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High genetic variability of vagrant polar bears illustrates importance of population connectivity in fragmented sea ice habitats

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Abstract

Projections by the Intergovernmental Panel on Climate Change (IPCC) and sea ice forecasts suggest that Arctic sea ice will decline markedly in coming decades. Expected effects on the entire ecosystem include a contraction of suitable polar bear habitat into one or few refugia. Such large-scale habitat decline and fragmentation could lead to reduced genetic diversity. Here we compare genetic variability of four vagrant polar bears that reached Iceland with that in recognized subpopulations from across the range, examining 23 autosomal microsatellites, mitochondrial control region sequences and Y-chromosomal markers. The vagrants' genotypes grouped with different genetic clusters and showed similar genetic variability at autosomal microsatellites (expected heterozygosity, allelic richness, and individual heterozygosity) as individuals in recognized subpopulations. Each vagrant carried a different mitochondrial haplotype. A likely route for polar bears to reach Iceland is via Fram Strait, a major gateway for the physical exportation of sea ice from the Arctic basin. Vagrant polar bears on Iceland likely originated from more than one recognized subpopulation, and may have been caught in sea ice export during long-distance movements to the East Greenland area. Although their potentially diverse geographic origins might suggest that these vagrants encompass much higher genetic variability than vagrants or dispersers in other regions, the four Icelandic vagrants encompassed similar genetic variability as any four randomly picked individuals from a single subpopulation or from the entire sample. We suggest that this is a consequence of the low overall genetic variability and weak range-wide genetic structuring of polar bears – few dispersers can represent a large portion of the species' gene pool. As predicted by theory and our demographic simulations, continued gene flow will be necessary to counteract loss of genetic variability in increasingly fragmented Arctic habitats. Similar considerations will be important in the management of other taxa that utilize sea ice habitats.

Introduction

Many species persist in landscapes where patches suitable for foraging or reproduction are situated in a matrix of non-suitable habitat (Hanski & Gaggiotti, 2004). Highly mobile species are more likely to disperse among habitat patches, facilitating gene flow and thereby counteracting the loss of genetic variability in individual demes (e.g. Hamrick & Godt, 1996; Keyghobadi, 2007). However, connectivity in fragmented habitats can be reduced by numerous anthropogenic factors, such as extinction of some patches, reduced area of habitat fragments, or decreased permeability of the matrix (Gascon *et al.*, 1999; Fischer & Lindenmayer, 2007). Increased habitat fragmentation along with population size reductions can thus negatively impact demographic stability in individual patches, and reduce the genetic variability of the entire species (Baum *et al.*, 2004; Hanski & Gaggiotti, 2004; Fischer & Lindenmayer, 2007).

Several ice-dependent mammal specialists such as polar bears *Ursus maritimus*, Arctic foxes *Vulpes lagopus* and ringed seals *Pusa hispida* utilize the Arctic sea ice for foraging, reproduction and dispersal (e.g. Amstrup, 2003; Geffen *et al.*, 2007; Kelly *et al.*, 2010; Norén *et al.*, 2011). Arctic sea ice also facilitates dispersal of several terrestrial taxa, such as gray wolves *Canis lupus* in the Canadian Arctic archipelago (Carmichael *et al.*, 2008). Sea ice is currently declining, and forecasts suggest an ice-free Arctic ocean during summers in the next few decades (Overland & Wang, 2013; IPCC 2014; Laidre *et al.*, 2015*b*). However, current and projected sea ice conditions vary across the Arctic (Amstrup, Marcot & Douglas, 2008). In several of the 19 polar bear subpopulations that are recognized by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.*, 2010) (Fig. 1), particularly those in the divergent and the seasonal ice ecoregions (*sensu* Amstrup *et al.*, 2008) (Fig. 1), negative impacts of sea ice loss on body condition have been documented (Stirling, Lunn & Iacozza, 1999; Obbard *et al.*, 2006; Rode, Amstrup & Regehr, 2010; Rode *et al.*, 2012). This is expected to result in the decline of several polar bear subpopulations (Durner *et al.*, 2009; Hunter *et al.*, 2010; Molnár *et al.*, 2010; Bromaghin *et al.*, 2015), and also in multiple ecosystem-wide effects (Post *et al.*, 2013).

Durner *et al.* (2009) projected that seasonally stable polar bear habitat will likely contract into one or few regions by the late 21st century: projections from nine out of ten evaluated global circulation models indicated an extensive decline of summer habitat, with the Canadian Arctic Archipelago and Greenland remaining as a refugium, and additional suitable habitat in the east Siberian, Laptev and/or Kara Sea. These regions would be isolated from each other each summer (Durner *et al.*, 2009), fragmenting the polar bear distribution. Recent sea ice projections for the Canadian Arctic Archipelago have confirmed that its northern-most regions

