

Spatial variation in Arctic hare (*Lepus arcticus*) populations around the Hall Basin

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Abstract

Arctic environments have relatively simple ecosystems. Yet, we still lack knowledge of the spatio-temporal dynamics of many Arctic organisms and how they are affected by local and regional processes. The Arctic hare (*Lepus arcticus*) is a large lagomorph endemic to high Arctic environments in Canada and Greenland. Current knowledge about this herbivore is scarce and the temporal and spatial dynamics of their populations are poorly understood. Here we present observations on Arctic hares in two sites on north Greenland (Hall and Washington lands) and one adjacent site on Ellesmere Island (Judge Daly Promontory). We recorded a large range of group sizes from 1 to 135 individuals, as well as a substantial variation in hare densities among the three sites (Hall land: 0 animals / 100 km², Washington land 14.5-186.7 animals / 100 km², Judge Daly Promontory 0.18-2.95 animals / 100 km²). However, pellet counts suggested that both Hall land and Judge Daly Promontory hosted larger populations at other times. We suggest that our results could have been caused by three spatially differentiated populations with asynchronous population fluctuations. With food limitation being a likely driver behind the observed variation, we argue that food limitation likely interacts with predation and competition in shaping the spatial dynamics of Arctic hares in this region.

Keywords

synchrony, population dynamics, geographic variation, Ellesmere Island, north Greenland, Lagomorpha

Introduction

Spatially and temporally coupled fluctuations in population size and dynamics, i.e. population synchrony, have been observed in many vertebrate populations (Liebhold et al. 2004). Population synchrony can have profound ecological consequences and understanding synchrony can thus improve our knowledge of how ecological processes influence population regulation and the distribution of fitness within and across populations (Gaillard et al. 2000). It can also be important for conservation and environmental management since it may influence extinction rates (Heino et al. 1997; Palmqvist and Lundberg 1998). Spatiotemporal coupling can arise from demographic linking of populations through dispersal processes (Holmes et al. 1994; Molofsky 1994), congruent dependence of some exogenous factors (i.e. the ‘Moran effect’, Moran 1953), or by trophic interactions with organisms that are themselves synchronized (Ims and Steen 1990; Selås 1997). However, local environmental factors and general climatic conditions can interact with these broad effects in shaping population synchrony at various spatial scales (Bjørnstad et al. 1999; Kendall et al. 2000).

The Arctic hare (*Lepus arcticus*) is a large lagomorph endemic to the high-Arctic environments of Canada and Greenland (Best and Henry 1994). The distribution of the Arctic hare encompasses Greenland, Canadian Arctic islands, and parts of the Canadian mainland east of the Mackenzie River and north of the tree line. The Arctic hare is strongly dependent on willows (*Salix* sp.) for forage (Klein and Bay 1994), which likely is caused by their higher digestibility for hares compared to other Arctic plants (Klein and Bay 1995). Despite the fact that there are only a few mammalian herbivore species in the high Arctic, knowledge about the Arctic hare is scarce and mostly based on information from the southern part of the distribution (Best and Henry 1994). Population density has for example only been reported from Newfoundland (~1/ km², Mercer et al. 1981). Arctic hares may gather in large groups of up to several hundred individuals (Parker 1977), and irregular temporal fluctuations in population size have been reported (Banfield 1951, Mech 2005). There are also reports of seasonal migrations, although these migrations may not occur throughout the species’ range (Best and Henry 1994). However, the temporal and spatial dynamics of Arctic hare populations are poorly understood.

Here we present observations on local variation of Arctic hare populations in three areas around the Hall Basin, two in northern Greenland, and one on Ellesmere Island, Canada. The observations were made as part of ecological fieldwork undertaken during an international expedition to the Petermann glacier region organized by the US National Science Foundation and the Swedish Polar Research Secretariat (<http://polar.se/en/expedition/petermann-2015/>).

Methods

We conducted the study on one site on central Hall land (81.5945 N / 60.7027 W), one site on Washington land (80.2585 N / 60.7958 W), both north Greenland, as well as one site on Judge Daly Promontory on Ellesmere Island (81.3833 N / 65.2430 W), Nunavut, Canada (Figure 1). The sites were visited 3-13 August (Hall land), 15-18 August (Washington land) and 19-26 August (Judge Daly Promontory) in 2015.

