

Human impacts on the distribution, abundance and population genetics of the Svalbard reindeer

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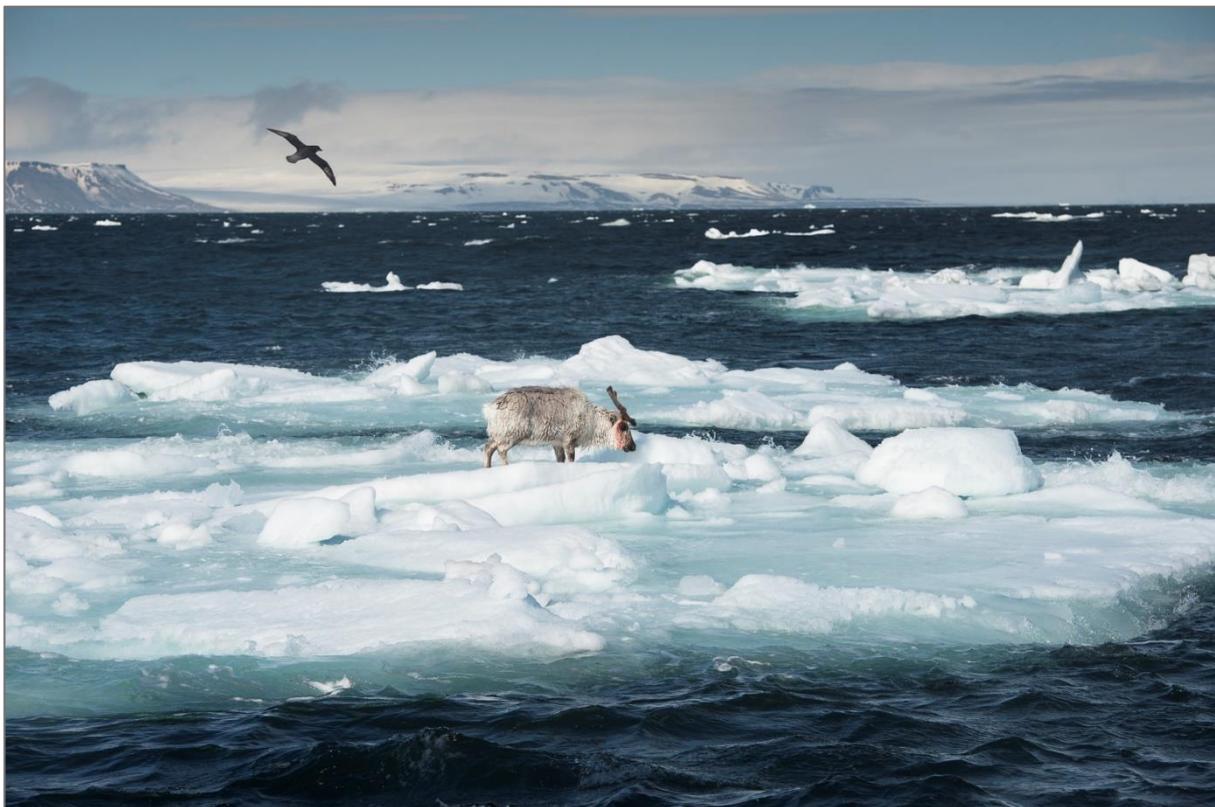


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SVALBARDS
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Sammendrag (in Norwegian)

Funn av pellets i eldre torvlag tyder på at svalbardreinen ankom øygruppa for mer enn 5000 år siden. Fra oppdagelsen av Svalbard i 1596 ble bestanden utsatt for et økende jakttrykk, noe som medførte en kraftig bestandsreduksjon og, etter hvert, utdøelse over store områder. Dette førte til et totalvern fra 1925. Målet med dette prosjektet var å framskaffe forvaltningsrelevant kunnskap om hvordan menneskelig aktivitet – inkludert historiske (dvs. høsting) og samtidige påvirkninger (dvs. klimaendringer) – har forårsaket endringer i svalbardreinenens utbredelse og antall, samt påvirket dens bestandsgenetikk gjennom effekter på isolasjon og utdøelses-rekoloniseringsprosesser. Resultatene viser at reinen nå er reetablert i de aller fleste isfrie områdene på Svalbard, dvs. områdene hvor det opprinnelig befant seg reinsdyr før menneskets ankomst til øygruppa. Analyser av tellingene våre viser dog at enkelte bestander fortsatt er i en reetableringsfase, dvs. bestandstettheten er betydelig lavere enn forventet ut i fra vegetasjonsdekket. På grunn av denne fortsatte veksten, samt sannsynlige effekter av økt planteproduksjon relatert til klimaendringer, er vårt estimat på totalantall rein på Svalbard (ca. 22000 individer) mer enn dobbelt så høyt som det forrige estimatet (fra 2009), som var basert på sporadiske tellinger fordelt over flere tiår. De genetiske analysene viser at det, på tross av generelt lav genetisk variasjon hos svalbardreinen, er en sterk romlig genetisk differensiering mellom bestander. Deler av disse romlige forskjellene i bestandsgenetikk forklares av direkte og indirekte effekter av historisk overhøsting, og særlig gjennom reintroduksjoner av rein fra Adventdalen til områder ved Kongsfjorden og Forlandssundet. Videre viser våre sammenligninger av DNA fra eldre beinsamlinger med moderne DNA at den historiske overhøstingen førte til et tap av genetisk variasjon. I seinere tid har bestandsgenetikken også blitt påvirket av reduksjonen i sjøisdekket vinterstid, siden sjøis fungerer som en 'landskapskorridor' for utveksling av individer, og derved genetisk materiale, mellom for eksempel reintroduserte og naturlig rekoloniserte bestander. I dag og i nær framtid er det svært sannsynlig at klimaoppvarmingen endrer beitebetingelsene dramatisk, og fortsatt tap av sjøis på fjordene og mellom øyene vil øke den genetiske isolasjonen og faren for lokale utdøelser over deler av Svalbard. Slike raske og dramatiske klimaendringer kan i sin tur true det evolusjonære potensialet og levedyktigheten til denne endemiske underarten av rein, noe som bør tas hensyn til i forvaltnings- og bevarings spørsmål.

Summary

Ancient feces records from peat layers suggest that the Svalbard reindeer have been present on the archipelago for at least 5000 years. From the 17th century onwards, harvest gradually reduced the population size and caused reindeer extirpations across large parts of the archipelago. Eventually, this led to full protection of the Svalbard reindeer in 1925. The aim of this project was to improve the knowledge basis for current and future reindeer management by assessing changes in distribution and abundance of the Svalbard reindeer sub-species, and by analyzing how the isolation, extirpation-recolonizations, and genetics of the different populations have been influenced by past (i.e. harvest) and current (i.e. climate change) anthropogenic drivers. We find that most unglaciated areas, i.e. those originally occupied by reindeer, are now recolonized. However, our reindeer surveys suggest that the recovery from overharvest is still in progress, since several newly recolonized areas have substantially lower reindeer densities than expected based on the available vegetation. Because of the still ongoing recovery, and documented vegetation 'greening' effects of climate warming, our estimate of the current total Svalbard reindeer abundance (ca. 22000 individuals) is more than twice the previous estimate based on counts in the period before 2009. In spite of overall low genetic variation in Svalbard reindeer, there were strong spatial patterns of genetic differentiation between populations. Part of this observed genetic differentiation in space was explained by the past harvest-induced extirpations and subsequent reintroductions (by humans) to peninsulas in Kongsfjorden and Forlandssundet. Furthermore, comparison of DNA from our ancient bone collection with modern samples indicated that the historical overharvest caused a loss of genetic variation. More recently, loss of sea ice has influenced the population genetics, since sea ice (and fjord ice) is important for dispersal among populations. Poor sea ice conditions in recent decades have therefore restricted exchange of individuals between, for instance, reintroduced and remnant reindeer populations. In the future, climate warming in summer and winter will continue to affect the tundra feeding conditions, and lack of sea ice as a dispersal corridor between populations will increase the isolation and local extirpation risk in parts of Svalbard. Such rapid and dramatic climate change effects may eventually threaten the evolutionary potential and persistence of the entire sub-species and should be accounted for in future management and conservation actions.

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Extended summary

The Svalbard reindeer is a wild reindeer subspecies that is endemic to Svalbard. According to old feces samples from peat deposits, the reindeer have probably been present on the archipelago for at least 5000 years. Their origin is most likely Eastern. From the 17th century onwards, harvest gradually reduced the population size, leading to local extirpations and, in turn, full protection of the reindeer in 1925. Sporadic population counts across parts of the archipelago during the late 20th and early 21st century indicated a population size of approximately 10,000 reindeer. However, this estimate has been regarded as highly uncertain, and the level of recovery from past regional extirpations due to overharvest have been poorly known. Especially in the light of current and future impacts of climate change, such as sea-ice loss, obtaining knowledge on the distribution, abundance and genetic diversity of the reindeer has therefore been pinpointed as a major management goal.

