Research Article

A Century of Conservation: The Ongoing Recovery of Svalbard Reindeer

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ABSTRACT Several caribou and reindeer (*Rangifer tarandus*) populations have experienced recent population declines, often attributed to anthropogenic stressors such as harvesting, landscape fragmentation, and climate change. Svalbard reindeer (*R. t. platyrhynchus*), the wild reindeer subspecies endemic to the high-Arctic Svalbard archipelago, was protected in 1925, after most subpopulations had been eradicated by harvest. Although direct pressure from harvest has ceased, indirect anthropogenic stressors from environmental changes have increased in this climate change hot spot. An assessment of the current distribution and abundance is therefore urgently needed. We combined distance sampling (300 km transects, $n = 489$ reindeer groups) and total counts (1,350 km^2, $n = 1,349$ groups) to estimate the Svalbard reindeer distribution and abundance across its entire range, which we compared with historical data from the literature and radiocarbon-dated bones. Reindeer have now recolonized nearly all non-glaciated land (i.e., areas occupied prior to human presence), and their spatial variation in abundance reflects vegetation productivity. Independent of vegetation productivity, however, recently recolonized areas have lower reindeer densities than areas not subject to past extirpation. This suggests that recovery from past overharvesting is still in progress. These incompletely recovered areas are potential targets for increased monitoring frequency and maintaining strict conservation to follow the Svalbard management goal (i.e., virtually untouched wilderness areas). Because of such ongoing recolonization, possibly combined with vegetation greening effects of recent warming, our status estimate of Svalbard reindeer abundance (22,435 [95% CI = 21,452–23,425]) is more than twice a previous estimate based on opportunistic counts. Thus, although our study demonstrates the successful outcome of strict harvesting control implemented a century ago, current and future population trajectories are likely shaped by climate change. © 2019 The Authors. *Journal of Wildlife Management* Published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS abundance, distance sampling, distribution, *Rangifer tarandus platyrhynchus*, spatial density modeling, subfossil bone, Svalbard reindeer, wildlife monitoring.

Determining the distribution and abundance of species across their entire range is difficult to achieve but important for evaluating conservation status (Yoccoz et al. 2001, Pollock et al. 2002, Jones 2011, Martin et al. 2015). Comparisons of a species' current state in relation to its past extent and future predictions can inform about a species' capability to expand or its vulnerability to extinction (Brown 1984, Acevedo et al. 2011). Over the last century, several deer species have increased in abundance through range

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expansion and density increase, following hunting restrictions, changes in land use, and translocations (Côté et al. 2004, Milner et al. 2006, Putman et al. 2011). In contrast, at higher latitudes, caribou and reindeer (*Rangifer tarandus*) have experienced declines in abundance in parts of their global range, and even some local or regional extirpations (Lorenzen et al. 2011). Anthropogenic factors such as harvesting, landscape fragmentation, and climate change have often been proposed as the main causes of these declines (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Gunn et al. 2011, Uboni et al. 2016). In many cases, the population trends are based on time-series of counts, which are often characterized by poor levels of spatial and temporal replication, without any assessment of uncertainties. This may result in dubious inferences, locally and on a circumpolar scale. Nonetheless, there is little doubt that several

large herds have been severely decimated, with potentially huge socioeconomic and ecosystem implications (Festa-Bianchet et al. 2011).

Arctic wildlife was extensively exploited in the seventeenth to twentieth centuries (Vekhov 1999, Conservation of Arctic Flora and Fauna 2013). As it became clear that many Arctic species were overharvested, they became protected or put under strict management regimes throughout the twentieth century. Effects of climate change and landscape and seascape alterations now represent other, potentially negative stressors (Klein 2005, Post et al. 2013, Laidre et al. 2015). Much of the Arctic has recently experienced an increase in temperature (Intergovernmental Panel on Climate Change [IPCC] 2014) and extreme rain-on-snow events in winter led to population die-offs of some large Arctic ungulate populations (Miller and Gunn 2003, Rennert et al. 2009, Hansen et al. 2013, Forbes et al. 2016). Continued and accurate (i.e., precise and unbiased; Williams et al. 2002) monitoring of the distribution and abundance of reindeer populations is therefore important to guide current management, evaluate past conservation actions, and predict future changes.

