Biological Conservation 253 (2021) 108936

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Restoration of transborder connectivity for Fennoscandian brown bears (*Ursus arctos*)

Alexander Kopatz [a,*], Oddmund Kleven [a], Ilpo Kojola [b], Jouni Aspi [c], Anita J. Norman [d], Göran Spong [d], Niclas Gyllenstrand [e], Love Dalén [e], Ida Fløystad [f], Snorre B. Hagen [f], Jonas Kindberg [a,d], Øystein Flagstad [a]

[a] *Norwegian Institute for Nature Research, Trondheim, Norway*
[b] *Natural Resources Institute Finland, Rovaniemi, Finland*
[c] *Department of Biology, University of Oulu, Oulu, Finland*
[d] *Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden*
[e] *Swedish Museum of Natural History, Stockholm, Sweden*
[f] *Norwegian Institute for Bioeconomy Research, Svanvik, Norway*

ARTICLE INFO

Keywords:
Brown bear
Genetic structure
Male gene flow
Microsatellites
Migration
Recovery
Ursus arctos
Wildlife monitoring
Y chromosome

ABSTRACT

Knowledge about the connectivity among natural populations is essential to identify management units for effective conservation actions. Conservation-minded management has led to the recovery of large carnivore populations in northern Europe, possibly restoring connectivity between the two separated, but expanding brown bear (*Ursus arctos*) populations on the Scandinavian peninsula to the west and Karelia, a part of the large Eurasian population, to the east. The degree of connectivity between these populations has been poorly understood, therefore we investigated the extent of connectivity between the two populations using autosomal microsatellites and Y chromosome haplotypes in 924 male bears (the dispersing sex), sampled during a period of 12 years (2005–2017) across the transborder area where these two populations meet. Our results showed that the two populations are not genetically isolated as reported in earlier studies. We detected recent asymmetrical gene flow at a rate (individuals per generation) of 4.6–5.5 (1%) from Karelia into Scandinavia, whereas the rate was approximately 27.1–34.5 (8%) in the opposite direction. We estimated historical gene flow of effective number of migrants to be between 1.7 and 2.5 between the populations. Analyses of Y chromosome markers supported these results. Successful recovery and expansion of both populations led to the restoration of connectivity, however, it is asymmetric, possibly due to different recovery histories and population densities. By aligning monitoring between neighboring countries, we were able to better understand the biological processes across the relevant spatial scale.

1. Introduction

Since isolation can be detrimental to populations and may ultimately threaten species survival (Frankham, 2005), wildlife conservation efforts often seek to establish and maintain inter-population connectivity. It is important to note that demographic connectivity (i.e. the dispersal of individuals) does not necessarily result in genetic connectivity (i.e. successful reproduction and gene flow) (Mills and Allendorf, 1996; Lowe and Allendorf, 2010; Driscoll et al., 2014; Vasudev and Fletcher Jr, 2016; Robertson et al., 2018). Genetic connectivity has substantial impact on the effective size of a population. For small populations in particular, an increase of genetic variation can substantially increase its ability to adapt to a changing environment, directly influencing persistence, viability, and long-term survival (Frankham, 2005; Waples and Gaggiotti, 2006; Broquet and Petit, 2009; Laikre et al., 2009; Driscoll et al., 2014). Measuring or monitoring of connectivity may be beneficial also for recovering populations to evaluate the success of conservation and management actions (Heller and Zavaleta, 2009; Beger et al., 2010; Driscoll et al., 2014; Iftekhar and Pannell, 2015; Ralls et al., 2018).

Assessing connectivity can be challenging, especially on broader, transnational scales, when distances among populations are large and span beyond the average individual dispersal distance of the target

---

[*] Corresponding author at: Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway.
E-mail address: alexander.kopatz@nina.no (A. Kopatz).

https://doi.org/10.1016/j.biocon.2020.108936
Received 14 July 2020; Received in revised form 13 November 2020; Accepted 17 December 2020

species (Flagstad et al., 2003; Vilà et al., 2003; Fischer et al., 2017). Because of this and because connectivity is often not balanced or symmetric, transborder assessment of populations across the entirety of their distribution range is preferable (Beger et al., 2010; Sundqvist et al., 2016; Thornton et al., 2018). Moreover, uneven sample sizes and discontinuous sampling, both spatially and temporally, can lead to potential biases (Schwartz and McKelvey, 2008; Frantz et al., 2009; Puechmaille, 2016). Such biases, sometimes caused by different management strategies as well as dissimilar monitoring and sampling schemes, must be addressed (Dallimer and Strange, 2015; Bischof et al., 2016; Thornton et al., 2018; Gervasi et al., 2019). If the distribution of the target species straddle administrative boundaries, transboundary collaboration and harmonization of monitoring may lead to greatly improved data (Thornton et al., 2018; Gervasi et al., 2019). The development of genetic, and specifically non-invasive genetic sampling, provides managers and researchers with tools necessary for collaboration and harmonization (Schwartz et al., 2007). Once harmonized, genetic information enables the study of the degree of genetic differentiation and connectivity, i.e. gene flow among nations, regions and populations. Genetic data is particularly important as demographic connectivity alone is not a feasible indicator for successful reproduction and thus genetic connectivity (Allendorf et al., 2010; McMahon et al., 2014; Shafer et al., 2015).

For most of the previous two centuries, large carnivores in Europe were heavily persecuted and eventually extirpated from many areas, with only a few fragmented populations surviving (Woodroffe, 2000; Dalerum et al., 2009). For example, the once continuous Fennoscandian brown bear (*Ursus arctos*) population was heavily decimated in Sweden, and animals could only be found in a few, remote areas (Swenson et al., 1995). In Norway, one isolated population is assumed to have survived in southern Norway (Elgmork, 1994), and in Finland, bears were eventually only present in the eastern regions at the border to Russia (Kojola and Laitala, 2000). The hunting led to fragmentation of the Scandinavian and Karelian brown bear populations (Curry-Lindahl, 1972; Swenson et al., 1995), a situation similar to other large carnivores in the area, such as grey wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*) in northern Europe (Hellborg et al., 2002; Flagstad et al., 2003; Vilà et al., 2003; Flagstad et al., 2004). Although conservation minded legislation and management in the second part of the 20th century initiated the recovery of large carnivore populations in northern Europe (Chapron et al., 2014), several populations are still threatened by fragmentation and isolation in many regions and also from increasing conflicts with humans (Ripple et al., 2014). Moreover, climate change may further challenge the persistence and survival of large carnivore populations (Hoffmann et al., 2011; Ripple et al., 2014; Haddad et al., 2015; Bar-On et al., 2018).

The brown bear (*Ursus arctos*) population has staged a successful return across Fennoscandia where the number of individuals on the Scandinavian Peninsula (Sweden, Norway) in the West and Karelia (northern Norway, Finland) in the East have increased (Fig. 1), mainly during the 1990s (Swenson et al., 1995; Sæther et al., 1998; Swenson et al., 1998; Kojola and Laitala, 2000; Kojola et al., 2006; Kojola and Heikkinen, 2006; Swenson et al., 2017). The Scandinavian population comprises mainly bears from Sweden but also individuals in the transborder area in central and southern Norway. The population size estimates increased from the 1960s until the 2010s by a factor of five while the eastern population of Karelia including Finland and northeastern Norway increased by a factor of ten. A similar pattern was seen for range expansion, where a documented change factor of four was reported for Scandinavia and three for Karelia (Chapron et al., 2014). Latest reports estimated approximately 2877 brown bears in Sweden (Kindberg and Swenson, 2018) and 2291 in Finland (Heikkinen and Kojola, 2018) and a minimum number of 125 individuals in Norway (Fløystad et al., 2018).