The aim of this project was to assess the current status of the Svalbard reindeer sub-species in the context of historical changes, and to analyze how population genetic patterns in space and time have been influenced by past and current anthropogenic drivers. Most of the results presented have been published in two peer-reviewed scientific articles (Le Moullec et al. 2019, Peeters et al. 2019a). It has already been well documented that, around the time of protection, reindeer were eradicated from large parts of the archipelago (northern parts of Isfjorden, southern, northwestern, and northeastern Spitsbergen, Barentsøya, Hinlopen, Kong Karls Land). We combined two abundance estimation methods – distance sampling (300 km transects, $n = 489$ reindeer groups observed) and total counts (1,350 km², $n = 1,349$ reindeer groups observed) – to estimate the reindeer distribution and abundance across their entire range, which we compared with historical data from the literature and radiocarbon-dated bones from our tundra surveys. We find that reindeer have now recolonized nearly all non-glaciated land, which according to the ancient bone collection (ranging back to 3600 years ago) corresponds well with the range occupied prior to human presence on the archipelago. The spatial variation in reindeer abundance largely reflects vegetation productivity, but when accounting for this ‘greenness’ effect, recently recolonized areas show lower reindeer densities than areas not subject to past extirpation. This confirms anecdotal observations that many areas have been recolonized very recently, and that the recovery from overharvesting is still in progress. Because of this, possibly combined with vegetation greening effects related to recent climate warming, our estimate of total reindeer abundance (ca. 22000 individuals) is more than twice the previous estimate published only ten years ago.

To evaluate population-genetic implications of past overharvest and current climate change, we genotyped 411 reindeer from 25 sampling sites throughout the entire subspecies’ range, at 19 microsatellite loci. Bayesian clustering analysis showed a genetic structure composed of eight ‘populations’, of which two were admixed. Overall population genetic differentiation was high (mean $F_{ST} = 0.21$). Genetic diversity was low (allelic richness = 2.07-2.58; observed heterozygosity = 0.23-0.43) and declined towards the outer distribution range, where populations showed significant levels of genetic inbreeding. Coalescent estimates of effective

population sizes and migration rates suggested evolutionary source-sink dynamics with the central population (Nordenskiöld Land) as the main source. The population genetic structure revealed strong isolation by glaciers and open water, and high connectivity by dispersal across winter sea ice. However, the observed patterns of natural genetic isolation were modified by the signature of the past harvest-induced extirpations, subsequent reintroductions (to Ny-Ålesund and Daudmannsøyra), and recent lack of sea/fjord ice. Finally, based on comparison of modern and ancient DNA, i.e. bones originating from the period prior to human presence, we find strong indicative evidence that the historical overharvest caused a substantial loss of genetic variation.

Thus, although effects of the past overharvest and regional extirpations can still be observed, our study has demonstrated a successful outcome of the strict harvest control implemented a century ago. The results suggest that past (i.e. harvest) and current (i.e. climate change) anthropogenic stressors may have interactive effects on large-scale ecological and evolutionary processes. These processes are particularly vulnerable in isolated island systems like Svalbard. Negative effects of the rapid winter warming, with more frequent rain-on-snow and icing events, are currently overruled by the effects of longer and warmer summers, but this balance may change in the future. Continued loss of sea ice as a dispersal corridor between islands and across fjords is expected to further increase the genetic isolation and local extirpation risk of the reindeer populations. Such rapid and dramatic climate change effects may eventually threaten the evolutionary potential and persistence of the sub-species and should be accounted for in future management and conservation actions.

1. Background and aim

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is a wild reindeer subspecies that is endemic to the high-Arctic Svalbard archipelago. Being the only large herbivore, and by far the most abundant herbivore in terms of biomass, it represents a key species for community-level dynamics on the Svalbard tundra (Hansen et al. 2013) and an indicator of environmental change (Ims and Ehrich 2013). The reindeer also represent important direct (i.e. hunting) and indirect value (i.e. tourism, recreation) for both visitors and locals, including trappers. Given the rapid climate change in this region, improving our knowledge on the distribution, abundance, and genetic diversity of the reindeer populations is therefore among the highest priorities for the management authorities (Governor of Svalbard 2009).

According to fecal records from old peat layers, the reindeer have probably been present on the archipelago for at least 5000 years (Van der Knaap 1989, Forman et al. 2000). Historical reports indicate that reindeer were found across most vegetated areas in Svalbard in the period following human's first arrival (polar expeditions, whaling), which was in 1596. Reindeer represented an important source of food for both whalers and trappers, and gradually more efficient means of hunting eventually led to overexploitation in the 19th and early 20th centuries. Thus, at the turn of the century, the reindeer were entirely (or very close to) extirpated from large parts of Svalbard, including northern parts of Isfjorden, southern, northwestern, and northeastern Spitsbergen, Barentsøya, Hinlopen, and Kong Karls Land (Wollebæk 1926, Lønø 1959). Reindeer hunting was banned in 1925, after which a slow recolonization seems to have occurred (Lønø 1959, Governor of Svalbard 2009). Although the knowledge on the current reindeer distribution and abundance has been poor (also in relation to the past), a total abundance of ca. 11000 individuals (Governor of Svalbard 2009) was estimated in 2009 based on scattered population counts during the last few decades. It was then concluded that the reindeer had probably recolonized most, yet not all, of their original habitat.

Although the direct anthropogenic effects of overharvest have ceased (around 200 reindeer are now shot annually by local hunters and trappers; Hansen et al. 2012), other human-caused stressors linked with global warming have now appeared. In particular, climate change has caused more frequent rain-on-snow events, resulting in ice-locked pastures and reduced survival and fecundity (Albon et al. 2017), while a longer and warmer summer season have led to shorter periods of snow cover, vegetation 'greening' (Vickers et al. 2016), and improved forage abundance (Albon et al. 2017, Hansen et al. 2019). The net outcome of generally poorer winter feeding conditions versus improved summer seasons seems to vary locally, such as from the inland to the coast (Hansen et al. 2019), and may also change with continued warming. On top of this, the sea-ice conditions in Svalbard have changed recently, with less frequent ice cover on fjords and between islands (Onarheim et al. 2014, Prop et al. 2015). It is well recognized that sea-ice can play a major role as dispersal corridor for Arctic ungulates (Jenkins et al. 2016, Leblond et al. 2016), but the population-genetic effects of more isolated Svalbard reindeer sub-populations have remained unknown.

The aim of this project was therefore to assess how the combination of these past (i.e. overharvest) and current (i.e. climate change) anthropogenic drivers shape the distribution, abundance, and population-genetic patterns of the Svalbard reindeer at the sub-species level. To achieve this, we combine previous data and information from the literature with our data and samples from two main expeditions across Svalbard in summers 2015-16. More specifically, we counted reindeer using established methodology (Le Moullec et al. 2017), sampled carcasses and feces for modern DNA, and collected bones and antlers for radiocarbon-dating and ancient DNA. Most of the results presented are from two articles published in peer-reviewed scientific journals (Le Moullec et al. 2019, Peeters et al. 2019a).

2. Methods

2.1. The study species

The oldest record of Svalbard reindeer presence was determined from fecal pellets found in peat layers dated to ca. 5000 years ago (Van der Knaap 1989). Recent genetic analyses estimated a population expansion in the same period and showed a phylogeny supporting a Eurasian origin of the subspecies (Kvie et al. 2016). The reindeer live in a predator-free environment (but see Derocher et al. 2000) and use relatively small seasonal home ranges (Tyler 1987), although dispersal between ranges (valleys, peninsulas) is documented in response to poor winter conditions (e.g. Hansen et al. 2010, Loe et al. 2016). Reindeer habitat use in summer is mainly shaped by the quality and quantity of available plant forage (Van der Wal et al. 2000, Hansen et al. 2009). Accordingly, the proportion of vegetation cover explained local summer distribution of reindeer monitored by 'distance sampling' and total counts on two peninsulas close to Ny-Ålesund (Le Moullec et al. 2017).

The management goal on Svalbard is that wildlife remains virtually untouched (Governor of Svalbard 2009). Accordingly, recreational reindeer hunting is presently strictly regulated and primarily occurs within the management area of Nordenskiöld Land, where ca 200 reindeer are harvested per year (Hansen et al. 2012). However, hunting has occurred since the 17th century, mainly in coastal areas, with expansion across the archipelago in the late 19th century with the establishment of mining communities, year-round trapping and overwintering sailing expeditions (Øritsland 1986). Reports from Hoel (1916) suggested that reindeer were present in all non-glaciated land in the middle of the 19th century. However, the subsequent high hunting pressure caused local extinction in parts of the archipelago (Hoel 1916, Wollebæk 1926, Governor of Svalbard 2009), and led to a ban on hunting in 1925. Lønø (1959) found that four reindeer metapopulations were remaining in the late 1950s (Figure 1A). Since then, reports based on opportunistic counts have provided updated estimates of regional reindeer abundance approximately every decade, and recorded new areas of recolonisation (Norderhaug 1970, Øritsland 1986, Governor of Svalbard 2009). Abundance records from previous reports can be informative but should be interpreted with care, since they lack information on survey design, sampling effort and estimate uncertainty.

