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Movement Ecology

RESEARCH

Intraseasonal variations in the spatial behaviour of an Arctic predator

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Abstract

Background In highly constrained ecosystems such as in the Arctic, animals must constantly adjust their movements to cope with the highly versatile environmental conditions. However, to date most studies have focused on interseasonal differences in spatial behaviour, while intraseasonal dynamics are less described.

Methods To fill this knowledge gap, we studied the movement patterns of an Arctic predator, the arctic fox (*Vulpes lagopus*) at the intraseasonal scale. To unravel temporal patterns in space use and movement metrics, we used GPS data collected on 20 individual foxes between 2017 and 2023 in North-East Greenland.

Results We showed that weekly full and core home range sizes (estimated by means of Autocorrelated Kernel Density Estimates), and daily mean relative turning angles stayed constant throughout the summer. Conversely, daily distance travelled, mean daily speed and daily proportion of 'active' time showed intraseasonal variations. These fine-scale metrics had a hump-shaped distribution, peaking in mid-July, with males and non-breeding foxes travelling longer distances and being faster. Site-specific patterns were also identified, with foxes having smaller territories in the two most productive sites but moving shorter distances and at lower speeds at the poorest site.

Conclusion Our study provides novel insights into how predators adjust their space use and behaviour to intraseasonal variations in environmental conditions. Specifically, we show that different movement metrics show different intraseasonal patterns. We also underline the importance of considering small spatiotemporal scales to fully understand predators' spatial behaviour.

Keywords Autocorrelated Kernel density estimate, GPS telemetry, Greenland, Home range, Movement ecology, Spatiotemporal patterns, *Vulpes lagopus*

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Background

Animals cope with their ever-changing environment by modulating their behaviour at different spatiotemporal scales [1, 2]. From one year to another, individuals from a variety of species can indeed adjust their behaviour according to previous experience and changing environmental conditions [3–6]. On the other hand, within a single year, animals can adapt their behaviour following seasonal variations in environmental and biological parameters [7–9]. More specifically, animals can adjust their movements according to temporal variations in biotic and abiotic parameters. This is particularly true for carnivores, which are impacted by both seasonal variations in environmental parameters and complex changes in prey distribution and behaviour. For example, female red fox (*Vulpes vulpes*) travel longer distances in summer, when foraging time increases [10]. Coyotes (*Canis latrans*) adjust their foraging behaviour and resources selection to avoid moving in costly landscapes during the snow season [11]. Animals are thus able to adjust their behaviour according to environmental variations at different temporal scales to make better use of their habitat.

Animal movements are also adjusted according to temporal variations in energetic needs, owing for instance to their breeding status or the age of their young [12, 13]. These energetic needs have to be met within the individual's home range, the area where an animal can express all the behaviours needed to survive and reproduce [14], which can consequently follow temporal variations too [15–18]. For instance, red wolves (*Canis lupus rufus*) home range sizes are larger in autumn and winter when resources are relatively scarce, and smaller in spring when cubs are highly dependent [19]. This expansion-contraction pattern in home range sizes according to resources availability and biological constraints is found in a variety of other species [20–22], suggesting a generalised and adaptive pattern.

However, clear seasonal changes in movement patterns are not always identified [23], probably because intraseasonal processes are at play at a smaller scale. For instance, various animal species adjust their movements according to short time variations in snow cover [11], temperature [24], landscape composition [25], or constraints owing to the development of the progeny [26]. Grey wolves (*Canis lupus*), for example, display more energy-costly behaviours during the pup rearing season [26]. Dingoes (*Canis dingo*) travel less when temperatures are too high in summer [24]. As such, several movement patterns can greatly change within a single season, according to different biotic and abiotic parameters that can potentially interact.

Although movement patterns have been extensively studied at the interseasonal scale (e.g. [11, 27–29]), intraseasonal studies are comparatively scarce. There is evidence that vertebrates can change their behaviour [30], habitat selection [31], diet [32], ultimately influencing their movement patterns [13, 29] within a few days or weeks. Overlooking intraseasonal changes can hence lead to spurious conclusions [11, 18, 33] and ultimately impede conservation efforts, for instance because animals can switch the location of their home range within a single season [34]. It is therefore crucial to better understand intraseasonal movements to draw more comprehensive conclusions and complement our knowledge on interseasonal patterns.

The Arctic tundra is an ideal study system to look at intraseasonal variations in wildlife behaviour. Indeed, this ecosystem is subject to extreme and rapid changes in climatic variations and its fauna has evolved to cope with these changes [35]. The arctic fox (*Vulpes lagopus*) is for instance able to intensively feed on pulsed resources [36, 37], cached food [38], or increase reproductive output when prey are abundant [36, 39]. To date, most research on arctic fox spatial behaviour has focused on the summer season [40, 41], with home ranges and movement metrics being estimated at yearly or seasonal time-scales (e.g. [42–44]). Studies investigating intraseasonal variations are virtually lacking. Furthermore, and because arctic foxes' behaviour and ecology can strongly change between study areas as a result of prey specialisation and environmental constraints [39, 42], it appears crucial to conduct comparative analyses between different study areas. It is hence essential to assess the intraseasonal changes in arctic fox space use in different areas to better understand its capacity to adjust its behaviour within the rapidly changing tundra ecosystem.

Our study aims at describing the intraseasonal spatial behaviour of the arctic fox at three sites in Northeast Greenland. We hypothesise that the combination of environmental, biological and ecological constraints would force arctic foxes to adjust their movements at a short, intraseasonal scale (Fig. 1).