Low-lying areas of Hall land and Judge Daly Promontory are of marine origin (England 1985, 1997) and emerged due to postglacial rebound, whereas elevated areas of Judge Daly Promontory and Washington land emerged from deglaciation of the Greenland ice sheet (England 1997; Bennike 2002). All three areas likely emerged approximately 8,000 years ago (England 1985; England 1997; Bennike 2002). The site on Hall land consisted of a broad valley with shallow slopes, with altitudes of 50–300 meters above sea level (asl). Land rise through postglacial rebound is an ongoing process in the region, and areas below approximately 100 m asl were almost entirely devoid of vegetation and consequently had very limited traces of herbivorous activity. The sites on Washington land and Judge Daly Promontory included undulating valleys and mountain slopes at altitudes of 250–600 m asl (Washington land) and 100–350 m asl (Judge Daly Promontory). The soil in all three areas consisted of clay and silt sediments at lower elevations and comparatively coarser-grained moraines at higher elevations. All three areas had sparse vegetation with an average

vegetation cover of approximately 10%. Plant communities were characterized by stands of very low (2–3 cm height) growth willow (*Salix arctica*) or communities with mixed grasses and forbs. Moist areas were characterized by various *Carex* species. Apart from Arctic hares, the terrestrial vertebrate herbivore community included caribou (*Rangifer tarandus*), muskoxen (*Ovibus muscatus*), collared lemmings (*Dicrostonyx groenlandicus*), ptarmigan (*Lagopus muta*), and snow geese (*Chen caerulescens*). The predator community consisted of wolves (*Canis lupus*), Arctic foxes (*Vulpes lagopus*), ermines (*Mustela erminea*), snowy owls (*Bubo scandiacus*), ravens (*Corvus corax*), long-tailed and parasitic jaegers (*Stercorarius longicaudus & parasiticus*), and gyrfalcon (*Falco rusticolus*).

We recorded observations of Arctic hares while walking in each study area. We recorded distances and locations walked using hand-held GPS units (Fig 1). All three areas contained open habitat without high vegetation, and arctic hares are conspicuous and easy to detect in this environment (Mech 2005). Weather was constant through the observation period and typical of a high Arctic dry and cold climate. In all areas, our activity ranged from 08.00 am to 03.00 am. Although we benefited from 24 h daylight, we were mostly active during mid-day to evenings. For each Arctic hare observation, we recorded the distance and azimuth to the observed animals using visual estimation and a hand-held compass, as well as noting the group size. Overall, we accumulated observations during 134 km of walking on Hall land, 78 km on Washington land and 135 km on Judge Daly Promontory. We augmented data on direct observations with pellet counts, which we conducted in plots placed along 1-km long transects. At each study area, 10 transects were randomly placed using stratified random protocol. We placed a grid with 3 x 3 km cells over each study area, and within each cell, we randomly selected transect starting points with the constraint that two coordinates were not allowed to be closer than 2 km to prevent overlap. Logistical and weather limitations (early snow) did not allow us to collect a full set of data on Judge Daly Promontory (7 transects). Transects were laid out along each cardinal direction from the starting coordinate in a rotating schedule. Each transect had 5 sample stations placed 250 m apart. At each sample station, we placed a 25 x 25 m square, which corners and center were hosting one square plot comprising 1 m², so that each transect included 25 plots of 1 m². We counted all hare pellets present within each 1 m² plot and also recorded the presence or absence of willows as well as total vascular vegetation cover. We also recorded all plant species present in each 25 m square.

We used distance-based techniques to estimate hare densities from the visual observations (Buckland et al. 2001). Although distance sampling may be prone to methodological biases (e.g. different visibility across study areas and different detectability among study organisms), we applied the method to only one species in an open environment which is ideal for long-distance observations (Mech 2005). We conducted one distance model grouped across the two study areas with hare observations (i.e. Washington Land and Judge Daly Promontory), including observed group size as aggregation size. We believe that this approach was appropriate since all areas were surveyed using the same technique, hosted very similar habitats, and we surveyed only one species. In addition, we ran one model for both areas because the low number of observations on Judge Daly Promontory would have made an estimation of detection function highly unreliable when based on data exclusively from this area. We used the raw perpendicular distances and a hazard-rate detection function (Buckland et al. 2004). We used a mixed generalized linear model with a binomial error structure and a logit link to compare the probability that a given 1 m² plot contained Arctic hare pellets among the three areas. This mixed model also allowed us to evaluate the relationship between presence of willows and hare pellets. We opted for comparing pellet occurrences using a binary classification rather than densities since it may give a less biased assessment of the spatial variation of herbivore abundance when clusters of herbivore pellets can occur (Isaacs et al. 2013). This mixed model used the presence or absence of hare pellets in a given plot as response variable, while fixed terms were set as study area, willow presence within the corresponding 25 m sample station as well as the 2-way interaction. We also compared the proportion of 1 m² plots containing willows between the three areas in a similar mixed model, using the presence or absence of willows as response variable and study area as a fixed factor. In both