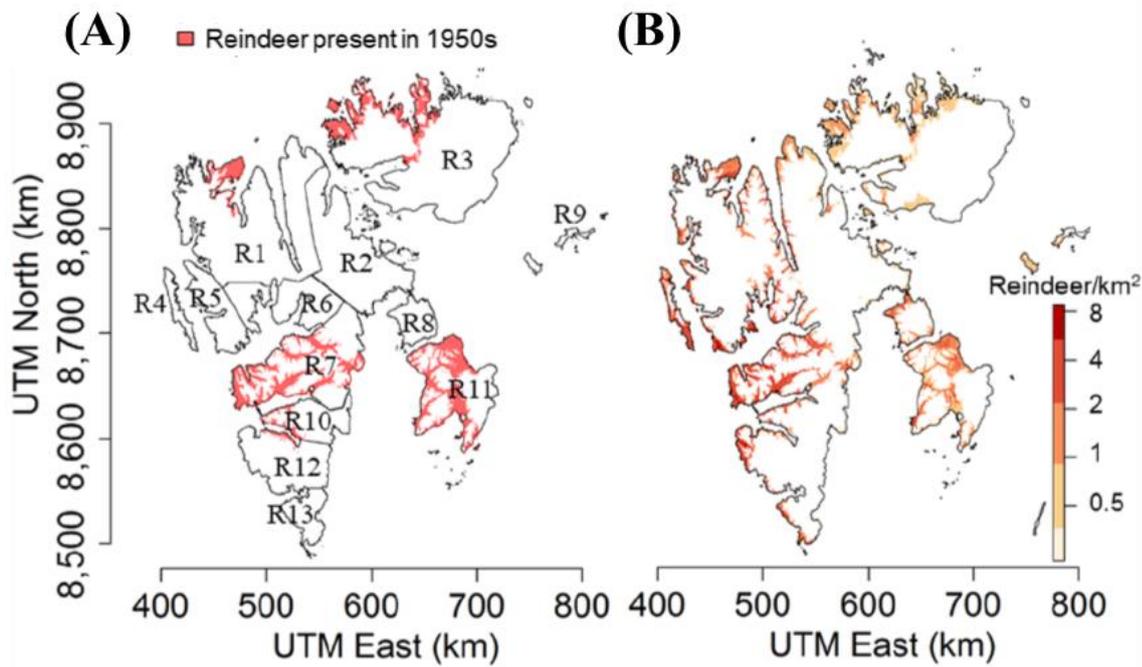


Figure 1. (A) Svalbard reindeer distribution in the period following protection 1925–1959 (Lønø 1959) and the extent of the reindeer management areas (R1–R13) in Svalbard (black lines). (B) Current predicted Svalbard reindeer density obtained using models based on distance sampling. UTM = Universal Transverse Mercator.

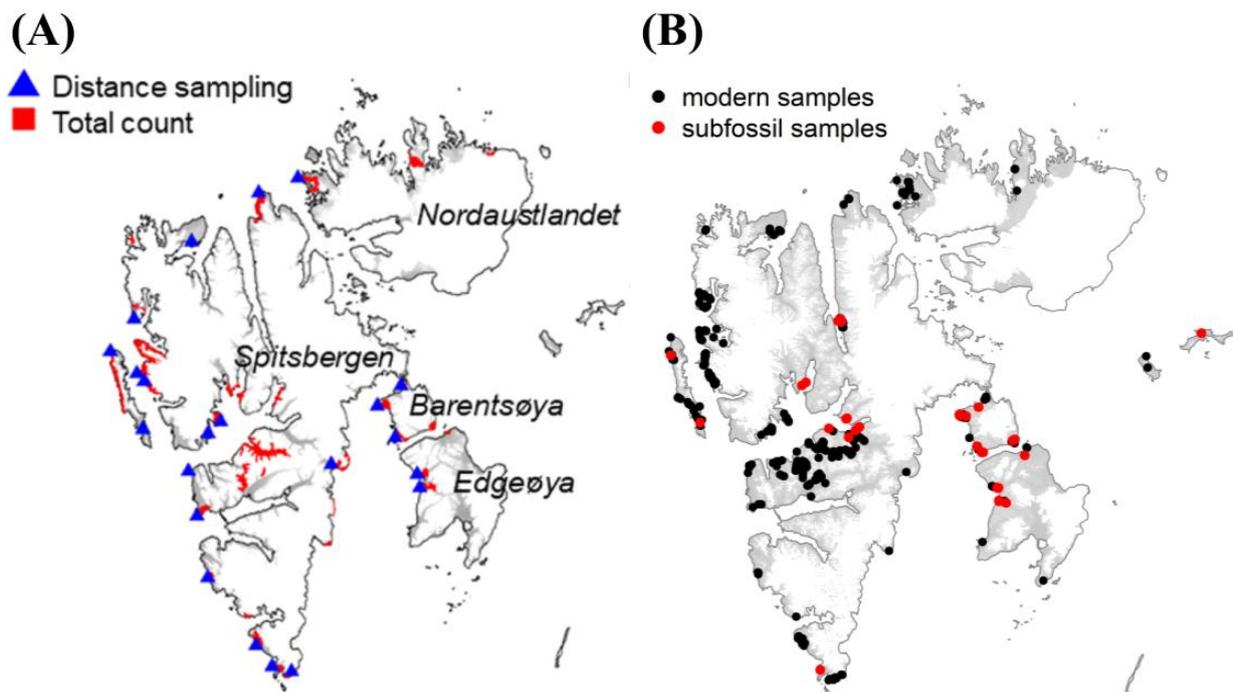


Figure 2. Overview of the field surveys and sampling sites during summers 2013–2016 for Svalbard reindeer abundance, distribution and genetics. (A) Study sites and methods for abundance estimation. The blue triangles, marking distance sampling areas, are shifted 3 km east for visual clarity. (B) Sampling sites for modern genetic samples (black dots) and radiocarbon-dated sub-fossil bones or antlers (red dots).

2.2 The reindeer surveys: abundance counts, bone sampling, and DNA collection

Data on reindeer distribution, abundance and genetics were mainly collected based on field surveys during summers 2013-16 (Figure 2). Transportation was made possible by ships (RV Lance, RV Helmer Hanssen), sailboat, zodiac, and helicopter. The north-western part of Spitsbergen was covered by monitoring campaigns in 2014, and sampling sites spread around the rest of Svalbard were covered in 2015-16. For estimation of reindeer (presence and) abundance, we surveyed 22 sites using distance sampling in wide, open plains (Buckland et al. 2001) and 33 sites using total counts in well-delimited areas (Figure 2A), as described in Le Moullec et al. (2017). For more details on the collection of reindeer abundance data, see Le Moullec et al. (2019).

Cold arctic environments preserve exposed bones and antlers (Van der Knaap 1989). We therefore collected subfossil bones and antlers from the areas in which we monitored reindeer abundance (Figures 2B and 3), to assess reindeer presence before human arrival in Svalbard. We typically found the bones lying on the tundra, partially nested into the ground or in cavities. We had the bones radiocarbon (^{14}C) dated at Uppsala Angströmlaboratoriet or at the Norwegian University of Science and Technology National Laboratory of Age Determination. We calibrated all ^{14}C dates to calendar ages (AD) using OxCal version 4.3 (Bronk Ramsey 2016) with the dataset IntCal13 (Reimer et al. 2016). For more details on the subfossil bone and antler collection and the radiocarbon-dating analysis, see Le Moullec et al. (2019).

During the population counts and capture-mark-recapture programs near Ny-Ålesund and in the Reindalen valley-system, we collected samples from carcasses (skin, bone or antler) and live reindeer (skin or hair from marked individuals included in mark-recapture programs, or fresh feces from unmarked individuals) for population genetic analysis. In total, we collected modern DNA from 411 individuals from 25 sampling sites across the Svalbard archipelago (Figure 2B). For more details on the DNA sampling, see Peeters et al. (2019a). We also extracted ancient DNA from a subsample of radiocarbon-dated bones and antlers for genetic analyses and comparison with modern DNA samples to investigate the potential loss of genetic diversity due to overharvesting (Côté et al. 2002). Preliminary results from this study are presented in this report further below.



Figure 3. A 680-year-old bone found on the tundra in Edgeøya.

2.3. Reindeer abundance estimation: distance sampling and total counts

To assess the current distribution and abundance status of the Svalbard reindeer in light of past overharvest, and the protection in 1925, we used extensive field surveys covering multiple environmental and geographical gradients, using distance sampling and total counts (Figure 2A). We developed spatial density models of the relationship between reindeer density and patterns of past local extirpations and vegetation productivity. We then used these to estimate the spatial distribution and abundance of reindeer, which we compared with observational data of past distribution (1950s) and abundance (late 20th century), and with radiocarbon-dated subfossil bones that inform about reindeer presence before hunting.

For distance sampling, we followed the protocols by Le Moullec et al. (2017) and walked 86 distance sampling line transects (~300 km) on large open plains, detecting reindeer with the naked eye. We conducted surveys in weather with good visibility, and we noted covariates that potentially influenced detection probability at the transect level: sky cover, wind speed, horizon background, observer, and year of sampling.

In contrast to distance sampling, total counts assume that all animals within a defined area are detected with certainty. This method has previously been evaluated for Svalbard reindeer using repeated total counts, and information from re-sightings of marked animals suggested the method was precise and unbiased, as long as certain guidelines were followed (Le Moullec et al. 2017). For instance, the counting area has to be well-delimited and relatively small for the area to be fully covered in one day. Although total counts can be more precise than distance sampling, they are not as adapted to cover large areas of open plains as is distance sampling (Le Moullec et al. 2017). We recorded all reindeer and their positions on a topographic map (1:100,000). For more details on the distance sampling and total counts data, see Le Moullec et al. (2017, 2019).