First, since foxes from Greenland live in a harsh environment with rapidly fluctuating resources [36, 45], we predict that home range sizes should be relatively large and fluctuate during the summer season, with larger home ranges during periods of food scarcity but smaller home ranges in areas with greater food availability. Second, because (1) foraging activity to feed growing cubs peaks during summer (2), in synchrony with resource accessibility (e.g., rodents being easier to catch in the absence of the protective snow cover) and availability (e.g., migratory birds), and because (3) foxes must also prepare for the harsh Arctic winter (e.g., by caching food), we predict that several movement metrics (i.e., weekly distance travelled, mean speed, turning angles and active time) should increase at the beginning of the summer as energetic needs increase, with a peak

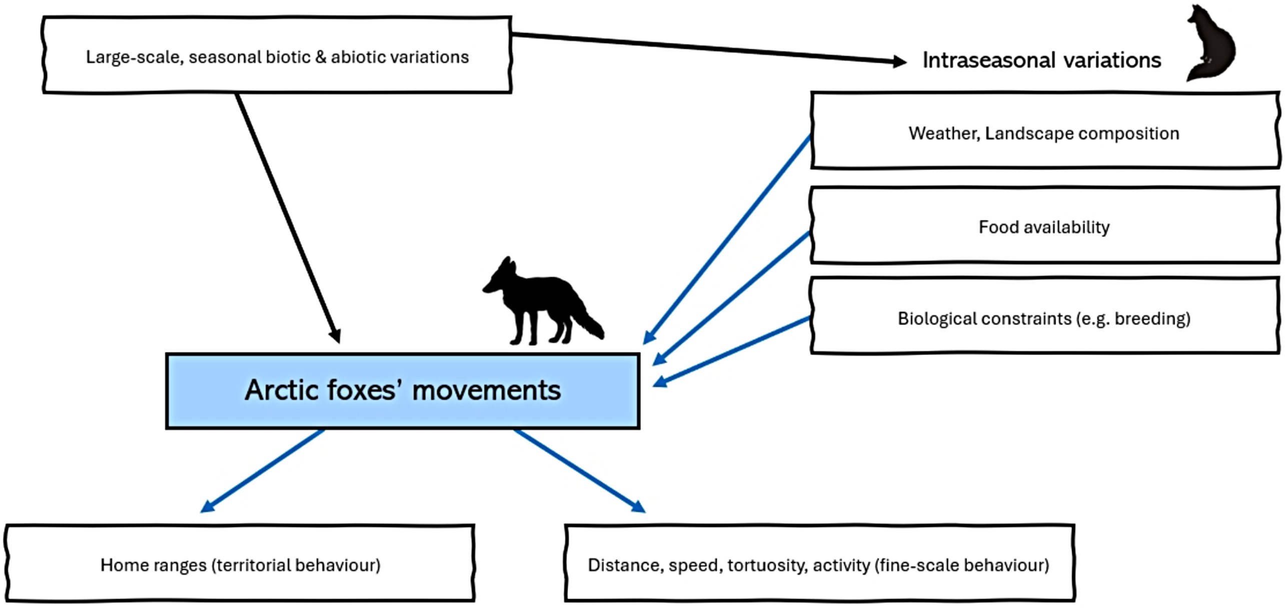

Fig. 1 Diagram representing the hypothesised main factors driving temporal changes in arctic foxes' movements. In this study, we focus on the impact of variations in biotic and abiotic factors on the movement patterns of arctic foxes at the intraseasonal scale (blue arrows). Territorial behaviour depicts larger spatial scale patterns, whereas fine-scale behaviour depicts small-scale movement decisions

in mid-summer when food needs and feeding opportunities are assumed to be maximal, before decreasing as resources become less abundant.

Materials and methods

Study areas and species

Data were collected at three study sites located in Northeast Greenland (Fig. 2): Hochstetter Forland (75.15°N, 19.70°W), Zackenberg (74.47°N, 20.57°W) and Karupelv Valley (72.50°N, 24.00°W), all being characterised by the shrub Tundra subzone biome (mean summer temperature < 10 °C; vegetation cover: 5–50% and scattered; [46]). The three study areas differ in terms of topography, vegetation cover, and resources richness ([37], *pers. comm.*). Hochstetter is characterised by lowlands and a graminoid cover, with numerous migratory birds in summer but an otherwise rather poor prey community. Karupelv is a large valley dominated by heath, with a relatively high rodents' abundance. Zackenberg is intermediate in its vegetation cover, being made of both heath and graminoids, and regularly benefits from the presence of muskox carcasses.

The terrestrial vertebrate community consists of breeding birds (mostly migratory shorebirds and wildfowl) and six mammal species [48]. The collared lemming (*Dicrostonyx groenlandicus*), whose population dynamics follow 4–5 year cycles [45, 49; Supporting Information S1, Table S1.1], form the prey base for most terrestrial vertebrate predators in the region [36, 45]. The arctic fox is the main terrestrial predator in the region (i.e., resident and most widespread; [36]). It mainly feeds on lemmings when present, but has a generalist diet and readily consumes birds, eggs, other small mammals, and even carcasses [37]. Although most individuals seem to be year-round residents in Northeast Greenland, some can disperse in winter or at least perform extensive extraterritorial movements, especially in times of food scarcity [50]. Arctic foxes are also capable of intensively moving within their territories [41], mostly to forage, travel between preferred feeding grounds and cache food [40]. Arctic foxes are generally monogamous and form long-lasting breeding pairs, although polygamy can be observed [52]. Two foxes of a same breeding pair generally have a high overlap between their territories, whereas there commonly is little overlap between the territories of arctic foxes that belong to different pairs [40, 53]. During the breeding season (June-August; [51]), under favourable conditions, foxes give birth to 4–6 cubs or even larger litters sizes in times of food abundance [55]. Both males and females provide parental care [52], although the female spends significantly more time in the den at the beginning of the breeding season because of the need to suckle the pups [53]. In mid-summer, when the cubs are rapidly growing and food is provided by both parents, the intensity of feeding is greater than in late summer, when cubs are more independent, although food provisioning is modulated by food availability [53]. As they get older, arctic fox cubs progressively start to travel farther from the den, eventually dispersing away from their parents' territory [53].