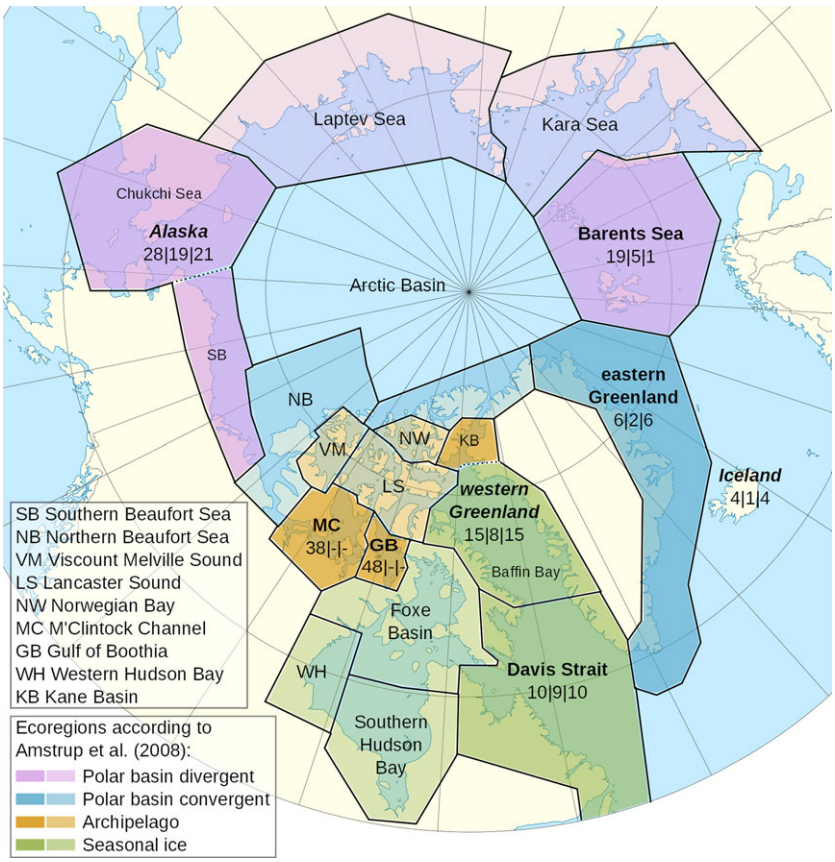

Figure 1 Map of all 19 polar bear subpopulations recognized by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.*, 2010), showing the numbers of analyzed samples per subpopulation and marker system (mtDNA|Y chromosome|autosomal microsatellites). Dark and light colors: sampled and unsampled subpopulations/ecoregions as defined by Amstrup *et al.* (2008), respectively. Subpopulation data from Chukchi Sea and Southern Beaufort Sea were combined and analyzed jointly (Alaska), as were data from Kane Basin and Baffin Bay (western Greenland), indicated by dotted lines. Modified from the Arctic Ocean location map by Tentotwo (Wikimedia Commons) under Creative Commons Attribution-Share Alike 3.0 Unported.

will retain polar bear habitat the longest (Hamilton *et al.*, 2014). Should suitable habitat eventually indeed contract into one single region, range-wide fragmentation would still occur on intermediate time scales (Durner *et al.*, 2009; Peacock *et al.*, 2015).

Loss of genetic variability in fragmented habitats can be counteracted by gene flow, mediated by long-distance movements of individuals beyond their natal areas (Keyghobadi, 2007). Besides the opportunity for passive drifting on sea ice (Amstrup & Gardner, 1994; Mauritzen *et al.*, 2003), polar bears have the capacity for active dispersal across large distances (Ferguson *et al.*, 1999; Laidre *et al.*, 2013). Extreme examples of individual movements are one satellite-tracked female covering almost 7200 km within 576 days, moving on sea ice from northern Alaska to northern Greenland (Durner & Amstrup, 1995) and another female swimming 687 km within 9 days in the Beaufort Sea, followed by additional 1800 km swimming and walking over sea ice (Durner *et al.*, 2011). Although long-distance swimming may come at energetic and reproductive costs (Durner *et al.*, 2011), such long-distance vagrants or dispersers could have the potential to reach and reproduce in other subpopulations, helping to retain their demographic stability and genetic variability (Vilà *et al.*, 2003).

Here we evaluate the genetic variability of vagrant polar bears that arrived on Iceland between 2008 and 2011. While Iceland is currently not part of the circumpolar distribution of polar bears (Obbard *et al.*, 2010), more than 500 polar bears have been recorded reaching Iceland's shores since the 9th century, including about 50 individuals in the past 100 years (Haraldsson & Hersteinsson, 2004). This recurrent influx of polar bears beyond their range may be a consequence of the high and rapid sea ice export out of the Arctic basin through Fram Strait, which plays an important role in regulating the amount of sea ice and freshwater in the Arctic Ocean and the Nordic Seas (Fahrbach *et al.*, 2001). The passage is approximately 500 km wide, separating northeastern Greenland from the Svalbard archipelago in the east, and ice drift rates can be as high as 80 km per day (Perovich, Tucker & Krishfield, 1989).

Although ecological conditions on Iceland preclude the establishment of a sustainable polar bear subpopulation (Amstrup, 2003), the individuals that reached Iceland illustrate the species' capacity for long-distance gene flow, even beyond current range boundaries. Hypothetically, vagrant individuals might only represent a small part of the species' gene pool, for example due to shared ancestry in a common source subpopulation. This would decrease the likelihood that a subpopulation would receive novel genetic variants from immigrants. However, consistent with the high dispersal capability of polar bears, genetic differentiation among the 19 recognized subpopulations is low (Paetkau *et al.*, 1999; Edwards *et al.*, 2011; Miller *et al.*, 2012*b*; Campagna *et al.*, 2013; Bidon *et al.*, 2014; Cronin *et al.*, 2014; Malenfant, Coltman & Davis, 2015; Peacock *et al.*, 2015). Further, a study that included data from 18 of the recognized subpopulations detected gene flow among clusters of subpopulations (Peacock *et al.*, 2015). However, to our knowledge, no previous study has evaluated genetic aspects of long-distance dispersing or vagrant polar bears.

