High connectivity in a long-lived high-Arctic seabird, the ivory gull *Pagophila eburnea*

Glenn Yannic1,2,3,16 · Jonathan M. Yearsley4 · Roberto Sermier5 · Christophe Dufresnes5 · Olivier Gilg1,6 · Adrian Aebischer5,7 · Maria V. Gavrilo8,9 · Hallvard Strøm10 · Mark L. Mallory11 · R. I. Guy Morrison12 · H. Grant Gilchrist13 · Thomas Broquet14,15

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**Abstract**  Species may cope with rapid habitat changes by distribution shifts or adaptation to new conditions. A common feature of these responses is that they depend on how the process of dispersal connects populations, both demographically and genetically. We analyzed the genetic structure of a near-threatened high-Arctic seabird, the ivory gull (*Pagophila eburnea*) in order to infer the connectivity among gull colonies. We analyzed 343 individuals sampled from 16 localities across the circumpolar breeding range of ivory gulls, from northern Russia to the Canadian Arctic. To explore the roles of natal and breeding dispersal, we developed a population genetic model to relate dispersal behavior to the observed genetic structure of worldwide ivory gull populations. Our key finding is the striking genetic homogeneity of ivory gulls across their entire distribution range. The lack of population genetic structure found among colonies, in tandem with independent evidence of movement among colonies, suggests that ongoing effective dispersal is occurring across the Arctic Region. Our results contradict the dispersal patterns generally observed in seabirds where species movement capabilities

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are often not indicative of dispersal patterns. Model predictions show how natal and breeding dispersal may combine to shape the genetic homogeneity among ivory gull colonies separated by up to 2800 km. Although field data will be key to determine the role of dispersal for the demography of local colonies and refine the respective impacts of natal versus breeding dispersal, conservation planning needs to consider ivory gulls as a genetically homogeneous, Arctic-wide metapopulation effectively connected through dispersal.

**Keywords**  
Natal dispersal · Breeding dispersal · Effective number of breeders · Population genetic structure · Overlapping generation model

**Introduction**

The distribution of natural habitats worldwide is currently changing as a direct consequence of global climate trends, and this is happening particularly fast in the Arctic, where climate warming is maximal (ACIA 2004; IPCC 2007). Species that live in the Arctic or in other rapidly changing environments might cope with this rapid change by shifting their distributions, by adjusting through phenotypic plasticity or by evolving adaptations to the new local climatic conditions (reviewed by Parmesan 2006; Gienapp et al. 2008; Chen et al. 2011; Hoffmann and Sgro 2011; Gilg et al. 2012). These responses partly depend on the process of dispersal, that is, the movement of individuals between birth and reproduction (natal dispersal), and possibly between successive reproduction events (breeding dispersal). Besides its role in the spatial structure and demographic dynamics of populations, dispersal is important in the context of habitat change because it is one key driver of the potential rate of spread of a population and, as the process by which genes are moved among populations, it influences the rate of adaptation to changing conditions and the potential for evolutionary rescue (Bell and Gonzalez 2011; Travis et al. 2013). Thus, understanding, predicting and managing biodiversity responses to rapid climate change demand a full consideration of a species’ dispersal characteristics and their demographic and genetic consequences.

We focus here on the ivory gull *Pagophila eburnea*, a bird that completes its life cycle entirely in the Arctic. Over its entire breeding range (Canadian Arctic, Greenland, Svalbard and Russian Arctic islands), it breeds either on inland cliffs and “nunataks,” i.e., rocky outcrops emerging from icecaps, or on high-Arctic barren islands or flatlands (Mallory et al. 2008; Gilg et al. 2009). In Canada, where the status of the species has been designed “Endangered” (COSEWIC 2006), studies indicated that 80% of the breeding population was lost during the past 20 years (Gilchrist and Mallory 2005). The species is listed as Near Threatened by the IUCN (BirdLife International 2012), and an international circumpolar “Conservation Strategy and Action Plan” has been presented by leading seabird experts from Arctic countries to gain more insight into how this bird responds to increasing threats from disappearance of sea ice habitat, natural resource exploration and increased contaminant loads (Gilchrist et al. 2008).