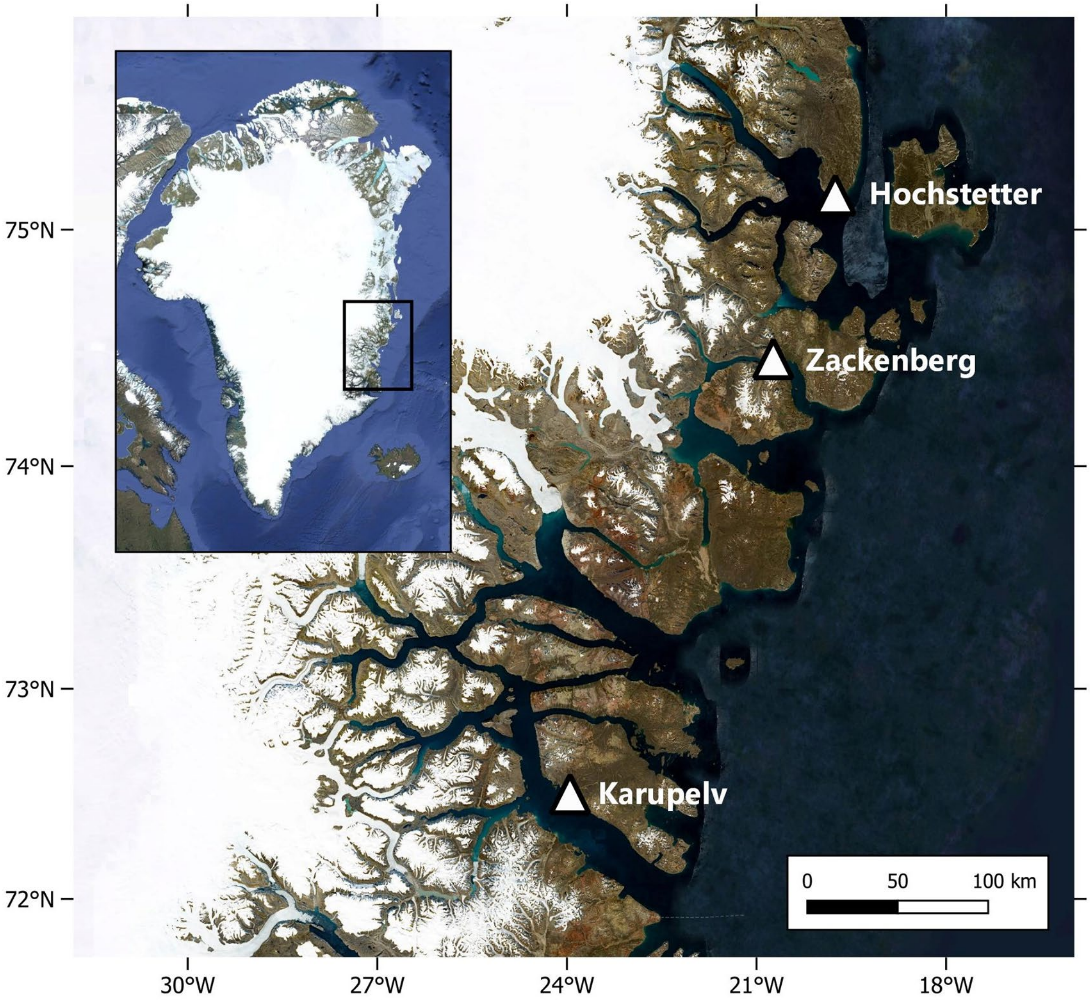

Fig. 2 Map of the three study areas in Northeast Greenland. Background map © Satellite Mediumres 2021, MapTiler © OpenStreetMap contributors [47]

Fox trapping and tracking

From 2017 to 2023, we captured a total of 24 adult foxes at the three study sites (Supporting Information S2, Table S2.1). Foxes were sexed and their breeding status was determined upon capture. For males that were captured away from their den, breeding status was assessed using camera traps or direct observations at the den. Foxes were trapped close to field camps and at breeding dens, using Tomahawk cage traps or padded leg-hold traps (model Victor No. 1 Soft-Catch®, Oneida Victor Ltd, USA). All foxes were fitted with GPS collars powered by a solar panel connected to a rechargeable battery and using UHF transmission for remote data download (collar weight: 100–120 g; < 3.5% of body mass for all foxes; collar models: "RadioTag-14" from Milsar Ltd, Nicosia, Cyprus, and "Felis" from Ecotone Telemetry, Gdynia, Poland; Milsar Base Station with UHF download [2.4 GHz ISM Band], Omnidirectional 2.4 GHz ISM band "Rubber Duck" type antenna). The collars were programmed with a location interval of 1 to 5 min in summer (depending on the study area and period). We removed all GPS positions with (1) dilution of precision values ≥ 10 (2), unrealistic speed values (i.e., more than 20 km/h between GPS positions; [44]), and (3) collected over the 48 h following capture [56]. Five foxes were dismissed from subsequent analyses because they had too short tracking periods (i.e., < 5 days). We then only kept GPS positions collected between the 1st of June and the 31st of August (summer months), when foxes are assumed to be the most territorial because of the need to feed and raise dependent cubs [54]. This data filtering left us with a total of 333,642 GPS positions (mean ± SD per fox-year: 12,357 ± 10,020; range 3,067–30,909; Supporting Information S2, Table S2.1) collected from 20 individuals (9 females, 10 males, 1 undetermined): 5 from Hochstetter, 8 from Karupelv and 7 from Zackenberg. Since several foxes were recaptured and followed for several successive years, this resulted in 27 fox-years of data (Supporting Information S2, Table S2.1). Finally, to standardise time-interval between all GPS positions we resampled our dataset using the *redisltraj()* function of the *adehabitatLT* R package [57] to keep only one position per 4 min, as recommended by Poulin et al. [41].

Intraseasonal variations in weekly home range sizes

Following Gable et al., 2018 [32], we divided our dataset into 7-days periods (thereafter referred as "weekly bins") to assess intraseasonal variations in space use (i.e. home range sizes), starting on June 1st (i.e., 1st weekly bin = 1–7 June, 2nd bin = 8–14 June, etc.) and ending August 30th. We could not monitor all foxes simultaneously and for the same duration (Supporting Information S3, Table S3.1-S3.2). Hence, not all foxes had overlapping tracking periods. However, dividing the summer season into bins allowed us to compare foxes within the exact same tracking bins, and excluding foxes of different bins (whose movements could have been driven by different constraints). A weekly scale was chosen to estimate home range sizes because preliminary analyses showed that at least 5 days were needed for the foxes to cover their entire territory (Supporting Information S4, Fig. S4.1). As such, having calculated home ranges at a smaller scale would not have correctly depicted arctic foxes' intraseasonal territorial behaviour. Similar weekly intervals have previously been used to study variations in intraseasonal movements [58, 59]. Thus, 13 non-overlapping weekly bins were defined to cover the entire summer season. To compare bins with similar sample sizes, we only estimated home ranges for weekly bins with full data coverage (i.e., 7 days). To investigate space use of foxes, we then calculated home range (HR) sizes at two different spatial scales: full and core HRs, with the latter representing the most intensely used area of the individual's HR. HRs were estimated using the autocorrelated Kernel Density Estimator (aKDE) implemented in the "*amt*" R-package [60] to account for spatial and temporal autocorrelation in our data. The 95% isopleth depicted the full HR size, as used in other arctic fox studies [41, 61], and the 50% isopleth the core HR [62]. These HR metrics are widely used in wildlife ecology [15]. To allow for comparison of the HR sizes between individuals, we used the same smoothing parameter h, calculated as the mean of the reference method (h_{ref}) for each fox-year. We then used the mean of all these values ($h = 574$ m) as the constant h when calculating the HRs for all individuals [51, 63]. We then estimated weekly HR values for each weekly bin and for each fox-year.