For analysis of abundance based on the distance sampling and total counts data, we extracted information about four covariates from digital maps across the reindeer summer range in Svalbard (i.e., <200m asl, without glacier and moraines, 11,600 km²). First, the maximum normalized difference vegetation index (NDVI) is a measure of primary production at the peak of the growing season. Second, we reproduced the map of reindeer presence and absence from Lønø (1959) as a binary map (1 × 1 km pixel resolution) with areas where reindeer were recorded as previously extirpated=0 and areas with presence=1. The land classified as having past extirpation represented 60% of Svalbard (Figure 1A). Third, we extracted Universal Transverse Mercator [UTM] east to investigate a possible longitudinal gradient in reindeer abundance, and fourth, UTM north to investigate a possible latitudinal gradient. We produced maximum NDVI maps (i.e., NDVI in Svalbard; Karlsen et al. 2018) by taking the averaging NDVI pixel values (240 × 240 m resolution, ranging between 0 and 1) over 2013 to 2016. The NDVI maps were based on data from the MODIS-satellite and do not cover latitudes >80°N. To get estimates of NDVI for the northernmost latitudes, we used a vegetation map based on LANDSAT-satellite images (30 × 30 m spatial resolution; Johansen et al. 2012). We predicted NDVI values north of 80°N based on the relationship between NDVI and vegetation categories in the data from farther south in Svalbard. The NDVI values ranged from 0 to 0.89 in Svalbard (0.29 ± 0.19, mean ± SE) at peak growing season. See Le Moullec et al. (2019) for more details and a description of the statistical analyses of the abundance data.

2.4. Genetic analyses

Using the modern DNA samples, we first analyzed the population genetic structure of Svalbard reindeer across their distribution range, and spatial patterns of genetic diversity, inbreeding and differentiation among sampling sites (Peeters et al. 2019a). For this, we used microsatellite markers, which are highly variable, neutral regions of nuclear DNA. This enabled us to detect patterns of recolonization and isolation and to delineate populations in distinct genetic units, which information the management can use to assign conservation units of Svalbard reindeer. Secondly, we performed landscape genetics analysis to better understand how the recolonization from overharvesting and gene flow between reindeer populations was restricted by landscape barriers (open water, glaciers and mountains) or mediated by dispersal across sea ice. For this, we estimated 'ecological distances' between individuals from different sampling sites. These were estimated by least-cost path and circuit theory analyses, but here we only show results for least-cost distances, as the conclusion from both methods are identical. For more details on the genetic analyses, see Peeters et al. (2019a).

We also performed a pilot study of genetic diversity in some of the radiocarbon-dated sub-fossil ('ancient') samples. These were compared with the genetic signature in modern DNA to investigate the potential loss of genetic diversity due to overharvesting. For this we analyzed microsatellites in nuclear DNA, but also mitochondrial DNA to make our samples comparable with modern samples from a previous study on the colonization of Svalbard (Kvie et al. 2016).

3. Results and Discussion

3.1. Changes in reindeer distribution and abundance

We found support for the claim of Hoel (1916) that reindeer occupied all non-glaciated lands of Svalbard prior to regional extinctions from overharvesting (Figure 1A, Le Moullec et al. 2019). Ancient bones older than documented human presence (1596) were recovered from 10 sampled management areas (Table 1). Since protection in 1925, recolonization of locally extinct populations happened progressively and in the 21st century all the reindeer management areas on Svalbard were reoccupied by reindeer (Figure 1B, Table 2). The areas that had viable reindeer populations throughout the 20th century included the regions with the highest present abundance of reindeer. Today's abundance estimates for Svalbard are the largest ever recorded with an estimated total population size of 22435 individuals [21452:23425] (mean [95% confidence interval]).

Table 1. Summary table of the age of radiocarbon dated (^{14}C) subfossil bone (with associated standard error) for each management area, as well as the area surface and its density estimate. Both uncalibrated radiocarbon dates Before Present (BP, i.e. before 1950) and calibrated dates to calendar ages (AD) were reported. The area surface comprise land below 200 m, without glaciers or moraines. Density estimates for distance sampling ($\hat{\lambda}_{\text{DS}}$) and total count ($\hat{\lambda}_{\text{TC}}$) methodologies represented the ratio between abundance estimates from Table 2 and the respective area surface.

Area	Lab. ref.	^{14}C date (BP)	Calendar age (AD)	Area (km^2)	$\hat{\lambda}_{\text{DS}}$	$\hat{\lambda}_{\text{TC}}$
R1 NW Spitsbergen	TRa-10913	1545±10	429-560	1986	~ 1.8	~ 1.4
R2 NE Spitsbergen	NA*	NA*	NA*	457	~ 0.9	~ 0.4
R3 NE-Land	TRa-12741	460±10	1428-1448	2702	~ 0.7	~ 0.5
R4 PK Forland	Ua-49962	371±35	1440-1640	416	~ 3.1	~ 2.0
R5 Ny-Ålesund	TRa-12740	1250±20	680-857	416	~ 3.3	~ 2.3
R6 N Isjorden	Ua-49956	376±32	1440-1640	552	~ 2.8	~ 1.9
R7 Nordenskiöld	TRa-10895	375±15	1452-1619	1834	~ 2.9	~ 5.2
R8 Barentsøya	TRa-10897	395±15	1444-1613	393	~ 1.6	~ 0.9
R9 Kong Karl land	TRa-10882	660±15	1282-1388	190	~ 0.7	~ 0.3
R10 Nathorstland	NA*	NA*	NA*	209	~ 1.9	~ 2.3
R11 Edgeøya	TRa-10899	470±25	1412-1454	1761	~ 1.4	~ 2.2
R12 Hornsund	NA*	NA*	NA*	426	~ 2.9	~ 2.3
R13 S Spitsbergen	TRa-10883	620±15	1295-1396	246	~ 2.2	~ 1.4
Total	-	-	-	11600	~ 1.8	~ 1.9

* No bones were sent to ^{14}C dating.

Table 2. Chronological summary of Svalbard reindeer distribution and abundance across the 13 management areas (R1–R13) in Svalbard, Norway (<200 m, without glacier and moraines). We report evidence of Svalbard reindeer presence (¹⁴C dated bones) before documented human presence (1600). Distribution information and opportunistic counts were reported for 1925–1954 presence information (Lønø 1959), 1954–1958 abundance information (Lønø 1959), in 1980–1982 (Øritsland 1986), and 1969–2008 (Governor of Svalbard 2009). We compared abundance estimations (\bar{x}) from the distance sampling (column ‘Today DS’) and the total counts (column ‘Today TC’) methodologies (2013–2016), also showing their difference and the respective 95% confidence interval (column ‘Difference’). *n* represents the number of study sites per management area.

Management area	Before 1600	1925–1954	~1959	~1986	~2009	Today DS			Today TC			Difference	
						\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	95% CI
R1 NW Spitsbergen	Present	Present	300	>1,000	800	3,617	537	3	2,727	116	3	-890	-1,966; 187
R2 NE Spitsbergen	NA ^a	0	0	NA	50–70	422	133	0	160	27	0	-261	-527; 5
R3 NE-Land	Present	Present	400	>500	300	1,994	751	1	1,372	93	3	-622	-2,106; 862
R4 PK Forland	Present	0	0	0	5–15	1,301	173	2	818	56	1	-483	-838; -127
R5 Ny-Ålesund	Present	0	0	50	300	1,375	148	3	959	65	3	-415	-732; -99
R6 N Isjorden	Present	0	0	0	80	1,550	171	1	1,068	73	4	-483	-847; -118
R7 Nordenskiöld Land	Present	Present	>200	4,500	4,000	5,349	629	3	9,455	268	5	4,106	2,765; 5,446
R8 Barentsøya	Present	0	0	500	500	621	175	3	357	48	4	-264	-620; 91
R9 Kong Karl land	Present	0	0	NA	109	132	69	0	51	19	0	-81	-222; 60
R10 Nathorstland	NA ^a	0	25	200	80	406	54	0	490	57	2	84	-70; 239
R11 Edgeøya	Present	Present	800	2,000	2,700	2,488	839	2	3,799	202	3	1,311	-381; 3,002
R12 Hornsund	NA ^a	0	0	300	1,000	1,250	126	1	992	73	2	-258	-543; 26
R13 S Spitsbergen	Present	0	0		200	536	70	3	339	42	3	-197	-358; -36
Total			>1,725	>9,050	~10,154	21,079	2,983	22	22,615	401	33	1,536	-4,363; 7,435

^a No bones were sent to ¹⁴C dating.

Based on the distance sampling methodology, the main covariate affecting reindeer spatial density was ‘greenness’, i.e. NDVI (Figure 4). In addition, reindeer density was lower in the East than in the West for similar values of NDVI (i.e., negative longitudinal gradient). The estimated abundance across Svalbard based on distance sampling was 21079 ± 2983 (one standard error). The total count surveys resulted in the observation of 1349 reindeer clusters (3898 individuals) in an area of $\sim 1350 \text{ km}^2$, of which 42% was not subject to past extinction. As for distance sampling, NDVI was the main covariate explaining variation in reindeer densities (Figure 4). Furthermore, in the total count models, the areas where reindeer were known to be present throughout the 20th century had on average higher estimated reindeer abundances than areas where reindeer were reported to be extinct. The estimated total reindeer population size was very similar to the estimate obtained from models based on distance sampling (22615 ± 401).

