of food inside territories have previously been observed in spotted hyenas *Crocuta crocuta* (Hofer and East 1993), red foxes *Vulpes vulpes* (Tsukada 1997) and wolves (Messier 1985). Our results thus lend further support to the hypothesis that this type of predator commuting system appears when prey abundance strongly fluctuates inside territories, whereas a predictable food source is within reaching distance of the territory (Hofer and East 1993, Tsukada 1997). However, as reported for coyotes, the availability of a nearby feeding range does not necessarily ensure its use, even when the amount of resources is low inside the territory (Patterson and Messier 2001). The establishment of a commuting system over other movement tactics in predators is not yet completely understood (Hofer and East 1993). Arctic foxes are capable of detecting resources over dozens of kilometers (Lai et al. 2015), which may allow them to efficiently locate marine resources in the vicinity of their territories. Resident foxes seemed to obtain sufficient resources on the land-fast ice of the narrow inlet (10–30 km wide) separating Bylot Island from Baffin Island (Fig. 1C–D) and they usually left their territory for less than three days in a row. Territorial scent marks can persist up to 25 days in wolves (Peters and Mech 1975). If this applies to foxes, commuting trips allow them to obtain marine food without a high risk of losing their territory, since their absence may not exceed the lifetime of scent marks. Taken together, these may explain why our study population uses a commuting system rather than a seasonal migration from the tundra to the sea ice or long-distance tracking of the lemming resource, which both could have been expected from arctic foxes based on the literature.

The prevalence of range residency in winter despite lemming fluctuations shows a strong attachment of foxes to their territories. Interestingly, the rare loop migrants that we detected all had their territories outside of the goose colony, highlighting site fidelity even without a predictable resource. In short-lived species, it is important to consider if the expected future reproductive success can compensate for the cost incurred upon long-distance movements (Switzer 1993). Wild arctic foxes live only 3–4 years on average (Audet et al. 2002, Angerbjörn et al. 2004). Instead of tracking the rodent resource, it may be more beneficial for a fox to keep a territory once it is acquired and reproduce when the conditions allow, a site-tenacious strategy similar to that of the long-tailed skua *Stercorarius longicaudus* (Andersson 1976, Barraquand et al. 2014). This strategy may be even more advantageous for foxes that have access to additional resources, such as those in the goose colony, as suggested by their decreased propensity to become nomads or migrants. A territory close to the goose nesting colony is valuable not only because eggs can be easily stored, thus potentially increasing winter survival, but also because they give higher breeding prospects in summer, especially during low lemming abundance (Giroux et al. 2012). Foxes may be more attached to areas where food availability is higher. In northern Alaska, arctic foxes in the Prudhoe Bay oil field were resident over the winter while individuals located in an undeveloped area presented mixed tactics including long-distance movements on the sea ice, a difference likely attributable to anthropogenic foods available in the Prudhoe Bay area (Pamperin 2008, Lehner 2012). However, in the alpine tundra of Norway, arctic foxes ($n = 3$ dens followed) also appear to adopt a 'sit-and-wait' strategy, maintaining their territories instead of tracking lemming availability (Strand et al. 1999). Tracking other arctic fox populations facing different ecological conditions will thus be an important future step. Although we did not observe the mass emigrations of foxes described in the literature (Wrigley and Hatch 1976), this could be because we did not track juveniles. Future work should focus on this segment of the population.

The likelihood of foxes to become nomads or migrants highly increased with age. The exclusion of older individuals from their territories may further be supported by the fact that dens left by these foxes were sometimes occupied by new breeders (Supplementary material Appendix 2 Table A2). It is unknown, however, if the new individuals arrived in the territory before or after the original territory holder left. Breeding dispersal allowing offspring to stay at the natal site may be a form of parental investment in female North American red squirrels *Tamiasciurus hudsonicus*, with older females more likely to bequeath their territories (Berteaux and Boutin 2000). In the case of arctic foxes, this would however require both members of the pair to leave the territory, which was not always the case (Supplementary material Appendix 2 Table A2). Further investigation is needed to clarify if territory acquisition occurs through takeover, inheritance or filling of vacancy.