Ivory gulls are capable of traveling thousands of kilometers either on single foraging trips or to reach wintering grounds in the north Pacific (Bering Sea and Sea of Okhotsk) and in the northwest Atlantic (Davis Strait and Labrador Sea) where most of the world population is thought to spend the winter (Mallory et al. 2008; Gilg et al. 2010). However, most seabirds have an extraordinary ability to travel long distances and yet show evidence of restricted gene flow and exhibit high levels of philopatry, sometimes returning to breed within a few meters of their natal nest (Friesen et al. 2007). A species’ movement capabilities thus do not automatically inform us about demographic and genetic connectivity among colonies. This is the “seabird paradox”, i.e., the apparent paradox between high vagility and low effective dispersal (Milot et al. 2008).

Dispersal may take place at different stages of an individual’s life. For ivory gulls, natal dispersal may happen during the two first years of life before the individual becomes sexually mature and joins a breeding colony. However, the behavior of ivory gulls during that time is almost completely unknown. In addition, adult ivory gulls may disperse among colonies from one breeding season to the next. Such breeding dispersal could effectively contribute to demographic and genetic exchanges among colonies, but our knowledge of these aspects for ivory gulls currently relies only on incidental observations (O. Gilg, A. Aebischer and M. L. Mallory, unpubl. data).

Here we take a genetic approach to investigating dispersal in order to complement ongoing mark–recapture and satellite tracking efforts (Gilg et al. 2010; Spencer et al. 2014). Genetic data can complement other approaches to measure dispersal by either providing direct information on individual movements (e.g., through parentage or population assignment) or indirect signatures of dispersal patterns (e.g., through analyses of genetic structure). Disentangling the effects of natal dispersal and breeding dispersal on realized gene flow is, however, challenging, and has rarely been addressed in the molecular ecology literature (Broquet and Petit 2009), although Rousset (2001) and Laporte and Charlesworth (2002) present general class-structured models that lay the foundations to such an endeavor.

The aim of this study was to explore population structure and spatial dispersal pattern in the ivory gull and to
infer natal versus breeding dispersal among colonies. For that purpose, we analyzed a genetic dataset representative of the entire species range and developed a population genetic model to infer lower bounds on natal and breeding dispersal consistent with the observed genetic structure of ivory gull populations worldwide.

Materials and methods

Study species

The ivory gull is a long-lived high-Arctic seabird (annual survival estimated to 0.86; Stenhouse et al. 2004; and maximum record 28 years; Mallory et al. 2012), which is associated with sea ice all year round (Gilg et al. 2010; Spencer et al. 2014). Breeding colonies are scattered in Arctic Canada, Greenland, Svalbard and the northern islands of Russia in the Barents and Kara seas (Table 1). The current total global population of the ivory gull was estimated to be approximately 19,000–27,000 breeding pairs (BirdLife International 2012). The Russian population is estimated to number in the range of 14,500–22,000 individuals (Gavrilov 2011). The population in Canada has declined since the 1980s (Mallory et al. 2008). In Norway (Svalbard), the population probably declined in the first part of last century, but after 1970, the trend is uncertain (Mallory et al. 2008). Population trends in Greenland are unclear due to sparse historical information (Gilg et al. 2009). Ivory gulls are thought to first breed after their second year, based on the fact that they acquire adult plumage in their second winter, and that individuals in less than full adult plumage are rarely seen at breeding colonies (Mallory et al. 2008). Unlike most gulls, which regularly lay three eggs, the ivory gull usually lays 1–2 eggs, more rarely three eggs. Most of the world population is thought to spend the winter in two main wintering grounds (Mallory et al. 2008): the north Pacific (Bering Sea and Sea of Okhotsk) and the northwest Atlantic (Davis Strait and Labrador Sea, Fig. 1).

Sample collection

Field works took place in summers 2006 to 2012, during the breeding season (late June to August). Sample locations were distributed across the entire breeding range of the species, including the Canadian Arctic Archipelago, northeastern Greenland, Svalbard Archipelago, Franz Josef Land Archipelago, Severnaya Zemlya Archipelago and Kara Sea islands (16 sampling locations overall, listed in Table 1 and Fig. 1). We collected samples in either breeding colonies or opportunistically near two military stations where ivory gulls are attracted by food remains (namely Alert, Canada and Station Nord, Greenland). Three nondestructive DNA sampling methods (mouth swabs, plucked feathers and blood) and a noninvasive sampling method (shed feathers) were used. Pieces of tissue were also opportunistically collected on dead birds.

