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Long-term population decline of a genetically homogeneous continental-wide top Arctic predator

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Genetic analysis can provide valuable information for conservation programmes by unravelling the demographic trajectory of populations, estimating effective population size or inferring genetic differentiation between populations. Here, we investigated the genetic differentiation within Snowy Owls *Bubo scandiacus* in North America, a species identified as vulnerable by the IUCN, to (1) quantify connectivity among wintering areas, (2) evaluate current genetic diversity and effective population size, and (3) infer changes in the historical effective population size changes from the last millennia to the recent past. The Snowy Owl, a highly mobile top predator, breeds across the Arctic tundra, a region especially sensitive to current climate change. Using single-nucleotide polymorphism (SNP)-based analyses on Snowy Owls sampled across the North American non-breeding range, we found an absence of genetic differentiation among individuals located up to 4650 km apart. Our results suggest high genetic intermixing and effective dispersal at the continental scale despite documented philopatry to non-breeding sites in winter. Reconstructing the population demographic indicated that North American Snowy Owls have been steadily declining since the Last Glacial Maximum *c.* 20 000 years ago, and concurrently with global increases in temperature. Conservation programmes should now consider North American Snowy Owls a single, genetically homogeneous continental-wide population which is probably sensitive to the long-term global warming occurring since the Last Glacial Maximum.

Keywords: *Bubo scandiacus*, conservation, effective population size, genetic structure, population reconstruction, single-nucleotide polymorphism, Snowy Owl.

INTRODUCTION

Natural ecosystems are currently changing at an unpreceded rate as a consequence of global climate change (IPCC, 2018; Taylor *et al.* 2020). These

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changes are particularly apparent in the Arctic, where climate warming is estimated to be three times as fast as the global average (ACIA 2004, Box *et al.* 2016, Meredith *et al.* 2020). Species that live in the Arctic are therefore facing a variety of changes and challenges (Gilg *et al.* 2012) and may respond by shifting their geographical ranges, adjusting behaviour or phenotypes, or adapting to the new local conditions (Parmesan 2006, Brown *et al.* 2019, Kelly 2019). In a scenario where environments are changing quickly and in complex ways, genetic information may be an efficient tool to inform conservation and management programmes (Schwartz *et al.* 2007, Hohenlohe *et al.* 2021, Hoban *et al.* 2021a). Understanding genetic structure allows the dispersal of individuals and hence connectivity among populations to be inferred. The genetic structure of populations is also important for wildlife conservation because it provides a baseline of the geographical scale at which programmes should be implemented and helps to define populations and management units (Fraser & Bernatchez 2001, Funk *et al.* 2012, Yannic, St-Laurent, *et al.* 2016). Furthermore, genetic tools provide key information on the current effective population size of populations (an essential parameter for monitoring vital rate; Hoban *et al.* 2013, 2021b), are useful when calculating the loss of diversity due to inbreeding or intraspecific hybridization, and help predict the ability of populations to persist and adapt to new environmental conditions (Hoffmann & Sgrò 2011). In addition, the long-term demographic trajectory of a species may also be retrieved from genetic data (Cristofari *et al.* 2018, Cole *et al.* 2019, Cleary *et al.* 2021), which can help us to understand how species have responded to past major climatic and environmental changes. Thus, understanding, predicting and managing biodiversity responses to rapid climate change demands a full consideration of the genetic differentiation within a species, an assessment of the species' evolutionary potential and knowledge of demographic trends.

The Snowy Owl *Bubo scandiacus*, declining according to the IUCN (BirdLife International 2020), provides a case study where conservation actions may be informed and refined using genetic information. This owl is a highly mobile top predator which breeds exclusively on the Arctic tundra (Holt *et al.* 2020). In Canada, Snowy Owls are declining at an estimated rate of −0.03 to −2.85% per year, depending on the region (Christmas bird counts; Meehan *et al.* 2018). Using very different estimation and extrapolation methods, the Nearctic Snowy Owl breeding population was first estimated at *c.* 290 000 individuals (Rich *et al.* 2004) and then more recently at *c.* 28 000 mature individuals (Potapov & Sale 2012). Both estimates are, however, probably inaccurate because they are not based on actual continental-wide surveys (Fuller *et al.* 2003, Therrien *et al.* 2014, Holt *et al.* 2020).

Currently, there is little genetic information on Snowy Owl populations. A previous study based on mitochondrial DNA (mtDNA) concluded that the phylogeographical differentiation across the geographical range of the species is low, suggesting one global panmictic population (Marthinsen *et al.* 2009). These authors estimated the global species effective population size (*Ne*) at *c.* 14 000 individuals. This estimate, derived from mtDNA, corresponds to the female *Ne* and does not equate to the whole census population size as it is considered by IUCN (BirdLife International 2020). Indeed, not only is *Ne* not a direct proxy for census population size (e.g. Ferchaud *et al.* 2016), this estimate disregards the number of breeding males or the variance in reproductive success among individuals (Storz *et al.* 2001, Wang *et al.* 2016). Therefore, further research using genome-wide nuclear data would provide a better understanding of the genetic structure of the population and a more accurate estimate of the current effective population size of Snowy Owls.

Snowy Owls exhibit a diversity of movement strategies throughout the year (McCabe *et al.* 2021). During the non-breeding season, individuals regularly overwinter in the Canadian Prairies and the American Great Plains (Chang & Wiebe 2018), and throughout the entire temperate regions of North America during irruption years (Kerlinger & Lein 1988, Robillard *et al.* 2016, Therrien *et al.* 2017, Holt *et al.* 2020). Conversely, some individuals stay in the Arctic throughout winter (Therrien *et al.* 2011, Robillard *et al.* 2018). Snowy Owls from the central regions of North America appear to follow similar and constant migration routes from breeding to winter areas (Curk *et al.* 2020, K. L. Wiebe pers. comm.) and other studies have concluded there is some site fidelity to wintering areas by Snowy Owls (Therrien *et al.* 2011, Robillard *et al.* 2018). In contrast, individuals from the eastern part of the North American continent have non-regular and unpredictable movement patterns (Therrien *et al.* 2014, Robillard *et al.* 2018). In summer, there is evidence that Snowy Owls use breeding sites far apart in consecutive years, e.g. 725 km on average, up to 2224 km, for individuals in eastern Canada (Therrien *et al.* 2014) and 1088 km for individuals in northern Alaska (Fuller *et al.* 2003), suggesting a lack of breeding site fidelity for the species (Therrien *et al.* 2014, Doyle *et al.* 2017, Holt *et al.* 2020). The large-scale movements of the species among breeding and non-breeding seasons suggest there could be widespread connectivity among populations. Thus, because Snowy Owls in different parts of their geographical range exhibit both regular and predictable migratory movements and also large-scale unpredictable movements, our primary objective was to study how such movements affect the overall genetic structure of the species at a continental scale.

Using single-nucleotide polymorphism (SNP) data, we specifically tested whether the large dispersal capacity of the species resulted in a high degree of genetic mixing or whether, on a continental scale within North America, the owls showed sufficient wintering site fidelity and non-random migration patterns to exhibit population structure. In a conservation context, we also attempted to estimate the current effective population size (*Ne*) of the species in North America. Our last objective was to investigate the long-term population trajectory of Snowy Owls in North America since the Last Glacial Maximum (~ 21 000 years ago) and beyond. Understanding how past shifts in climate may have affected population size might provide insight into the resilience of wildlife to climate change in the near future. Past climatic fluctuations deeply affect long-term (historical) effective population size for Arctic terrestrial (Prost *et al.* 2010, Lorenzen *et al.* 2011, Yannic *et al.* 2014) and marine species (Louis *et al.* 2020, Cleary *et al.* 2021), but this has never been explored for Snowy Owls, an important species which structures the Arctic trophic network (Legagneux *et al.* 2012, Gauthier *et al.* 2013).

METHODS

Sample collection

We used feathers (n = 74), blood (n = 2) and tissue (liver (n = 48), muscle (n = 26)) from Snowy Owls collected via live-trapping or carcass collection (brought to rehabilitation centres, government agencies and veterinary laboratories). Sample collection covered most of the southern non-breeding region in North America, including British Columbia (n = 50), Saskatchewan (n = 29), Minnesota (n = 3), Ontario (n = 1), Wisconsin (n = 9), Michigan (n = 16), Maryland (n = 3), Pennsylvania (n = 2), New York (n = 34), Québec (Nunavik; n = 1), Nova Scotia (n = 1) and Prince Edward Island (n = 1; Fig. 1, Table 1, Supporting Information Table S1). Sampling spanned a distance of 4650 km. We collected samples during winter between 2012 and 2018 (except for two samples that were collected in 2007 and 2008). For each individual, we assessed sex and age-class (first year or adult) according to morphological and moult measurements (Solheim 2012). The spatial distribution of the samples was slightly clustered into four groups (i.e. wintering areas) according to longitude (see Fig. 1): West (W: British Columbia); Central (C: Saskatchewan); Great Lakes areas (GL: Michigan, Wisconsin, Ontario and Maryland) and East (E), which included all other individuals (including the one from Nunavik; Fig. 1).