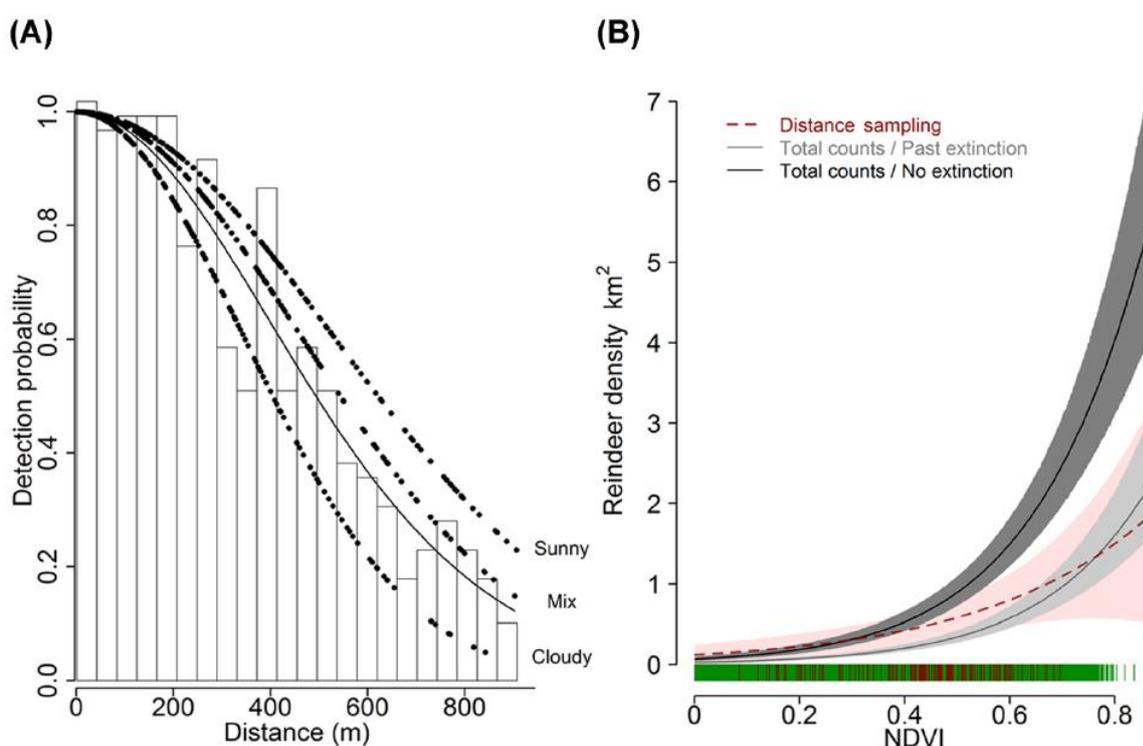


Figure 4. Svalbard reindeer detection and density functions obtained from monitoring programs in Svalbard, Norway (2013–2016). (A) The detection function of distance sampling line transects progressively decreases with a half normal rate (full line) until the truncation distance of 908 m. Detectability was influenced by weather (i.e., sunny, partly cloudy [mix], or cloudy sky). Each full dot represents a reindeer cluster distance fitted on a continuous scale so that the histogram of cluster observation frequency could be plotted for visual illustration. (B) The density functions of distance sampling (red dashed line) and total counts (full lines) increase exponentially with vegetation productivity (i.e., max. normalized difference vegetation index [NDVI]). Total counts density was influenced by areas with past local population extirpation (grey) or no past extirpation (black), due to overharvesting a century ago. The longitude covariate was fixed for mid-Svalbard. The shaded curves represent 95% confidence intervals and the bars along the x-axis show the NDVI pixels values from the areas covered by total counts (green) and the areas covered by distance sampling segments (red).

Although recovery time and the trajectory since overharvesting can be difficult to predict, population recovery can take decades (Hutchings 2000, Suding et al. 2016). The reproductive biology of the species, the number of recolonizing/translocated individuals, their sex and age and feedbacks between biotic and abiotic factors will influence population growth rates. The experimental translocation of 12 reindeer (three males and nine females) from central Svalbard to the Ny-Ålesund area on the northwest coast in 1978 illustrates this well (Aanes et al. 2000). After a century of reindeer absence, the translocation resulted in an immediate exponential population increase, followed by a severe population crash in 1994 likely due to the interplay between overgrazing, demography and extreme weather events (Kohler and Aanes 2004, Hansen et al. 2007, 2019). Subsequently, population size stabilized in the early 2000s. The first known dispersal events to neighbouring peninsulas (Sarsøyra, Kaffiøyra) occurred 16 years or more after the translocation event. Further to the west, but still not far from Ny-Ålesund, the abundance of reindeer on Prins Karls Forland was estimated to only ca. 15 individuals one decade ago (Governor of Svalbard 2009). Based on the analysis of our population counts, the abundance there may now be as high as ca. 1,000 reindeer (Table 2). At larger spatial scales, recovery in such a fragmented landscape often takes even longer than what was observed locally in the Ny-Ålesund area, which is also expected given the highly sedentary behaviour of Svalbard reindeer (Tyler 1987, Côté et al. 2002). We could therefore expect that similar recovery trajectories for naturally recolonized populations across Svalbard have probably delayed the full recolonization of the archipelago into the 21st century.

The two abundance estimation methodologies applied here (i.e., distance sampling and total counts) led to quite similar abundance estimates for the entire Svalbard, even though they were partly conducted at different sites, with different harvest histories. This was likely facilitated by extensive spatial replication, since at the time of survey, a specific subpopulation could by coincidence be in an eruptive phase, or a post-crash phase. However, distance sampling model selection, as opposed to total counts model selection, did not detect an effect of past extinction history on reindeer abundance. A main reason for this discrepancy was that landscapes suited for distance sampling methodology (i.e., wide coastal plains) were also the areas accessible by hunting expeditions. Therefore, most of the line transects were located in regions with past extinctions, which led to low statistical power for detecting a difference. Accordingly, the distance sampling density function estimated reindeer densities to be between the density functions obtained from total counts for past extinction or no extinction (Figure 4B). This resulted in a tendency for distance sampling to underestimate reindeer abundance in non-extinct regions, and vice versa in regions where reindeer had been extinct, when compared to the estimates from total counts. Two of the non-extinct regions (Nordenskiöld Land and Edgeøya) are characterized by inland valleys (suitable for total counts) with the highest reindeer density. The underestimation by distance sampling in these two regions (only significantly different from total counts estimates in Nordenskiöld Land, Table 2) explained most of the difference in the overall Svalbard abundance estimates across methodologies. Furthermore, the variance estimation differed between the two methodologies, with higher precision for total counts than distance sampling estimates.

Distance sampling models account both for uncertainties due to detection and density errors, while total counts models assume no detection errors and, thus, less uncertainty (Le Moullec et al. 2019). We also had 2.5 times higher sample size in the total counts than the distance sampling methodology.

The carrying capacity of the tundra (i.e. how many reindeer it can support) is expected to increase as the climate warms and the vegetation is gradually 'greening' (Albon et al. 2017, Hansen et al. 2019). The climate gradient towards the East, currently characterised by a relatively cold climate and short growing seasons (Nordli et al. 2014, Macias-Fauria et al. 2017), likely explains the associated negative gradient in reindeer density. Even with a similar NDVI value at the peak of the growing season, the carrying capacity may be lower towards the East due to a longer snow-cover season. We also suspect that the colder climate towards the East affects plant community composition, possibly with lower overall forage quality for reindeer due to, for instance, more moss-dominated communities. The tendency for higher aggregation of reindeer towards the East, as indicated by the total counts model, may also be due to such differences in the spatial distribution of high-quality forage. However, on the east coast, the retreat of the sea-ice in spring has on average been two weeks earlier per/decades since 1979 (Prop et al. 2015), and this has led to reduced cooling from local breeze and enhanced 'greening' (Macias-Fauria et al. 2017). Hence, one could expect eastern regions of Svalbard to soon approach the growing conditions of today's warmer western regions.

Reindeer are the only ungulates on the Svalbard tundra and represent the largest biomass of secondary producers. Changes in reindeer abundance therefore have important top-down and bottom-up effects on the ecosystem. Although the system is mainly bottom-up regulated (Ims et al. 2013), reindeer have undoubtedly changed vegetation communities in recolonised regions by depleting lichens (Van der Wal et al. 2001, Hansen et al. 2007) and altering vegetation communities from moss to graminoid-dominated tundra (Van der Wal 2006). These changes are due to both grazing, trampling and increased fertilisation from feces and carcasses, affecting both above- and belowground processes (Van der Wal and Brooker 2004, Van der Wal et al. 2004). Furthermore, reindeer carcasses are a major food source for Arctic foxes and contribute strongly to their population dynamics in some areas (Fuglei et al. 2003, Eide et al. 2012, Hansen et al. 2013). The increase in reindeer distribution and abundance demonstrated here, in part due to recent climate warming (Hansen et al. 2019), implies on average more numerous and more widespread carcasses on the tundra, which can improve the carrying capacity for Arctic foxes. This may have knock-on effects on reproduction success of ground nesting birds, including geese (Fuglei et al. 2003), through increased predation rates on young. Unravelling the implications of such potential trophic cascades (Ims et al. 2007) in response to changing ungulate abundance require continuous efforts in ecosystem monitoring (Côté et al. 2004, Ims et al. 2013).