On the high-Arctic Svalbard archipelago, the endemic subspecies of wild reindeer, the Svalbard reindeer (*R. t. platyrhynchus*), was overharvested until its protection in 1925 (Wollebæk 1926, Lønø 1959). Hunting has occurred since the seventeenth century, mainly in coastal areas, but it expanded dramatically across the archipelago in the late nineteenth 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 nineteenth century. However, the subsequent high hunting pressure caused local extirpation in parts of the archipelago (Hoel 1916, Wollebæk 1926, Governor of Svalbard 2009). At the time of protection, only 4 metapopulations remained (Lønø 1959). Since then, reports based on opportunistic counts have provided updated estimates of regional reindeer abundance approximately every decade, and recorded new areas of recolonization (Norderhaug 1970, Øritsland 1986, Governor of Svalbard 2009). Abundance records from previous reports can be informative but should be interpreted with care because they lack information on survey design, sampling effort, and estimate uncertainty.

The management goal in Svalbard is that wildlife remain virtually untouched (Governor of Svalbard 2009). Accordingly, recreational reindeer hunting has been strictly regulated since 1983 in central parts of Svalbard and primarily occurs within the management area of Nordenskiöld Land, where approximately 200 reindeer/year are harvested (Stien et al. 2012). Svalbard reindeer live in a predator-free environment (except documented kills by polar bear (*Ursus maritimus*); Derocher et al. 2000) and use relatively small seasonal home ranges (Tyler 1987, Tyler and Øritsland 1989), although displacement is documented in response to poor winter conditions (Stien et al. 2010, Loe et al. 2016). Reindeer habitat use is mainly shaped by the quality and quantity of available forage (Van der Wal et al. 2000, Hansen et al. 2009, Loe et al. 2016). Accordingly, the

proportion of vegetation cover explained local abundance of reindeer monitored by distance sampling and total counts on 2 peninsulas (Le Moullec et al. 2017). Although direct anthropogenic pressure from hunting has virtually ceased, climatic factors have changed (IPCC 2014). In particular, warmer and longer summers cause increased plant biomass (i.e., Arctic greening; Van der Wal and Stien 2014, Vickers et al. 2016), potentially improving the carrying capacity of the system (Albon et al. 2017, Hansen et al. 2019b). Conversely, increasingly frequent rain-on-snow events associated with winter warming affect Svalbard reindeer population growth negatively (Kohler and Aanes 2004, Hansen et al. 2013), though mainly at high population densities (Hansen et al. 2019a) and with different strength across populations (Hansen et al. 2019b). Together these ongoing environmental changes and past conservation actions demand an assessment of Svalbard reindeer responses in terms of distribution and abundance.

Our main objective was to estimate the current Svalbard reindeer distribution and abundance across the archipelago to evaluate the success of the 1925 conservation action and identify the main factors influencing spatial density. We expected that spatial variation in reindeer abundance was positively correlated with gradients in vegetation productivity (Le Moullec et al. 2017) but possibly modified by past overharvest and associated local extirpations. Thus, if recovery from overharvest is still ongoing, this would predict a lower than expected (based on vegetation productivity) reindeer density in previously extirpated areas.