DNA extraction

We used Qiagen DNeasy Blood and Tissue kits (Qiagen, Inc., Valencia, CA, USA) to extract genomic DNA following the manufacturer's instructions and assessed DNA quality and checked for DNA degradation on agarose gels. We quantified DNA concentration for each sample using the QuantiFluor dsDNA System kit (Promega), using samples with a minimum DNA concentration of 3.20 ng/μL after extraction for subsequent double-digested RAD sequencing (ddRADSeq) library preparation.

ddRADSeq library construction and sequencing

We built four ddRADSeq libraries from the Snowy Owl genomic DNA following a modified version of the protocol in Peterson *et al.* (2012) and detailed in Gagnon *et al.* (2019). We randomized the individuals for each wintering area in each library. The Genomic DNA (100 ng) was digested using the enzymes *Sbf*I and *Msp*I and fragments selected between 300 and 500 bp using the Blue-Pippin size-selection system (Sage Science). To

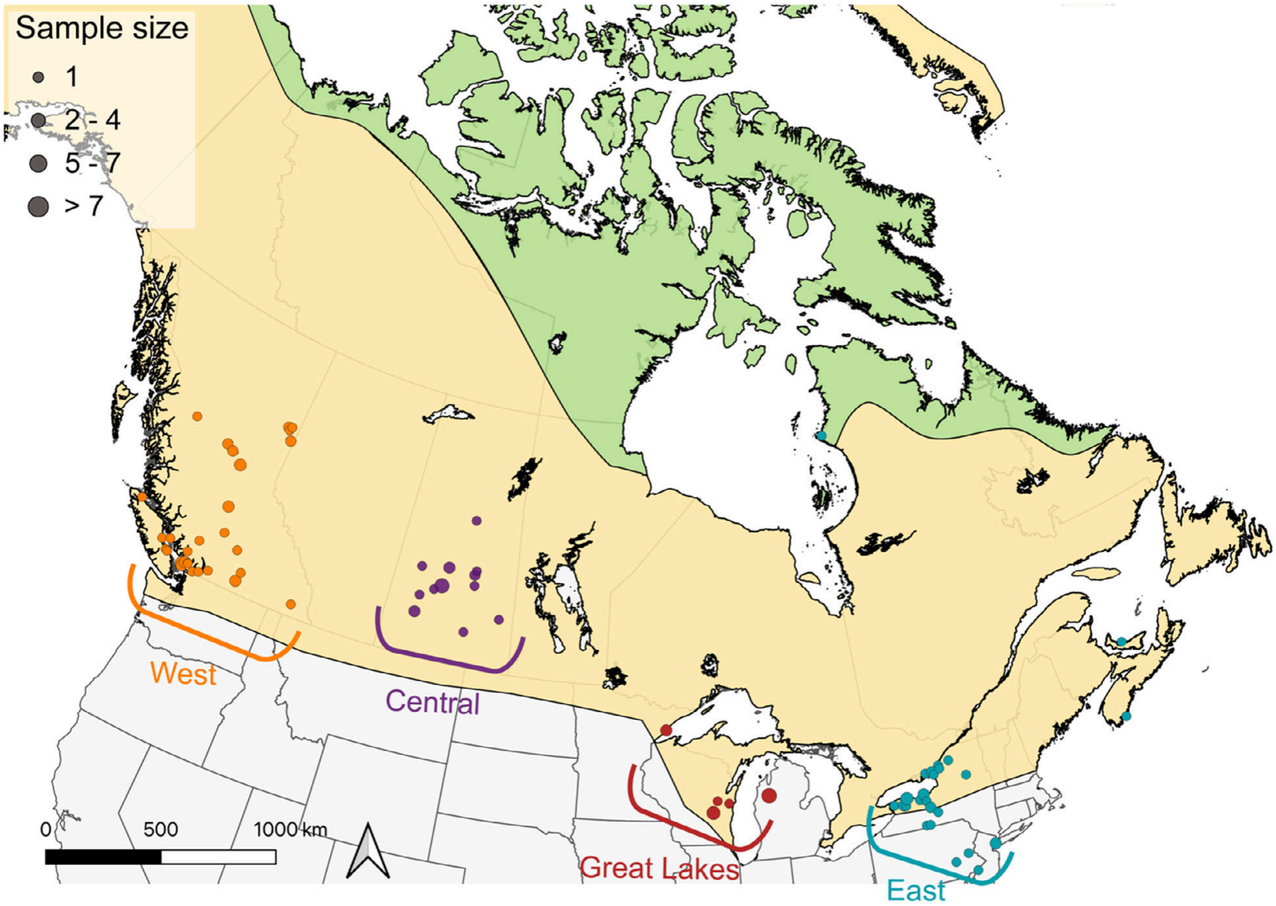


Figure 1. Sampling sites of wintering Snowy Owls (n = 150) collected during November–March between 2007 and 2018. Green areas represent the geographical year-round range and yellow areas represent the non-breeding range of the species according to BirdLife International (2020). [Colour figure can be viewed at wileyonlinelibrary.com]

control for library quality and consistency, we replicated 15.2% of our samples (n = 28) following the recommendations of Mastretta-Yanes *et al.* (2015). We included 47 samples per library including replicates and a negative control. The four libraries were then sequenced on two full lanes (two libraries per lane) of a paired-end (2 × 125 bp) Illumina Hi-Seq 2500 (Fasteris SA, Switzerland).

Table 1. Sampling distribution of Snowy Owls by sex or age for each wintering area in North America between 2007 and 2018.

	Wintering area				
	West	Central	Great Lakes	East	Total
Sex					
Male	24	14	13	18	69
Female	25	14	9	24	72
Unknown	1	1	5	0	7
Age					
Adult	28	5	13	25	71
First year	20	24	12	15	71
Unknown	2	0	4	2	8
Total	50	29	29	42	150

ddRADSeq data processing

We used Stacks 1.44 (Catchen *et al.* 2011, 2013) to demultiplex data, build a *de novo* SNP catalogue and call genotypes. Following Mastretta-Yanes *et al.* (2015), we tested different sets of Stacks core parameters (ustack −m (2 to 6), −M (2 to 6), −max_locus_stacks (2 to 6) and cstack −n (0 to 5); Supporting Information Figs S1 and S2) by varying one parameter at a time while holding the others at their default values. We then selected the set of parameters that minimized error rates between replicates (n = 28 pairs) and maximized the amount of data recovered. The optimal values were: −m (5), −M (2), −max_locus_stacks (3) and −n (2; error rates for each set of parameters are presented in Figs. S1 and S2). To produce the final dataset, we ran Stacks with all parameters set to their optimal values. We performed the next filtering steps in R 3.6.2 (R Core Team 2021) from the original VCF file obtained from Stacks and by keeping only loci that were typed for at least 85% of samples and only samples that were typed for at least 80% of loci. We then used the *dartR* (Gruber *et al.* 2018) and *Radiator* (Gosselin *et al.* 2017) packages in R and PDGspider (Lischer & Excoffier 2012) to convert SNP VCF files to other formats (e.g. genlight; Jombart 2008).

Population genetic structure, genetic distance and isolation-by-distance

We used complementary analyses to quantify population genetic structure. Unless mentioned, all analyses were in R 3.6.2 (R Core Team 2021). We first used principal component analysis (PCA), considering the *a priori* defined wintering regions with the function *glPCA* using the package Adegenet 2.1.1 (Jombart 2008). Next, to compute pairwise F_{ST} among regions according to Weir and Cockerham (1984), we used *gl.fst.pop* in the *dartR* package (Gruber *et al.* 2018; see Supporting Information Appendix S1). Also, we performed a discriminant analysis of principal components (DAPC; Jombart *et al.* 2010; also implemented in the package Adegenet (Jombart 2008)) to infer the number of genetic clusters that best fit our data. In addition, we used a maximum likelihood approach using Admixture 1.3 software (Alexander *et al.* 2009) to estimate the number of populations underlying the genetic dataset based on individual relatedness without our *a priori* wintering regions. Finally, we tested for isolation-by-distance at the individual level using the natural logarithm of Euclidean distance and relatedness (i.e. *beta*, according to Weir & Goudet 2017) distance matrices between each pair of individuals. An extended description of the methods is provided in Appendix S1.

Descriptive genetic diversity

We calculated the observed heterozygosity (*Ho*) and the expected heterozygosity (*He*) for each locus using the function *gl.Ho* and *gl.Hs* in the *dartR* (Gruber *et al.* 2018) package in R 3.6.2 (R Core Team 2021). We also computed *Ho* and *Hs* for each wintering area. To test whether a significant difference in *Hs* among wintering areas can exist, we performed a linear mixed model (LMM) implemented in the lme4 R package (Bates *et al.* 2015) with wintering area as the fixed effect and the locus ID as a random effect. We verified linearity assumptions of model residuals and then computed a post-hoc Tukey test to contrast wintering areas.

Contemporary effective population size (*Ne*)

We used NeEstimator 2.1 (Do *et al.* 2014) to estimate the contemporary effective population size (*Ne*) of Snowy Owls in North America. We used the linkage disequilibrium (LD) method with a random mating model. Following Waples and Do (2010), we excluded rare alleles (i.e. those SNPs with a minor allele frequency ≤ 0.05) to avoid estimation bias.