Here we compare the level of genetic variability found in four vagrant polar bears that arrived on Iceland to that in several polar bear subpopulations recognized by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.*, 2010) (Fig. 1). Our analyses are based on data from autosomal microsatellites, mitochondrial control region sequences, and Y-chromosomal sequence and microsatellite haplotypes, including previously published (Lindqvist *et al.*, 2010; Hailer *et al.*, 2012; Miller *et al.*, 2012*b*; Campagna *et al.*, 2013; Bidon *et al.*, 2014) and newly generated data (the latter mainly to produce comparable microsatellite datasets, given known variation in allele sizes obtained from different instruments and size markers; e.g. Morin *et al.*, 2009). Further, we use forward-time simulations to model genetic drift in a small polar bear population under complete isolation or with ongoing immigration to investigate the importance of connectivity among subpopulations.

Materials and methods

Sampling and data

We obtained 58 samples from across the polar bear range (Fig. 1), including 41 blood or tissue samples from Chukchi Sea and Southern Beaufort Sea (divergent ecoregion) and from Baffin Bay and Davis Strait (seasonal ice ecoregion), four tissue samples from vagrant individuals reaching Iceland, and 13 DNA samples from Barents Sea (divergent ecoregion), Kane Basin (Archipelago ecoregion), eastern Greenland (convergent ecoregion), Baffin Bay, Alaska (Chukchi Sea and Southern Beaufort Sea), and from a captive animal with unclear geographic ancestry. In addition, we used previously published data from 112 individuals (Lindqvist *et al.*, 2010; Hailer *et al.*, 2012; Miller *et al.*, 2012*b*; Campagna *et al.*, 2013; Bidon *et al.*, 2014) from Alaska and the Barents Sea (divergent ecoregion), and from Gulf of Boothia and M'Clintock Channel (Archipelago ecoregion) (Fig. 1) that was collated from GenBank. The captive animal was excluded from some analyses. Detailed information on each individual is provided in Table S1. We note that our sampling for some subpopulations is relatively limited (Hale, Burg & Steeves, 2012). We therefore merged the individuals from less well-sampled subpopulations with those of adjacent and not strongly differentiated subpopulations (based on Paetkau *et al.*, 1999; Cronin, Amstrup & Scribner, 2006; Peacock *et al.*, 2015): Baffin Bay and Kane Basin were merged as 'western Greenland', Southern Beaufort Sea and Chukchi Sea as 'Alaska'.

Mitochondrial DNA: PCR amplification, sequencing and analysis

A hypervariable 681-bp fragment of the mitochondrial control region was already published for 51 of the 58 samples (Hailer *et al.*, 2012; Bidon *et al.*, 2014) (Table S1), the remaining seven individuals were sequenced (ENA accession

Table 1 Mitochondrial genetic variability of polar bears from different subpopulations (Fig. 1)

Subpopulation	*n*	*S*	N_H	$H_d \pm$ SD	$\pi \pm$ SD
Vagrants[a]	4	8	4	1.00 ± 0.18	0.007 ± 0.005
Barents Sea	19	7	8	0.88 ± 0.04	0.003 ± 0.002
Eastern Greenland	6	6	4	0.80 ± 0.17	0.003 ± 0.002
Western Greenland	15	13	7	0.89 ± 0.05	0.006 ± 0.004
Davis Strait	10	5	4	0.53 ± 0.18	0.002 ± 0.001
Alaska	28	11	7	0.74 ± 0.07	0.005 ± 0.003
Total/average	82	19	20	0.88 ± 0.02	0.005 ± 0.003

Analyses are based on sequences from a 681 bp long fragment from the mtDNA control region.

n sample size (number of individuals); *S*, number of segregating sites; N_H number of distinct haplotypes; H_d haplotype diversity; π, nucleotide diversity.

[a]Vagrant polar bears reaching Iceland were analyzed as a group.

Table 2 Genetic variability of polar bears from different subpopulations (Fig. 1) at 23 autosomal microsatellites

Subpopulation	*n*	$H_E \pm$ SD	$H_O \pm$ SD	A_R
Vagrants[a]	4	0.72 ± 0.05	0.67 ± 0.05	3.5
Eastern Greenland	6	0.66 ± 0.04	0.64 ± 0.04	3.2
Western Greenland	15	0.70 ± 0.03	0.66 ± 0.03	3.3
Davis Strait	10	0.71 ± 0.04	0.66 ± 0.03	3.4
Alaska	21	0.68 ± 0.03	0.66 ± 0.02	3.3
Total/average[b]	58	0.70	0.66	3.3

n, sample size (number of individuals); H_E expected heterozygosity; H_O observed heterozygosity; A_R rarefied allelic richness (see Appendix S1).

[a]Vagrant polar bears reaching Iceland were analyzed as a group.

[b]Includes two samples that were not counted in any of the shown subpopulation groupings (one from the Barents Sea and one captive).

numbers: LN613410-LN613416) as described in Hailer *et al.* (2012). Primers and PCR conditions are listed in Table S2.

We added 26 previously published control region sequences (681 bp) to a final alignment containing 84 individuals, including 19 sequences from the Barents Sea (Miller *et al.*, 2012*b*) and seven from Alaska (Lindqvist *et al.*, 2010; Miller *et al.*, 2012*b*). For a second, shorter alignment, we collated 86 additional sequences with a length of 470 bp from the M'Clintock Channel and Gulf of Boothia subpopulations (Campagna *et al.*, 2013), yielding a total of 170 individuals (Fig. 1; Table S1).

We calculated estimates of within-population variability for five different subpopulations and for the vagrants (see Table 1) in Arlequin 3.5 (Excoffier & Lischer, 2010). Phylogenetic relationships among inferred haplotypes were determined based on median-joining networks constructed using Network 4.612 (Bandelt, Forster & Röhl, 1999) and based on phylogenetic trees using BEAST 1.7.4 (Drummond *et al.*, 2012). A spatial analysis of variance was performed in SAMOVA v1.0 (Dupanloup, Schneider & Excoffier, 2002) to identify groups of subpopulations (*K*) that are geographically homogenous and genetically maximally differentiated from each other. Details on mtDNA analyses are provided in Appendix S1.