STUDY AREA

The archipelago of Svalbard (76–81°N and 10–34°E, 59,793 km^2; Fig. 1A), Norway, is located in the high-Arctic between the Barents Sea and the Greenland Sea. The principal islands are Spitsbergen, Nordaustlandet, Edgeøya, and Barentsøya. Glaciers cover 61.6% (36,860 km^2) of the land surface, and only 16.1% is vegetated (8,536 km^2; Johansen et al. 2012). The vegetated areas are typically located along the coast and in inland valleys in central Spitsbergen and on Edgeøya, and they are mainly confined to areas below 200 m above sea level (asl). Thus, the study took place from 2013 to 2016 in the lowlands (i.e., <200 m asl) characterized by open landscape, where reindeer predominantly occur in summer. The vegetated landscape is highly fragmented and characterized by peninsulas separated by open water and tidewater glaciers on the coast and high mountains (~1,700 m) with U-shaped valleys inland. The bioclimatic zones of Svalbard comprise polar deserts with plant species such as Svalbard poppy (*Papaver dahlianum*), saxifrages (*Saxifraga* spp.), and drabas (*Draba* spp.); Northern Arctic tundra with polar willow (*Salix polaris*) and purple saxifrage (*Saxifraga oppositifolia*); and Middle Arctic tundra with Arctic bell-heather (*Cassiope tetragona*) on acidic substrate and mountain avens (*Dryas octopetala*) on alkaline substrate (Jónsdóttir 2005). The plant growing season lasts for 1 to 3 months (Jónsdóttir 2005). The dominant terrestrial Svalbard fauna includes resident herbivores (i.e., the Svalbard reindeer and the Svalbard rock
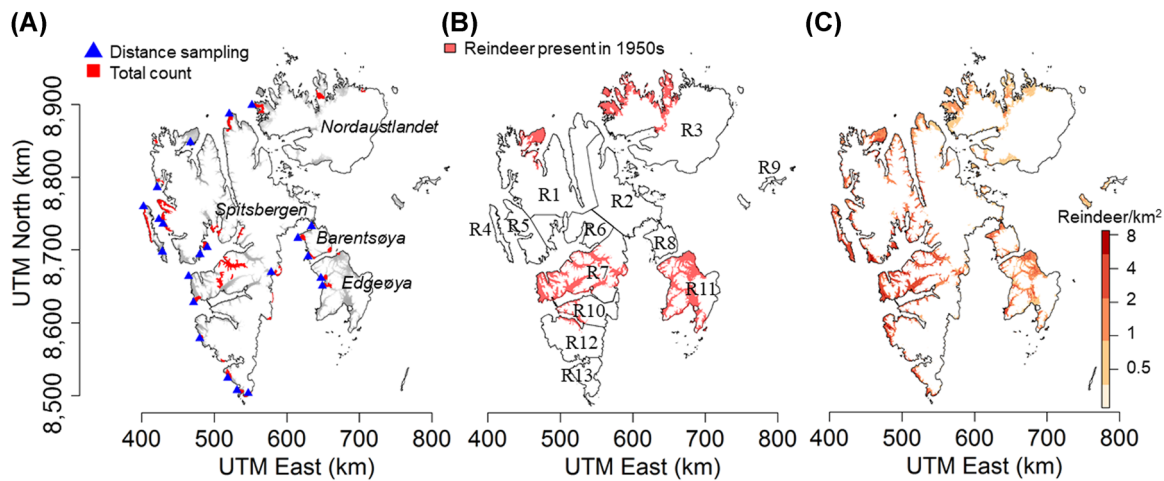
Figure 1. Maps of Svalbard, Norway. A) Overview of the study sites and the methods used for abundance estimation for Svalbard reindeer (2013–2016). The blue triangles, marking distance sampling areas, are shifted 3 km east for visual clarity. B) Svalbard reindeer distribution in the period following protection 1925–1959 (Lønø 1959) and the extent of the reindeer management areas (R1–R13) in Svalbard (black lines). C) Current predicted Svalbard reindeer density obtained using models based on distance sampling.

ptarmigan [*Lagopus muta hyperborean*]), migratory herbivores (i.e., pink-footed goose [*Anser brachyrhynchus*] and barnacle goose [*Branta leucopsis*]), and a main tundra predator and scavenger (i.e., Arctic fox [*Vulpes lagopus*]; Ims et al. 2013). The oldest record of Svalbard reindeer presence was determined from fecal pellets found in peat layers dated to approximately 5,800 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 western and central parts of Svalbard are influenced by the Atlantic warm water current giving an oceanic climate that is milder than in eastern parts. The temperature in Svalbard over the past century (1898–2012) was approximately 4.5°C in summer and −14°C in winter, and has increased with a rate of 1°C and 2.9°C per 100 years in summer and winter, respectively (Nordli et al. 2014). Glaciers in Svalbard have shrunk by approximately 7% over the past 30 years (Nuth et al. 2013), potentially offering more habitat for reindeer, but vascular plant community establishment is slow on these nutrient-poor soils (Hodkinson et al. 2003). Since the discovery of the archipelago in 1596, whaling and other harvesting (∼17–19th century), mining (19–20th century), and tourism (21st century) have been the dominant human activities on the archipelago.

METHODS

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. 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 dated subfossil bones that inform about reindeer presence before hunting.

Reindeer Field Data Collection

We collected field data of Svalbard reindeer abundance in summer (Jul–Aug) 2013–2016. The northwestern part of Spitsbergen was covered by a monitoring campaign in 2013–2014, and sampling sites spread around the rest of Svalbard were covered in 2015–2016. 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 (Fig. 1A), as described in Le Moullec et al. (2017). Monitoring Svalbard reindeer on foot do not require a particular statement of animal care, but all the field work was approved by the Governor of Svalbard (RIS-ID 6618, 10015, 10128, 2372 and 2373).