Intraseasonal variations in movement metrics

To investigate fine-scale intraseasonal variations in foxes' movements, we estimated all the remaining movement metrics at the daily scale, following Papageorgiou et al., 2021 [64]. Each fox-year was divided into tracking days, corresponding to the Julian days during which the fox was tracked (thereafter, "Julian day"). We could therefore obtain up to 92 tracking-days per fox-year (i.e. if this fox was followed for the three summer months). To compare days with similar sample sizes, we estimated daily metrics only if the fox was tracked for the entire day (i.e. 24 h of tracking). For each Julian day of each fox-year, we then calculated daily distance travelled, mean daily speed, mean relative turning angle, and proportion of active time to depict foxes' fine-scale spatial behaviour. These metrics were chosen because they are linked to multiple components of predators' behaviour such as hunting or travelling [65–67] and are commonly used in studies of predators' movements [24, 26, 68, 69]. Daily distance travelled was calculated by summing all distances between successive GPS positions for a given Julian day within individual fox-years. Speed was estimated by dividing the distance between two consecutive GPS positions by the time difference between these positions. Mean daily speed was then calculated by averaging all speed values of the given Julian day within individual fox-years. Relative turning angle (thereafter, turning angle) was defined as the angle between a given GPS position and the following one, where values close to 0 indicate straight, directed movements (i.e. travel) and greater values indicate tortuous paths (i.e. foraging, hunting; [69]). Mean daily values were then calculated for each Julian day within individual fox-year. Finally, to estimate the proportion of active time, we first categorised GPS positions into "active" (i.e., speed between two successive locations > 0.04 m/s [56] ; and "resting" states (i.e., when ≤ 0.04 m/s), and then divided the number of active periods by the total number of GPS positions of the bin. The 0.04 m/s threshold was determined based on visual observations of our data (*results not shown*) and on the mean speed of actives foxes calculated by Clermont et al. [40].

Statistical analyses

In total, after data processing, our data covered 119 weekly bins (range: 1–11 per fox-year) and 483 Julian days (2–67 per fox-year ; Supporting Information S3, Table S3.1-S3.2). We modelled all our response variables (i.e., the different movement metrics) using Generalised Additive Mixed Models (GAMMs), with a Gaussian distribution of residuals, using the *mgcv* R package [71], to examine temporal patterns. Individual movement metrics were first modelled as a function of the spline of weekly bin (full and core home ranges) or Julian day (daily distance, mean speed, mean turning angle, and proportion of active time), with a fixed regression smoother (k) of 3 (i.e., cubic spline) to identify any intraseasonal effect. These models were then compared with a constant model, which acted as a null model using the Bayesian Information Criterion (BIC, [67]). We chose the BIC criterion because it allows the selection of more accurately stabilised models [72]. If the constant model had a lower BIC score, no intraseasonal temporal pattern was assumed for the metric. In a second step, we conducted three different rounds of model selection to explore the impact of additional predictive variables: sex (Male/Female), breeding status (Breeding/Non-breeding), and study area (Hochstetter/Karupelv/Zackenberg). We could not integrate all predictors into a single model because of convergence issues owing to our small sample size. For each predictive variable, we built four different models: a constant model, a model with the predictive variable only, a model with the additive effects of weekly bin or Julian day and an additional predictive variable, and a model with both the single effects and the interaction between the two. The model with the lowest BIC was considered the best model (Supporting Information S5, Table S5.1). When two models were equivalent (i.e. delta BIC < 2), the most parsimonious (i.e. with the smallest number of predictive variables) was selected [73]. Despite the fact that sea ice can be used by arctic foxes, thereby having the potential to influence their movements [74], we did not include sea ice availability in our analyses. Indeed, we restricted our study period to the summer (1st of June – 31st of August), when sea ice is generally not used by the foxes. Moreover, arctic foxes in our study area are not known to extensively use the sea-ice in summer, as only 4 foxes used sea ice within the study period, and in a very limited proportion *(data not shown).*

Fox-year was included as random factor to account for repeated measures of individual foxes. Preliminary analyses showed that fitting a random slope on fox-year better fitted full and core home range data, and fitting a random intercept better fitted daily movement metrics, so we adjusted the random factor accordingly. Despite the fact that lemming densities can significantly impact arctic foxes' movements [51, 75] we could not include this variable to our models because our data were strongly unbalanced, with very few lemming peaks (Supporting Information S1, Table S1.1). Furthermore, including lemming density to the model would have been redundant with the "fox-year" variable. In fact, we only had one estimation of lemming density per year and per site, so the "lemming density" variable was indirectly included in the "fox-year" variable. All data were analysed using the R software (version 4.3.2; [76]).

Table 1 Summary table of the best model for the weekly full (**A**) and core (**B**) home ranges according to study area. Values represent estimated parameters ± standard error (factor variables) or estimated degree of freedom (numeric variables). Reference category for study areas = Hochstetter

	Study area			
	Intercept	**Karupelv**	**Zackenberg**	**S(Bin number)**
Full home range (A)	90.00 ± 10.68	-41.83 ± 15.20	-47.46 ± 12.01	17.71
Core home range (B)	24.33 ± 2.57	-13.92 ± 3.68	14.38 ± 2.88	18.29

S(Bin number) = spline of bin number

Results

Home range sizes

Weekly full HR sizes ranged from 9.9 to 242.3 km^2 (mean ± SD: 55.2 ± 38.5 km^2) and core HRs between 1.6 and 47.7 km^2 (13.0 ± 9.1 km^2). Full and core HR sizes differed between study areas (Supporting Information S5; Table S5.1) and were significantly larger at Hochstetter than at the two other sites (Table 1; Fig. 3). Overall, HR sizes remained relatively constant throughout the summer.