During the recovery process, and despite indications of long-distance dispersal of individuals (Støen et al., 2006; Manel et al., 2007), several studies reported considerable genetic differentiation among brown bears from the Scandinavian and Karelian population. The largest differentiation was found between the brown bears from Scandinavia and individuals from Finland and northwestern Russia (Schregel et al., 2012; Kopatz et al., 2014; Schregel et al., 2015). Numerous studies have assessed the genetic structure of the Scandinavian brown bear population and reported subdivision into southern, central and northern genetic clusters (Manel et al., 2004; Xenikoudakis et al., 2015; Schregel et al., 2017). Studies on the genetic structure of the Karelian population showed that it is subdivided into a northern and southern genetic cluster in Finland (Tammeleht et al., 2010; Kopatz et al., 2014), but the differentiation between these two units has been decreasing (Hagen et al., 2015), most likely as a result of considerable immigration of bears from Russia into the southern part of the population (Kopatz et al., 2014). Despite the quantity of studies assessing connectivity between Scandinavia and Karelia, a comprehensive analysis with continuous sampling has been lacking, especially across the crucial, transborder area between northern Sweden and northern Finland. Only a single study, analysing Y-haplotype diversity and distribution among male brown bears in northern Europe (Schregel et al., 2015), had samples from this area included. The results corroborated with earlier studies and showed strong genetic differentiation and low connectivity between the

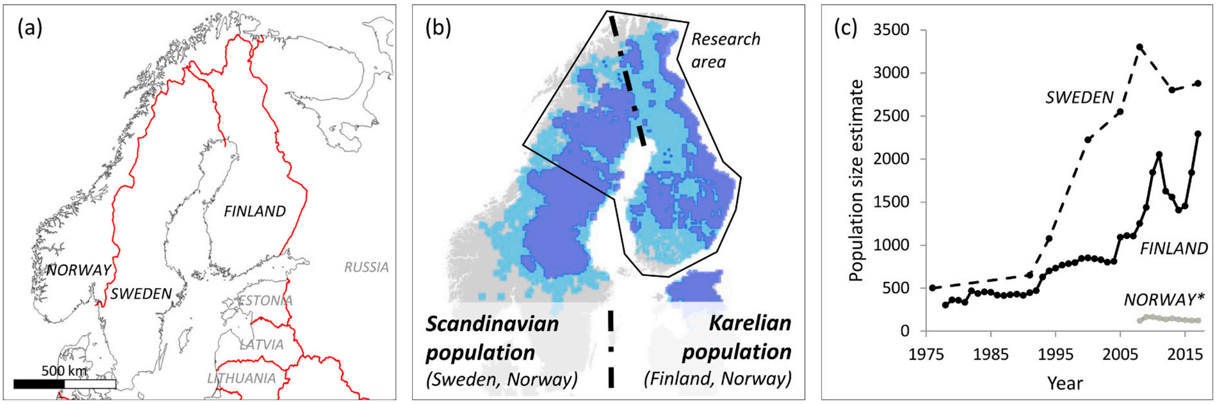

Fig. 1. Study area, distribution and estimated population sizes for the brown bear in northern Europe. a) A map of northern Europe indicating b) the current distribution of the Scandinavian and Karelian brown bear population: permanent (dark blue) and occasional presence (light blue; map by Large Carnivore Initiative for Europe, modified) and the research area outlined. Previously described population border (Chapron et al., 2014) is indicated by a black, dotted line. c) Trajectory of the estimated number of individuals in Sweden 1976–2017 (dotted), Finland 1978–2017 (solid) and minimum number* for Norway 2008–2017 (grey) based on harvest and genetic sampling.

populations from Scandinavia and Karelia.

Given the substantial increase in population size and the associated range expansion of both brown bear populations (Chapron et al., 2014), as well as the dispersal capacity of male brown bears (Bartoń et al., 2019), it is surprising that earlier studies have shown such low levels of connectivity. Therefore, we designed a study focusing exclusively on the dispersing sex with continuous sampling of male brown bears from large parts of Fennoscandia. In total, we analyzed autosomal microsatellites and Y chromosome haplotypes of 924 males, sampled during a period of 12 years (2005–2017), representing the upper limit of one brown bear generation (Tallmon et al., 2004). Our main objective was to address whether inter-population and transborder connectivity has been restored by measuring gene flow, and to estimate the number of migrants. Specifically, we tested if migration surpasses the one-migrant-per-generation rule. That number is the suggested lower limit on the number of reproducing migrants required to counter negative effects of reduced genetic variation caused by isolation in small populations (Mills and Allendorf, 1996), and is also the minimum conservation goal in the current Swedish brown bear management plan if the estimated population size in the country would decrease below 2350 individuals (Naturvårdsverket, 2016).

2. Material and methods

2.1. Data collection and molecular analyses

We used 12 microsatellite genotypes from 924 individuals. Most individuals were sampled noninvasively, but some were genotyped from tissue samples of legally harvested brown bears from northern Sweden, Norway and Finland. Of the total amount, 32 individuals were genotyped with eight microsatellites, instead of twelve. Of the 924 sampled individuals, 826 individuals were also genotyped at nine Y-chromosomal microsatellite loci (see Appendix A Supplementary data, Table S1). Aligning with data collection patterns and previous studies, samples of brown bears from Sweden and Norway, i.e. Scandinavia, were grouped administratively, by county: Västerbotten, Norrbotten, Troms and Finnmark. In Finland, we grouped the samples based on latitude into northern and southern Finland with the 65° latitude as separator line. The northern part approximately represents the reindeer husbandry area in Finland, a partly fenced area for semi-domestic reindeer to roam freely during summer, where special legislation for large predator removal is keeping the population density for large carnivores to a minimum (Fig. S1).

The tissue samples for DNA analysis were collected from dead animals, harvested legally and provided by the National Veterinary Institute of Sweden and the Natural Resources Institute Finland. No ethics permissions were required, as sample collection of tissue and noninvasive samples did not involve live animals and was performed by the respective national monitoring authorities of Sweden, Finland and Norway.

2.2. Genetic structure

We used a discriminant (DAPC) as well as spatial principal components analysis (sPCA) method in the package ADEGENET (Jombart, 2008) in R 3.5.2 (R Development Core Team, 2019) to quantify the population genetic structure (see Appendix A Supplementary data). DAPC and sPCA apply multivariate clustering in which individual genotypes are grouped by genetic similarity to visualize hierarchical structure not assuming any specific population genetic model or arbitrarily defined populations (Jombart et al., 2010). We ran the software STRUCTURE (Pritchard et al., 2000) to identify population genetic clusters (see Appendix A Supplementary data). In STRUCTURE it is assumed that within populations, the loci are at Hardy-Weinberg equilibrium and linkage equilibrium. We estimated pairwise F_{ST} (Weir and Cockerham, 1984) among the identified genetic clusters with the program ARLEQUIN version 3.5.2.2 (Excoffier and Lischer, 2010).

2.3. Gene flow and migration

We assessed connectivity among the geographic regions by estimating self-recruitment and directional gene flow with the program BAYESASS Version 3 (Wilson and Rannala, 2003). The algorithm applies a Bayesian, non-equilibrium population assignment method to reveal recent, unidirectional gene flow among populations. BAYESASS estimates the posterior probability of each genotype's migration-history (see Appendix A Supplementary data). The effective number of migrants per generation was estimated for Norrbotten and Finland by multiplying the migration rate with the estimated population size, as effective sizes were not available (Kindberg and Swenson, 2017; Heikkinen and Kojola, 2018; Kindberg and Swenson, 2018). We repeated the BAYESASS-analysis for brown bears sampled 2007–2012 and 2013–2017 in Norrbotten, Troms, Finnmark and northern Finland in order to have even sample sizes between groups to test whether there may have been a trajectory of migration on a temporal scale. We also used the private allele method (Slatkin, 1985) included in the program GENEPOP (Rousset, 2008) to estimate the effective number of migrants among the regions per generation, and specifically between Norrbotten and Finland. In addition, we estimated the number of migrants between the identified genetic clusters in Norrbotten and Finland by applying Wright's statistics (Wright, 1949) and utilizing the pairwise F_{ST}-results.

2.4. Distribution of male lineages

We used previously published Y-haplotypes (Schregel et al., 2015) and newly genotyped samples to assess the distribution of male lineages across the study area using eight Y microsatellite markers (see Appendix A Supplementary data).