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. The study was designed to meet the 4 main assumptions outlined by Buckland et al. (2001). First, to ensure animals were distributed independently of transect lines, we randomly drew a latitude (or a longitude) for the first line. To cover the study area, we positioned additional transects in parallel to this random line, 2–3 km apart. Second, reindeer on or close to the transect line were always detected because visibility was good on these open plains. Third, the tameness of Svalbard reindeer helped ensure that we measured the position of a detected single reindeer or cluster (i.e., group) before any animals moved in response to the observer (Reimers et al. 2011). Fourth, we made accurate measurements. We used a rangefinder (Nikon laser 1200S, Tokyo, Japan) to measure the distance and a compass to record the angle from the observer to the animal in the center of the cluster. Additionally, we recorded the coordinates of the observer's position to allow for calculation of the position of the reindeer. When the distance to the animal was outside the rangefinder limits

(∼500 m), we used maps (1:100,000) with the support of a handheld global positioning system (GPS) to pinpoint positions. We conducted surveys in weather with good visibility, and we noted covariates that potentially influenced detection probability at the transect level: sky cover (cloudy, partly cloudy, sunny), wind speed (low: <5 m/s, high: >5 m/s), horizon background (mountain, sea, horizon), observer (4 observers participated and conducted 50, 21, 9, and 6 transects, respectively), and year of sampling. We also extracted terrain ruggedness values along transects (i.e., at the segment level) from a 20×20-m spatial resolution map (uncertainty of 5–10 m).

Total counts.—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 and 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 sampling effort to be equal across the area covered in one day. Although total counts are 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). In some suitable cases, we conducted total counts together with distance sampling. The observer conducting total counts was then always a distance behind the observer conducting distance sampling, to avoid affecting the distance sampling study design. Total count observers could deviate from their route to get the best overview of the landscape for scanning with binoculars. When several observers were involved, they walked routes no more than 1 km apart from each other and communicated by very high frequency (VHF) radio to avoid double counts. We recorded reindeer cluster size and positions on a topographic map (1:100,000).

Subfossil bones and antlers.—Cold arctic environments preserve exposed bones and antlers (Van der Knaap 1989). We collected subfossil bones, including antlers from the areas in which we monitored reindeer abundance, to assess reindeer presence before human arrival in Svalbard. This was documented as being in 1596 when Svalbard was discovered by W. Barents. We typically found the bones lying on the tundra, partially nested into the ground or in cavities. We had all bones ^{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).

Spatial Covariates

We extracted information about 4 covariates from digital maps across the reindeer summer range in Svalbard (i.e., <200 m asl, without glacier and moraines, 11,600 km^2, hereafter referred as Svalbard). 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 (Fig. 1B). Third, we extracted Universal Transverse Mercator [UTM] east to investigate a possible longitudinal gradient in reindeer abundance (ranging from 402,330 to 824,490), and fourth, UTM north to investigate a possible latitudinal gradient (ranging from 8,495,405 to 8,978,525).

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 (further details in Fig. S1, available online in Supporting Information). The NDVI values ranged from 0 to 0.89 in Svalbard (0.29 ± 0.19, mean $\pm$ SE) at peak growing season.

Statistical Analysis

The distance sampling and total count methods allow the true density parameter (λ) to vary depending on environmental predictors (Z_i) associated with pixel i. We fitted models in R version 3.3.1 (R Core Team 2016). We computed the model for distance sampling with the packages Distance (Miller 2014) and dsm (Miller et al. 2016) using the functions ds and dsm, and computed the model for the total count with the package pscl (Zeileis et al. 2008) and the function hurdle (Zuur et al. 2009:261).

Distance sampling.—Before analysis of the reindeer abundance data, we removed the 5% of observations with the longest observed distances from the transect line (Buckland et al. 2001), leading to a maximum observed distance of 908 m (i.e., transect width = 1,816 m). Within this distance range there was no evidence of a correlation between cluster size and detection distance ($r = 0.04$, 95% CI = −0.05–0.13). We divided transects into smaller segments to allow for habitat heterogeneity along the line and extracted covariates at the segment level (Miller et al. 2013). We cut each transect into equal segment lengths, and we determined the number of segments by the ratio between transect length and the initial target length of 1,300 m (rounding down to the nearest integer), resulting in an average segment length of $1,560 \pm 281$ m. Initial segment lengths smaller than 1,300 m showed signs of spatial autocorrelation in residuals (investigations started at 250 m; Table S1, available online in Supporting Information). The choice of segment length did not affect the overall abundance estimates across Svalbard, or estimates of encounter rate significantly (Table S1).