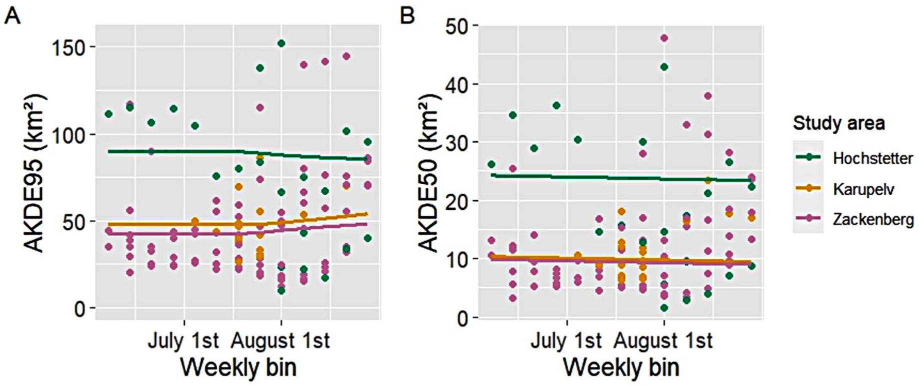

Fig. 3 Intraseasonal temporal pattern in foxes' weekly full (**A**) and core (**B**) home range sizes according to study area (*n* = 119 fox-weeks). Each point represents the weekly full (**A**) and core (**B**) home range size, calculated by means of autocorrelated Kernel Density Estimation (aKDE) (95% and 50% aKDEs for full and core HRs, respectively) for the given week. The lines depict predictions from the best model, considering the effects of all components present in the model, including random effects

Movement metrics

Daily distance travelled and mean speed showed similar temporal patterns. On average, arctic foxes moved 40.88 ± 11.84 km (mean ± SD) per day (range: 10.47–83.53 km). Mean daily speed was 1.67 ± 0.49 km/h (range: 0.45–3.49 km/h). Both daily distance travelled and speed followed quadratic intraseasonal variations (Table 2): arctic foxes travelled relatively short distances at low speed at the beginning of the summer, with daily distances and speed gradually increasing to reach a peak in mid-July. Then, both metrics continuously decreased to reach a minimum at the end of the summer period (Fig. 4). Additionally, there was a small additive effect of sex, breeding status, and study area on daily distances and speed (Table 2). Females (39.38 ± 9.30 km) and breeding individuals (38.07 ± 11.59 km) moved shorter distances over the whole summer compared with males (41.93 ± 13.53 km) and non-breeding individuals (44.54 ± 11.15 km ; Fig. 4A-B). Conversely, males (1.73 ± 0.57 km/h) and non-breeding individuals (1.83 ± 0.45 km/h) moved more rapidly than females (1.58 ± 0.38 km/h) and breeding individuals (1.54 ± 0.49 km/h) on average (Fig. 4D-E). Regarding study area, foxes from Hochstetter had smaller daily distances travelled (31.39 ± 12.31 km) and lower speeds (1.31 ± 0.51) than foxes from Karupelv (43.47 ± 11.77 km ; 1.81 ± 0.49) and Zackenberg (40.73 ± 11.58 km ; 1.65 ± 0.48), whose daily distances and speeds were similar overall (Fig. 4C-F).

Mean proportion of active time was 61.32 ± 9.90% (range: 24–89%). As for daily distances travelled and mean speed, activity showed a hump-shaped distribution, being at its maximum in mid-July, reaching a minimum at the end of August, with intermediate values at the beginning of the summer (Table 2 ; Fig. 5). Sex, breeding status and study area had no effect on this metric (Supporting Information S5, Table S5.1).

Conversely, there was no clear intraseasonal variation in mean daily relative turning angle (Supporting Information S6, Fig. S6.1). Daily turning angles stayed relatively similar throughout the summer, without showing distinct peaks nor fluctuations. Mean daily relative turning angle was 0.01 ± 0.09 radians (range: -0.20–0.27).

Discussion

We found that home range sizes and mean turning angles of arctic foxes did not show clear intraseasonal variations throughout the summer in Northeast Greenland. Conversely, daily distance travelled, mean speed and proportion of active time showed intraseasonal variations with a hump-shaped distribution, being at their highest in mid-July. Sex, breeding status and study area had contrasting impacts on our metrics. Together, these results show that arctic foxes remain very territorial throughout the summer, but that they can adjust some components

Table 2 Summary table of the best models (Julian day only (**A**), Julian day + sex (**B**), Julian day + breeding status (**C**) and Julian day + study area (**D**)) for daily distance travelled (km), mean daily speed (km/h), and proportion of active time (%). Values represent estimated parameters ± standard error (factor variables) or estimated degree of freedom (numeric variables). Reference category = female for sex, breeding for breeding status and Hochstetter for study area; S(Julian day) = spline of Julian day

	Julian day (A)		**Sex (B)**			**Breeding status (C)**			**Study area (D)**			
	Intercept	**S(Julian day)**	**Intercept**	**Male**	**S(Julian day)**	**Intercept**	**Non-breeding**	**S(Julian day)**	**Intercept**	**Karupelv**	**Zackenberg**	**S(Julian day)**
Daily distance travelled	39.35 ± 1.68	1.97	38.31 ± 2.47	1.47 ± 3.51	1.97	38.57 ± 2.17	1.97 ± 3.48	1.97	34.97 ± 4.14	5.34 ± 5.03	5.19 ± 4.79	1.97
Mean daily speed	1.61 ± 0.07	1.97	1.55 ± 0.10	0.09 ± 0.15	1.97	1.57 ± 0.09	0.10 ± 0.15	1.97	1.45 ± 0.17	0.23 ± 0.21	0.17 ± 0.20	1.97
Proportion of active time	60.37 ± 1.42	1.95	-	-	-	-	-	-	-	-	-	-