Population trajectory reconstruction

We reconstructed the population history of Snowy Owls using the Stairway Plot 2 method (Liu & Fu 2020). The Stairway Plot infers detailed population demographic history using the site frequency spectrum (SFS: Liu & Fu 2015) from DNA sequence data. This method uses a flexible, multi-epoch model as used in the Skyline Plot method (Strimmer & Pybus 2001, Navascués *et al.* 2017) and based on the expected composite likelihood of a given SNP frequency spectrum (SFS). This provides information on the history of population effective size (*Ne*) over time until the recent past. We estimated the folded SFS using the VCF file and a Python script, *EasySFS* (https://github.com/isaacovercast/easySFS; Covercast 2017) and included the total number of observed nucleic sites (both polymorphic and monomorphic sites). The 'two-epoch' model, with 67% of sites for training and 200 bootstraps, was used as recommended. We tested four different numbers of breaking points (i.e. to define the boundaries of each epoch; Liu & Fu 2020) as described in Liu and Fu (2015), i.e. 74, 149, 223 and 298. We assumed a mutation rate of 1.9×10^{-9}, which is a recent estimate for birds in general (Zhang *et al.* 2014), and a generation time of 7.93 years (a generally accepted value; BirdLife International 2020). However, because we have no information on the mutation rate in Snowy Owls and because there is also some uncertainty over generation times in the literature (e.g. 4.7 years (Heggøy *et al.* 2017) vs. 7.93 years (BirdLife International 2020)), we ran sensitivity analyses using various mutation rates retrieved from the literature on birds (e.g. $\mu = 2.3 \times 10^{-9}$, Smeds *et al.* 2016; $\mu = 1.9 \times 10^{-9}$, Nam *et al.* 2010, Zhang *et al.* 2014) and ranges of generation times. We also added the major past glaciation events to the resulting Stairway Plot (Clark *et al.* 2009, 2012, Mann *et al.* 2009).

RESULTS

SNP genotyping

After the *de novo* SNP calling and filtering procedure, the dataset encompassed 13 793 SNPs distributed over 5987 loci. We only kept the SNPs that had less than 15% of missing data, i.e. that were typed for at least 85% of birds. Individuals scored on average 5767 SNPs ± 198 sd, resulting in 3.7% missing data in the genotype matrix. Error rates estimated on the 13 793 SNPs obtained from replicated samples were 0.004 ± 0.003 and dropped to 0.003 ± 0.002 when considering single SNP per loci (n = 5987 SNPs). For subsequent analyses, we only considered a single SNP per locus, for a final dataset consisting of 5987 SNPs genotyped on 150 Snowy Owl individuals.

Population genetic structure, genetic distance and isolation-by-distance

Results from the PCA (Fig. 2a), the DACP (Supporting Information Fig. S3) and Admixture (Fig. 2c; Supporting Information Fig. S4) were congruent and all revealed a single genetic cluster (K = 1). When Admixture was conducted separately on each dataset of yearling owls vs. the adult owls, both also revealed a single genetic cluster (K = 1). Pairwise F_{ST} between wintering areas averaged 7 e^{-5} ± 3 e^{-4} (Fig. 2b). However, pairwise F_{ST} analysis on adults from W and E, the two most distant wintering areas, revealed a small but significant genetic differentiation ($F_{ST} = 0.002$; $P = 0.017$; Fig. 1, Supporting Information Table S2), which also held for the adult females between W and E ($F_{ST} = 0.002$; $P = 0.006$; Table S2) and the adult females between W and GL ($F_{ST} = 0.001$; $P = 0.042$; Table S2). There was also a low genetic differentiation between males from W and C ($F_{ST} = 0.002$; $P = 0.042$; Table S2). Global F_{IS} was 0.0332 ± 0.2431. Mean F_{IS} values were low to moderate (but all significantly different from zero; all Wilcoxon signed rank tests, $P < 0.001$) and were similar within wintering areas: W = 0.037 ± 0.19; C = 0.038 ± 0.21; GL = 0.048 ± 0.22; E = 0.040 ± 0.20.

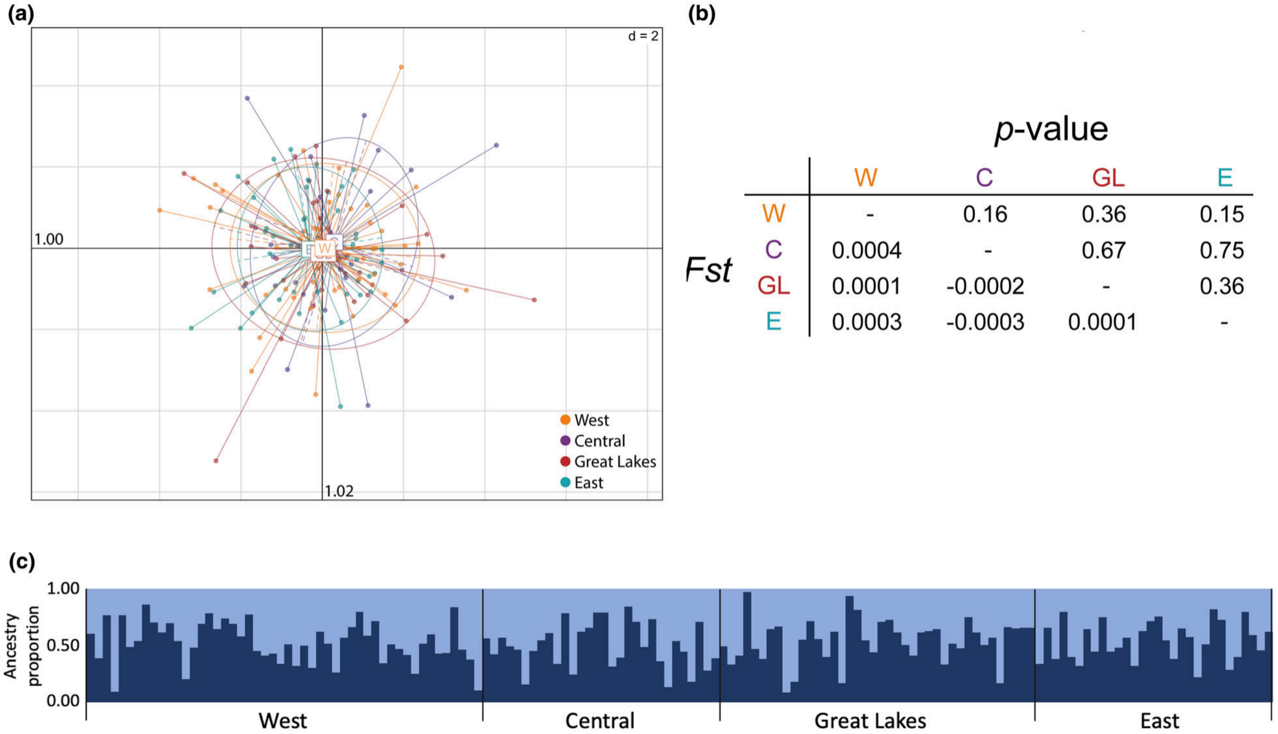
On average, genetic relatedness was 0.017 ± 0.014 (Supporting Information Fig. S6), and the maximum value between two individuals was 0.093, one sampled in the E wintering area (New York) and one in the GL area (Michigan; 2763 km apart). The minimum value between the two individuals was 1.98×10^{-6}, one from the E (New York) and one from the GL areas (Wisconsin; 2457 km apart). Genetic distance was similar within and between wintering areas (Fig. S6) and between adults and first year birds (Fig. S6). We did not find any pattern of isolation-by-distance (at a scale of 4650 km) either at the individual level (i.e. relatedness vs. ln-transformed geographical distance: Mantel's $r = 0.005$, $P = 0.39$ and LMM slope = –8.87 e^{-5}, 95% CI –1.86 e^{-4} to 9.30 e^{-6}) or at the population level (i.e. $F_{ST}/(1–F_{ST})$ vs. ln-transformed geographical distance: Mantel's $r = –0.258$, $P = 0.70$ and LMM; slope = –3.69 e^{-4}, 95% CI –6.8 e^{-4} to 4.75 e^{-5}).

Descriptive genetic diversity

At the locus scale, the average observed heterozygosity (*Ho*) per locus was 0.142 ± 0.143 sd and the expected heterozygosity per locus (*He*) was 0.148 ± 0.140. At the wintering area scale, we found a significant decrease of gene diversity from West to East (*Hs*; slope = –1.847 e^{-2}, se = 5.664 e^{-3}, 95% CI –0.0296 to –0.00737; Supporting Information Fig. S5).

Current effective population size (*Ne*)

Using the LD method with the lowest allele frequency set at 0.05, the current effective population size (contemporary *Ne*) for the North American population of Snowy Owls was estimated to be 15 792 individuals (95% CI: 10 850–



p-value

Fst	W	C	GL	E
W	-	0.16	0.36	0.15
C	0.0004	-	0.67	0.75
GL	0.0001	-0.0002	-	0.36
E	0.0003	-0.0003	0.0001	-

Figure 2. (a) PCA of all the individuals according to their wintering areas. The number of retained PCs was 100. The number of dimensions (d) of the PCA is 2. Colour codes: orange = West (W, British Columbia, $n = 50$), purple = Central (SK, Saskatchewan, $n = 29$), red = Great Lakes (GL, $n = 29$) and green = East (E, $n = 42$). The boxes with the letter are the centroid of each group. (b) Pairwise F_{ST} values among wintering areas (W-West, C-Central, GL-Great Lakes, E-East) and the associated *P*-values are displayed in the table. (c) CLUMPAK results for $K = 2$ from 10 runs of Admixture, without any prior allowing for the number of clusters (*K*) in the model to vary from 1 to 10. We generated random seeds for each run ($\beta < 0.0001$). [Colour figure can be viewed at wileyonlinelibrary.com]

28 950). Excluding singleton alleles only, the *Ne* value was 15 401 (95% CI: 12 782–19 366).