Y chromosome markers: data compilation and analysis

We used 3.1 kb of Y-specific sequence data and one Y-linked microsatellite marker (*369.1*) from 39 male polar bears (Bidon *et al.*, 2014; Aarnes *et al.*, 2015) to construct a statistical parsimony haplotype network in TCS 1.21 (Clement, Posada & Crandall, 2000). These individuals had previously been sexed, using the approach of Bidon *et al.* (2013). This dataset includes the only male among the four vagrants that reached Iceland. In addition, sequences (3.1 kb) and microsatellite data for *369.1* were extracted from genomic sequence data of five males from Alaska and the Barents Sea (Miller *et al.*, 2012*b*). Details and haplotype data are provided in Fig. 1 and the Appendices S1 and S2.

Autosomal microsatellites: PCR amplification, fragment and data analysis

Each of the 58 samples was genotyped at 30 autosomal microsatellite loci in seven multiplex reactions as described in Appendix S1 and Table S2. Standard population genetic procedures were applied to test for Hardy–Weinberg equilibrium and linkage disequilibrium (Appendix S1) and to calculate diversity indices for four different subpopulations and the vagrants (see Table 2). A Principle Coordinate Analysis (PCoA) was calculated in GenAlEx 6.5 (Peakall & Smouse, 2006, 2012) using all 58 individuals, based on a standardized pairwise genetic distance matrix. To determine population genetic structuring without pre-assigning individuals to sampling localities, we used the program STRUCTURE v2.3.1 (Pritchard, Stephens & Donnelly, 2000). Details and genotype data are provided in Appendices S1 and S3.

Using R (R Core Team 2015), we randomly picked genotypes with replacement from our dataset to evaluate the variability of polar bears dispersing in other regions than Fram Strait, and evaluated their genetic variability as described above.

We performed forward-time simulations in EASYPOP 2.0.1 (Balloux, 2001) to evaluate the impact of continued immigration on the loss of genetic variability through genetic drift in two different demographic scenarios. Loss of genetic variability in an effective population of ten individuals was simulated (1) with no immigration and (2) receiving immigrants at a rate of one individual per generation from a large effective source population of 2000 individuals. Details are provided in Appendix S1.

Results

Mitochondrial and Y-chromosomal markers

In a 681-bp-fragment from the mitochondrial control region of 82 polar bears from the Barents Sea, Alaska, eastern Greenland, western Greenland, and the Davis Strait, i.e. from

all four ecoregions according to Amstrup *et al.* (2008), and including four vagrant individuals that reached Iceland (Fig. 1), we found 19 segregating sites that defined 20 haplotypes. Haplotype diversity for the entire dataset was 0.88 ± 0.02 (mean $\pm$ SD) and nucleotide diversity was 0.005 ± 0.003 (Table 1). Overall, genetic structuring was weak among polar bear subpopulations. In a BEAST analysis, most branches had posterior support values below 0.95 (Fig. S1), except for one branch grouping haplotypes that were carried by individuals sampled in Alaska, western Greenland and Iceland. In a network of genetic variation, haplotypes from different subpopulations were closely related to each other (Fig. 2a). All four vagrant individuals carried different mitochondrial haplotypes that were not particularly closely related to each other. In our SAMOVA that excluded vagrant polar bears, F_{SC} (genetic distance within groups) was minimized and significant for $K = 4$ groups of subpopulations (Fig. S2). However, no corresponding F_{CT} value (genetic differentiation among groups) was significant, so $K = 1$ could not be rejected. A similar lack of pronounced spatial population structuring was obtained from analyses of an extended mtDNA dataset from 170 polar bears, based on shorter (470-bp) control region sequences (Fig. S2 and S3; details in Appendix S1).

We identified seven haplotypes in a network of genetic variation at Y-linked sequence data and one Y-linked microsatellite (locus *369.1*) from 44 male polar bears. These haplotypes were separated by seven mutational steps (Fig. 2b). The only single nucleotide polymorphism in the dataset was the same as already described in Bidon *et al.* (2014), separating five polar bears from Alaska and western Greenland from the remaining individuals. The five newly typed individuals [genome data from Miller *et al.* (2012*b*)] had three different Y-chromosomal haplotypes (Fig. 2b), each of them previously reported by Bidon *et al.* (2014). This included four samples from Svalbard (in the Barents Sea), a region yet uncharacterized for Y-linked markers, which carried two closely related haplotypes. The Y-chromosomal haplotype of the male polar bear that arrived on Iceland (all other samples of vagrants came from females) was also found in the Davis Strait and in western Greenland (Fig. 2b).

Autosomal microsatellites

We screened 30 autosomal microsatellite loci that had originally been developed for brown bears (Paetkau, Shields & Strobeck, 1998; Kleven *et al.*, 2012), American black bears