We adopted a 2-stage approach to spatial modeling of the distance sampling data (Miller et al. 2013, Buckland 2015, Antún et al. 2018). We modeled detection and density functions as linear functions of environmental predictors on

the log-link scale (Appendix I, available online in Supporting Information). First, we modeled detection probabilities by fitting a half-normal detection function and hazard rate key function, with covariates of the distance data. We compared models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and chose the detection function that best fit the data to move to the next step. Second, we modeled the density function for the abundance of individuals per segment area in the function dsm when accounting for group size and setting segment length as an offset. We built a quasi-Poisson model including all 4 covariates that potentially influenced reindeer density (i.e., NDVI, past extirpation [factor], UTM east, and UTM north). We then adopted a backward model selection approach where we removed 1 non-significant variable at a time according to its t-statistic and associated P-value. We fitted models using the restricted maximum likelihood (REML) framework. Finally, we investigated the residuals from the selected models for normality, autocorrelation, and plots of linear predictor and fitted values.

Total counts.—We split the study areas covered by total counts into pixels of 240×240 m, matching the resolution of the NDVI map, and allocated animal observations to these pixels. Because the resulting spatial data contained a large number of pixels with no animal observations and some pixels with a high number of animal observations leading to overdispersion, we used a hurdle model (Zuur et al. 2009). We assumed a binomial distribution for the presence of ≥ 1 reindeer in pixel i given a probability of presence (π_i). For pixels with a reindeer present, we modeled the number of animals observed (μ_i) assuming either a zero-truncated Poisson or a negative binomial distribution. The zero-truncated negative binomial distribution with dispersion parameter (θ) gave the best fit to the data. We fit covariates in the model for π_i assuming a logit-link function, and in the model μ_i assuming a log-link function giving:

$$\text{logit}(\pi_i) = \gamma_o + \gamma_1 \cdot Z_i \qquad (1)$$

and

$$\log(\mu_i) = \nu_o + \nu_1 Z_i. \qquad (2)$$

The expected density of reindeer in pixel i is then given as (modified from Zuur et al. 2009):

$$\lambda_{TC.i} = \frac{\pi_i}{1 - P_o} \cdot \mu_i, \qquad (3)$$

where

$$P_o = \frac{\theta}{\mu_i + \theta}. \qquad (4)$$

We performed model selection based on a full model that included all 4 density covariates in the presence-absence (π_i) and the count model (μ_i). We selected the model with least parameters and a ΔAIC < 2.

Predictions and comparison of methods.—We predicted reindeer abundance across their summer range in Svalbard and within each of 13 management areas (Fig. 1B) defined by the Governor's office in Svalbard (Governor of Svalbard 2009) on a prediction grid of 240×240 m. Previous reports used similar spatial delimitations, making comparisons of abundance estimates possible. We also predicted density with variance estimation (Appendix II, available online in Supporting Information) across the covariate gradients (i.e., NDVI from 0 to 1, setting other covariates at their mean). Finally, we computed the difference between total counts and distance sampling abundance estimates and associated 95% confidence intervals as described in Le Moullec et al. (2017). We obtained the overall Svalbard abundance estimate by weighted (i.e., inverse standard error) arithmetic mean estimates from total count and distance sampling data. We obtained the standard error of the estimate by simulation and reported it as a 95% confidence interval.

RESULTS

We found support for the claim of Hoel (1916) that reindeer occupied all non-glaciated lands of Svalbard prior to regional extirpations from overharvesting. We recovered subfossil bones older than documented human presence (1596) from all 10 sampled regions (Table 1 and Table S2, available online in Supporting Information). Since protection in 1925, recolonization of locally extirpated populations happened progressively and in the twenty-first century all the reindeer management areas in Svalbard were re-occupied by reindeer (Table 1). The areas that had viable reindeer populations throughout the twentieth 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 mean population size of 22,435 (95% CI = 21,452–23,425).

The distance sampling surveys resulted in the observation of 489 reindeer clusters (866 individuals, after truncation) along 189 line-segments, corresponding to a covered area of approximately 540 km^2, of which 29% was not subject to past extirpation (Fig. 1). Cluster size was on average 1.77 ± 1.17. The half-normal detection function best fitted the data (Table S3, available online in Supporting Information). Weather was the only covariate that affected detection probabilities (Table S3, available online in Supporting Information). As expected, sunny weather led to higher detectability than a partly cloudy or cloudy sky (Table 2; Fig. 2A). The average detection probability was 0.57 ± 0.02 and 50% of the reindeer clusters were detected at approximately 500 m (Fig. 2A). The NDVI values along segments were on average 0.43 ± 0.14 (min. = 0.07, max. = 0.72; Fig. 2B). The main covariate affecting reindeer spatial density was NDVI (Table S4, available online in Supporting Information; Fig. 2B). In addition, density was lower in the East than in the West for similar values of NDVI (i.e., negative longitudinal gradient; Table 2). Past extirpation was not selected as a covariate influencing density. Accordingly, the distance sampling density function fell between the 2 density functions obtained from total counts