Population trajectory reconstruction

The Stairway Plot approach showed that the coalescence *Ne* of Snowy Owls in North America has declined steadily in recent times (Fig. 3). There was an expansion of *Ne* around 100 000 years ago, followed by a long period of stability. Coalescence *Ne* then started to decline around 6000 years ago, which coincides with an acceleration of deglaciation in North America between 6000 and 8000 years ago. This is also approximately timed with the beginning of the Holocene period, which was characterized by global temperature increases. During the Little Ice Age period (*c*. 1400–1700 CE), the rate of decline in coalescence *Ne* apparently slowed down. The decline started to speed up again around 200 years ago, approximately at the onset of the worldwide retreat of glaciers and the acceleration of air temperature warming (Fig. 3). We cannot infer population changes for the last 100 years because of the uncertainties in the final steps of the Stairway Plot method (Liu & Fu 2015, 2020). The sensitivity analysis showed that despite using different values for mutation rate or generation time, all demography simulations resulted in a declining trend (Supporting Information Fig. S7).

DISCUSSION

Continent-scale genetic homogeneity

Using recombining DNA markers, our results all indicate that populations at the continental scale are genetically homogeneous in North America. Two non-mutually exclusive hypotheses could explain the absence of genetic differentiation on a 4500-km scale: breeding dispersal and juvenile (natal) dispersal. Irrespective of their wintering areas, if owls disperse widely during the prebreeding period or between successive reproduction events (i.e. breeding dispersal; Clobert *et al.* 2012), individuals from different wintering areas may come into contact, mate and breed together in the high Arctic. There is some evidence that Snowy Owls have low breeding site fidelity and that long distances may separate breeding sites in consecutive years (Fuller *et al.* 2003, Therrien *et al.* 2014, Doyle *et al.* 2017, Holt *et al.* 2020). Thus, mating is probably panmictic and not related to the winter area of birds.

A second possibility is that high juvenile dispersal from the site of birth to the site of reproduction is driving genetic mixing. Natal dispersal distance is typically much larger than breeding dispersal in many birds (Clobert *et al.* 2012) and probably plays a role in genetic intermixing in other owl species such as the Northern Spotted Owl *Strix occidentalis caurina* (Miller *et al.* 2018) but nothing is known about natal dispersal in Snowy Owls. This hypothesis could explain the absence of genetic differentiation if juveniles are dispersing among wintering areas during the first years of life, i.e. before their first reproduction. Alternatively, genetic homogenization could occur as a result of periodic winter irruptions when, after a summer with high productivity linked to abundant lemming prey in the Arctic, large numbers of juveniles travel farther south than average during their first winter (Kerlinger & Lein 1988, Potapov & Sale 2012, Holt *et al.* 2020). High gene flow is probably facilitated by the high mobility and nomadic behaviour of the species, allowing breeding dispersal and natal dispersal or a combination of both at long distance (Yannic, Yearsley, *et al.* 2016).

The pairwise F_{ST} values among winter areas of Snowy Owls (ranging from −0.0003 to 0.0004) are low compared with the range of values based on SNPs from other raptor species. It is a challenge to compare differentiation between species as the scale of the study and the ecology of the species varied. However, Gousy-Leblanc *et al.* (2021) recently reviewed genetic differentiation within raptors according to the scale of the study and reported values for four species based

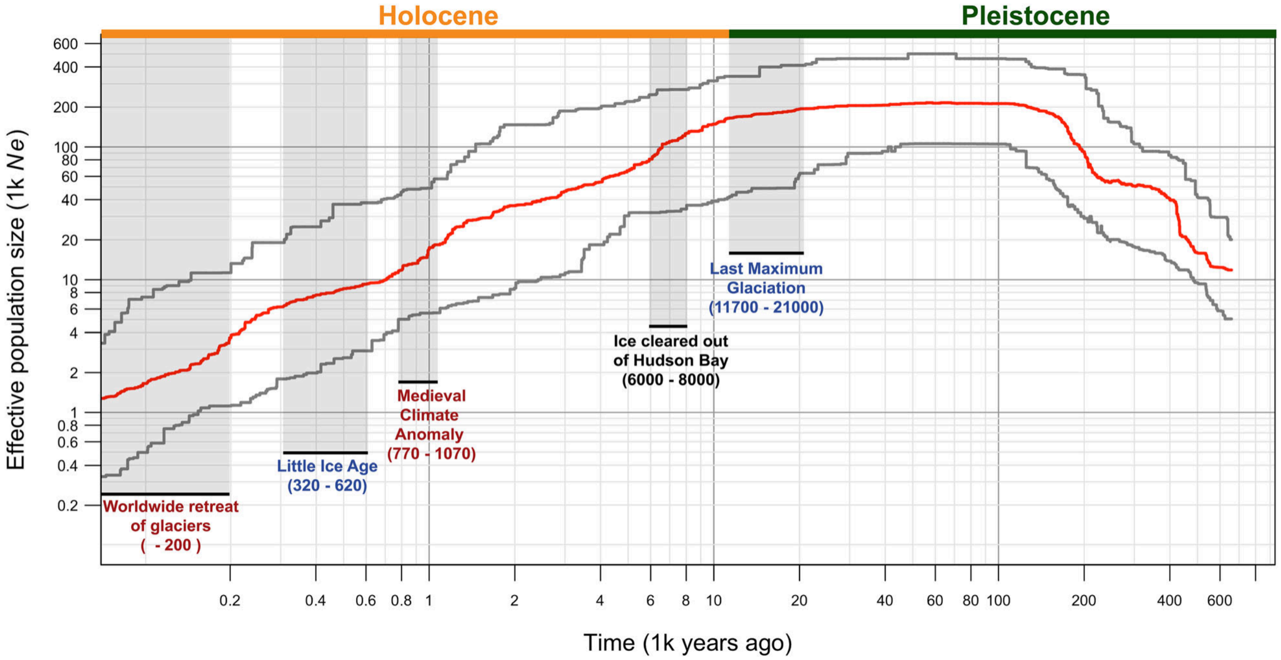


Figure 3. Reconstruction of the effective population size of the Snowy Owl population (*Ne*) from 600 000 years ago until 100 years ago in North America, assuming a mutation rate of 1.9×10^{-9} and a generation time of 7.93 based on Stairway Plot 2 (Liu & Fu 2020). The method precludes reliable estimates for the most recent 100 years. Grey lines indicate the 95% CI. Light grey areas represent glaciation events according to Clark *et al.* (2009, 2012) and Mann *et al.* (2009). Events in red are characterized by higher temperature and events in blue by lower temperatures. [Colour figure can be viewed at wileyonlinelibrary.com]

on data from breeding grounds at smaller scales than our current study and with different ecology than Snowy Owls (i.e. fully sedentary or partially migratory species): Great Grey Owl *Strix nebulosa* F_{ST} = 0.03–0.15 (Mendelsohn *et al.* 2020), Prairie Falcon *Falco mexicanus* F_{ST} = 0.01–0.03 (Doyle *et al.* 2018), both species in their North America Southern range, Bald Eagle *Haliaeetus leucocephalus* F_{ST} = 0.037–0.203 (Judkins *et al.* 2019) and Northern Goshawk *Accipiter gentilis* F_{ST} = 0–0.093 (Geraldes *et al.* 2019), both species in their North American range. All estimates were at least an order of magnitude higher than those we found in Snowy Owls, even though the sampled range was smaller, and none of these species had movements as nomadic as those observed in Snowy Owls. Although F_{ST} comparisons across studies are challenging (Gousy-Leblanc *et al.* 2021), our results for Snowy Owl suggest that the species exhibits much less broad-scale genetic differentiation in comparison with other raptor species.

Conversely, the Gyrfalcon *Falco rusticolus*, an Arctic raptor that inhabits similar habitats as the Snowy Owl, shows genetic differentiation between the continental populations of Greenland and Iceland, despite the high dispersal capability of the species (Johnson *et al.* 2007). For the Eurasian Arctic Peregrine Falcon *Falco peregrinus*, four distinct genetic groups were detected at the continental scale, which supposedly arose from the use of distinct population-specific migration routes, and fidelity to breeding and non-breeding areas (Gu *et al.* 2021). At such a large scale and for species with a high dispersal capacity, various factors such as fidelity to breeding or non-breeding areas, low breeding and natal dispersal, the use of distinct migration routes, and the interplay between those factors could impede gene flow among populations, promoting genetic differentiation.

Current genetic diversity and effective population size (contemporary Ne)

For Snowy Owls, we found a slight but statistically different level of genetic diversity between the most distant regions, i.e. the western and eastern regions in North America. This could be explained by the potential inclusion (i.e. via migration) of individuals in the ‘western’ category, which originated from Alaska or Russia but whose dispersal was not far enough to reach the eastern population (Fuller *et al.* 2003, Holt *et al.* 2020). Such heterogeneous migration could have slightly influenced allele frequencies across the circumpolar distribution, while not greatly impacting the genetic differentiation overall. Indeed, we observed that the highest *Hs* occurred in the west. The North American population should nonetheless be considered one population unit genetically.