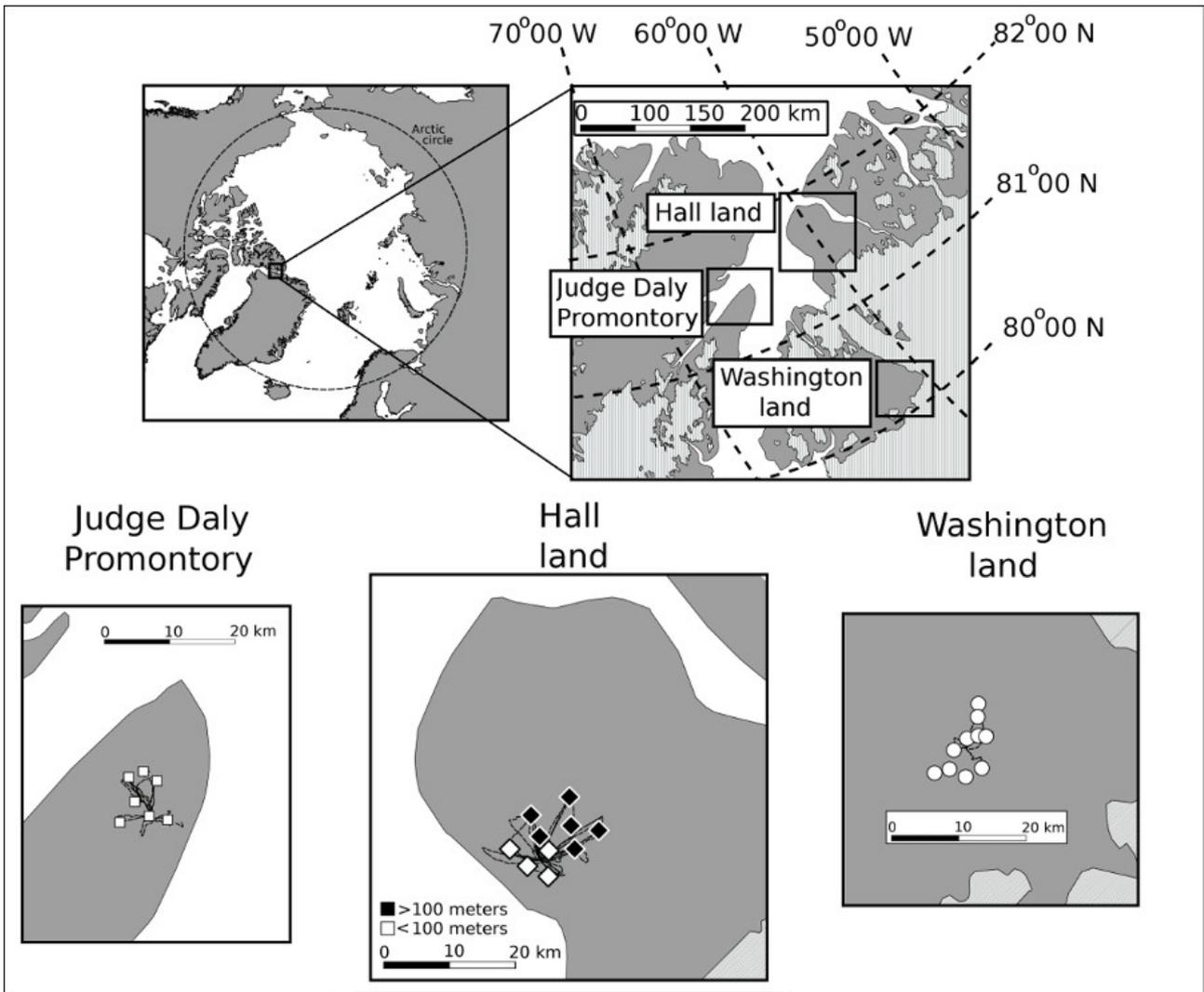


Figure 1. Map of the Hall basin region, including our three study areas with the location of sample transects used for pellet counts and vegetation surveys as well as the tracks walked for distance sampling. For Hall land, the transect points are divided to those below and above 100 meters of altitude, since we noted a distinct shift in vegetation communities at this elevation.