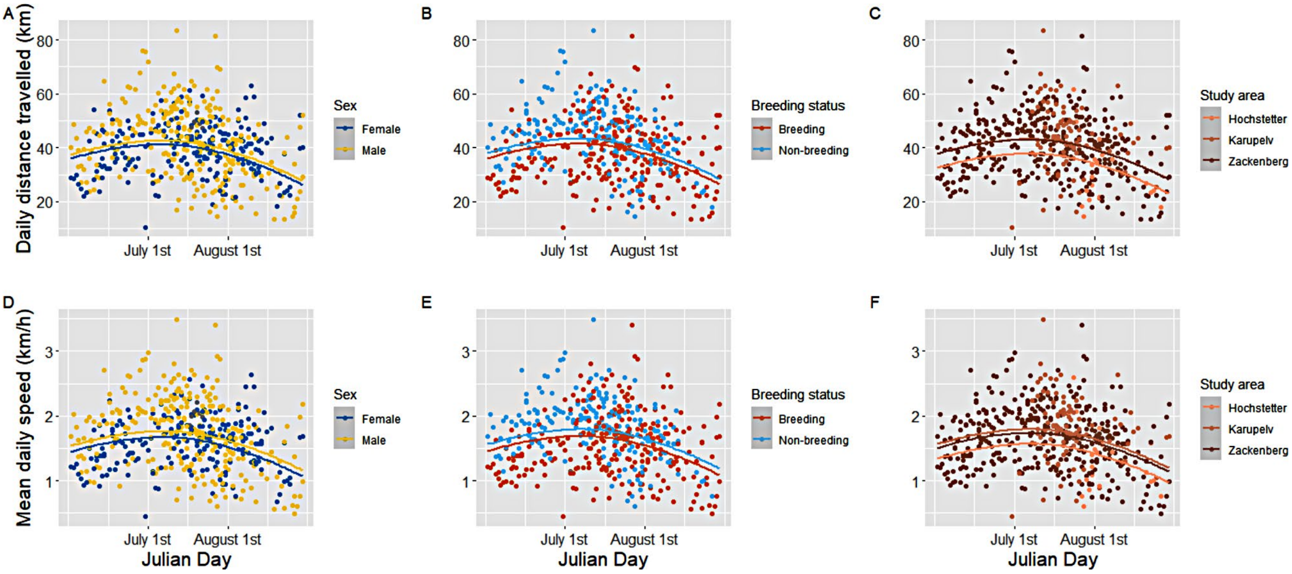

Fig. 4 Intraseasonal temporal pattern in arctic foxes' daily distance travelled (**A-C**) and mean daily speed (**D-F**) according to summer Julian day (*n* = 483 Julian days) + sex (**A, D**), Julian day + breeding status (**B, E**), Julian day + study area (**C, F**). Each point represents the daily distance travelled (**A-C**) or the mean daily speed (**D-F**) of an individual fox during the given Julian day. The lines depict predictions from the best model, considering the effects of all components present in the model, including random effects

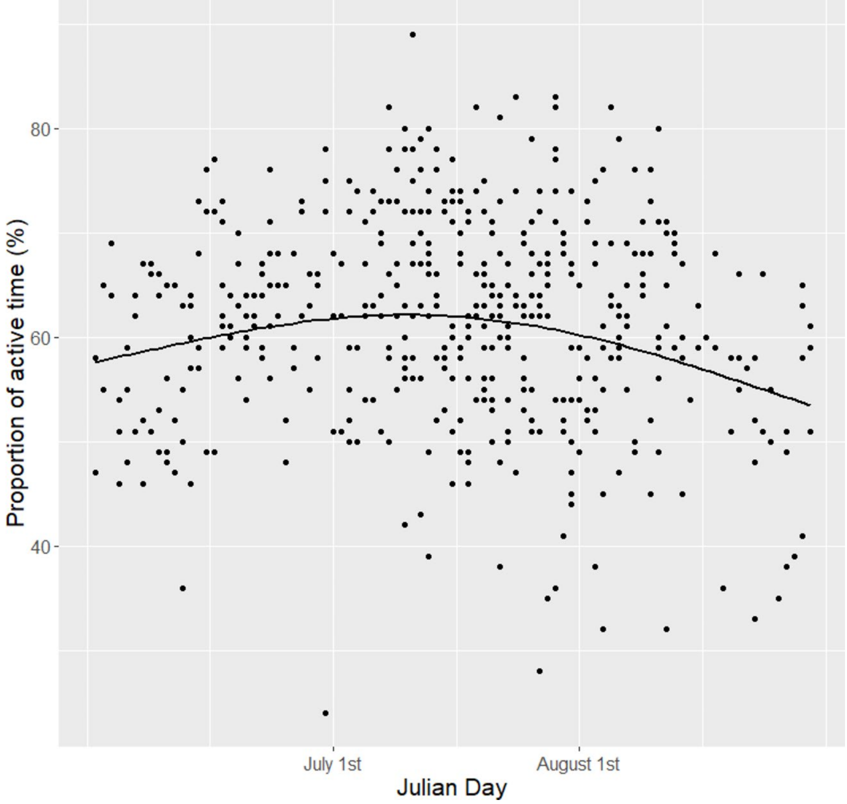

Fig. 5 Intraseasonal temporal pattern in arctic foxes' proportion of active time according to summer Julian day (*n* = 483 Julian days). Each point represents the proportion of time the fox was considered 'active' for the given Julian day. The lines depict predictions from the best model, considering the effects of all components present in the model, including random effects

of their fine-scale behaviour over small spatiotemporal scales. Thereafter we explore potential explanations for our results.

Territoriality

Both core and full home range sizes did not significantly vary within the summer season, which likely reflects the territorial behaviour of arctic foxes. Indeed, fox species generally establish and maintain their territories over long periods [29]. In Northeast Greenland, where lemmings (which form the basis of the food chain) have cyclic population dynamics [36, 45, 50], the absence of intraseasonal variations likely reflects an adaptive strategy to cope with rapid intraseasonal changes in food availability [49], a process referred to as the 'Obstinate strategy' [77]. This theory posits that, in environments where resources fluctuate, animals should maintain sufficiently large territories to prepare for potential future periods of food scarcity. This has already been observed in some red fox populations where individual home ranges remained stable despite significant environmental changes [78]. Setting or extending a territory is very energy-costly (i.e., due to behaviours such as patrolling, defending; [70, 72]). As such, it is probably beneficial for the foxes to maintain the same territory throughout long periods of time (i.e., at least during the entire summer season), rather than constantly adjusting it to short time fluctuations [53, 79].