3. Results

3.1. Genetic structure

The mean likelihood of Bayesian clustering was not conclusive for a specific number of clusters (see Appendix A Supplementary data, Fig. S2). The approaches by Evanno et al. (2005) suggested $K = 2$ (Fig. S3) and Puechmaille (2016) suggested $K = 4$ as the most likely number of genetic clusters (Fig. S4). The bar plots illustrating the assignment of each genotype for the clusters $K = 2$ to $K = 5$ are shown in Fig. S5. Based on previous studies assessing the genetic population structure of brown bears in northern Europe, $K = 2$ as well as $K = 4$ number of genetic clusters are representative of the hierarchical genetic subdivision present. $K = 2$ clusters highlights the east-west division, Scandinavia vs. Karelia, while the substructure with $K = 4$ clusters is representative of further genetic differentiation within the main clusters, namely Västerbotten, Norrbotten/Troms in Scandinavia versus northern Finland/Finnmark and southern Finland in Karelia (Fig. 2a, Figs. S6, S7). While most genotypes of the clusters showed a large degree of geographical grouping (northern Karelia), distribution of genotypes also displayed clear spatial overlap (northern Karelian and northern Scandinavian, northern and southern Karelian population; Fig. 2b). Genotypes sampled in Västerbotten, Troms, Finnmark and southern Finland were mainly assigned to one genetic cluster. Overall, we found 72 (7.79%) genotypes with mixed ancestry and thus ambiguous cluster assignment ($q < 0.7$). In Scandinavia, we identified six genotypes assigned to genetic clusters in Karelia. Another five genotypes sampled in Scandinavia were not clearly assigned but showed higher assignment values (q) for Karelian origin. We found 20 genotypes in the Karelian population, which originated from Scandinavia, plus six admixed genotypes with a higher assignment for Scandinavia (Fig. 2a, Fig. S7). Overall, the differentiation among the genetic clusters showed moderate but significant pairwise F_{ST}-values; $F_{ST} = 0.09$ between Norrbotten/

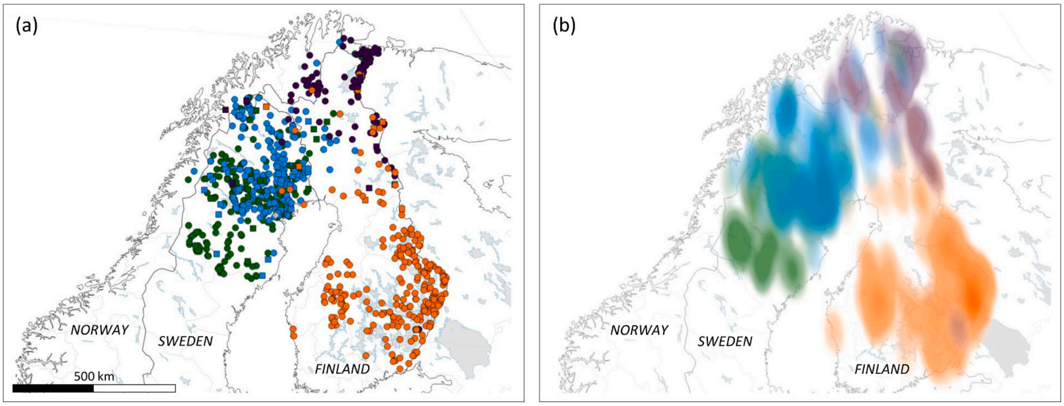

Fig. 2. Genetic population structure of the analyzed male brown bears. a) Locations of the male microsatellite genotypes and their assignment to a genetic cluster. Colors correspond to $K = 4$ clusters (see also Figs. S6 and S7). Genotypes with unambiguous assignment values ($q \geq 0.7$) are shown in circles, admixed genotypes ($q < 0.7$) as squares, and b) displaying the left figure as a heatmap to illustrate geographic distribution and density of individuals representing each of the genetic clusters.

Troms and northern Finland/Finnmark in the transborder area (Table S2).

The DAPC- and sPCA-analysis showed a very similar picture of the genetic clustering among brown bears. In the DAPC, genotypes from individuals collected in Scandinavia overlapped and grouped closely together (Fig. S8), whereas genotypes sampled in Karelia formed three other clusters with considerable overlap. Also, genotypes from northern Karelia and northern Scandinavia showed substantial overlap, suggesting connectivity among neighboring populations of brown bears in the study area. The Monte Carlo simulations of the sPCA suggested highly significant global structure ($p < 0.001$) and an absence of local structure ($p = 0.656$) and indicated distinct hierarchical clustering. The first four global PCs were retained as they had the greatest differentiation between eigenvalues relative to the rest (Fig. 3). No local PCs were retained. The first PC indicated a strong east-west divide, i.e. Scandinavian vs. Karelian population, however, with individuals at the western edge in northern Finland showing higher similarity to the Scandinavian population (Fig. 3a). The second PC indicated a strong north-south divide close to Sweden's northern border and along that latitude (Fig. 3b). The three PCs with the Scandinavian, northern and southern Karelian assigned genotypes are represented in the color plot and illustrate the immigration of individuals from Scandinavia into northern Finland, with more genotypes of Scandinavian origin found in northern Norway and Finland (Fig. 3c).

3.2. Gene flow and migration

All runs with BAYESASS were consistent and convergent (Table 1, Figs. S9, S10) and showed that self-recruitment was lowest in northern Finland with 68% and Troms with 82%. High self-recruitment was found with about 89% in Norrbotten, 91% in Västerbotten, 93% in Finnmark and 98% in southern Finland. While we estimated about 8% influx per generation from Norrbotten into northern Finland, the influx from northern Finland into Norrbotten was 0.1%. The results show that Norrbotten receives about 0.3% of genes from Finnmark and 0.6% from southern Finland, which sums up to 1% of influx of eastern genotypes into Norrbotten per generation. Relatively high rates of immigration were estimated for Troms with approximately 9% from Norrbotten, 4% from Finnmark and 1% from northern Finland per generation. Northern Finland also seemed to receive considerable gene flow from several directions. In addition to Norrbotten (8%), high rates of gene flow were also estimated from Finnmark and southern Finland (12% and 9%, respectively). On a temporal scale gene flow between Norrbotten and northern Finland appeared stable with low influx of bears from Finland to Sweden. Gene flow from the east to the west further north, however, may have increased, as suggested by the directional migration rates from northern Finland and Finnmark into Troms (Table S3).

We identified 8 migrants (four F0- and four F1-migrants) from the Karelian population in Scandinavia and 24 migrants (15 F0- and 9 F1-

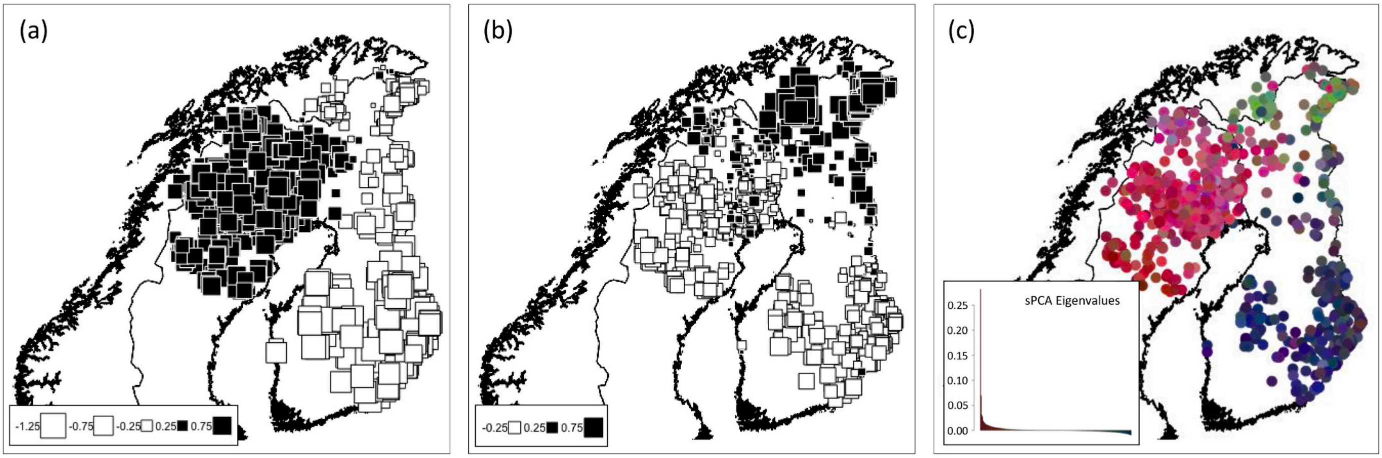

Fig. 3. Spatial Principal Component Analysis (sPCA) of the analyzed male brown bears. a) sPCA 1 displaying the east-west divide while b) sPCA 2 shows the north-south divide. Both sPCAs represent genetic differentiation on the global scale while c) the third sPCA shows little sub-differentiation within the Scandinavian and Karelian population, at the local scale.

Table 1

Percentage of self-recruitment and directional migration of male brown bears in northern Europe. Self-recruitment estimates are presented in the diagonal cells (in bold), directional migration estimates are given above and below the diagonal including standard deviations (*SD*) among the regions; incl. Västerbotten (VB), Troms (TR), Norrbotten (NB), northern Finland (NF), Finnmark (FM) and southern Finland (SF).