The average expected heterozygosity (0.148 ± 0.140 sd) at the locus scale for Snowy Owls is slightly lower compared with the *He* values computed with SNPs for three other species of raptors, although it is challenging to compare *He* values when the proportion of the species range sampled varies across studies. Two species that were partial migrants displayed genetic differentiation at large scale and they were both sampled in North America: *He* = 0.293 in the Bald Eagle across most of its range (Judkins *et al.* 2019) and *He* = 0.340 in the Golden Eagle *Aquila chrysaetos* only for the Nearctic part of its range, similarly to our study (Doyle *et al.* 2016). One obligate migrant species, the Prairie Falcon *Falco mexicanus*, showed no population genetic differentiation at a large scale with *He* = 0.332 (Doyle *et al.* 2018). However, *He* in Snowy Owls is quite similar to the Burrowing Owl *Athene cunicularia*, another nomadic facultatively migrant species (*He* = 0.112) which exhibited population genetic differentiation at a low scale, although only a small part of its range was sampled (Mueller *et al.* 2018).

Although Snowy Owls appear to have lower gene diversity than other raptors, the estimated current effective population size of the species in North America (*contemporary Ne* = 15 792 individuals) is large enough to preserve the evolutionary potential of the population and allow it to persist and adapt in a changing environment as suggested by population modelling (see Kamath *et al.* 2015 and Hoban *et al.* 2021b). In general, a minimum *Ne* of 100 individuals is recommended to prevent loss of genetic diversity by genetic drift and an *Ne* of 1000 individuals to maintain long-term evolutionary potential (Frankham *et al.* 2014). In a conservation context, *Ne/Nc*, where *Nc* is the number of individuals counted in a census population, is important for disentangling the relative effects of population size and genetic factors on the persistence of species (Frankham 1995, Palstra & Ruzzante 2008, Ferchaud *et al.* 2016, Waples 2016). Considering our estimated *contemporary Ne* of 15 792 individuals

(95% CI: 10 850–28 950) and an *Nc* of about 30 000 individuals in North America (Rosenberg *et al.* 2016, BirdLife International 2020), we can calculate a *contemporary Ne/Nc* ratio of about 0.57 (range 0.36–0.96). Estimates of *Nc* for Snowy Owls are extremely uncertain and may be as low as 7000–8000 pairs in North America (Potapov & Sale 2012, BirdLife International 2020). *Ne/Nc* ratio values derived from these lower *Nc* estimates would then be around 1.05 (0.77–1.81). Nonetheless, all these *Ne/Nc* values are higher than those in many other avian taxa (Frankham 1995), so our results suggest that the North American population as a whole does not face an imminent risk of inbreeding depression or genetic impoverishment.

Past population trajectory

Demographic reconstruction suggests that the population size of Snowy Owls in North America has declined over the last few 1000 years, starting around the Last Glacial Maximum (LGM). A recent reconstruction of demographic history in the Peregrine Falcon, another Arctic raptor, resulted in a similar population size trajectory as the North American Snowy Owl (i.e. expansion during the LGM and a steady decline since the beginning of the Holocene; Gu *et al.* 2021). Perhaps an increase in the total area of tundra habitat may explain the population expansion during the LGM and the subsequent decline in the population that occurred when the tundra began to contract northward (Gu *et al.* 2021). Similarly, the population size of Snowy Owls may be closely matched to the amount of Arctic tundra because the species breeds exclusively in that habitat. An implication is that large and long-term environmental changes over the last few 1000 years, and in particular temperature increases since the LGM (Clark *et al.* 2009), may have greatly affected the population size of Snowy Owls. Indeed, population reconstructions showed that temperature increases reduced the effective population size of three penguin genera (*Eudyptes*, *Pygoscelis* and *Aptenodytes*) in Antarctica (Cole *et al.* 2019), highlighting ecosystem-wide responses to climate changes in the Antarctic Ocean in the past. Similarly, the climate warming that occurred after the LGM in the Northern Hemisphere has reduced effective population sizes, genetic diversity and census counts of other Arctic species such as the Polar Bear *Ursus maritimus* (Miller *et al.* 2012) and the Arctic Fox *Vulpes lagopus* (Larsson *et al.* 2019). Global warming has also been implicated as a major factor in the mass extinction of Late Quaternary megafauna in the Northern Hemisphere (Lorenzen *et al.* 2011, Lord *et al.* 2020, Stewart *et al.* 2021; but see Sandom *et al.* 2014).

Globally, the warming period of the Holocene has had an important influence on population size and range distribution of small mammals, such as lemmings (Prost *et al.* 2010, 2013, Lanier *et al.* 2015, Fedorov *et al.* 2020), which are the main prey of breeding Snowy Owls. Thus, climate change has the potential to influence entire ecosystems in the Arctic by disrupting the main trophic links between species; Snowy Owls may have declined since the mid-Holocene both as a direct result of higher temperatures (e.g. physiological stress) and due to the indirect effect of the climate-induced population reductions and geographical range contractions of its main prey, i.e. the small mammals in the Arctic.

CONCLUSION

Our findings should help further define some research priorities for Snowy Owls identified by Holt *et al.* (2020). First, the lack of significant genetic differentiation over the span of a continent spanning > 4500 km does not support the hypothesis that well-separated migration routes, i.e. north–south corridors to distinct winter grounds, are serving to isolate distinct breeding populations of North American Snowy Owls. Secondly, and potentially most concerning, our results showed that Snowy Owls have experienced a continuous decline in numbers since the end of the LGM (18 000–21 000 years ago) in North America. Although our estimate of the current effective population size does not suggest that Snowy Owls are at risk for imminent genetic problems, the finding that the owls were highly sensitive to global changes in the past implies that the population size may decline more precipitously in the future if Arctic warming accelerates, as predicted by many models of climate change. Finally, the climate warming that occurred after the LGM in the Northern Hemisphere and its accelerating rate with human-induced global change now may have completely shaped the many trophic links between a top predator in decline and his prey across biomes.

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AUTHOR CONTRIBUTIONS

Marianne Gousy-Leblanc: Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; validation; visualization; writing – original draft. **Jean-François Therrien:** Conceptualization; investigation; resources; supervision; writing – review and editing. **Thomas Broquet:** Data curation; formal analysis; software; validation; writing – review and editing. **Delphine Rioux:** Resources. **Nadine Curt-Grand-Gaudin:** Resources. **Natalie Tissot:** Resources. **Sophie Tissot:** Resources. **Ildiko Szabo:** Resources; writing – review and editing. **Laurie Wilson:** Resources; writing – review and editing. **Jack T. Evans:** Resources. **Victoria Bowes:** Resources. **Gilles Gauthier:** Resources; validation; writing – review and editing. **Karen L. Wiebe:** Resources; writing – review and editing. **Glenn Yannic:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Nicolas Lecomte:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL NOTE

All live captures followed Canadian Animal Care Committees guidelines.

Data Availability Statement

The SNP data set (vcf) can be found on Figshare: https://figshare.com/s/f1f01dc772d2f8c8698c. Raw genomic data (Fastq files) are available under the NCBI Sequence Read Archive (SRA) database (BioProject ID: PRJNA932710).

REFERENCES

ACIA 2004. *Impacts of a Warming Arctic-Arctic Climate Impact Assessment*. Cambridge, United Kingdom: Cambridge University Press.

Alexander, D.H., Novembre, J. & Lange, K. 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**: 1655–1664.

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**: 1–48.

BirdLife International. 2020. Species factsheet: Bubo scandiacus, *IUCN Red List for Birds*. http://www.birdlife.org on 12/04/2020.

Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.-J.W., Brown, C.J., O'Connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Pandolfi, J.M., Parmesan, C. & Richardson, A.J. 2016. Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob. Change Biol.* **22**: 1548–1560.

Brown, R., Bhatt, U.S., Euskirchen, E.S. & Romanovsky, V.E. 2019. Key indicators of Arctic climate change: 1971–2017. *Environ. Res. Lett.* **14**: 45010.

Catchen, J.M., Amores, A., Hohenlohe, P., Cresko, W. & Postlethwait, J.H. 2011. Stacks: Building and genotyping loci de novo from short-read sequences. *G3 Genes Genomes Genet.* **1**: 171–182.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A. & Cresko, W.A. 2013. Stacks: An analysis tool set for population genomics. *Mol. Ecol.* **22**: 3124–3140.

Chang, A.M. & Wiebe, K.L. 2018. Habitat selection by wintering male and female snowy owls on the Canadian prairies in relation to prey abundance and a competitor, the great horned owl. *J. Field Ornithol.* **89**: 64–77.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W. & McCabe, A.M. 2009. The last glacial maximum. *Science* **325**: 710–714.