Table 3. Overview of sampling sites, number of reindeer sampled (*n*), their Origin (natural, reintroduced, or mixed), whether they were locally extinct from harvesting (Ext., Lønø, 1959), and genetic diversity estimates. Populations are here defined by their genetic structure according to cluster analyses (see Figure 5B). AR = allelic richness; H_o = observed heterozygosity; uH_E = unbiased expected heterozygosity; F_{IS} = inbreeding coefficient

Population	Sampling site	<i>n</i>	Origin	Ext.	AR	H_o	uH_E	F_{IS}
North	Reinsdyrflya	6	Natural	No	–	0.19	0.30	0.37
Spitsbergen	Mitrahalfvøya	18	Natural	Yes	1.80	0.25	0.27	0.07
	Danskøya	3	Natural	Yes	–	–	–	–
	Mosselhalvøya	3	Natural	Yes	–	–	–	–
Wijdefjorden	Wijdefjorden	29	Natural	Yes	2.28	0.37	0.39	0.03
West	Brøggerhalvøya	27	Reintro.	Yes	2.03	0.35	0.34	-0.03
Spitsbergen	Sarsøyra	18	Reintro.	Yes	2.12	0.33	0.34	0.03
	Kaffiøyra	31	Reintro.	Yes	2.01	0.31	0.34	0.07
	Prins Karls Forland	22	Reintro.	Yes	2.13	0.31	0.36	0.13
North Isfjorden	Bohemanflya/Erdmannflya	19	Mixed?	Yes	2.17	0.35	0.38	0.09
Central	Sassendalen	20	Natural	No	2.21	0.43	0.42	-0.03
Spitsbergen	Adventdalen	33	Natural	No	2.23	0.40	0.42	0.04
	Colesdalen/Reindalen	52	Natural	No	2.25	0.44	0.43	-0.04
	Grøndalen/Hollenderdalen	14	Natural	No	2.08	0.44	0.38	-0.15
	Nordenskiöld Coast	8	Natural	No	–	–	–	–
	Agardhbukta	1	Natural	No	–	–	–	–
South	Breinesflya	11	Natural	Yes	2.02	0.23	0.33	0.30
Spitsbergen	Sørflya/Øyrlandet	17	Natural	Yes	1.90	0.29	0.32	0.07
	Storvika	4	Natural	Yes	–	–	–	–
	Kvalvågen	2	Natural	?	–	–	–	–
East Svalbard	Barentsøya	30	Natural	Yes	2.08	0.31	0.34	0.10
	Edgeøya	18	Natural	No	2.06	0.26	0.34	0.25
	Svenskøya	2	Natural	Yes	–	–	–	–
Nordaustlandet	Storsteinhalvøya	17	Natural	No	1.82	0.22	0.30	0.27
	Rijpfjorden	6	Natural	No	–	0.24	0.24	-0.03

3.2. Reindeer population genetics: a result of overharvest and sea-ice conditions

Svalbard reindeer is known to have very low genetic diversity compared to other populations and subspecies of reindeer and caribou (Røed 2003, Yannic et al. 2014). Estimates of allelic richness and observed and expected heterozygosity were highest for sampling sites in Nordenskiöld Land, Central Spitsbergen, and similar to the findings of previous studies of local population genetics in Central Spitsbergen (Côté et al. 2002). However, genetic diversity estimates decreased towards sampling sites further away from the center of their distribution range, most notably in North Spitsbergen and Nordaustlandet (Table 3, Figure 5A). These locations also had higher estimates of genetic inbreeding (Table 3). This pattern confirms to the central-marginal hypothesis (Eckert et al. 2008) and relates to the higher probability of migration between central (migration sources) and peripheral populations (migration sinks) than among peripheral populations. Coalescent estimates of migration rates also confirmed evolutionary source-sink dynamics with Central Spitsbergen as the main source for gene flow (see Peeters et al. 2019a). Nevertheless, it is worth noting that three (out of four) populations that survived extensive harvesting in the past (Reinsdyrflya, Nordaustlandet and Edgeøya) have among the lowest levels of genetic diversity. Furthermore, the reintroduced sites in West Spitsbergen (Brøggerhalvøya, Kaffiøyra, Sarsøyra, Prins Karls Forland) have lower levels of genetic diversity than their source population (Adventdalen in Nordenskiöld Land), yet not as low as other peripheral sites. This strongly indicates a reduction in the number of alleles due to a founder bottleneck due to the reintroduction in 1978. However, the loss of genetic diversity due to genetic drift (i.e. random loss) may have been restricted as the population in Brøggerhalvøya grew rapidly after reintroduction.

The analysis of population genetic structure revealed up to six distinct genetic clusters that were furthermore characteristic for six distinct regions of Svalbard: North Spitsbergen (or Northwest-Spitsbergen National Park), West Spitsbergen, Central Spitsbergen, South Spitsbergen, East Svalbard (Barentsøya, Edgøya) and Nordaustlandet (Figure 5B). However, Wijdefjorden and North Isfjorden showed a high degree of admixture indicated by a mixed cluster origin in reindeer samples. North Isfjorden revealed a strong similarity with Central Spitsbergen, but also with West Spitsbergen, suggesting that this population has been partly recolonized from the reintroduced Daudmannsøyra in the east and Nordenskiöld Land along the inner parts of Isfjorden. This was also confirmed by genetic estimates of recent migration rates (Peeters et al. 2019a). Wijdefjorden showed a strong mixture from the remnant Reinsdyrflya in North Spitsbergen and West/Central Spitsbergen (Figure 5B), which resulted in elevated levels of allelic richness and genetic heterozygosity (Table 4). When excluding the reintroduced sites from the analysis, Wijdefjorden was characterized as a separate cluster, suggesting that this population is an important contact zone for gene flow.

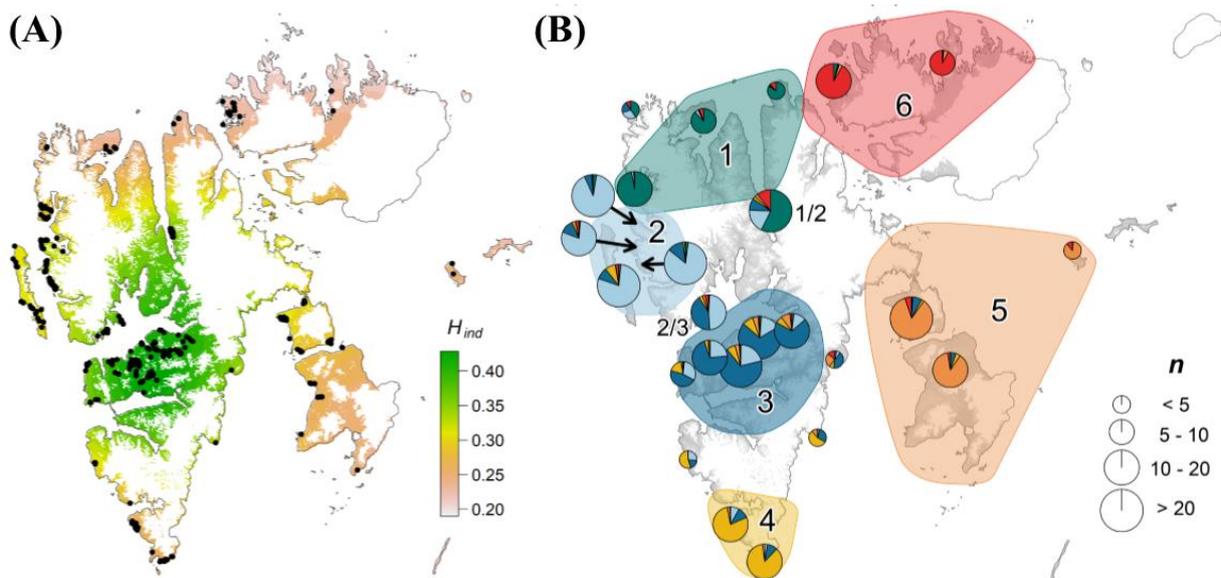


Figure 5. Population genetic diversity and structure of Svalbard reindeer. (A) Spatial variation in individual genetic diversity (H_{ind}), showing a reduction from Central Spitsbergen towards populations at the edge of their distribution range. Black dots show individual samples ($n = 411$). (B) Population genetic structure analyses suggested six clusters, i.e. genetically distinct ‘populations’. These six clusters were delineated as follows: North Spitsbergen (1, green), the reintroduced West Spitsbergen (2, light blue), Central Spitsbergen (3, dark blue), South Spitsbergen (4, yellow), East Svalbard (5, orange) and Nordaustlandet (6, red). The colors in the pie charts indicate the proportion of cluster origins among individuals sampled at 25 sites, whereas the size of pie charts indicate the number of individuals sampled. Wijdefjorden (1/2) and North Isfjorden (2/3) were characterized by a high mixture of cluster origins.

Thus, based on our population genetic analysis, we identified eight populations with strong differentiation in their genetic structure, six populations defined by the six genetic clusters and two populations showing mixed genetic origins (Table 4). Estimates of genetic differentiation (F_{ST} -values) indicated high levels of genetic isolation (Table 5). North Spitsbergen was extremely isolated from other populations of Svalbard, with F_{ST} -values between 0.3 - 0.4 (i.e. ca 0.4 - 0.5 migrants per generation), except for Wijdefjorden, which appeared to be partly recolonized from Reinsdyrflya.

Svalbard reindeer were assumed to be extirpated in South Spitsbergen before the 1820s, and this region was probably recolonized by a gradual southward expansion from Central Spitsbergen since the 1960s (Norderhaug, 1970). The low genetic diversity and the strong genetic differentiation between these two populations, as shown here, may indicate that South Spitsbergen may have held a small remnant population after harvesting was banned. Nevertheless, continuous range expansion can result in a gradual loss of genetic diversity due to cumulative bottlenecks and founder events. Similar loss of genetic diversity during range expansion has been observed in muskox that colonized high Arctic Canadian islands and Greenland, leading to extremely high genetic differentiation among populations (Hansen et al., 2018). Thus, a harvest-induced extirpation followed by successive founder events is the most plausible explanation for the genetic signature in South Spitsbergen, especially

considering the small available habitat patches and fragmented landscape along the southwest coast. This was also confirmed by evolutionary estimates of migration, suggesting higher gene flow from Central to South Spitsbergen than in the opposite direction (Peeters et al. 2019a).