			Population											
			Scandinavian						Karelian					
			From VB	*SD*	From TR	*SD*	From NB	*SD*	From NF	*SD*	From FM	*SD*	From SF	*SD*
Population	Scandinavian	To VB	**0.906**	*0.024*	0.006	*0.006*	0.073	*0.024*	0.005	*0.005*	0.005	*0.005*	0.005	*0.005*
		To TR	0.018	*0.016*	**0.823**	*0.038*	0.093	*0.037*	0.012	*0.011*	0.043	*0.021*	0.011	*0.011*
		To NB	0.082	*0.013*	0.018	*0.005*	**0.891**	*0.014*	0.001	*0.001*	0.003	*0.002*	0.006	*0.002*
	Karelian	To NF	0.010	*0.008*	0.011	*0.007*	0.083	*0.017*	**0.680**	*0.011*	0.125	*0.022*	0.091	*0.019*
		To FM	0.004	*0.003*	0.013	*0.006*	0.019	*0.008*	0.031	*0.013*	**0.931**	*0.015*	0.004	*0.004*
		To SF	0.002	*0.002*	0.002	*0.002*	0.002	*0.002*	0.008	*0.006*	0.002	*0.002*	**0.983**	*0.007*

Standard deviations (*SD*) in italics.

migrants) from Scandinavia were identified in the Karelian population (Tables S4, S5). Estimates of the number of brown bears in the region reported 463–549 brown bears in Norrbotten and 326–415 bears in northern Finland (reindeer-husbandry area) and 1965–2279 bears in the southern part of Finland (Kindberg and Swenson, 2017; Heikkinen and Kojola, 2018). Based on these numbers and our estimates of gene flow, Norrbotten received 0.46–0.55 effective immigrants from northern Finland, 1.39–1.65 bears from Finnmark, and, 2.78–3.29 bears from southern Finland per generation. The total sum of brown bears immigrating from the neighboring populations in the east to Norrbotten thus adds up to 4.6–5.5 individuals effectively per generation. In the opposite direction, from Norrbotten, 27.1–34.5 bears immigrate into northern Finland and 3.9–4.6 bears into southern Finland per generation.

The private allele method estimated $Nm = 1.70$ as the effective number of migrants between Norrbotten and northern Finland (Table S6). The number of effective migrants between southern Finland and Norrbotten was $Nm = 0.57$ and between Finnmark and Norrbotten $Nm = 1.05$ bears. When comparing only Norrbotten and the whole of Finland, $Nm = 1.27$ was the estimated effective number of migrants. Based on the pairwise F_{ST}-values the estimate of the effective number of migrants between the genetic cluster of Norrbotten/Troms versus northern Finland/Finnmark was $Nm = 2.53$ and between Norrbotten/Troms and southern Finland $Nm = 1.67$.

3.3. *Distribution of male lineages*

Based on the eight Y chromosome microsatellites, we identified a total of 28 different haplotypes, of which seven (five in Karelia, two in Scandinavia) had not been detected previously (Fig. 4, Fig. S11). The Karelian population displayed a high diversity of Y-haplotypes with 26 haplotypes identified, while we found only six haplotypes present in Scandinavia. Six individuals carrying haplotype 2.07 and 1.01, previously detected only in Karelia, were sampled in Norrbotten and Troms. One haplotype previously detected only in the Russian Republic of Komi (haplotype 2.28; Schregel et al., 2015), was detected in an individual sampled in Troms. Haplotypes 2.05 and 2.08 were dominant in the Scandinavian population and we found 20 individuals carrying haplotype 2.05 in Finland and 10 in Finnmark (Fig. 4a). Also, we identified four individuals with haplotype 2.08 in northern Finland, suggesting gene flow from Scandinavia into the Karelian population (Fig. 4b).

4. Discussion

The successful recovery and range expansion of the Karelian and Scandinavian brown bear populations led to the restoration of the once lost connectivity and we identified individuals migrating from Karelia to Scandinavia for the first time. Connectivity and gene flow were asymmetric with a higher immigration rate of individuals from Scandinavia to Karelia than the opposite direction. The analysis of male lineages supported these results with comparably more brown bears carrying distinctive haplotypes from Scandinavia that were identified in the Karelian population than vice versa.

Overall, the genetic structure was characterized by a distinctive and strong east-west-subdivision between the brown bear populations of Scandinavia and Karelia. The north-south division within the Scandinavian and the Karelian population represents further, internal substructure with considerable geographical overlap (Figs. 2, 3, Figs. S6, S7) and has been documented by earlier studies. These suggest that the underlying genetic subdivision is still pronounced (Manel et al., 2004; Tammeleht et al., 2010; Kopatz et al., 2014; Schregel et al., 2017), likely caused by long-term historical-ecological processes (Xenikoudakis et al., 2015), and possibly also stabilized by the effect of regular, annual

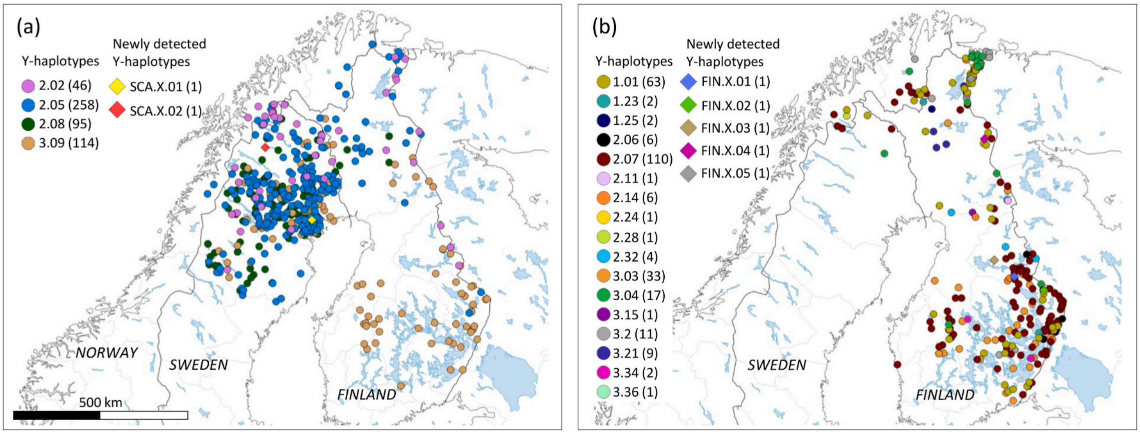

Fig. 4. Sampling locations of the brown bears carrying the different male Y-haplotypes found (number in brackets) in the study area. a) Scandinavian, with six different Y-haplotypes, and b) Karelian brown bear population, with a total of 26 different Y-haplotypes identified.

harvest in this largely human-dominated landscape (Klemen and Adamic, 2008; Krofel et al., 2012; Kojola et al., 2020). This indicates a possibly time-lagged response to population expansion (Ewers and Didham, 2006). Our results showed higher values for immigration from the two expanding populations since the previous assessment, where immigration of eight brown bears from Scandinavia into the Karelian population was reported (Kopatz et al., 2014). However, in the latter and another previous study (Schregel et al., 2012), connectivity between Scandinavia and Finland has not been assessed with continuous sampling suggesting that an earlier reconnection may have been missed. In addition, our results suggest a migration corridor through the northernmost parts of Norway as a few individuals from Troms were assigned to Karelia and some in Finnmark were assigned to Scandinavia by microsatellite as well as Y chromosome data. Genetic differentiation in our study was also slightly lower compared to the numbers reported in an earlier study (Schregel et al., 2012). However, F_{ST} is determined based on the frequency of common alleles, which usually have been in the population already for many generations and therefore the method is reflective of long, historical time periods (Whitlock and McCauley, 1999; Yamamichi and Innan, 2012). Thus, the F_{ST} most likely retains the signal from the severe demographic bottleneck and subsequent separation experienced in the past rather than reflecting recent changes.