Clark, P.U., Shakun, J.D., Baker, P.A., Bartlein, P.J., Brewer, S., Brook, E., Carlson, A.E., Cheng, H., Kaufman, D.S., Liu, Z., Marchitto, T.M., Mix, A.C., Morrill, C., Otto-Bliesner, B.L., Pahnke, K., Russell, J.M., Whitlock, C., Adkins, J.F., Blois, J.L., Clark, J., Colman, S.M., Curry, W.B., Flower, B.P., He, F., Johnson, T.C., Lynch-Stieglitz, J., Markgraf, V., McManus, J., Mitrovica, J.X., Moreno, P.I. & Williams, J.W. 2012. Global climate evolution during the last deglaciation. *Proc. Natl. Acad. Sci. U.S.A.* **109**: E1134–E1142.

Cleary, A.C., Hoffman, J.I., Forcada, J., Lydersen, C., Lowther, A.D. & Kovacs, K.M. 2021. 50,000 years of ice and seals: Impacts of the last glacial maximum on Antarctic fur seals. *Ecol. Evol.* **11**: 14003–14011.

Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (eds) 2012. *Dispersal Ecology and Evolution*. Oxford: Oxford University Press.

Cole, T.L., Dutoit, L., Dussex, N., Hart, T., Alexander, A., Younger, J.L., Clucas, G.V., Frugone, M.J., Cherel, Y., Cuthbert, R., Ellenberg, U., Fiddaman, S.R., Hiscock, J., Houston, D., Jouventin, P., Mattern, T., Miller, G., Miskelly, C., Nolan, P., Polito, M.J., Quillfeldt, P., Ryan, P.G., Smith, A., Tennyson, A.J.D., Thompson, D., Wienecke, B., Vianna, J.A. & Waters, J.M. 2019. Receding ice drove parallel expansions in Southern Ocean penguins. *Proc. Natl. Acad. Sci. U.S.A.* **116**: 26690–26696.

Covercast, I. 2017. *easySFS*. Github repository.

Cristofari, R., Liu, X., Bonadonna, F., Cherel, Y., Pistorius, P., Le Maho, Y., Raybaud, V., Stenseth, N.C., Le Bohec, C. & Trucchi, E. 2018. Climate-driven range shifts of the king penguin in a fragmented ecosystem. *Nat. Clim. Change* **8**: 245–251.

Curk, T., Pokrovsky, I., Lecomte, N., Aarvak, T., Burnham, K., Dietz, A., Franke, A., Gauthier, G., Jacobsen, K.-O., Kidd, J., Lewis, S.B., Øien, I.J., Solheim, R., Wiebe, K., Wikelski, M., Therrien, J.-F. & Safi, K. 2020. Arctic avian predators synchronise their spring migration with the northern progression of snowmelt. *Sci. Rep.* **10**: 7220.

Do, C., Waples, R.S., Peel, D., Macbeth, G.M., Tillett, B.J. & Ovenden, J.R. 2014. NeEstimator v2: re-implementation of software for the estimation of contemporary effective population size from genetic data. *Mol. Ecol. Resour.* **14**: 209–214.

Doyle, J.M., Katzner, T.E., Roemer, G.W., Cain, J.W., Millsap, B.A., McIntyre, C.L., Sonsthagen, S.A., Fernandez, N.B., Wheeler, M., Bulut, Z., Bloom, P.H. & Andrew DeWoody, J. 2016. Genetic structure and viability selection in the golden eagle (*Aquila chrysaetos*), a vagile raptor with a Holarctic distribution. *Conserv. Genet.* **17**: 1307–1322.

Doyle, F.I., Therrien, J.-F., Reid, D.G., Gauthier, G. & Krebs, C.J. 2017. Seasonal movements of female snowy owls breeding in the Western north American Arctic. *J. Raptor Res.* **51**: 428–438.

Doyle, J.M., Bell, D.A., Bloom, P.H., Emmons, G., Fesnock, A., Katzner, T.E., LaPré, L., Leonard, K., SanMiguel, P., Westerman, R. & Andrew DeWoody, J. 2018. New insights into the phylogenetics and population structure of the prairie falcon (*Falco mexicanus*). *BMC Genomics* **19**: 233.

Fedorov, V.B., Trucchi, E., Goropashnaya, A.V., Waltari, E., Whidden, S.E. & Stenseth, N.C. 2020. Impact of past climate warming on genomic diversity and demographic history of collared lemmings across the Eurasian Arctic. *Proc. Natl. Acad. Sci. U.S.A.* **117**: 3026–3033.

Ferchaud, A.-L., Perrier, C., April, J., Hernandez, C., Dionne, M. & Bernatchez, L. 2016. Making sense of the relationships between Ne, Nb and Nc towards defining conservation thresholds in Atlantic salmon (*Salmo salar*). *Heredity* **117**: 268–278.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: A review. *Genet. Res.* **66**: 95–107.

Frankham, R., Bradshaw, C.J.A. & Brook, B.W. 2014. Genetics in conservation management: Revised recommendations for the 50/500 rules, red list criteria and population viability analyses. *Biol. Conserv.* **170**: 56–63.

Fraser, D.J. & Bernatchez, L. 2001. Adaptive evolutionary conservation: Towards a unified concept for defining conservation units. *Mol. Ecol.* **10**: 2741–2752.

Fuller, M., Holt, D. & Schueck, L. 2003. Snowy owl movements: Variation on the migration theme. In Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*: 359–365. Berlin: Springer.

Funk, W.C., McKay, J.K., Hohenlohe, P.A. & Allendorf, F.W. 2012. Harnessing genomics for delineating conservation units. *Trends Ecol. Evol.* **27**: 489–496.

Gagnon, M., Yannic, G., Perrier, C. & Côté, S.D. 2019. No evidence of inbreeding depression in fast declining herds of migratory caribou. *J. Evol. Biol.* **32**: 1368–1381.

Gauthier, G., Bêty, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevallier, C., Lai, S., Tarroux, A. & Berteaux, D. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philos. Trans. R. Soc. B Biol. Sci.* **368**: 20120482.

Geraldes, A., Askelson, K.K., Nikelski, E., Doyle, F.I., Harrower, W.L., Winker, K. & Irwin, D.E. 2019. Population genomic analyses reveal a highly differentiated and endangered genetic cluster of northern goshawks (*Accipiter gentilis laingi*) in Haida Gwaii. *Evol. Appl.* **12**: 757–772.

Gilg, O., Kovacs, K.M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R.A., Meltofte, H., Moreau, J., Post, E., Schmidt, N.M., Yannic, G. & Bollache, L. 2012. Climate change and the ecology and evolution of Arctic vertebrates: Climate change impacts on Arctic vertebrates. *Ann. N. Y. Acad. Sci.* **1249**: 166–190.

Gosselin, T., Lamothe, M. & Grewe, P. 2017. *Radiator: RADseq Data Exploration, m Anipulation and Visualization Using R*. R package version 1.1.9. https://doi.org/10.5281/zenodo.3687060.

Gousy-Leblanc, M., Yannic, G., Therrien, J.-F. & Lecomte, N. 2021. Mapping our knowledge on birds of prey population genetics. *Conserv. Genet.* **22**: 685–702.

Gruber, B., Unmack, P.J., Berry, O.F. & Georges, A. 2018. DARTR: An R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Mol. Ecol. Resour.* **18**: 691–699.

Gu, Z., Pan, S., Lin, Z., Hu, L., Dai, X., Chang, J., Xue, Y., Su, H., Long, J., Sun, M., Ganusevich, S., Sokolov, V., Sokolov, A., Pokrovsky, I., Ji, F., Bruford, M.W., Dixon, A. & Zhan, X. 2021. Climate-driven flyway changes and memory-based long-distance migration. *Nature* **591**: 259–264.

Heggøy, O., Aarvak, T., Øien, I.J., Jacobsen, K.-O., Solheim, R., Zazelenchuk, D., Stoffel, M. & Kleven, O. 2017. Effects of satellite transmitters on survival in snowy owls *Bubo scandiacus*. *Ornis Nor.* **40**: 33.

Hoban, S.M., Hauffe, H.C., Pérez-Espona, S., Arntzen, J.W., Bertorelle, G., Bryja, J., Frith, K., Gaggiotti, O.E., Galbusera, P., Godoy, J.A., Hoelzel, A.R., Nichols, R.A., Primmer, C.R., Russo, I.-R., Segelbacher, G., Siegismund, H.R., Sihvonen, M., Vernesi, C., Vilà, C. & Bruford, M.W. 2013. Bringing genetic diversity to the forefront of conservation policy and management. *Conserv. Genet. Resour.* **5**: 593–598.

Hoban, S., Bruford, M.W., Funk, W.C., Galbusera, P., Griffith, M.P., Grueber, C.E., Heuertz, M., Hunter, M.E., Hvilsom, C., Stroil, B.K., Kershaw, F., Khoury, C.K., Laikre, L., Lopes-Fernandes, M., MacDonald, A.J., Mergeay, J., Meek, M., Mittan, C., Mukassabi, T.A., O'Brien, D., Ogden, R., Palma-Silva, C., Ramakrishnan, U., Segelbacher, G., Shaw, R.E., Sjögren-Gulve, P., Veličković, N. & Vernesi, C. 2021a. Global commitments to conserving and monitoring genetic diversity are now necessary and feasible. *Bioscience* **71**: 964–976.

Hoban, S., Paz-Vinas, I., Aitken, S., Bertola, L., Breed, M.F., Bruford, M., Funk, C., Grueber, C., Heuertz, M. & Hohenlohe, P. 2021b. Effective population size remains a suitable, pragmatic indicator of genetic diversity for all species, including forest trees. *Biol. Conserv.* **253**: 108906.