Table 1. 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 (^{14}C dated bones) before documented human presence (1600). Distribution information and opportunistic counts were reported for 1925–1954 presence information by Lønø (1959), 1954–1958 abundance information by Lønø (1959), in 1980–1982 by Øritsland (1986), and 1969–2008 by Governor of Svalbard (2009). We compared abundance estimations from total counts (TC) and distance sampling (DS) methodologies (2013–2016) with their difference and 95% confidence interval. The columns with symbol *n* represent the number of study sites per management area.

Management area	Before 1600	1925–1954	~1959	~1986	~2009	Today DS $\bar{x}$	SE	*n*	Today TC $\bar{x}$	SE	*n*	Difference $\bar{x}$	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 ^{14}C dating.

(see below) in areas with and without past extirpation (Fig. 2B). The estimated abundance across Svalbard based on distance sampling was 21,079 ± 2,983 (Table 1; Fig. 1C; Fig. S2, available online in Supporting Information).

The total count surveys resulted in the observation of 1,349 reindeer clusters (3,898 individuals) in an area of approximately 1,350 km^2, of which 42% was not subject to past extirpations (Fig. 1). The NDVI values within total count survey areas were on average 0.41 ± 0.18 (range = 0.00–0.84). We selected the model with ∆AIC = 0.51 (i.e., least parameters and a ∆AIC < 2; Table S5, available online in Supporting Information), which had a dispersion parameter $\theta = -0.95 \pm 0.21$. As for distance sampling, NDVI was the main covariate explaining variation in reindeer densities using total count surveys (Fig. 2B) and longitude also affected densities (Table 2; Table S5, available online in Supporting Information). However, the

effect of longitude on reindeer abundance was complex, the probability of observing ≥1 reindeer decreased from West to East, whereas the expected number of reindeer present when ≥1 reindeer was observed increased from West to East (Table S6, available online in Supporting Information). Furthermore, in the total count models, the areas where reindeer were known to be present throughout the twentieth century had on average higher estimated reindeer abundances than areas where reindeer were reported to have been extirpated (Table 2). The estimated total reindeer population size (22,615 ± 401) was similar to the estimate obtained from models based on distance sampling (Table 1; Fig. S3, available online in Supporting Information).

DISCUSSION

This study represents a counter example to the many reindeer population status assessments reporting recent local

Table 2. Covariate coefficient estimates of the selected distance sampling and total counts models of monitored Svalbard reindeer, Norway, 2013–2016. Distance sampling modeling was divided into a detection function and a density function both linear on the log-scale. Total counts modeling was divided into a presence-absence function linear on the logit-scale and a count function linear on the log-scale. NDVI = maximum normalized difference vegetation index.