models, we also included sample station nested within transect as a random effect structure to account for spatial interdependence. Because of the apparent effect of the concurrent land rise process on plant communities, and subsequently also on herbivore distribution, we have only used data above 100 m asl from Hall land, since we detected no pellet in any plots below this altitude. We conducted post-hoc comparisons by evaluating pair-wise differences in least square means with Tukey adjustments of the p-values to control for multiple comparisons (Lenth et al. 2016). Data analyses were conducted in R 3.3.0 for linux (<http://www.r-project.org>) using the contributed packages Distance (Miller 2015), lmer (Bates et al. 2015), lsmeans (Lenth et al. 2016), and mrds (Lakke et al. 2015).

Results

We made 13 observations of Arctic hares on Washington land, 3 on Judge Daly Promontory, and no observations while walking on Hall land. However, we did observe one individual adjacent to our study area on Hall land during a helicopter transport. Group sizes varied from single individuals to 135 animals, with the largest groups observed on Washington land (Table 1). Density of hares per 100 km² was estimated to 14.5-187 individuals (95% C.I.) on Washington land, and 0.18-2.95 individuals on Judge Daly Promontory (Table 1). We observed hare pellets in 49 % of the surveyed plots on Hall land, 71 % of the plots on Washington land, and in 16% of the plots on Judge Daly Promontory. Densities ranged from 0.67 to 11.2 pellets / m² (Table 1). There were significant differences among the three areas in the proportion of sample plots that contained hare pellets ($\chi^2=8.98$, $df=2$, $p=0.01$), with Judge Daly Promontory having had a significantly lower proportion of plots with pellets compared to Washington lands ($Z=2.96$, $p=0.01$). There was also a trend for Judge Daly Promontory to have had a lower proportion of plots with pellets compared to Hall land ($Z=2.29$, $p=0.06$). There were no difference in proportion of plots with pellets between Hall and Washington lands ($Z=0.77$, $p=0.72$). Willow and hare pellets presences were positively related ($\chi^2=79.1$, $df=1$, $p<0.001$). This effect did not differ among the three areas ($\chi^2=3.38$, $df=2$, $p=0.18$), although the three areas differed in the proportion of plots containing willows ($\chi^2=16.3$, $df=2$, $p<0.01$, Table 1). Washington land had a higher proportion of plots containing willows than both Judge Daly Promontory ($Z=4.59$, $p<0.001$) and Hall land ($Z=2.72$, $p=0.02$). There were no differences between Hall land and Judge Daly Promontory ($Z=1.91$, $p=0.14$).

Discussion

Our observations suggested markedly different population densities among the three sites, with current populations densities being substantially higher on Washington land compared to both Judge Daly Promontory and Hall land. However, since Arctic hare pellets may remain in high Arctic environment for up to a decade (Krebs et al. 2003), our pellet counts indicated that both Hall land and Judge Daly Promontory had larger populations than the current ones at other times. We suggest three potential explanations for these results. First, the three sites contain spatially differentiated populations with separate population dynamics. This interpretation would imply a substantial asynchrony in Arctic hare population dynamics across this region, and contrast the large scale synchrony found in boreal snowshoe hare (*Lepus americanus*) populations (Krebs et al. 2013). Alternatively, all three sites consist of one single hare population. Our contrasting number of observations would then suggest that the hares are moving across the region in a synchronized fashion. However, although seasonal migrations have been suggested for Arctic hares (Best and Henry 1994), we question whether the limited dispersal abilities of lagomorphs (e.g., Krebs et al. 2013) would permit such movements. Finally, we appreciate that our different observations could have been caused by observational bias, and not necessarily reflect contrasting densities. However, Arctic hares are highly conspicuous and easy to observe in high Arctic environments (Mech 2005), and conditions were similar in our three study areas. Hence, we do not believe that the lack of observations in Hall land, and the low number of observations on Judge Daly Promontory were

Table 1. Sampling effort (expressed as distance walked for observations and total number of 1 m² plots used for pellet count and plant surveys), number of Arctic hare (*Lepus arcticus*) observations while walking, observed Arctic hare group sizes, and estimated Arctic hares densities on Hall land, Washington land and Judge Daly Promontory as well as proportion of plots containing Arctic hare pellets and willow (*Salix arctica*) and corresponding hare pellet density. Values indicate mean \pm 1 SE.