Table 4. Genetic diversity and population size estimates of the eight populations. n = sample size; AR = allelic richness; AR_P = allelic richness of alleles unique to each population (excluding Wijdefjorden and North Isfjorden which had mixed cluster origins); H_O = observed heterozygosity; uH_E = unbiased expected heterozygosity; F_{IS} = inbreeding coefficient (bold estimates are significantly larger than zero); N_c = estimated census population size with standard error (SE); N_d = population density (N_c / km^2); N_e = effective population size 95% confidence intervals.

Population	n	AR	AR_P	H_O	uH_E	F_{IS}	$N_c \pm SE$	N_d	N_e (95% CI)
North Spitsbergen	27	2.07	0.20	0.24	0.30	0.19	2,678 \pm 400	1.84	36.2 (11.1; ∞)
Wijdefjorden	29	2.58	–	0.37	0.39	0.03	572 \pm 81	1.97	219.9 (36.3; ∞)
West Spitsbergen	98	2.42	0.02	0.33	0.35	0.07	1,887 \pm 241	2.88	100.2 (47.8; 437.9)
North Isfjorden	19	2.45	–	0.35	0.38	0.09	1,730 \pm 184	2.87	38.5 (13.5; ∞)
Central Spitsbergen	119	2.55	0.07	0.43	0.43	0.00	5,581 \pm 650	2.97	221.1 (106.1; 1593.1)
South Spitsbergen	28	2.35	0.13	0.27	0.34	0.20	648 \pm 82	2.26	21.6 (10.8; 67.2)
East Svalbard	50	2.36	0.15	0.29	0.34	0.16	3,289 \pm 1,085	1.38	108.5 (35.7; ∞)
Nordaustlandet	23	2.08	0.16	0.23	0.30	0.25	1,922 \pm 710	0.77	63.3 (14.0; ∞)

Table 5. Pairwise genetic differentiation (F_{ST}) among the eight populations. High F_{ST} -values indicate strong differentiation due to isolation.

Population	North Spitsbergen	Wijdefjorden	West Spitsbergen	North Isfjorden	Central Spitsbergen	South Spitsbergen	East Svalbard	Nordaustlandet
North Spitsbergen								
Wijdefjorden	0.158							
West Spitsbergen	0.342	0.144						
North Isfjorden	0.370	0.194	0.084					
Central Spitsbergen	0.317	0.163	0.064	0.051				
South Spitsbergen	0.361	0.164	0.123	0.222	0.134			
East Svalbard	0.370	0.277	0.197	0.188	0.158	0.262		
Nordaustlandet	0.374	0.207	0.166	0.215	0.160	0.198	0.219	

The observed patterns of genetic diversity and population genetic structure were best understood when investigating effects of landscape barriers, connectivity across sea ice and past harvest-induced extinctions followed by natural recolonizations or human-mediated reintroductions. F_{ST} -values increased linearly with distance between natural (i.e. not reintroduced) sampling sites, a pattern referred to as isolation-by-distance (IBD) (Figure 6A). However, the IBD relationship showed an increasing spread in F_{ST} with distance and an intermediate correlation ($r = 0.48$). We thus estimated ecological or least-cost distances between individuals at different sampling sites. When least-cost distances accounted for high resistance (i.e. low movement probability) across open water, glaciers, and steep mountain slopes, the resulting pattern of isolation-by-resistance (IBR) explained the genetic differentiation much better ($r = 0.63$) than IBD (Figure 6B). Furthermore, when incorporating low resistance (i.e. high movement probability) across winter sea ice (using a map for sea ice occurrence in March between 1986-2015), even more variation in F_{ST} was explained ($r = 0.70$, Figure 6C).

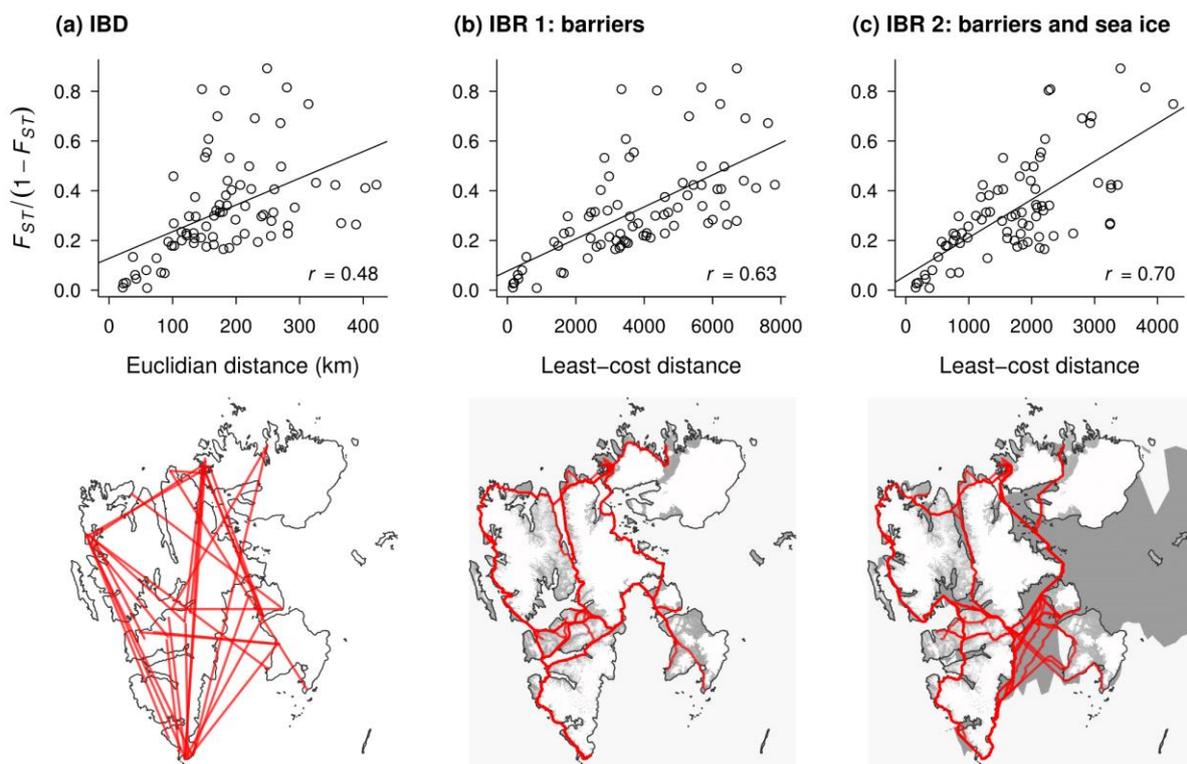


Figure 6. Natural patterns of gene flow in Svalbard reindeer were best explained by geographic distances correcting for landscape barriers (open water, glaciers, mountains) and connectivity across winter sea ice. The graphs show pairwise genetic differentiation (F_{ST}) between sampling sites (excluding sites from reintroduced populations) as a function of (a) Euclidian or “straight-line” distance, (b) least-cost or “ecological” distance correcting for barriers, and (c) least-cost distance correcting for barriers and connectivity across winter sea ice. Regression lines are shown in black with Pearson correlations (r). The maps below illustrate connectivity and dispersal routes for the respective landscape models for 30 random pairs of individuals (red lines) on transition maps with low (white) to high (dark grey) dispersal probability. No transition map was used for IBD.

However, these patterns of IBD and IBR were obscured when including genetic data from reintroduced sites in our analyses (Figure 7). When comparing reintroduced sites with each other or with sampling sites from their source population (Nordenskiöld Land), a linear increase in F_{ST} with distance was clear for both IBD and IBR (Figure 7, middle panel), although this increase was not as strong as when comparing natural sites only. Moreover, when comparing reintroduced sites with natural sites that were genetically different from the reintroduction source, we found an inverse relation between F_{ST} and distance metrics (Figure 7, right panel). This relation was mainly influenced by a very high differentiation between recently recolonized and reintroduced sites near Kongsfjorden and Krossfjorden, West Spitsbergen. Here, the reindeer population of Brøggerhalvøya had grown exponentially after reintroduction, but crashed during the severe winter in 1993-1994, leading to the dispersal and recolonization of reindeer to Sarsøyra and Kaffiøyra the following years (Aanes et al. 2000). During this period, Mitrahalvøya in Krossfjorden (<20 km north of Kvadehuken on Brøggerhalvøya) was also recolonized, but the origin of reindeer was only based on speculations (Scheie & Grøndahl, 1990). Now, our results from the genetic structure analysis can clearly confirm that Mitrahalvøya was recolonized by reindeer from North Spitsbergen and has shown no sign of immigration from the reintroduced Brøggerhalvøya, as F_{ST} -values were as high as 0.41. It is also worth noting that sea ice occurrence has rapidly decreased during the past few decades along the west coast of Spitsbergen, and now occurs only rarely in the inner parts of fjords (Onarheim et al. 2014, Nilsen et al. 2016). Overall, these results suggest a very strong genetic differentiation over short distances due to past harvest-induced extinctions followed by reintroductions and recent lack of dispersal across sea ice.