Hoffmann, A.A. & Sgrò, C.M. 2011. Climate change and evolutionary adaptation. *Nature* **470**: 479–485.

Hohenlohe, P.A., Funk, W.C. & Rajora, O.P. 2021. Population genomics for wildlife conservation and management. *Mol. Ecol.* **30**: 62–82.

Holt, D.W., Larson, M.D., Smith, N., Evans, D. & Parmelee, D.F. 2020. The snowy owl (*Bubo scandiacus*). In Billerman, S.M. (ed) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology.

IPCC. 2018. *Global Warming of 1.5° C. An IPCC Special Report on the Impacts of Global Warming of 1.5° C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. Sustainable Development, and Efforts to Eradicate Poverty* [V. Masson-Delmotte, P. Zhai, HO Pörtner, D. Roberts, J. Skea, PR Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, JBR Matthews, Y. Chen, X. Zhou, MI Gomis, E. Lonnoy, T. Maycock, M. Tignor, T. Waterfield (eds.)]. http://www.ipcc.ch/report/sr15

Johnson, J.A., Burnham, K.K., Burnham, W.A. & Mindell, D.P. 2007. Genetic structure among continental and Island populations of gyrfalcons: Gyrfalcon population structure. *Mol. Ecol.* **16**: 3145–3160.

Jombart, T. 2008. Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**: 1403–1405.

Jombart, T., Devillard, S. & Balloux, F. 2010. Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genet.* **11**: 94.

Judkins, M.E., Couger, B.M., Warren, W.C. & Van Den Bussche, R.A. 2019. A 50K SNP array reveals genetic structure for bald eagles (*Haliaeetus leucocephalus*). *Conserv. Genet.* **21**: 65–76.

Kamath, P. L., Haroldson, M. A., Luikart, G., Paetkau, D., Whitman, C., & Van Manen, F. T. 2015. Multiple estimates of effective population size for monitoring a long-lived vertebrate: an application to Y ellowstone grizzly bears. *Molecular Ecology* **24**: 5507-5521.

Kelly, M. 2019. Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Philos. Trans. R. Soc. B Biol. Sci.* **374**: 20180176.

Kerlinger, P. & Lein, M.R. 1988. Population ecology of snowy owls during winter on the Great Plains of North America. *Condor* **90**: 866–874.

Lanier, H.C., Gunderson, A.M., Weksler, M., Fedorov, V.B. & Olson, L.E. 2015. Comparative Phylogeography highlights the double-edged sword of climate change faced by Arctic- and alpine-adapted mammals. *PLoS One* **10**: e0118396.

Larsson, P., Götherström, A., Androsov, S., Germonpré, M., Bergfeldt, N., Fedorov, S., Eide, N.E., Sokolova, N., Berteaux, D., Angerbjörn, A., Flagstad, Ø., Plotnikov, V., Norén, K., Díez-del-Molino, D., Dussex, N., Stanton, D.W.G. & Dalén, L. 2019. Consequences of past climate change and recent human persecution on mitogenomic diversity in the Arctic Fox. *Philos. Trans. R. Soc. B Biol. Sci.* **374**: 20190212.

Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L. & Krebs, C.J. 2012. Disentangling trophic relationships in a high Arctic tundra ecosystem through food web modeling. *Ecology* **93**: 1707–1716.

Lischer, H.E.L. & Excoffier, L. 2012. PGDSpider: An automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics* **28**: 298–299.

Liu, X. & Fu, Y.-X. 2015. Exploring population size changes using SNP frequency spectra. *Nat. Genet.* **47**: 555–559.

Liu, X. & Fu, Y.-X. 2020. Stairway plot 2: Demographic history inference with folded SNP frequency spectra. *Genome Biol.* **21**: 280.

Lord, E., Dussex, N., Kierczak, M., Díez-del-Molino, D., Ryder, O.A., Stanton, D.W., Gilbert, M.T.P., Sánchez-Barreiro, F., Zhang, G. & Sinding, M.-H.S. 2020. Preextinction demographic stability and genomic signatures of adaptation in the woolly rhinoceros. *Curr. Biol.* **30**: 3871–3879.

Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., Ugan, A., Borregaard, M.K., Gilbert, M.T.P., Nielsen, R., Ho, S.Y.W., Goebel, T., Graf, K.E., Byers, D., Stenderup, J.T., Rasmussen, M., Campos, P.F., Leonard, J.A., Koepfli, K.-P., Froese, D., Zazula, G., Stafford, T.W., Aaris-Sørensen, K., Batra, P., Haywood, A.M., Singarayer, J.S., Valdes, P.J., Boeskorov, G., Burns, J.A., Davydov, S.P., Haile, J., Jenkins, D.L., Kosintsev, P., Kuznetsova, T., Lai, X., Martin, L.D., McDonald, H.G., Mol, D., Meldgaard, M., Munch, K., Stephan, E., Sablin, M., Sommer, R.S., Sipko, T., Scott, E., Suchard, M.A., Tikhonov, A., Willerslev, R., Wayne, R.K., Cooper, A., Hofreiter, M., Sher, A., Shapiro, B., Rahbek, C. & Willerslev, E. 2011. Species-specific responses of late quaternary megafauna to climate and humans. *Nature* **479**: 359–364.

Louis, M., Skovrind, M., Samaniego Castruita, J.A., Garilao, C., Kaschner, K., Gopalakrishnan, S., Haile, J.S., Lydersen, C., Kovacs, K.M., Garde, E., Heide-Jørgensen, M.P., Postma, L., Ferguson, S.H., Willerslev, E. & Lorenzen, E.D. 2020. Influence of past climate change on phylogeography and demographic history of narwhals, *Monodon monoceros*. *Proc. R. Soc. B Biol. Sci.* **287**: 20192964.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. & Ni, F. 2009. Global signatures and dynamical origins of the little ice age and medieval climate anomaly. *Science* **326**: 1256–1260.

Marthinsen, G., Wennerberg, L., Solheim, R. & Lifjeld, J.T. 2009. No phylogeographic structure in the circumpolar snowy owl (*Bubo scandiacus*). *Conserv. Genet.* **10**: 923–933.

Mastretta-Yanes, A., Arrigo, N., Alvarez, N., Jorgensen, T.H., Piñero, D. & Emerson, B.C. 2015. Restriction site-associated DNA sequencing, genotyping error estimation and *de novo* assembly optimization for population genetic inference. *Mol. Ecol. Resour.* **15**: 28–41.

McCabe, R.A., Therrien, J.-F., Wiebe, K.L., Gauthier, G., Brinker, D., Weidensaul, S. & Elliott, K. 2021. Landscape cover type, not social dominance, is associated with the winter movement patterns of snowy owls in temperate areas. *Auk* **138**: ukaa082.

Meehan, T.D., LeBaron, G.S., Dale, K., Michel, N.L., Verutes, G.M. & Langham, G.M. 2018. Abundance trends of birds wintering in the USA and Canada, from Audubon Christmas bird counts, 1966-2017, version 2.1. National Audubon Society, New York, NY, USA.

Mendelsohn, B., Bedrosian, B., Love Stowell, S.M., Gagne, R.B., LaCava, M.E.F., Godwin, B.L., Hull, J.M. & Ernest, H.B. 2020. Population genomic diversity and structure at the discontinuous southern range of the great gray owl in North America. *Conserv. Genet.* **21**: 693–706.

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J. & Muelbert, M.M.C. 2020. Polar regions. In Pörtner, H.-O., Roberts, D.C., Masson-Delmott, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B. & Weyer, N.M. (eds) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. https://www.ipcc.ch/srocc/

Miller, W., Schuster, S.C., Welch, A.J., Ratan, A., Bedoya-Reina, O.C., Zhao, F., Kim, H.L., Burhans, R.C., Drautz, D.I., Wittekindt, N.E., Tomsho, L.P., Ibarra-Laclette, E., Herrera-Estrella, L., Peacock, E., Farley, S., Sage, G.K., Rode, K., Obbard, M., Montiel, R., Bachmann, L., Ingolfsson, O., Aars, J., Mailund, T., Wiig, O., Talbot, S.L. & Lindqvist, C. 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. *Proc. Natl. Acad. Sci. U.S.A.* **109**: E2382–E2390.

Miller, M.P., Davis, R.J., Forsman, E.D., Mullins, T.D. & Haig, S.M. 2018. Isolation by distance versus landscape resistance: Understanding dominant patterns of genetic structure in northern spotted owls (*Strix occidentalis caurina*). *PLoS One* **13**: e0201720.

Mueller, J.C., Kuhl, H., Boerno, S., Tella, J.L., Carrete, M. & Kempenaers, B. 2018. Evolution of genomic variation in the burrowing owl in response to recent colonization of urban areas. *Proc. R. Soc. B Biol. Sci.* **285**: 20180206.

Nam, K., Mugal, C., Nabholz, B., Schielzeth, H., Wolf, J.B., Backström, N., Künstner, A., Balakrishnan, C.N., Heger, A., Ponting, C.P., Clayton, D.F. & Ellegren, H. 2010. Molecular evolution of genes in avian genomes. *Genome Biol.* **11**: 17.