Recent, directional migration rates per generation were suggestive of asymmetrical gene flow between the Scandinavian and Karelian population. Considering the size of the populations, the estimated migration rates are rather low indicating that the successful restoration of connectivity is likely to be a relatively recent event. Estimates of gene flow based on the private allele method were lower than the estimates based on Bayesian analyses. Both estimates suggest recent establishment of connectivity, as private alleles in large populations have usually been introduced to the gene pool relatively recently, thus rare and therefore the method should be sensitive to contemporary migration (Slatkin and Takahata, 1985; Slatkin, 1987; Yamamichi and Innan, 2012). Albeit low and stable across the study period, the level of gene flow from the Karelian population into Scandinavia surpassed the suggested one-migrant-per-generation rule and thus meets the minimum conservation goal (Mills and Allendorf, 1996; Wang, 2004; Naturvårdsverket, 2016).

Connectivity enables gene flow between populations, thereby increasing genetic variation and the ability of a population to react to a changing environment. This is especially important for small and fluctuating populations as they often require a higher number of migrants for successful, long-term connectivity and enhancement of genetic diversity (Vucetich and Waite, 2000; Greenbaum et al., 2014). However, the brown bear population size in northern Europe has been increasing steadily for two decades, with a current estimate of more than 5000 bears (Heikkinen and Kojola, 2018; Kindberg and Swenson, 2018). As such, one reproducing migrant per generation in both directions should ensure the maintenance of genetic variation and long-term viability of Fennoscandian populations (Frankham, 2005). For deeper assessment on the asymmetry of dispersing individuals, spatially explicit methods should be applied to understand the potential effects of environmental features and landscape resistance (Elliot et al., 2014; Oriol-Cotterill et al., 2015) on connectivity. We found several F1-migrants indicating successful reproduction of immigrants in both populations. Therefore, data from female brown bears should be included in future analyses, as the detected gene flow should lead to juvenile females with mixed ancestry (Vasudev and Fletcher Jr, 2016; Robertson et al., 2018). An analysis that explicitly combines genetic and geographical information would give further important insights, enabling further investigation of connectivity across northern Europe.

The uneven distribution of Y-haplotypes corresponded to the asymmetric gene flow identified. An earlier study assessing the Y-haplotype distribution of brown bears across northern Europe and northwestern Russia (Schregel et al., 2015) detected four different Y-haplotypes in Scandinavia, of which, two were distinctive for brown bears in Scandinavia and two were found across Fennoscandia (Schregel et al., 2015). Our results further reveal that migration of Scandinavian brown bears into the northern Karelian population occurred. Additionally, we identified seven new haplotypes, five of which were found in the Karelian population and two in Scandinavia. The striking difference in haplotype diversity between the Scandinavian and Karelian population is highly suggestive of differing population histories and recovery processes. The Karelian population is supported by a large influx of bears from Russia (Kopatz et al., 2014) and this strong connection seems consistent over several decades as indicated by records of observed border crossings of individuals from Russia to Finland (Pullianen, 1990). The Scandinavian population on the other hand seems to have primarily recovered independently from the Karelian population as indicated by the prominent genetic structure and low variation of Y-haplotypes present. Nonetheless, two haplotypes are shared between both populations and, although rare, single immigration events from Karelia to Scandinavia may have occurred in the past. Further investigation into this is warranted and can be achieved by genotyping historical samples (Schregel et al., 2015; Xenikoudakis et al., 2015).

Earlier studies on the matrilineal phylogeography of brown bears in northern Europe identified two highly divergent clades: bears from northern Scandinavia and Karelia belonging to the eastern lineage and bears from southern Scandinavia belonging to the western clade (Taberlet and Bouvet, 1994; Taberlet et al., 1995; Davison et al., 2011; Ersmark et al., 2019). Our study did not include samples from the southern part of the Scandinavian population. Nonetheless, previous mtDNA-analyses and mitogenomic data showed differences in haplotype diversity between Scandinavia and Finland and genetic substructure, similar to the subdivision identified by autosomal markers and explained by natal philopatry of female bears (Saarma et al., 2007; Keis et al., 2013; Norman et al., 2013; Xenikoudakis et al., 2015). Due to the pronounced display of philopatry by female bears (Swenson et al., 1998; Støen et al., 2006), we focused in our study on the dispersing sex in order to be able to identify gene flow and individual migrants. A targeted study, assessing maternal lineages may however illuminate the role and challenges of female bears in the region, especially within the contact zone.

Asymmetric connectivity is not uncommon, especially between transboundary populations that are managed differently (Beger et al., 2010; Sundqvist et al., 2016; Thornton et al., 2018). However, the reasons for the asymmetry in our study remains underexplored and is likely related to varying brown bear densities in Scandinavia and Karelia, specifically in the zone connecting both populations, namely the neighboring areas of Norrbotten in northern Sweden and the reindeer husbandry region in northern Finland. No density estimates from these regions are available, however, estimates on population sizes resulted in a higher number of individuals in northern Sweden and may indicate a higher density of bears compared to the reindeer husbandry area in northern Finland (Heikkinen and Kojola, 2018; Kindberg and Swenson, 2018). While the number of bears in Sweden are kept stable with regulated hunting quotas, the number of bears in the Finnish reindeer husbandry area is kept to a minimum due to special management and legislation for large carnivore removal to counter damages by predation on semi-domestic reindeer (Kojola and Heikkinen, 2006; Kopatz et al., 2012; Kojola et al., 2020). Also, brown bears in northern Finland have been less frequently observed than in central and eastern Finland (Kojola et al., 2006), partly due to the low density of volunteers and lack of will among reindeer herders to actively contribute to the large carnivore observation network (Rasmus et al., 2020). Nonetheless, the data available suggests a much lower density of brown bears, especially of females that could produce migrating males, in that region, reflected in the relatively low self-recruitment rate for northern Finland. The Finnish reindeer husbandry area has therefore been characterized as a peripheral part of the Finnish brown bear population (Kojola et al., 2020). From these lines of evidence, it appears that the possibility of migration and thus gene flow between Karelia and Scandinavia through this area seems rather limited. All knowledge considered indicates that the reindeer husbandry region can be characterized as a sink-area with constant removal of individuals (Lowe and Allendorf, 2010; Stoner et al., 2013). However, this area is receiving migrants compensating for low local recruitment with bears from the neighboring regions of higher bear densities and stable populations in Sweden, Norway and likely Russia as well as the expanding population in southern Finland (Kojola et al., 2003; Kindberg et al., 2011; Hagen et al., 2015). Source-sink-dynamics in the northern European brown bear should be investigated further through analyses of individual dispersal and migration of also female bears.

The process of population recovery from the severe demographic and genetic bottleneck (Swenson et al., 1998; Kopatz et al., 2014; Xenikoudakis et al., 2015) seems to have begun earlier in the Scandinavian population (Fig. 1a; Swenson et al., 2017), and thus allowed the expansion front to reach the boundary areas to the east sooner, therefore enabling earlier immigration of individuals into the Karelian population (Kopatz et al., 2014). This earlier start might now be reflected in the asymmetrical migration rates, with more individuals from Scandinavia entering Karelia. The Karelian brown bear population has also been recovering as suggested by an increasing estimated population size and expansion towards the west since the early 2000s (Kojola et al., 2006; Kojola and Heikkinen, 2006). Based on our results, the Karelian expansion front is only presently reaching northern Scandinavia and is represented by a few Karelian individuals detected in northern Scandinavia (Hagen et al., 2015; Kopatz et al., 2017).

4.1. *Implications for conservation management*

Brown bears are capable of long-distance dispersal (Bartoń et al., 2019). However, due to a high conflict level with humans, and potentially substantial environmental and climatic changes, large carnivore populations will remain vulnerable and continued responsive management and conservation is therefore necessary (Heller and Zavaleta, 2009; Hoffmann et al., 2011; Ripple et al., 2014; Haddad et al., 2015; Iftekhar and Pannell, 2015; Bar-On et al., 2018). Also the brown bear's reproductive rate is sensitive to high harvest quotas (Bischof et al., 2018), therefore the populations should be closely monitored and carefully managed. A next step could be the development of a collaborative, regular transborder monitoring and management program across northern Europe (Liu et al., 2020; Mason et al., 2020), taking scale-dependent processes into account, such as inter-population but also local and intra-population processes (Kool et al., 2012). Here specifically, the establishment of a DNA-based monitoring program including regular sampling of non-invasive genetic material and assessment of the brown bear population in Finland, as is currently applied in Sweden and Norway, would enable close monitoring of the whole Fennoscandian population, and with that, allowing for further study on the trajectory of the recently established connectivity including the number of immigrants. Indeed, such an approach would enable continuous assessment of migration and if it remains sufficient, which is important as a single effective migrant per generation may not be sufficient to counter possible negative genetic effects (Nathan et al., 2017). Prioritization of such an effort would also contribute with important data for management decisions to protect family groups in the Finnish reindeer husbandry area (Kojola et al., 2020) and give valuable insights into population expansion dynamics.