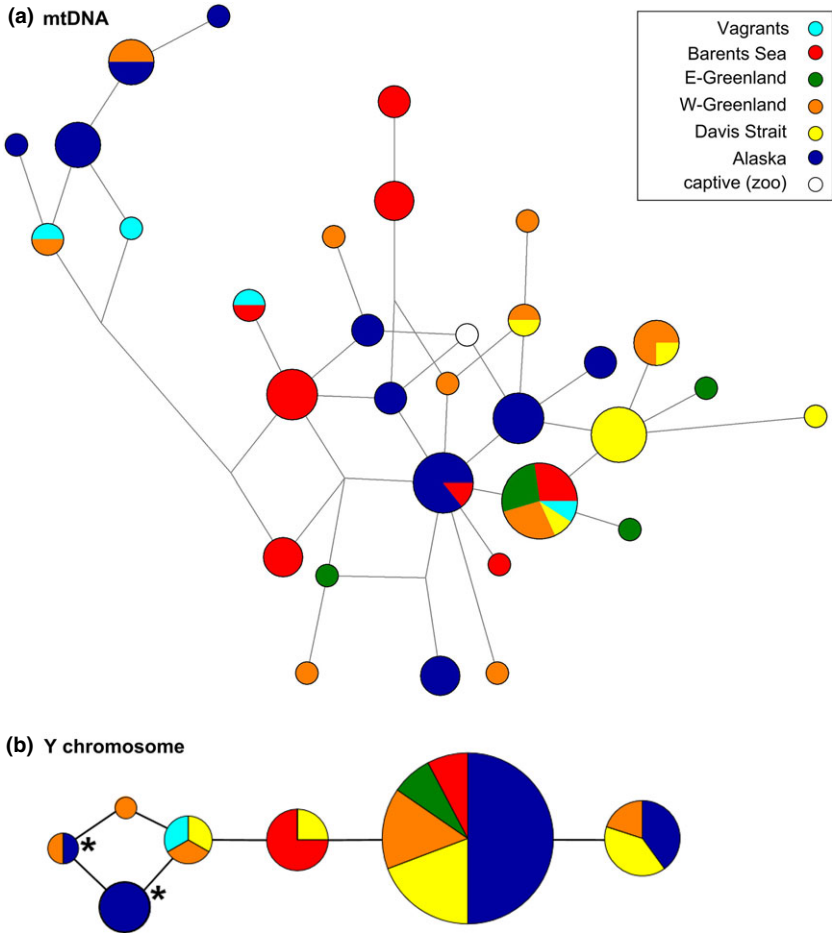

Figure 2 Haplotype networks of uniparentally inherited markers in polar bears from different subpopulations across their range. (a) Median joining network of genetic variation at a 681 bp fragment of the mitochondrial control region in 83 polar bears. (b) Statistical parsimony network of Y chromosome haplotypes, inferred from the unweighted combination of 3.1 kb sequence data and microsatellite locus *369.1*. *Haplotype determined by a single nucleotide polymorphism.

(Paetkau & Strobeck, 1994), Asiatic black bears (Kitahara *et al.*, 2000) or polar bears (Paetkau *et al.*, 1995) for utility and variability in 58 polar bear samples covering subpopulations from all four ecoregions (Amstrup *et al.*, 2008). Seven loci failed in PCR or were monomorphic in polar bears, leaving 23 microsatellite loci (Tables S2 and S3) for all following analyses. This included thirteen brown bear loci from Kleven *et al.* (2012), which here are shown to be highly polymorphic in polar bears (Appendix S1). No linkage disequilibrium was found for any pair of loci in any subpopulation ($P > 0.05$ after sequential Bonferroni correction). We found significant departure from Hardy-Weinberg equilibrium in one instance in one subpopulation (locus *UarD1585* in western Greenland; $P < 0.001$).

In the analyzed subpopulations, expected heterozygosity (H_E) across autosomal loci ranged from 0.66 ± 0.04 (mean $\pm$ SD) in eastern Greenland to 0.71 ± 0.04 in the Davis Strait, and allelic richness (A_R) ranged from 3.2 in eastern Greenland to 3.4 in the Davis Strait (Table 2). The four vagrants that reached Iceland tended to show slightly higher variability when analyzed as a group ($H_E = 0.72 \pm 0.05$, $A_R = 3.5$). For comparison, four randomly picked genotypes from the most extensively sampled subpopulation (Alaska) yielded lower variability across 100 replicates (average $H_E = 0.67 \pm 0.04$, $A_R = 3.2$) than the vagrants, but with overlapping standard deviations. Similar estimates were obtained when randomly re-sampling four genotypes 100 times from across the entire range (average $H_E = 0.70 \pm 0.03$, $A_R = 3.3$). Both estimates from randomly picked individuals overlapped with estimates from recognized subpopulations, indicating the vagrants exhibited marginally but non-significantly higher variability than other individuals. The proportion of heterozygous loci per individual (individual heterozygosity) ranged from 30% to 87% in individuals from established subpopulations and from 57% to 87% in the vagrants.

A PCoA (Fig. 3a) revealed weak geographic structuring. All vagrants clustered at different positions in the plot. One vagrant was somewhat disjunct from other polar bears (but overall not strongly divergent), the other three vagrants clustered closely to individuals from Alaska or from eastern and western Greenland. Pairwise Θ_{ST} values between subpopulations were low and ranged from 0.012 (Davis Strait/western Greenland) to 0.044 (Alaska/Davis Strait) (Table S4). Despite low differentiation levels among subpopulations, most Θ_{ST} values were significant, except for the differentiation of Davis Strait and western Greenland. All pairwise comparisons including vagrants yielded low and non-significant Θ_{ST} values.

Admixture analyses using STRUCTURE confirmed weak population structuring. When not using the geographic sample origin as prior information, all individuals showed admixture for $K = 2$–10 clusters, proportional to the numbers of assumed clusters (Fig. 3b). A more pronounced signal of genetic structuring was obtained when including the geographic origin of each sample as prior information [locprior model (Hubisz *et al.*, 2009)] (Fig. 3c), but parameters α and r did not converge within 3 million iterations, despite multiple runs with different settings. Using the locprior model, ΔK was highest for $K = 3$, with Alaskan polar bears assigned to one cluster, individuals from the Davis Strait and western Greenland assigned to a second cluster and four eastern Greenlandic polar bears assigned to a third cluster. All vagrant individuals showed admixture, but each with a different clustering composition (Fig. 3c).