Fitness costs and benefits of the different tactics must be assessed to understand ultimate causes of tactics, but this is difficult. Mortality is often greater for animals moving into unfamiliar areas (Schwartz and Franzmann 1992, Ferreras et al. 2004, Hellgren et al. 2005), although it is not always the case (Koopman et al. 2000, Noyce and Garshelis 2011). In our study, the mortality rate was > 3 times higher for migrants and nomads than for residents, suggesting high risks associated with moving out of the familiar territory in the Arctic. In addition, reproduction was likely unsuccessful following five of the six loop migrations recorded, since foxes came back to their dens very late in the breeding season (late April or May). Of the 10 nomads that survived until spring, only four had settled and may have raised young (Supplementary material Appendix 2 Table A2). These observations suggest that long-distance movements may not be the optimal tactic in this population. Previous research on mobile terrestrial carnivores also suggested that large-scale resource tracking could be more costly than switching to a secondary prey (Valeix et al. 2012). This contrasts with avian rodent predators, for which breeding dispersal to track the spatial variation in rodent abundance improves breeding performance, especially in females (Therrien et al. 2014, Terraube et al. 2015). To better understand the costs and benefits of each movement tactic in arctic foxes, other parameters known to influence movements could be evaluated by future research. In particular, reproductive success during the previous season may strongly influence movement decisions, with many bird species adopting a 'win–stay, lose–switch' strategy, where site fidelity follows breeding success and dispersal follows breeding failure (Greenwood and Harvey 1982, Haas 1998, Hoover 2003). We did not have information on the previous breeding success (presence of pups) for all collared foxes and thus could not add this parameter in the analysis. However, examination of the foxes for which we had information indicated that the proportion of successful and failed breeders seemed similar among the nomads/migrants (80% versus 20%, $n = 20$) and the residents (72% versus 28%, $n = 67$; χ^2-test, $p = 0.46$). This suggests that the previous reproductive success may not affect the winter movement tactic in arctic foxes, while also highlighting that a very high proportion of nomads/migrants were previously successful breeders. Other parameters to consider may include population density (Nelson 1995), body condition (Brodersen et al. 2014) and seal carcass availability.

Through the translocation of nutrients and influence on predator–prey interactions, cross-ecosystem foraging by a highly mobile predator has important implications for community structure and ecosystem function (Lundberg and Moberg 2003, Nifong et al. 2015). Understanding winter movement patterns of arctic foxes is thus important for modelling ecosystem processes. For example, Gilg (2006) did not consider arctic fox winter predation when studying lemming dynamics in Greenland, assuming that foxes become "partly nomadic" in winter. Yet mixed movement tactics including high levels of residency can occur, as we have shown. Considering winter predation on lemmings by arctic foxes is critical on Bylot Island, where top–down forces shape ecosystem functioning (Legagneux et al. 2014). Our results also show the spatial scales at which the arctic fox, as a "mobile link" (Lundberg and Moberg 2003, Jeltsch et al. 2013), can affect communities and ecosystems. Allochtonous marine resources contributing to the Bylot terrestrial ecosystem (Tarroux et al. 2012) mainly originate locally, from the Navy Board Inlet and Eclipse Sound regions, while arctic fox nomadism can disperse pathogens and parasites at a very large scale across the Nearctic. As seen in other top predators foraging between adjacent ecosystems, individual-level behaviours, such as prey preference, can influence intrapopulation variation in movement patterns, which can in turn have an impact on ecosystem connectivity (Nifong et al. 2015). Compared to foxes close to the goose colony, which may rely more on cached food such as eggs, foxes located further away cross more often between the terrestrial and marine environments and may thus be more involved in the local ecosystem connectivity. Finally, potential negative impacts of the diminishing sea ice on arctic foxes have been raised (Roth 2002, Pamperin et al. 2008). While an earlier break-up of the sea ice may indeed impair long-distance movements, especially for homing foxes, resident populations may be less impacted if commuting trips occur mostly during winter.

In summary, we found that low lemming densities trigger winter fox movements only at a local scale, while access to a goose colony influences movements at both local and large scales. Hence, arctic foxes cope with food shortage by regularly crossing ecosystem boundaries instead of migrating or tracking food resources over long distances. This study using a terrestrial but mobile arctic predator shows the behavioural adjustments used to maintain range residency in a highly variable environment favoring migration or nomadism. Our results can thus help predict movement patterns in other species depending on cyclic prey (for example, *Lynx* species feeding on cyclic hares), or those relying on fluctuating migratory prey. Future studies of the determinants of movement strategies in flexible species should thus take into account their mobility, dietary flexibility and diversity of alternative food sources, whether resources are inside or outside of the territory, as well as the fitness outcomes of movement patterns.

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Supplementary material (Appendix oik-03948 at <www.oikosjournal.org/appendix/oik.03948>). Appendix 1–4.