Navascués, M., Leblois, R. & Burgarella, C. 2017. Demographic inference through approximate-Bayesian-computation skyline plots. *PeerJ* **5**: e3530.

Palstra, F.P. & Ruzzante, D.E. 2008. Genetic estimates of contemporary effective population size: What can they tell us about the importance of genetic stochasticity for wild population persistence? *Mol. Ecol.* **17**: 3428–3447.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.

Peterson, B.K., Weber, J.N., Kay, E.H., Fisher, H.S. & Hoekstra, H.E. 2012. Double digest RADseq: An inexpensive method for De novo SNP discovery and genotyping in model and non-model species. *PLoS One* **7**: 11.

Potapov, E. & Sale, R. 2012. *The Snowy Owl*. London: T&A Poyser.

Prost, S., Smirnov, N., Fedorov, V.B., Sommer, R.S., Stiller, M., Nagel, D., Knapp, M. & Hofreiter, M. 2010. Influence of climate warming on Arctic mammals? New insights from ancient DNA studies of the collared lemming *Dicrostonyx torquatus*. *PLoS One* **5**: e10447.

Prost, S., Guralnick, R.P., Waltari, E. & Fedorov, V.B. 2013. Losing ground: past history and future fate of arctic small mammals in a changing climate. *Glob. Change Biol.* **19**: 1854–1864.

R Core Team 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rich, T.D., Beardmore, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Inigo-Elias, E.E., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S. & Will, T.C. 2004. *Partners in Flight North American Landbird Conservation Plan*. Ithaca, NY: Cornell Lab of Ornithology.

Robillard, A., Therrien, J.F., Gauthier, G., Clark, K.M. & Bêty, J. 2016. Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl. *Oecologia* **181**: 423–433.

Robillard, A., Gauthier, G., Therrien, J.-F. & Bêty, J. 2018. Wintering space use and site fidelity in a nomadic species, the snowy owl. *J. Avian Biol.* **49**: jav-01707.

Rosenberg, K.V., Kennedy, J.A., Dettmers, R., Ford, R.P., Reynolds, D., Alexander, J.D., Beardmore, C.J., Blancher, P.J., Bogart, R.E., Butcher, G.S., Camfield, A.F., Couturier, A., Demarest, D.W., Easton, W.E., Giocomo, J.J., Keller, R.H., Mini, A.E., Panjabi, A.O., Pashley, D.N., Rich, T.D., Ruth, J.M., Stabins, H., Stanton, J.C. & Will, T. 2016. *Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States*. Partners in Flight Science Commitee. 119 pp.

Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. 2014. Global late quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. B Biol. Sci.* **281**: 20133254.

Schwartz, M., Luikart, G. & Waples, R. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends Ecol. Evol.* **22**: 25–33.

Smeds, L., Qvarnström, A. & Ellegren, H. 2016. Direct estimate of the rate of germline mutation in a bird. *Genome Res.* **26**: 1211–1218.

Solheim, R. 2012. Wing feather moult and age determination of snowy owls *Bubo scandiacus*. *Ornis Nor.* **35**: 48–67.

Stewart, M., Carleton, W.C. & Groucutt, H.S. 2021. Climate change, not human population growth, correlates with late quaternary megafauna declines in North America. *Nat. Commun.* **12**: 1–15.

Storz, J.F., Ramakrishnan, U. & Alberts, S.C. 2001. Determinants of effective population size for loci with different modes of inheritance. *J. Hered.* **92**: 497–502.

Strimmer, K. & Pybus, O.G. 2001. Exploring the demographic history of DNA sequences using the generalized skyline plot. *Mol. Biol. Evol.* **18**: 2298–2305.

Taylor, J.J., Lawler, J.P., Aronsson, M., Barry, T., Bjorkman, A.D., Christensen, T., Coulson, S.J., Cuyler, C., Ehrich, D. & Falk, K. 2020. Arctic terrestrial biodiversity status and trends: A synopsis of science supporting the CBMP state of Arctic terrestrial biodiversity report. *Ambio* **49**: 833–847.

Therrien, J.-F., Gauthier, G. & Bêty, J. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. *J. Avian Biol.* **42**: 363–369.

Therrien, J.-F., Gauthier, G., Pinaud, D. & Bêty, J. 2014. Irruptive movements and breeding dispersal of snowy owls: A specialized predator exploiting a pulsed resource. *J. Avian Biol.* **45**: 536–544.

Therrien, J.-F., Weidensaul, S., Brinker, D., Huy, S., Miller, T., Jacobs, E., Weber, D., McDonald, T., Lanzone, M., Smith, N. & Lecomte, N. 2017. Winter use of a highly diverse suite of habitats by irruptive snowy owls. *Northeast. Nat.* **24**: B81–B89.

Wang, I.J., Santiago, E. & Caballero, A. 2016. Prediction and estimation of effective population size. *Heredity* **117**: 193–206.

Waples, R.S. 2016. Making sense of genetic estimates of effective population size. *Mol. Ecol.* **25**: 4689–4691.

Waples, R.S. & Do, C. 2010. Linkage disequilibrium estimates of contemporary N_e using highly variable genetic markers: A largely untapped resource for applied conservation and evolution. *Evol. Appl.* **3**: 244–262.

Weir, B.S. & Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* **38**: 1358–1370.

Weir, B.S. & Goudet, J. 2017. A unified characterization of population structure and relatedness. *Genetics* **206**: 2085–2103.

Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., Dussault, C., Hundertmark, K.J., Irvine, R.J., Jenkins, D.A., Kolpashikov, L., Mager, K., Musiani, M., Parker, K.L., Røed, K.H., Sipko, T., Þórisson, S.G., Weckworth, B.V., Guisan, A., Bernatchez, L. & Côté, S.D. 2014. Genetic diversity in caribou linked to past and future climate change. *Nat. Clim. Change* **4**: 132–137.

Yannic, G., St-Laurent, M.-H., Ortego, J., Taillon, J., Beauchemin, A., Bernatchez, L., Dussault, C. & Côté, S.D. 2016. Integrating ecological and genetic structure to define management units for caribou in eastern Canada. *Conserv. Genet.* **17**: 437–453.

Yannic, G., Yearsley, J., Sermier, R., Dufresnes, C., Gilg, O., Aebischer, A., Gavrilo, M.V., Strøm, H., Mallory, M.L., Morrison, R.I.G., Gilchrist, H.G. & Broquet, T. 2016. High connectivity in a long-lived high-Arctic seabird, the ivory gull Pagophila eburnea. *Polar Biology*. **39**: 221–236.

Zhang, G., Li, C., Li, Q., Li, B., Larkin, D.M., Lee, C., Storz, J.F., Antunes, A., Greenwold, M.J., Meredith, R.W., Odeen, A., Cui, J., Zhou, Q., Xu, L., Pan, H., Wang, Z., Jin, L., Zhang, P., Hu, H., Yang, W., Hu, J., Xiao, J., Yang, Z., Liu, Y., Xie, Q., Yu, H., Lian, J., Wen, P., Zhang, F., Li, H., Zeng, Y., Xiong, Z., Liu, S., Zhou, L., Huang, Z., An, N., Wang, J., Zheng, Q., Xiong, Y., Wang, G., Wang, B., Wang, J., Fan, Y., da Fonseca, R.R., Alfaro-Nunez, A., Schubert, M., Orlando, L., Mourier, T., Howard, J.T., Ganapathy, G., Pfenning, A., Whitney, O., Rivas, M.V., Hara, E., Smith, J., Farre, M., Narayan, J., Slavov, G., Romanov, M.N., Borges, R., Machado, J.P., Khan, I., Springer, M.S., Gatesy, J., Hoffmann, F.G., Opazo, J.C., Hastad, O., Sawyer, R.H., Kim, H., Kim, K.-W., Kim, H.J., Cho, S., Li, N., Huang, Y., Bruford, M.W., Zhan, X., Dixon, A., Bertelsen, M.F., Derryberry, E., Warren, W., Wilson, R.K., Li, S., Ray, D.A., Green, R.E., O'Brien, S.J., Griffin, D., Johnson, W.E., Haussler, D., Ryder, O.A., Willerslev, E., Graves, G.R., Alstrom, P., Fjeldsa, J., Mindell, D.P., Edwards, S.V., Braun, E.L., Rahbek, C., Burt, D.W., Houde, P., Zhang, Y., Yang, H., Wang, J., Consortium, A.G., Jarvis, E.D., Gilbert, M.T.P., Wang, J., Ye, C., Liang, S., Yan, Z., Zepeda, M.L., Campos, P.F., Velazquez, A.M.V., Samaniego, J.A., Avila-Arcos, M., Martin, M.D., Barnett, R., Ribeiro, A.M., Mello, C.V., Lovell, P.V., Almeida, D., Maldonado, E., Pereira, J., Sunagar, K., Philip, S., Dominguez-Bello, M.G., Bunce, M., Lambert, D., Brumfield, R.T., Sheldon, F.H., Holmes, E.C., Gardner, P.P., Steeves, T.E., Stadler, P.F., Burge, S.W., Lyons, E., Smith, J., McCarthy, F., Pitel, F., Rhoads, D. &

Froman, D.P. 2014. Comparative genomics reveals insights into avian genome evolution and adaptation. *Science* **346**: 1311–1320.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supplementary materials on the method and results sections.