We performed forward-time simulations of genetic drift based on small populations with similar levels of genetic variability as encompassed by the polar bears that reached Iceland. Ten reproducing individuals were simulated assuming a ratio of effective to actual population size of 0.1 (Frankham, 1995; but see Palstra & Ruzzante, 2008), and an actual population size of 100 based on the size of the three smallest recognized subpopulations that include 94–278 polar bears (Obbard *et al.*, 2010). In a scenario of complete isolation, 36% ($\pm$3%) (mean $\pm$ SD) or 90% ($\pm$4%) of the genetic variability had been lost after 10 or 50 generations, respectively (Fig. 4). In contrast, when simulated populations were connected by migration at a rate of one individual per generation (roughly mirroring the historical records for Iceland), levels of expected heterozygosity remained relatively constant over time and only 15% ($\pm$4%) of the genetic variability had been lost after 50 generations.

Discussion

Comparably high genetic variability of vagrant polar bears on Iceland

Genetic characteristics of the four vagrant polar bears that reached Iceland show that relatively few individuals arriving at a given location can represent a substantial proportion of the species' gene pool. Individual heterozygosity of each of the four vagrants falls within the range observed among individuals sampled in recognized subpopulations. As a group, the vagrants encompass a slightly but non-significantly higher level of genetic variability than what is present in recognized subpopulations – despite the limited number of vagrants included in our study.

The high variability encompassed by the four vagrants might be the result of the particular sea ice conditions in Fram Strait. A likely route for polar bears arriving on Iceland is from the east coast of Greenland on pack ice that is exported out of Fram Strait, which is the primary region of sea ice export from the Arctic basin (Perovich *et al.*, 1989). The eastern Greenland subpopulation is geographically closest to Iceland and polar bears roam along the entire coastline (Laidre *et al.*, 2015*a*), so eastern Greenland has been assumed to be the source of polar bears reaching Iceland (Vetter, Gall & Skírnisson, 2015). However, our study suggests that besides the geographically proximate subpopulation of eastern Greenland, vagrants arriving on Iceland may come from subpopulations from all four ecoregions (Amstrup *et al.*, 2008): the vagrant individuals are most genetically similar to individuals from eastern Greenland, western Greenland, and Alaska, and each shows different clustering affinities for autosomal microsatellites. Further, the four

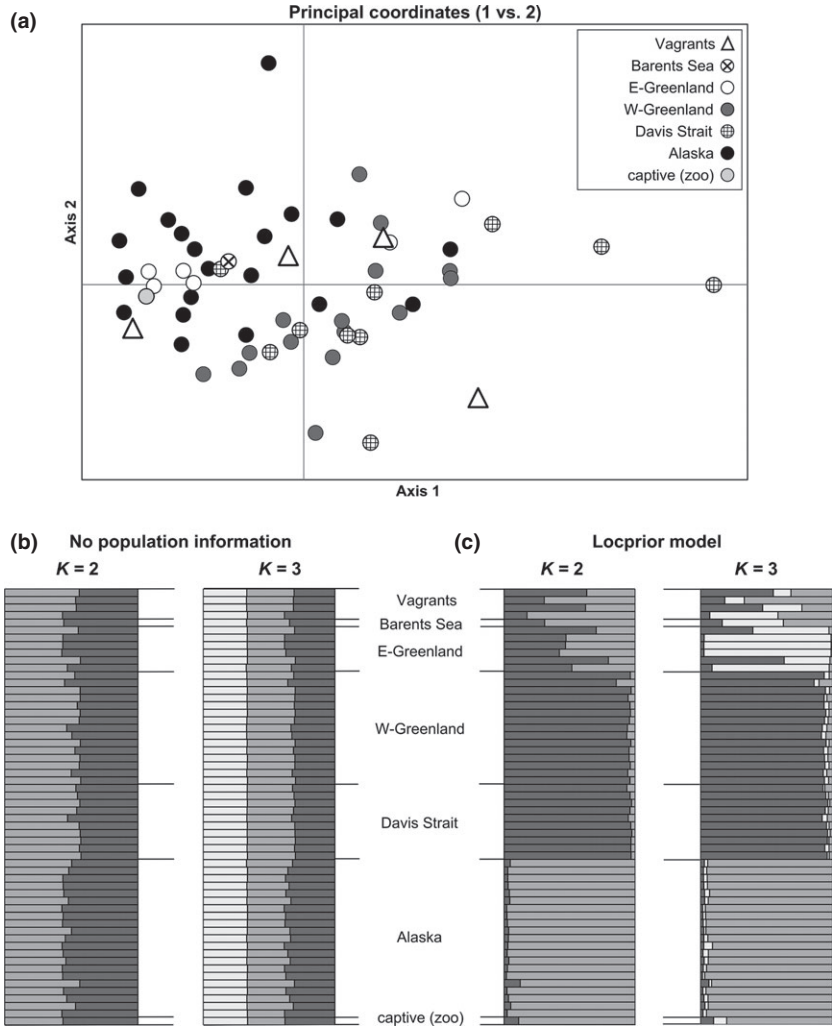

Figure 3 Genetic structuring of polar bears from different subpopulations across their range at autosomal microsatellite markers. (a) Principal Coordinate Analysis of 58 polar bears, genotyped at 23 autosomal microsatellite loci. (b) Admixture analyses in STRUCTURE of 58 individual autosomal genotypes without using any prior population information; (c) same as (b), but using the locprior model. Each color represents one cluster and each bar represents one individual.

individuals carry four different mitochondrial haplotypes, of which two belong to a statistically highly supported lineage otherwise found in Alaska, western Greenland and Canadian subpopulations (M'Clintock Channel and Gulf of Boothia). This signal from differentially inherited genetic markers suggests that the polar bears reaching Iceland may have had different geographic origins. However, the weak range-wide geographic structuring in polar bears precludes a definite assignment to a particular source region.