Area	Distance walked for observations (km)	Plots sampled for pellets and willows	Number of observations	Group size	Estimated density (animals / 100 km ²)	Proportion of plots with pellets	Density of pellets (pellets / 1 m ²)	Proportion of plots with willows
Hall land	134	250 (150) ^A	0	0	0	0.49 \pm 0.13 ^B	5.91 \pm 3.34 ^B	0.28 \pm 0.09 ^B
Washington land	78	250	13	31.4 \pm 12.5	52.0 \pm 34.1	0.71 \pm 0.05	11.2 \pm 2.91	0.57 \pm 0.07
Judge Daly Promontory	135	175	3	3.33 \pm 1.44	0.73 \pm 0.54	0.16 \pm 0.07	0.67 \pm 0.46	0.09 \pm 0.04

^A Numbers in brackets indicate transects > 100 m asl (below this altitude, no pellets and willow were recorded)

^B Data shown only for transects > 100 m asl

caused by any methodological bias. Such an interpretation is further supported by our varying sampling effort. We walked a substantially larger distance for observations in the area with no observed hares (Hall land) compared to the areas with the highest number of observations (Washington land).

Our study suggests a close spatial association between Arctic hares and willows. Such spatial associations have been recorded previously (Klein and Bay 1994; Schaefer et al. 1996), and agree with earlier observations suggesting a strong dietary importance of willows, especially during winter (Klein and Bay 1995; Larter 1999). Such dietary dependence could be driven by the dominance of willows in terms of available plant biomass rather than by selective feeding strategies, since Arctic hares appear to utilize other forage than willows if given the opportunity (Best and Henry 1994). Muskox, caribou, and ptarmigan similarly rely on willows for forage, but size-related differences in habitat use and movement patterns could allow coexistence despite the potential for competition in such low productive habitats (Klein and Bay 1994; Schaefer et al. 1996). Such partitioning is potentially further promoted by different requirements for winter snow conditions (Berg et al. 2008). However, we observed extremely low levels of plant biomass in the Hall basin region, and we observed animals or tracks (including pellets) of both muskoxen and caribou in our three study sites. Although Arctic ecosystems have been suggested to be regulated by top-down processes caused by predation (Krebs et al. 1999; Gilg et al. 2003; Legagneux et al. 2014), we highlight that food limitation may cause fluctuations in Arctic hare population sizes through bottom-up forces (e.g., Mech 2007).

Contrary to sub-Arctic species such as the mountain (*Lepus timidus*) and snowshoe hare, northern populations of Arctic hares remain white throughout the year (Best and Henry 1994). This makes them very conspicuous and subsequently potentially vulnerable to predation (Parker 1977). Social aggregations have been suggested as an efficient anti-predator strategy, and the well-developed sociality in Arctic hares has likely evolved as a defense against predation (Klein and Bay 1994). Although none of the high Arctic predators feed exclusively on Arctic hares, they have been recorded in the diet of Arctic populations of wolves (Marquard-Petersen 1998, see also Mech 2007), Arctic foxes (Dalerum and Angerbjörn 2000), and gyrfalcons (Booms and Fuller 2003). Because top-down driven population fluctuations generally are ascribed to specialist predators (e.g. Anderson and Erlinge 1977), we suggest that the lack of specialist hare predators in our area points to a limited destabilizing effect of predation on local and regional hare populations.

To conclude, we observed a large variation in the densities of Arctic hares among three sites across the Hall basin region in the High-Arctic. We suggest that this variation most likely was caused by asynchronous population fluctuations among three spatially distinct hare populations. We regard food limitation as a potential strong driver behind the observed variation. However, since predation is a likely cause for the gregarious behavior of Arctic hares and the hare populations were sympatric with muskoxen and caribou, two potential competitors, we argue that food limitation likely interact with predation as well as with intra- and inter-specific competition in shaping the spatial dynamics of Arctic hares in our study region. Determining at what spatial scales such interactions affect the spatial synchrony of Arctic herbivore populations is critical to deciphering the functioning of Arctic communities.

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