5. Conclusions

Genetic data enabled us to study and quantify population level processes across political borders of three nations with different management regimes. Without genetic information and use of several methods, such an assessment would be challenging. We achieved continuous sampling in the study area through intensified and focused sampling of the dispersing sex allowing us to assess gene flow effectively. Our research took advantage of regular and harmonized DNA-based brown bear monitoring in Sweden and Norway and illustrates its benefits for large scale transborder assessment of wildlife populations (Cayuela et al., 2018; Lamb et al., 2019) and how standardized genetic tools allow transnational evaluation of conservation and management actions (McMahon et al., 2014; Ralls et al., 2018; Liu et al., 2020; Mason et al., 2020). Our study highlights that conservation-driven management can lead to successful population recovery and restoration of connectivity for fragmented populations, including those of large carnivores.

CRediT authorship contribution statement

J.K. and Ø.F. conceived the study; A.K., O.K., J.K. and Ø.F. designed the study and together with A.N. and G.S. analyzed the data. I.K., J.A., G. S., N.G., L.D., I.F., S.H. contributed to sample and data collection. A.K., O.K., J.K. and Ø.F. led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

Data archiving statement

Georeferenced genotype data based on microsatellite markers and Y-chromosomal microsatellite markers for this study is available at the Dryad depository under the following URL: https://doi.org/10.5061/dryad.bk3j9kd9p.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding was provided by the Swedish Environmental Protection Agency and the Norwegian Environment Agency. We would like to thank Per Sjögren-Gulve for his support and Gernot Segelbacher, Rodolfo Jaffé, Marco Apollonio and two anonymous reviewers for valuable and constructive feedback. We further would like to thank Line Birkeland Eriksen, Hege Brandsegg, Merethe Hagen Spets and Sten Even Erlandsen (Norwegian Institute for Nature Research) as well as Rasa Bukontaite and Thomas Källman (Swedish Museum of Natural History) for the laboratory analyses, Sanna Kokko and Anita Kentällä (Natural Resources Institute Finland) and Henrik Brøseth (Rovdata) for support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108936.

References

Allendorf, F.W., Hohenlohe, P.A., Luikart, G., 2010. Genomics and the future of conservation genetics. Nat. Rev. Genet. 11, 697–709. https://doi.org/10.1038/nrg2844.

Bar-On, Y.M., Phillips, R., Milo, R., 2018. The biomass distribution on earth. Proc. Natl. Acad. Sci. 115, 6506. https://doi.org/10.1073/pnas.1711842115.

Bartoń, K.A., Zwijacz-Kozica, T., Zięba, F., Sergiel, A., Selva, N., 2019. Bears without borders: long-distance movement in human-dominated landscapes. Glob. Ecol. Conserv. 17, e00541 https://doi.org/10.1016/j.gecco.2019.e00541.

Beger, M., Linke, S., Watts, M., Game, E., Treml, E., et al., 2010. Incorporating asymmetric connectivity into spatial decision making for conservation. Conserv. Lett. 3, 359–368. https://doi.org/10.1111/j.1755-263X.2010.00123.x.

Bischof, R., Brøseth, H., Gimenez, O., 2016. Wildlife in a politically divided world: insularism inflates estimates of brown bear abundance. Conserv. Lett. 9, 122–130. https://doi.org/10.1111/conl.12183.

Bischof, R., Bonenfant, C., Rivrud, I.M., Zedrosser, A., Friebe, A., et al., 2018. Regulated hunting re-shapes the life history of brown bears. Nat. Ecol. Evol. 2, 116–123. https://doi.org/10.1038/s41559-017-0400-7.

Broquet, T., Petit, E.J., 2009. Molecular estimation of dispersal for ecology and population genetics. Annu. Rev. Ecol. Evol. Syst. 40, 193–216. https://doi.org/10.1146/annurev.ecolsys.110308.120324.

Cayuela, H., Rougemont, Q., Prunier, J.G., Moore, J.-S., Clobert, J., et al., 2018. Demographic and genetic approaches to study dispersal in wild animal populations: a methodological review. Mol. Ecol. 27, 3976–4010. https://doi.org/10.1111/mec.14848.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553%JScience.

Curry-Lindahl, K., 1972. The brown bear (*Ursus arctos*) in Europe: decline, present distribution, biology and ecology. In: Bears: Their Biology and Management. IUCN Publications New Series, Calgary, pp. 74–80.

Dalerum, F., Cameron, E.Z., Kunkel, K., Somers, M.J., 2009. Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biol. Lett. 5, 35–38. https://doi.org/10.1098/rsbl.2008.0520.

Dallimer, M., Strange, N., 2015. Why socio-political borders and boundaries matter in conservation. Trends Ecol. Evol. 30, 132–139. https://doi.org/10.1016/j.tree.2014.12.004.

Davison, J., Ho, S.Y.W., Bray, S.C., Korsten, M., Tammeleht, E., et al., 2011. Late-Quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. Quat. Sci. Rev. 30, 418–430. https://doi.org/10.1016/j.quascirev.2010.11.023.

Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., et al., 2014. The trajectory of dispersal research in conservation biology. Systematic review. PLoS One 9, e95053. https://doi.org/10.1371/journal.pone.0095053.

Elgmork, K., 1994. The decline of a brown bear *Ursus arctos* L. population in central South Norway. Biol. Conserv. 69, 123–129. https://doi.org/10.1016/0006-3207(94)90051-5.

Elliot, N.B., Cushman, S.A., Macdonald, D.W., Loveridge, A.J., Pettorelli, N., 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. J. Appl. Ecol. 51, 1169–1178. https://doi.org/10.1111/1365-2664.12282.

Ersmark, E., Baryshnikov, G., Higham, T., Argant, A., Castaños, P., et al., 2019. Genetic turnovers and northern survival during the last glacial maximum in European brown bears. Ecol. Evol. 9, 5891–5905. https://doi.org/10.1002/ece3.5172.

Evanno, G., Regnaut, S., Goudet, J., 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. Mol. Ecol. 14, 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117–142. https://doi.org/10.1017/S1464793105006949.

Excoffier, L., Lischer, H.E.L., 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10, 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x.

Fischer, M.L., Salgado, I., Beninde, J., Klein, R., Frantz, A.C., et al., 2017. Multiple founder effects are followed by range expansion and admixture during the invasion process of the raccoon (*Procyon lotor*) in Europe. Divers. Distrib. 23, 409–420. https://doi.org/10.1111/ddi.12538.

Flagstad, Ø., Walker, C.W., Vilà, C., Sundqvist, A.K., Fernholm, B., et al., 2003. Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. Mol. Ecol. 12, 869–880. https://doi.org/10.1046/j.1365-294X.2003.01784.x.

Flagstad, Ø., Hedmark, E.V.A., Landa, A., Brøseth, H., Persson, J., et al., 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. Conserv. Biol. 18, 676–688. https://doi.org/10.1111/j.1523-1739.2004.00328.x-i1.

Fløystad, I., Brøseth, H., Banken Bakke, B., Eiken, H.G., Hagen, S.B., 2018. In: naturforskning, N.i.f. (Ed.), Populasjonsovervåking av brunbjørn. DNA-analyse av prøver innsamlet i Norge i 2017. Norsk institutt for naturforskning, Trondheim, p. 65.

Frankham, R., 2005. Genetics and extinction. Biol. Conserv. 126, 131–140. https://doi.org/10.1016/j.biocon.2005.05.002.

Frantz, A.C., Cellina, S., Krier, A., Schley, L., Burke, T., 2009. Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? J. Appl. Ecol. 46, 493–505. https://doi.org/10.1111/j.1365-2664.2008.01606.x.

Gervasi, V., Linnell, J.D.C., Brøseth, H., Gimenez, O., 2019. Failure to coordinate management in transboundary populations hinders the achievement of national management goals: the case of wolverines in Scandinavia. J. Appl. Ecol. 56, 1905–1915. https://doi.org/10.1111/1365-2664.13379.

Greenbaum, G., Templeton, A.R., Zarmi, Y., Bar-David, S., 2014. Allelic richness following population founding events – a stochastic modeling framework incorporating gene flow and genetic drift. PLoS One 9, e115203. https://doi.org/10.1371/journal.pone.0115203.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., et al., 2015. Habitat fragmentation and its lasting impact on earth's ecosystems. Sci. Adv. 1, e1500052 https://doi.org/10.1126/sciadv.1500052.