We propose two complementary explanations why already a low number of polar bears can capture a large proportion of the species' gene pool. Notably, this reasoning is not restricted to Fram Strait, but is likely applicable to anywhere in the range.

First, polar bears show low overall genetic variability. Nucleotide diversity of polar bears is only circa 20–25% of that found in brown bears (Hailer *et al.*, 2012; Miller *et al.*, 2012*b*; Liu *et al.*, 2014). This large difference between the two species reflects severe population bottlenecks in polar bears (Miller *et al.*, 2012*b*; Liu *et al.*, 2014), but likely also their smaller distribution range and population size compared to brown bears (McLellan, Servheen & Huber, 2008; Wiig *et al.*, 2015).

Second, the largest proportion of genetic variance in polar bears is not found among subpopulations, but instead among individuals – regardless of their subpopulation origin. The high dispersal capability of polar bears (Ferguson *et al.*, 1999; Laidre *et al.*, 2013) enables them to cover considerable distances (Durner & Amstrup, 1995; Durner *et al.*, 2011). This has resulted in only weak range-wide population genetic structuring that is visible in our data from autosomal microsatellites, the Y chromosome and mtDNA. Similar low levels of population differentiation have been previously reported for mtDNA (Edwards *et al.*, 2011; Campagna *et al.*, 2013; Peacock *et al.*, 2015), autosomal microsatellites (Paetkau *et al.*, 1999; Peacock *et al.*, 2015), Y-chromosomal data (Bidon *et al.*, 2014), autosomal introns (Hailer *et al.*, 2012), and genome-wide data (Miller *et al.*, 2012*b*; Cahill *et al.*, 2013; Cronin *et al.*, 2014; Malenfant *et al.*, 2015).

Comparing estimates of population differentiation among polar bear subpopulations obtained from maternally inherited mtDNA and paternally inherited Y-chromosomal markers,

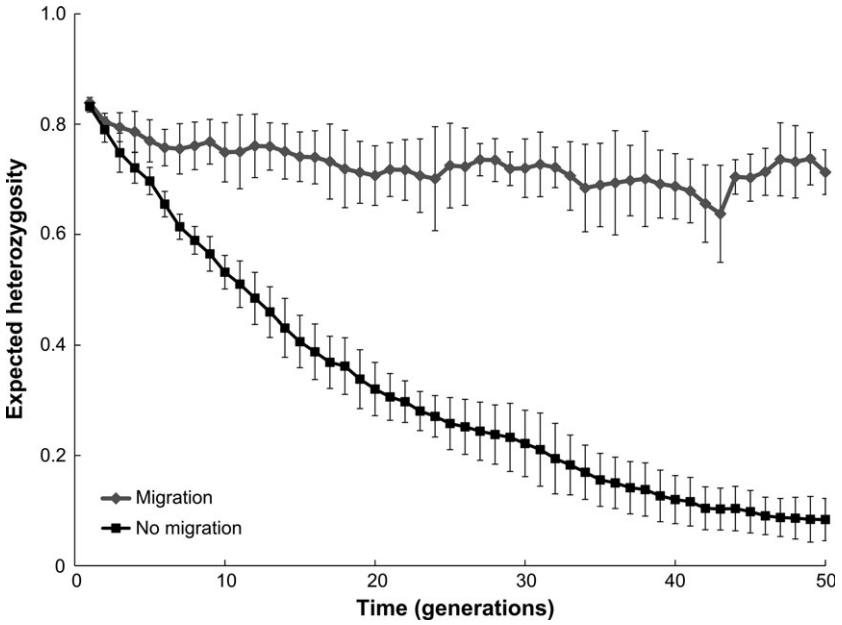

Figure 4 Simulated loss of genetic variability in a population of ten individuals. Two simulation scenarios were investigated: (1) migration at a rate of one individual per generation and (2) no migration. Lines are averages (±SD) across 10 simulations.

respectively, Bidon *et al.* (2014) did not observe pronounced differences between the two marker systems, implying less strongly sex-biased dispersal in polar than in brown bears (Bidon *et al.*, 2014). This is consistent with our results and with analyses of movement data that found males to travel similar (Laidre *et al.*, 2013) or only slightly larger (Amstrup *et al.*, 2001) mean distances than females.

Importance of long-distance dispersal for future genetic variability of polar bears

Some late Pleistocene polar bear populations appear to have become isolated in coastal regions south of the current range, near the Alaskan Admiralty, Baranof and Chichagof islands (Cahill *et al.*, 2013), Ireland (Edwards *et al.*, 2011) and Pleistocene Beringia (Barnes *et al.*, 2002). At these locations, polar bears hybridized with brown bears, leaving a genetic footprint in resident brown bear populations (Cahill *et al.*, 2013). These observations show that climate-related changes in Arctic habitats can isolate polar bear populations from their conspecifics.

Large-scale reductions in summer sea ice extent have been projected, fragmenting the remaining habitat into one or several regions by the late 21st century (Amstrup *et al.*, 2008; Durner *et al.*, 2009; Hamilton *et al.*, 2014). Until that time, polar bears will face intermediate levels of habitat fragmentation (Durner *et al.*, 2009; Peacock *et al.*, 2015), likely with regional differences: Amstrup *et al.* (2008) projected the convergent and Archipelago ecoregions to maintain polar bear habitat the longest, similar to projections by Durner *et al.* (2009), that, however, suggest local deviations from this large-scale pattern.