This overall intraseasonal stability contrasts with the interannual variations of home range sizes found at the same study sites and on Bylot Island (Canada), and attributed to changes in lemming densities [51, 75]. This suggests that arctic foxes may adjust their home range sizes to resource availability, but that they adopt different strategies at shorter (i.e. within the summer season) and longer time-scales (i.e. year). For instance, rather than adjusting the size of their home ranges during the summer season, arctic foxes could have adapted their fine-scale habitat selection patterns within a stable area [80, 81]. Research shows that arctic foxes exploit their territory heterogeneously and select different areas for different purposes. For instance, Canadian foxes select areas of high geese densities when hunting, but avoid these same areas when resting [82]. In Svalbard, arctic foxes preferentially select for hydric vegetated habitats over drier areas [68]. Similarly, denning habitats are located on sites with specific topography and landscape characteristics [83]. As such, it appears that the optimal short-term strategy is to adjust habitat selection patterns, whereas adjusting home-range sizes is a better long-term strategy. Studies on both small and large-scale habitat selection patterns of arctic foxes is needed to explore its potential link to variations in home range sizes [84].

Dietary switch and foraging behaviour

Daily distances travelled and mean speed peaked in mid-July, a pattern that could be explained by changes in foraging patterns. Indeed, at this period, arctic foxes feed on a great variety of prey [37], each of them having their own behaviour and anti-predator strategies. As a result, different prey items could require different foraging patterns, thereby changing foxes' movement metrics. For instance, in Svalbard, foxes feeding on geese and inland preys have higher mean speeds than foxes from coastal areas hunting on birds' cliffs [68]. Similarly, foxes attacking geese nests typically rush towards the nest to collect the eggs before being attacked by the incubating birds [85]. This behaviour also involves movements to bird nesting grounds and to food caches [40], which could be larger than distances travelled when more local preys are available. Therefore, the fact that several movement metrics reached a peak in mid-summer probably reflects a switch in hunting strategy owing to a switch in preys that require specific movement patterns to hunt or search for.

The proportion of active time peaked in mid-July, a period of relatively high food abundance in the Arctic. In our study areas, the abundance of migratory birds peaks in the middle of the summer with moulting geese and fledging shorebirds [37] providing an important food source for arctic foxes [37, 86]. At the same period, foxes in our study area also benefit from the presence of big mammals carcasses [37, 86], plants [36, 87] or even catch fish [88] and hunt seal pups [87]. Although arctic foxes specialise on rodents when available [36, 89], they still show a flexible and opportunistic diet [37]. As such, the peak in activity seen in mid-July could reflect a need for arctic foxes to capitalise on locally abundant but time-limited resources at this period. Then, as resources become scarcer and fat reserves are reconstituted, foxes would have been able to decrease their activity at the end of the summer. However, the fact that daily relative turning angles did not show intraseasonal variations suggest that arctic foxes did not significatively change their foraging behaviour throughout the summer. Higher absolute values (i.e. tortuosity) would have indicated an increase in foraging activity, and smaller absolute values an increase in straight travel movements [70]. As no intraseasonal variations were observed, we can assume that arctic foxes spent a relatively similar proportion of time foraging throughout the summer. Then, the mid-July peak in activity could be due to the fact that, as their fat reserves rebuild, arctic foxes were able to engage in more active behaviours such as socialising or territory defence. Fine-scale behavioural categorisation of arctic foxes' movements is needed to better understand their activity budget throughout the summer [40].

Site-specific constraints and food availability

Home ranges of foxes from the poorest area (i.e. Hochstetter) were significantly larger than those from the two other and richer areas (Karupelv and Zackenberg). It is well-established that home range size is negatively correlated with food abundance in most animal species [22, 90, 91], including arctic foxes ([42, 44, 50], but see [78]). Most of the summer prey items at Hochstetter consists of migratory breeding birds, an abundant but very temporary food source [37]. Although arctic foxes are known to actively capture and cache goose eggs in summer [38], they still need alternative food sources when birds are absent [92]. Foxes from Zackenberg benefit from the presence of muskox carcasses, whereas Karupelv experiences generally higher lemmings abundances [37]. Furthermore, the weather and topography of Zackenberg and Karupelv are more favourable to arctic foxes than those experienced at Hochstetter (*O. Gilg, pers. comm.*). As a result, foxes from Hochstetter probably need higher home range sizes to gather enough resources to cope with the relatively lower food abundance and harsher environmental conditions. Interestingly, despite having larger home ranges, foxes from Hochstetter tended to travel shorter daily distances compared with foxes from the two other areas. Their prey base at Hochstetter (i.e. including a large fraction on moulting geese in summer; [37]) probably requires foxes from this area to display a specific hunting behaviour. For instance, they might have to explore and exploit larger areas than at both other sites (e.g. travelling to distant flocks of moulting geese, resulting in larger home range sizes), but hunt by lying in wait (taking advantage of these spatially-clumped food resources) rather than opportunistically, thereby decreasing the daily distance travelled. Alternatively, this pattern could be linked to lemming cycles. In fact, Hochstetter was the only study area where we did not see a clear peak in lemmings' abundance over the study period (Supporting Information S1 ; Table S1.1). As arctic foxes generally move less when lemmings are abundant [63], we would expect individuals from Hochstetter to follow the same pattern, thereby reducing the difference between study areas. Comparative studies of the intraseasonal variations in arctic foxes' movements between low and high-lemming years are needed to explore this hypothesis. This is particularly relevant considering that lemmings' cycles are expected to decrease in intensity as a result of the ongoing climate change [93].

Our three study areas come with their unique combinations of biotic and abiotic characteristics [37], which probably led to this site-specific pattern. Hochstetter is the northernmost area, dominated by graminoid vegetation types [37] with an abundance of small ponds and lakes, a type of habitat that is a high-quality hunting area for arctic foxes feeding on moulting geese. Accordingly, foxes from Hochstetter may require less daily movement in order to locate food. However, due to the relatively smaller overall resources availability (moulting geese being only present in July), they still might have to maintain large home ranges to cover their nutritional needs as resources become depleted (see above). Topography and landscape configuration strongly impact the spatial behaviour of wildlife, leading to site-specific habitat selection and movement patterns [94, 95]. Some elements of the landscape, such as streams, can also facilitate the movements of canids [96]. Thus, the conditions experienced by the foxes in Hochstetter could favour smaller travel distances, but cannot compensate for the relatively lower food density.