Hagen, S.B., Kopatz, A., Aspi, J., Kojola, I., Eiken, H.G., 2015. Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. Proc. R. Soc. Lond. B Biol. Sci. 282, 20150092. https://doi.org/10.1098/rspb.2015.0092.

Heikkinen, S., Kojola, I., 2018. Suomen karhukannan tila ja pentuetuotto 2017, p. 8 pages. (Luke).

Hellborg, L., Walker, C.W., Rueness, E.K., Stacy, J.E., Kojola, I., et al., 2002. Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrial DNA analysis. Conserv. Genet. 3, 97–111. https://doi.org/10.1023/A:1015217723287.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142, 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Hoffmann, M., Belant, J.L., Chanson, J.S., Cox, N.A., Lamoreux, J., et al., 2011. The changing fates of the world's mammals. Philos. Trans. R. Soc. B Biol. Sci. 366, 2598–2610. https://doi.org/10.1098/rstb.2011.0116.

Iftekhar, M.S., Pannell, D.J., 2015. "Biases" in adaptive natural resource management. Conserv. Lett. 8, 388–396. https://doi.org/10.1111/conl.12189.

Jombart, T., 2008. adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129.

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. https://doi.org/10.1186/1471-2156-11-94.

Keis, M., Remm, J., Ho, S.Y.W., Davison, J., Tammeleht, E., et al., 2013. Complete mitochondrial genomes and a novel spatial genetic method reveal cryptic phylogeographical structure and migration patterns among brown bears in north-western Eurasia. J. Biogeogr. 40, 915–927. https://doi.org/10.1111/jbi.12043.

Kindberg, J., Swenson, J.E., 2017. Björnstammens storlek i Norrbottens län 2016, p. 6 pages. Skandinaviska björnprojektet.

Kindberg, J., Swenson, J.E., 2018. In: Björnprojektet, S. (Ed.), Björnstammens storlek i Sverige 2017. Skandinaviska björnprojektet, p. 6.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C., et al., 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. Wildl. Biol. 17, 114–123. https://doi.org/10.2981/10-100.

Klemen, J., Adamic, M., 2008. Fifty years of brown bear population expansion: effects of sex-biased dispersal on rate of expansion and population structure. J. Mammal. 89, 1491–1501.

Kojola, I., Heikkinen, S., 2006. Structure of expanded brown bear population at the edge of range in Finland. Ann. Zool. Fenn. 43, 258–262.

Kojola, I., Laitala, H.M., 2000. Changes in the structure of an increasing brown bear population with distance from core areas: another example of presaturation female dispersal? Ann. Zool. Fenn. 37, 59–64.

Kojola, I., Danilov, P.I., Laitala, H.M., Belkin, V., Yakimov, A., 2003. Brown bear population structure in core and periphery: analysis of hunting statistics from Russian Karelia and Finland. Ursus 14, 17–20.

Kojola, I., Hallikainen, V., Nygren, T., Pesonen, M., Ruusila, V., 2006. Trends and harvest in Finland's brown bear population. Ursus 17, 159–164.

Kojola, I., Hallikainen, V., Heikkinen, S., Nivala, V., 2020. Has the sex-specific structure of Finland's brown bear population changed during 21 years? Wildl. Biol. 2020 https://doi.org/10.2981/wlb.00575.

Kool, J.T., Moilanen, A., Treml, E.A., 2012. Population connectivity: recent advances and new perspectives. Landsc. Ecol. 28, 165–185. https://doi.org/10.1007/s10980-012-9819-z.

Kopatz, A., Eiken, H.G., Hagen, S.B., Ruokonen, M., Esparza-Salas, R., et al., 2012. Connectivity and population subdivision at the fringe of a large brown bear (*Ursus arctos*) population in North Western Europe. Conserv. Genet. 13, 681–692. https://doi.org/10.1007/s10592-012-0317-2.

Kopatz, A., Eiken, H.G., Aspi, J., Kojola, I., Tobiassen, C., et al., 2014. Admixture and gene flow from Russia in the recovering Northern European brown bear (*Ursus arctos*). PLoS One 9, e97558. https://doi.org/10.1371/journal.pone.0097558.

Kopatz, A., Eiken, H.G., Schregel, J., Aspi, J., Kojola, I., et al., 2017. Genetic substructure and admixture as important factors in linkage disequilibrium-based estimation of effective number of breeders in recovering wildlife populations. Ecol. Evol. 7, 10721–10732. https://doi.org/10.1002/ece3.3577.

Krofel, M., Jonozovič, M., Jerina, K., 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. Ursus 23, 91–103. https://doi.org/10.2192/ursus-d-10-00013.1.

Laikre, L., Nilsson, T., Primmer, C.R., Ryman, N., Allendorf, F.W., 2009. Importance of genetics in the interpretation of favourable conservation status. Conserv. Biol. 23, 1378–1381. https://doi.org/10.1111/j.1523-1739.2009.01360.x.

Lamb, C.T., Ford, A.T., Proctor, M.F., Royle, J.A., Mowat, G., et al., 2019. Genetic tagging in the Anthropocene: scaling ecology from alleles to ecosystems. Ecol. Appl. 29, e01876 https://doi.org/10.1002/eap.1876.

Liu, J., Yong, D.L., Choi, C.-Y., Gibson, L., 2020. Transboundary frontiers: an emerging priority for biodiversity conservation. Trends Ecol. Evol. 2671, 1–12. https://doi.org/10.1016/j.tree.2020.03.004.

Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19, 3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x.

Manel, S., Bellemain, E., Swenson, J.E., François, O., 2004. Assumed and inferred spatial structure of populations: the Scandinavian brown bears revisited. Mol. Ecol. 13, 1327–1331. https://doi.org/10.1111/j.1365-294X.2004.02074.x.

Manel, S., Berthoud, F., Bellemain, E., Gaudeul, M., Luikart, G., et al., 2007. A new individual-based spatial approach for identifying genetic discontinuities in natural populations. Mol. Ecol. 16, 2031–2043. https://doi.org/10.1111/j.1365-294X.2007.03293.x.

Mason, N., Ward, M., Watson, J.E.M., Venter, O., Runting, R.K., 2020. Global opportunities and challenges for transboundary conservation. Nat. Ecol. Evol. 4, 694–701. https://doi.org/10.1038/s41559-020-1160-3.

McMahon, B.J., Teeling, E.C., Höglund, J., 2014. How and why should we implement genomics into conservation? Evol. Appl. 7, 999–1007. https://doi.org/10.1111/eva.12193.

Mills, L.S., Allendorf, F.W., 1996. The one-migrant-per-generation rule in conservation and management. Conserv. Biol. 10, 1509–1518. https://doi.org/10.1046/j.1523-1739.1996.10061509.x.

Nathan, L.R., Kanno, Y., Vokoun, J.C., 2017. Population demographics influence genetic responses to fragmentation: a demogenetic assessment of the 'one migrant per generation' rule of thumb. Biol. Conserv. 210, 261–272. https://doi.org/10.1016/j.biocon.2017.02.043.

Naturvårdsverket, 2016. Nationell förvaltningsplan för björn – Förvaltningsperioden 2014–2019. Naturvårdsverket (Swedish Environment Protection Agency), Stockholm, p. 106.

Norman, A.J., Street, N.R., Spong, G., 2013. De novo SNP discovery in the Scandinavian brown bear (*Ursus arctos*). PLoS One 8, e81012. https://doi.org/10.1371/journal.pone.0081012.

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124, 1263–1273. https://doi.org/10.1111/oik.02224.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945.

Puechmaille, S.J., 2016. The program structure does not reliably recover the correct population structure when sampling is uneven: subsampling and new estimators alleviate the problem. Mol. Ecol. Resour. 16, 608–627. https://doi.org/10.1111/1755-0998.12512.

Pullianen, E., 1990. Recolonization of Finland by the brown bear in the 1970s and 1980s. Aquilo Ser. Zool. 21–25.

R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ralls, K., Ballou, J.D., Dudash, M.R., Eldridge, M.D.B., Fenster, C.B., et al., 2018. Call for a paradigm shift in the genetic management of fragmented populations. Conserv. Lett. 11, e12412 https://doi.org/10.1111/conl.12412.