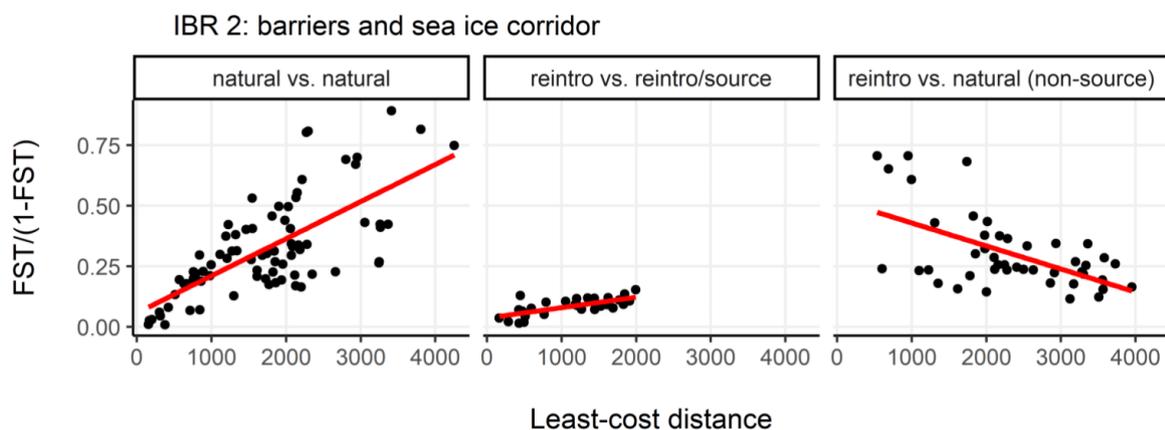


Figure 7. Genetic differentiation between pairs of sampling sites as a function of least-cost distance (i.e. correcting for barriers effects and sea ice connectivity) and population origin: only pairs of natural sites (left panel), only pairs of reintroduced sites or reintroduced sites paired with sites from Nordenskiöld Land (i.e. source of reintroduction; middle panel), and reintroduced sites paired with natural, non-source sites from Nordaustlandet, East Svalbard, North Spitsbergen and South Spitsbergen (right panel).

3.3 Ancient DNA: Loss of genetic variation due to overharvesting?

As a pilot study, we extracted reindeer DNA from 14 subfossil bones or antlers that were found on the tundra on Svalbard. Radiocarbon dating analyses indicated that these samples aged 4000-200 years old (Table 6). We analyzed mitochondrial DNA (mtDNA) in these “ancient” samples and compared them with published results from modern DNA samples (Kvie et al. 2016). Based on variation in mtDNA haplotypes, Kvie et al. (2016) determined that reindeer have likely colonized Svalbard from the Eurasian mainland by using Franz Josef Land as a stepping-stone along the way. The authors found 24 distinct haplotypes at one fragment of the mtDNA control region, but only one of these haplotypes was found in their 27 modern samples of Svalbard reindeer. In addition to this single common haplotype in modern samples, we found two unique haplotypes in three of our ancient samples (Table 6). The first unique haplotype was found in two subfossil antlers, one from Barentsøya (1605 years old) and one from North Isfjorden (376 years old). The second unique haplotype was found in a subfossil antler from Prins Karls Forland (368 years old). Reindeer were extirpated due to overharvesting in all three locations. A simple statistical test suggests that the genetic diversity in Svalbard reindeer mtDNA was significantly higher in ancient samples, i.e. before the period of overharvesting, than in modern samples.

We also compared DNA of ancient samples at 10 microsatellite loci with modern samples from the four populations that survived the extensive harvesting in the past (Peeters et al. 2019a). However, amplification of microsatellites proved challenging for ancient DNA and only 4 ancient samples had sufficiently high DNA yield to be genotyped at 8-10 loci. One sample from Barentsøya was heterozygous at a microsatellite locus, including one allele which was not found at this locus in modern samples (Peeters et al. 2019a). Also, analyses of individual genetic heterozygosity indicated that the oldest two samples, one from Barentsøya and one from Gipsdalen north of Isfjorden, had significantly higher genetic diversity than modern samples. The two samples from Wijdefjorden, which dated back to the time when the extensive reindeer harvest was still ongoing (Table 6), had average levels of genetic diversity comparable to modern samples, but suggested a rather mixed genetic signature. Overall, genetic diversity of Svalbard reindeer was likely already low due to a strong bottleneck at the time Svalbard was colonized, but the results from our pilot study suggest that a further loss of genetic diversity was induced by extensive overharvesting.

Table 6. Overview results of “ancient” DNA samples from subfossil antlers or bones with radiocarbon dates Before Present (BP, i.e. before 1950) and standard errors (\pm SE). “mtDNA” indicates the haplotype found (A, B or C, where A is the common haplotype found in modern samples from Kvie et al. (2016)), and “microsat” indicates which samples were successfully analyzed (x) at microsatellite markers for comparison with modern samples from Peeters et al. (2019a).

Region	Location	ID	^{14}C date (BP)	mtDNA	microsat
Barentsøya	Barentsøya SE	MLM80	3605 \pm 15	A	-
Barentsøya	Barentsøya SE	MLM84	420 \pm 15	A	-
Barentsøya	Barentsøya SW	MLM55	395 \pm 15	A	x
Barentsøya	Vossebukta	MB83	1350 \pm 20	A	-
Barentsøya	Vossebukta	MB79	1605 \pm 15	B	-
Edgeøya	Diskobukta	MLM12	1425 \pm 20	A	-
Isfjord North	Blomesletta	MB103	235 \pm 15	A	-
Isfjord North	Gipsdalen	M53	376 \pm 32	B	-
Isfjord North	Gipsdalen	M44	566 \pm 32	A	x
Nordenskiöld Land	Diabas	MLM154	380 \pm 10	A	-
Nordenskiöld Land	Sassendalen	M73	980 \pm 35	A	-
Prins Karls Forland	Forlandsletta	M95	368 \pm 31	C	-
Wijdfjorden	Austfjordnes	R36	175 \pm 10	A	x
Wijdfjorden	Austfjordnes	R20	85 \pm 10	A	x

4. Conclusions and future prospects

This study represents a contrast to the many reindeer and caribou population status assessments reporting recent local or regional declines in abundance (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Uboni et al. 2016). The available evidence shows a strong increase in Svalbard reindeer abundance following the 1925 management actions that banned hunting. Due to both range expansion and increased densities, reindeer now occupy the entire available and original (according to ancient bones) distribution range, more than half of which was free of reindeer for several decades following the protection. Our assessment of total population size gave estimates up to thirteen times higher than the minimum estimates from the late 1950s, and twice as high as an estimate based on opportunistic counts between 1969-2008. Vegetation productivity largely explained local reindeer abundance, but recently recolonized areas appeared to have lower reindeer densities than areas not subject to past extinction. This suggests that recovery from past overharvesting is still ongoing.

At present, the reindeer abundance is estimated to be ca 22000 individuals. Since the probability of extinction is inversely related to the effective population size (Beissinger and McCullough 2002, Lande et al. 2003), and given that high reindeer abundance also reflects a high effective population size, the subspecies is not of conservation concern today. However, this does not necessarily apply at the subpopulation level. Because of the naturally fragmented landscape and non-migratory behaviour, this reindeer subspecies exists in a system of semi-isolated subpopulations characteristic of a metapopulation (Hanski and Simberloff 1997). The largest subpopulations occur in wide 'inland' valleys where reindeer did not suffer from past extinction and are likely the most resilient to environmental stochasticity, such as extreme rain-on-snow and icing events (Hansen et al. 2019). In contrast, populations at the periphery, such as coastal peninsulas previously extirpated by overharvesting, have the lowest abundances (and densities). With global warming, sea-ice loss is now increasing the isolation of such subpopulations through a reduction in available dispersal corridors (Peeters et al. 2019a; see also Post et al. 2013, Jenkins et al. 2016). These coastal semi-isolated areas also have the highest current and expected future frequencies of rain-on-snow and icing events (Peeters et al. 2019b) and, thus, possibly elevated probabilities of local extinction. Although a metapopulation system can have a sustainable dynamic balance between local extinctions and recolonizations (Levins 1970), it took approximately a century for this subspecies to recover from overharvesting, i.e. the source-sink dynamics of the Svalbard reindeer may be too slow to track the speed of future climate change.

These effects of historical overharvest and current climate change on reindeer distribution and abundance have directly or indirectly led to changes in the population genetics, as well. Based on comparison of modern and ancient DNA, we found strong indications that the overharvest caused a (likely irreversible) loss of genetic variation. Compared with other reindeer and caribou, the overall genetic diversity of Svalbard reindeer is naturally very low, especially in the outer distribution range, where we found significant levels of genetic inbreeding. The observed patterns of natural genetic isolation were modified by the signature

of the past harvest-induced extirpations, subsequent reintroductions (to Ny-Ålesund and Daudmannsøyra), and recent lack of sea ice. Because parts of the large genetic differentiation between today's populations are explained by spatial variation in the potential for dispersal across winter sea ice, future sea-ice loss may have huge population-genetic consequences.

Although effects of the past overharvest and regional extirpations can still be observed, our study has demonstrated a successful outcome of the strict harvest control implemented a century ago. However, the results suggest that past (i.e. overharvest) and current (i.e. climate change) anthropogenic stressors may have interactive effects on large-scale ecological and evolutionary processes. These processes are particularly vulnerable in isolated island systems like Svalbard. Negative effects of the rapid winter warming, with more frequent rain-on-snow and icing events, are currently overruled by the effects of longer and warmer summers, but this balance may change in the future. Continued loss of sea ice as a dispersal corridor between islands and across fjords is expected to further increase the genetic isolation and local extirpation risk of the reindeer populations. Such rapid and dramatic climate change effects may eventually threaten the evolutionary potential and persistence of the sub-species and should be accounted for in future management and conservation actions.

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