Nutritional needs

We found that breeding foxes travelled shorter distances and were slower than non-breeding individuals, but the effect was biologically small. Raising cubs requires extensive parental care, with females suckling until mid-July and both parents having to guard the young, socialise, feed them and maintain the den [53, 80, 97]. These behaviours do not generally require extensive nor rapid movements (contrary to other behaviours such as travelling, [41]), potentially explaining why breeding foxes moved less and at lower speeds, and tended to be less active. However, the identified effect of breeding status might have been less important than expected because of the confounding effect of litter size. When conditions are optimal (e.g. high lemming densities), arctic foxes can give birth to extremely large litters [55]. The food demand of such large litters and the resulting energy costs for the parents are considerably larger than those of smaller litters [98]. Consequently, the parents of large litters might show behavioural patterns that strongly differ from foxes taking care of none or only a few cubs. Conversely, foxes with small litter sizes might behave similarly to those that did not reproduce at all. Perhaps most foxes in our study areas predominantly had very small litter sizes, thereby not allocating all their time-budget to parental care and behaving more like foxes without cubs. Regular behavioural observations conducted until the end of the summer season, either direct or via the use of camera-traps, and a strict count of litter sizes would provide useful information on the impact of breeding on arctic foxes' movements.

Also, in mid-July, arctic fox cubs start to emerge from the den and are less dependent on their mother's milk [99]. This means that the parents can leave them alone at the den and spend more time engaging in relatively active behaviours such as hunting (i.e. requiring to move greater distances and higher speeds). Foxes that do not breed probably also increase their hunting behaviour during summer, and thus the distance they travel searching for food at relatively high speed, to capitalise on abundant but time-limited resources to prepare for the harsh Arctic winter [100, 101]. Finally, males travelled greater distances and were faster compared with females, but the effect was small. Although sexual dimorphism in size and behaviour is limited in arctic foxes [51, 102], sex-specific movement patterns can still be observed in some areas, with males generally moving more than females [103, 104]. This pattern is commonly observed in other taxa, mostly because males are generally larger than females in mammals [105]. However, these differences are likely more explained by sex-specific behaviour patterns [100], with males spending more time searching for food during summer compared to females spending longer periods at the den to care for the cubs [53].

Limitations

Some of our foxes had relatively short tracking durations (Supporting Information S3; Table S3.1-S3.2). However, comparable studies on arctic foxes' movements used similar tracking durations [40, 41] and theoretical studies have shown that movement metrics can be correctly assessed if the frequency of GPS fixes is regular and their accuracy sufficiently precise [41, 106]. Additionally, the identified effects of sex and breeding status were biologically small and deserve more in-depth investigations. A rigorous study plan aiming at collecting balanced data on breeding foxes, litter sizes and sex-specific behavioural patterns would help confirming the patterns we observed. Our results are also difficult to compare with other canid studies because most of the latter only investigate spatial ecology at large temporal scales (e.g., seasonal, annual or interannual: [15, 43, 44, 101]), thereby overlooking shorter temporal components of spatial behaviour (but see [41]). We are also aware that our results may not be extrapolated to other regions where temporal variations in food resources or climatic conditions are less pronounced. Overall, ecological and biological parameters such as species diversity and demography tend to show more extreme variations in environments with strong seasonality compared with less seasonal environments [107–109]. As such, intraseasonal variations in some behaviours could be detectable only in areas where seasonality is strong enough [110]. However, our results on intraseasonal movements are complementary of studies investigating spatial behaviour at a larger temporal scale and in less seasonal environments, allowing a broader comprehension of predators' movements.

Conclusion

Our study shows that arctic foxes can adjust their movement patterns within a single season in Northeast Greenland. Daily distances, speed and proportion of active time showed a hump-shaped distribution throughout the summer. Daily distances and speed were impacted by sex, breeding status and study area with females, breeding individuals and foxes from the less productive site covering smaller distances and at a lower speed. Conversely, home range sizes and turning angle did not significantly vary during the season. However, home range sizes were larger in the less productive site. Our study thereby emphasis that variations in movement metrics can occur at an intraseasonal scale in summer. This underlines a need for researchers to carefully consider the behaviour of their model species at different spatiotemporal scales, wherever sufficiently strong temporal variations in resources and climatic conditions allow it [106]. We also recommend avoiding looking only at seasonal or yearly movements, but rather decompose study periods into smaller periods when possible [111]. This could prevent misinterpretations owing to, for instance, overlooking habitat-selection patterns and social constraints that occur at short spatiotemporal scales [112, 113].

Abbreviations

aKDE	Autocorrelated Kernel Density Estimation
BIC	Bayesian Information Criterion
GAMMs	Generalised Additive Mixed Models
GPS	Global Positioning System
HR	Home range
SD	Standard deviation

Supplementary Information

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Supplementary Material 1: Additional_file_1. Complementary information supporting our results, discussion and conclusion. Appendix S1 presents the lemming counts and cycle dynamics for the three study areas, Appendix S2 contains a summary of the GPS tracking data used in this study, Appendix S3 summarises the data available after cleaning in terms of weekly bins and Julian days, as well as their temporal distribution, Appendix S4 shows the asymptotic relationship between arctic foxes' home range size and the number of days used in home ranges calculations, Appendix S5 presents the model selection procedure. Appendix S6 displays additional intraseasonal relationships in arctic foxes' movement metrics.

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Author contributions

LB, DP, JM and OG conceived the study. NMS, JL, LHH, BS and OG collected the data. LB and DP analysed the data. LB wrote the manuscript with contributions from all authors. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

The datasets used and analysed during the current study can be visualized on Movebank (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1255926892 ; https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1255889609 ; https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1255911964) and are available from the corresponding author on reasonable request.

Declarations

Ethics approval

Captures, handling and tagging of arctic fox was approved by the Government of Greenland, Ministry of Domestic Affairs, Nature and Environment-NNPAN, under the permits numbers: C-17-3-28, C-18-3-11, C-19-3-3, C-20-3-19, C-21-3-22, C-22-3-29 and C-23-5-25 for Hochstetter Forland, C-17-23, C-18-24, C-19-36, C-20-33, C-21-33, C-22-35 and C-23-1084 for Karupelv Valley, C-17-3-11, C-18-3-6, C-19-3-11, C-20-3-4, C-21-3-4, C-22-3-4 for Zackenberg.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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