| Model part	Covariate		Coefficient	SE	*P*
Distance sampling					
Detection	Weather	Cloudy	5.84	0.06	
		Mix	6.14	0.11	
		Sunny	6.27	0.12	
Density	Intercept		−12.34	0.79	<0.001
	NDVI		3.15×10^{-3}	0.83×10^{-3}	<0.001
	Longitude		-3.84×10^{-6}	1.69×10^{-6}	0.02
Total counts					
Presence-absence	Intercept		−2.07	0.29	<0.001
	NDVI		$4.44.10 \times 10^{-3}$	0.27×10^{-3}	<0.001
	Longitude		-6.48×10^{-6}	0.57×10^{-6}	<0.001
	Not extirpated		0.67	0.07	<0.001
Count	Intercept		−1.84	0.44	<0.001
	NDVI		1.45×10^{-3}	0.42×10^{-3}	<0.001
	Longitude		2.32×10^{-6}	0.88×10^{-6}	<0.001
	Not extirpated		0.49	0.11	0.01
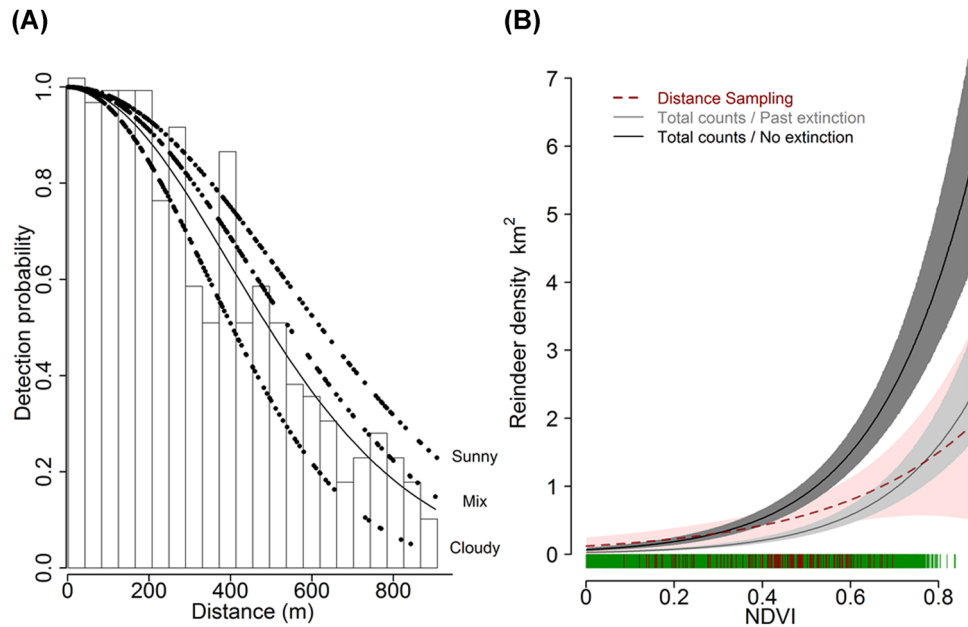
Figure 2. Svalbard reindeer detection and density functions obtained from monitoring programs in Svalbard, Norway (2013–2016). A) The detection function of distance sampling line transects progressively decreases with a half normal rate (full line) until the truncation distance of 908 m. Detectability 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).

or regional declines in abundance (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Uboni et al. 2016). The available evidence shows an increase in Svalbard reindeer abundance following the 1925 management actions that banned hunting. Because of range expansion and increased densities, reindeer now occupy the entire available and original (according to subfossil bones) distribution range (Table 1; Fig. 1), more than half of which was free of reindeer for several decades following protection. Furthermore, our assessment of total population size gave estimates up to 13 times higher than the minimum estimates from the late 1950s, and twice as high as an estimate based on opportunistic counts between 1969–2008 (Table 1). Vegetation productivity largely explained local abundance, but recently recolonized areas appeared to have lower reindeer densities than areas not subject to past extirpations. This suggests that recovery from past overharvesting is still ongoing.

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 and translocated individuals, their sex and age, and feedbacks between biotic and abiotic factors will influence population growth rates. The experimental translocation of 12 reindeer (3 males and 9 females) from central Svalbard to Ny-Ålesund area on the west coast in 1978 provides an example (Aanes et al. 2000). After a century of reindeer absence, the translocation resulted in an immediate exponential population increase, followed by a population

crash in 1994 likely due to the interplay between overgrazing, demography, and extreme weather events (Kohler and Aanes 2004, Hansen et al. 2007). Subsequently, population size stabilized in the early 2000s (Hansen et al. 2019b). The first known dispersal events to neighboring peninsulas occurred 16 years after the translocation event. This implies that regional recovery in this fragmented landscape takes longer than what was observed locally in the Ny-Ålesund area, which is also expected given the highly sedentary behavior of Svalbard reindeer (Tyler 1987, Côté et al. 2002). We could expect that similar recovery trajectories for naturally recolonized populations across Svalbard have probably delayed the full recolonization of the archipelago into the twenty-first century.

Distance sampling and total counts methods led to 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 because 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 extirpation history on reindeer abundance. A main reason for this discrepancy was that landscapes suited for distance sampling methodology (i.e., wide open plains such as elevated beaches) were also the areas accessible by hunting expeditions. Therefore, most of the line transects were located in regions with past extirpations, 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 extirpation or no extirpation (Fig. 2B). This resulted in a tendency for distance sampling to underestimate reindeer abundance in non-extirpated regions, and *vice versa* in regions where reindeer had been extirpated, when compared to the estimates from total counts. Two of the non-extirpated regions (Nordenskiöld Land and Edgeøya) are characterized by inland valleys (suitable for total counts) with the highest reindeer abundance. The underestimation by distance sampling in these 2 regions (only significantly different from total counts estimates in Nordenskiöld Land; Table 1) explained most of the difference in the overall Svalbard abundance estimates across methodologies. Furthermore, the variance estimation differed between the 2 methodologies, with higher precision for total counts than distance sampling estimates. Distance sampling models account for uncertainties due to detection and density errors, whereas total counts models assume no detection errors, and thus less uncertainty (Appendix II). We also had a sample size that was 2.5 times greater in total counts than distance sampling methodologies.