Rasmus, S., Kojola, I., Turunen, M., Norberg, H., Kumpula, J., et al., 2020. Mission impossible? Pursuing the co-existence of viable predator populations and sustainable reindeer husbandry in Finland. J. Rural Stud. https://doi.org/10.1016/j.jrurstud.2020.08.017.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. https://doi.org/10.1126/science.1241484.

Robertson, E.P., Fletcher, R.J., Cattau, C.E., Udell, B.J., Reichert, B.E., et al., 2018. Isolating the roles of movement and reproduction on effective connectivity alters conservation priorities for an endangered bird. Proc. Natl. Acad. Sci. 115, 8591. https://doi.org/10.1073/pnas.1800183115.

Rousset, F., 2008. genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Mol. Ecol. Resour. 8, 103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x.

Saarma, U., Ho, S.Y., Pybus, O.G., Kaljuste, M., Tumanov, I.L., et al., 2007. Mitogenetic structure of brown bears (*Ursus arctos* L.) in northeastern Europe and a new time frame for the formation of European brown bear lineages. Mol. Ecol. 16, 401–413. https://doi.org/10.1111/j.1365-294X.2006.03130.x.

Sæther, B.-E., Engen, S., Swenson, J.E., Bakke, Ø., Sandegren, F., 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. Oikos 83, 403–416. https://doi.org/10.2307/3546856.

Schregel, J., Kopatz, A., Hagen, S.B., Broseth, H., Smith, M.E., et al., 2012. Limited gene flow among brown bear populations in far Northern Europe? Genetic analysis of the east-west border population in the Pasvik Valley. Mol. Ecol. 21, 3474–3488. https://doi.org/10.1111/j.1365-294X.2012.05631.x.

Schregel, J., Eiken, H.G., Grøndahl, F.A., Hailer, F., Aspi, J., et al., 2015. Y chromosome haplotype distribution of brown bears (*Ursus arctos*) in Northern Europe provides insight into population history and recovery. Mol. Ecol. 24, 6041–6060. https://doi.org/10.1111/mec.13448.

Schregel, J., Kopatz, A., Eiken, H.G., Swenson, J.E., Hagen, S.B., 2017. Sex-specific genetic analysis indicates low correlation between demographic and genetic connectivity in the Scandinavian brown bear (*Ursus arctos*). PLoS One 12, e0180701. https://doi.org/10.1371/journal.pone.0180701.

Schwartz, M.K., McKelvey, K.S., 2008. Why sampling scheme matters: the effect of sampling scheme on landscape genetic results. Conserv. Genet. 10, 441. https://doi.org/10.1007/s10592-008-9622-1.

Schwartz, M.K., Luikart, G., Waples, R.S., 2007. Genetic monitoring as a promising tool for conservation and management. Trends Ecol. Evol. 22, 25–33. https://doi.org/10.1016/j.tree.2006.08.009.

Shafer, A.B.A., Wolf, J.B.W., Alves, P.C., Bergström, L., Bruford, M.W., et al., 2015. Genomics and the challenging translation into conservation practice. Trends Ecol. Evol. 30, 78–87. https://doi.org/10.1016/j.tree.2014.11.009.

Slatkin, M., 1985. Rare alleles as indicators of gene flow. Evolution 39, 53–65. https://doi.org/10.1111/j.1558-5646.1985.tb04079.x.

Slatkin, M., 1987. Gene flow and the geographic structure of natural populations. Science 236, 787–792. https://doi.org/10.1126/science.3576198.

Slatkin, M., Takahata, N., 1985. The average frequency of private alleles in a partially isolated population. Theor. Popul. Biol. 28, 314–331. https://doi.org/10.1016/0040-5809(85)90032-2.

Støen, O.-G., Zedrosser, A., Sæbø, S., Swenson, J.E., 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia 148, 356. https://doi.org/10.1007/s00442-006-0384-5.

Stoner, D.C., Wolfe, M.L., Mecham, C., Mecham, M.B., Durham, S.L., et al., 2013. Dispersal behaviour of a polygynous carnivore: do cougars *Puma concolor* follow source-sink predictions? Wildl. Biol. 19, 289–301. https://doi.org/10.2981/12-124.

Sundqvist, L., Keenan, K., Zackrisson, M., Prodöhl, P., Kleinhans, D., 2016. Directional genetic differentiation and relative migration. Ecol. Evol. 6, 3461–3475. https://doi.org/10.1002/ece3.2096.

Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R., et al., 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildl. Biol. 1 (11–25), 15.

Swenson, J.E., Sandegren, F., So-Derberg, A., 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. J. Anim. Ecol. 67, 819–826. https://doi.org/10.1046/j.1365-2656.1998.00248.x.

Swenson, J.E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R., et al., 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. Wildl. Biol. 2017 https://doi.org/10.2981/wlb.00251.

Taberlet, P., Bouvet, J., 1994. Mitochondrial DNA polymorphism, phylogeography, and conservation genetics of the brown bear *Ursus arctos* in Europe. Proc. R. Soc. Lond. B Biol. Sci. 255, 195–200. https://doi.org/10.1098/rspb.1994.0028.

Taberlet, P., Swenson, J.E., Sandegren, F., Bjärvall, A., 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear *Ursus arctos* in Scandinavia. Conserv. Biol. 9, 1255–1261.

Tallmon, D.A., Bellemain, E.V.A., Swenson, J.E., Taberlet, P., 2004. Genetic monitoring of Scandinavian brown bear effective population size and immigration. J. Wildl. Manag. 68, 960–965. https://doi.org/10.2193/0022-541X(2004)068[0960:GMOSBB]2.0.CO;2.

Tammeleht, E., Remm, J., Korsten, M., Davison, J., Tumanov, I., et al., 2010. Genetic structure in large, continuous mammal populations: the example of brown bears in northwestern Eurasia. Mol. Ecol. 19, 5359–5370. https://doi.org/10.1111/j.1365-294X.2010.04885.x.

Thornton, D.H., Wirsing, A.J., Lopez-Gonzalez, C., Squires, J.R., Fisher, S., et al., 2018. Asymmetric cross-border protection of peripheral transboundary species. Conserv. Lett. 11, e12430 https://doi.org/10.1111/conl.12430.

Vasudev, D., Fletcher Jr., R.J., 2016. Mate choice interacts with movement limitations to influence effective dispersal. Ecol. Model. 327, 65–73. https://doi.org/10.1016/j.ecolmodel.2016.01.014.

Vilà, C., Sundqvist, A.K., Flagstad, Ø., Seddon, J., Rnerfeldt, S.B., et al., 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. Proc. R. Soc. Lond. B Biol. Sci. 270, 91–97. https://doi.org/10.1098/rspb.2002.2184.

Vucetich, J.A., Waite, T.A., 2000. Is one migrant per generation sufficient for the genetic management of fluctuating populations? Anim. Conserv. 3, 261–266. https://doi.org/10.1111/j.1469-1795.2000.tb00111.x.

Wang, J., 2004. Application of the one-migrant-per-generation rule to conservation and management. Conserv. Biol. 18, 332–343. https://doi.org/10.1111/j.1523-1739.2004.00440.x.

Waples, R.S., Gaggiotti, O., 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol. Ecol. 15, 1419–1439. https://doi.org/10.1111/j.1365-294X.2006.02890.x.

Weir, B.S., Cockerham, C.C., 1984. Estimating F-statistics for the analysis of population structure. Evolution 38, 1358–1370. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x.

Whitlock, M.C., McCauley, D.E., 1999. Indirect measures of gene flow and migration: FST≠1/(4Nm+1). Heredity 82, 117–125. https://doi.org/10.1038/sj.hdy.6884960.

Wilson, G.A., Rannala, B., 2003. Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163, 1177.

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3, 165–173. https://doi.org/10.1111/j.1469-1795.2000.tb00241.x.

Wright, S., 1949. The genetical structure of populations. Ann. Eugenics 15, 323–354. https://doi.org/10.1111/j.1469-1809.1949.tb02451.x.

Xenikoudakis, G., Ersmark, E., Tison, J.L., Waits, L., Kindberg, J., et al., 2015. Consequences of a demographic bottleneck on genetic structure and variation in the Scandinavian brown bear. Mol. Ecol. 24, 3441–3454. https://doi.org/10.1111/mec.13239.

Yamamichi, M., Innan, H., 2012. Estimating the migration rate from genetic variation data. Heredity 108, 362–363. https://doi.org/10.1038/hdy.2011.83.