Late winter and early spring sea ice is currently permitting large-scale movements across subpopulation boundaries during the mating season (March–May) (Amstrup, 2003; Laidre *et al.*, 2013). However, already under current sea ice conditions, genetic differentiation among subpopulations is discernible (Paetkau *et al.*, 1999; Campagna *et al.*, 2013; Malenfant *et al.*, 2015; Peacock *et al.*, 2015). With projections of increasing duration of the ice-free season in summer (IPCC, 2014), the period available for dispersal across sea ice is expected to shorten over the next decades (Durner *et al.*, 2009; Peacock *et al.*, 2015). While these habitat changes are likely to lead to a merging of some of the currently recognized subpopulations (Paetkau *et al.*, 1999; Cronin *et al.*, 2006; Peacock *et al.*, 2015), other subpopulations are likely to become isolated from each other each summer (Obbard *et al.*, 2010).

As predicted by population genetic theory (Nei, Maruyama & Chakraborty, 1975), our genetic drift simulations revealed that genetic variability would decline severely within only few generations in a completely isolated population. In contrast, continued immigration decelerated the decline in genetic variability in our simulations. Indeed, genetic diversity decreased significantly in an isolated Italian brown bear *U. arctos* population within less than one generation (De Barba *et al.*, 2010), and gene flow into isolated wolf and bighorn sheep *Ovis canadensis* populations has been shown to assist in the preservation of genetic diversity (Vilà *et al.*, 2003; Miller *et al.*, 2012*a*). The comparably high genetic diversity observed in vagrant polar bears reaching Iceland and in randomly picked individuals implies that vagrant or dispersing polar bears can potentially carry novel genetic variants into other subpopulations. Hence, in the projected fragmented Arctic habitats of the 21st century, dispersing polar bears will likely become increasingly important for subpopulation connectivity, buffering against subpopulation size fluctuations and declines of genetic diversity.

Long-distance dispersal in the Arctic and its conservation implications

Even under scenarios where polar bears eventually may be restricted to one remaining refugium (Amstrup *et al.*, 2008; Durner *et al.*, 2009; Hamilton *et al.*, 2014), preservation of genetic diversity will be an important long-term management goal to safeguard evolutionary potential (Reed & Frankham, 2003). Hence, albeit not surprising from a theoretical standpoint, our results highlight an aspect that has not received much attention in polar bear management (Obbard *et al.*, 2010), possibly because it is difficult to influence (Crooks & Sanjayan, 2006): that factors contributing to maintained connectivity in fragmented habitats should receive conservation attention (Heller & Zavaleta, 2009).

Management decisions in the face of increased population fragmentation due to further sea ice loss are complex and will likely involve a mix of strategies ranging from the individual to the habitat level (Hodgson *et al.*, 2009) [see e.g. Sahanatien & Derocher (2012); Vongraven *et al.* (2012); Derocher *et al.* (2013) for a detailed discussion of effective polar bear management and conservation]. A reduction of greenhouse gas emissions on a global scale is expected to positively affect the amount and quality of sea ice habitat (e.g. Amstrup *et al.*, 2010; Laidre *et al.*, 2015*b*). Translocations of polar bears are difficult and considered an unviable option under most circumstances (Derocher *et al.*, 2013). Nevertheless, monitoring schemes of mortality, movement patterns, subpopulation status, physiology and sea ice concentration will yield important data for future management decisions (Sahanatien & Derocher, 2012; Vongraven *et al.*, 2012; Derocher *et al.*, 2013). This could include more targeted tagging studies in key areas, and intensified international cooperation to share and analyze movement data. One possible outcome of monitoring could be the identification of regions that are particularly important for subpopulation connectivity (Heller & Zavaleta, 2009). Further, continued genetic sampling will allow monitoring subpopulation differentiation and variability over time (Vongraven *et al.*, 2012).

Given recent climate projections (IPCC, 2014), population connectivity is likely to be reduced not only for polar bears, but for other Arctic species as well. Similar to polar bears, Arctic foxes currently show extensive levels of gene flow across most of their range with sea ice occurrence explaining regional variation in connectivity (Geffen *et al.*, 2007). Interestingly, Arctic foxes follow polar bears in their movements, scavenging on remains from their kills (Chesemore, 1968), so the population genetic structuring of these two carnivores is interrelated in multiple ways (Paetkau *et al.*, 1999; Dalén *et al.*, 2005; Norén *et al.*, 2011; Peacock *et al.*, 2015). Other terrestrial taxa utilize Arctic sea ice for dispersal as well, such as Canadian gray wolves (Carmichael *et al.*, 2008). Sea ice loss could therefore decrease connectivity and perhaps also genetic diversity in several species of conservation concern, with associated risk of reduced fitness and loss of evolutionary potential (Reed & Frankham, 2003).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Further details on analyses, additional results, supplementary figures and tables.

Fig. S1. Maximum clade credibility tree based on a 681 bp fragment of the mt control region in 84 polar bears.

Fig. S2. SAMOVA results for population structuring in polar bears, based on mtDNA control region sequences.

Fig. S3. Median joining network of genetic variation at a 470 bp fragment of the mitochondrial control region in 169 polar bears.

Table S1. Geographic origin, sequence information and subpopulation assignment of all individuals analyzed in this study.

Table S2. Primers (in 5′ to 3′ orientation) and amplification conditions of nuclear and mitochondrial loci.

Table S3. Comparison of genetic variability by locus per study area.

Table S4. Pairwise genetic differentiation among subpopulations.

Appendix S2. Y-linked SNP and microsatellite allele size data.

Appendix S3. Microsatellite allele sizes for 23 autosomal microsatellite markers.