Svalbard reindeer carrying capacity is expected to increase as the climate warms and the vegetation is gradually greening (Albon et al. 2017). The climate gradient towards the East, currently characterized by a relatively cold climate and short growing seasons (Nordli et al. 2014, Macias-Fauria et al. 2017, Pedersen et al. 2017), likely explains the associated negative gradient in reindeer density. Even with similar NDVI values at the peak of the growing season, the carrying capacity may be lower towards the East because of a longer snow-cover season. We also suspect that the colder climate to 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 to the East, as indicated by the total counts model, may also be due to such differences in the spatial distribution of high-quality forage in the colder East. On the east coast, however, the retreat of the sea ice in spring has on average been 2 weeks earlier per decade since 1979 (Laidre 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 (Pedersen et al. 2017).

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 recolonized 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 grazing, trampling, and increased fertilization 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 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 implies on average more numerous and more widespread carcasses on the tundra, which can improve the carrying capacity of Arctic foxes. This may have effects on reproduction success of ground-nesting birds, including geese (Fuglei et al. 2003), through increased predation on eggs and juveniles. Unraveling the implications of such potential trophic cascades (Ims et al. 2007) in response to changing ungulate abundance requires continuous efforts in ecosystem monitoring (Côté et al. 2004, Ims et al. 2013).

Following large-scale regional extirpations due to over-harvesting, the endemic Svalbard reindeer now occupies its entire historical range across Svalbard. At a global level, the abundances of the 12 reindeer subspecies found throughout the Arctic today appear to have declined, and the species has been listed as vulnerable (i.e., about 40% decline over the past 10–30 yr) by the International Union for Conservation of Nature (Gunn 2016). Large uncertainties underlie the observed trend, mainly because of a lack of spatiotemporal replication in the monitoring and an absence of assessment of precision associated with population counts. For some populations, however, the evidence for a decline is strong (Festa-Bianchet et al. 2011). Our study is an example of the opposite trend pattern (Hansen et al. 2019*b*). It highlights the importance of spatiotemporal heterogeneity in ecological factors and their responses across scales and, thereby, the need for proper spatial and temporal replication to capture heterogeneity in the dynamics, within and among subspecies.

At present, the abundance of the Svalbard reindeer subspecies is estimated to be approximately 22,000 individuals, twice the size of previous estimates based on opportunistic counts (Governor of Svalbard 2009). Because 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. This does not necessarily apply at the subpopulation level. Because of the naturally fragmented landscape and non-migratory behavior, 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 extirpations and are likely the most resilient to stochastic events. In contrast, populations at the periphery, inhabiting coastal peninsula previously extirpated by overharvesting, have the lowest abundances. With global warming, sea-ice loss is now increasing the isolation of such subpopulations through a reduction in available dispersal corridors (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. 2019) and, thus, possibly elevated probabilities of local extirpation. Although a metapopulation system can have a

sustainable dynamic balance between local extirpations and recolonizations (Levins 1970), bearing in mind that it took approximately a century for the subspecies to recover from overharvesting, the source-sink dynamics of the Svalbard reindeer may be too slow to track the speed of future climate change.

MANAGEMENT IMPLICATIONS

Because the endemic subspecies of wild Svalbard reindeer has been heavily overharvested and extirpated across large parts of its original range, this range-wide assessment of its current distribution and abundance represents an essential tool for developing adaptive management and conservation plans. In Svalbard, the overall environmental management goal is to conserve wilderness areas, keeping wildlife populations intact in virtually untouched ecosystems. Accordingly, an implication of the documented reindeer presence across the entire archipelago prior to human presence is that management should conserve all sub-populations across Svalbard. The extensive spatial replication of this study identifies areas with incomplete recovery as potential targets for increased monitoring frequency and specific conservation, such as maintaining strict harvest regulations. Furthermore, in such a slowly recolonizing subspecies inhabiting a patchy environment with substantial dispersal barriers, currently increasing because of sea-ice loss, particular attention should be paid to conservation of physically and genetically isolated subpopulations.

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DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: DOI: 10.5061/dryad.7351kt1 (Le Moullec, Pedersen, Stien, Rosvold, & Hansen, 2019).

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