Juveniles (chicks of the year) were sampled in two sites from Greenland in 2009: Amdrup Land and Station Nord (Table 1; Fig. 1) in order to perform parentage analyses. In these cases, buccal swabs and tissue samples were used as DNA sources. All other samples were taken from adult birds, where we considered two classes of individuals according to their breeding status. Field observations suggest that non-breeding adults visit or stay in colonies during the breeding season. Moreover, satellite transmitters indicated that breeding birds visited colonies as far as 200 km from their own breeding colony (O. Gilg and A. Aebischer, unpublished data). Hence in any one site, adult birds were classified as “breeding” only if they were seen hatching eggs or raising chicks, and “unknown status” otherwise. Thus, “unknown” birds included: (1) the non-breeding component of the population (the so-called floaters; Penteriani et al. 2011), but also (2) birds found in colonies but that were not reproducing locally and that may reproduce elsewhere in an unknown colony, and (3) birds that they were identified from shed feathers collected on the ground. This distinction is relevant for analyzing the genetic structure of colonies since non-breeding birds or individuals lacking information on their breeding location (all called here “unknown”) could be transient visitors. Due to field constraints, we generally have information on only one of these two classes of adults within each sampling site (reported in Table 1), either because samples were taken only from breeding individuals or because the breeding status was ignored altogether (e.g., shed feathers or transient birds). However, in one repeatedly visited site from Greenland (called Station Nord), we could collect precise mark–resight data on both breeding and unknown (see above) individuals, and obtain sizable samples from these two classes of birds (referred to as “breeding” and “unknown” in Table 1).

All samples from Greenland, Norway and Russia (Table 1) were obtained using nondestructive (collection of mouth swabs and plucked feathers) and noninvasive DNA sampling methods (collection of shed feathers) as described in Yannic et al. (2011). In addition, birds from Alert (Canada) were caught with rocket nets near a military base. Immediately following capture, a blood sample (about 0.3 ml) was collected from the brachial vein in heparinized micro-hematocrit capillary tubes, before release. Blood samples were centrifuged on site at 13,200 g for 15 min. Red blood cells and plasma were separated and stored frozen at –20 °C until laboratory analyses.
<table>
<thead>
<tr>
<th>ID</th>
<th>Country</th>
<th>Estimated regional population</th>
<th>Region</th>
<th>Site</th>
<th>Abbr.</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Status</th>
<th>DNA source</th>
<th>N</th>
<th>nA</th>
<th>Ar</th>
<th>H₀</th>
<th>Hₑ</th>
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<td>Station Nord</td>
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<td>Swab</td>
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<td>Swab/tissue</td>
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<td>Swab/tissue</td>
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<td>Swab/blood</td>
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<td>0.80</td>
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<td>14,500–22,000 pairs</td>
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<td>Nagurskoje</td>
<td>Nagu</td>
<td>80.72</td>
<td>48.22</td>
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<td>Shed feathers</td>
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<td>3.9</td>
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<td>58.39</td>
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<td>Shed feathers</td>
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<td>EvLi</td>
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<td>63.22</td>
<td>Adult unknown</td>
<td>Shed feathers</td>
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<td>90.76</td>
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<td>Shed feathers</td>
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<td>Domashny Island</td>
<td>Doma</td>
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<td>94.84</td>
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<td>Shed feathers/swab</td>
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<td>91.05</td>
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<td>Shed feathers</td>
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<td>96.75</td>
<td>Juvenile</td>
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<td>–</td>
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<td>#16</td>
<td>Kara Sea Islands</td>
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<td>Heiberg Islands</td>
<td>Heil</td>
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<td>Shed feathers</td>
<td>4</td>
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<td>#17</td>
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<td>Seymour Island</td>
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<td>Swab/plucked feathers</td>
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<td>0.78</td>
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<td>Adult unknown</td>
<td>Blood</td>
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<td>6.7</td>
<td>5.87</td>
<td>0.80</td>
<td>0.77</td>
</tr>
</tbody>
</table>

N gives the number of samples genotyped at 13 microsatellite markers. Statistics include number of alleles (nA), allelic richness (Ar; estimated for n ≥ 10 individuals and based on min. sample size of eight diploid individuals successfully genotyped at 13 loci), observed heterozygosity (H₀) and expected heterozygosity (Hₑ).

a Gilg et al. (2009); b Gilchrist et al. (2008); c Gavrilo (2011); d Environment Canada (2013)
DNA extraction and genotyping

Genomic DNA from all individuals was extracted from shed and plucked feathers, tissue, blood or buccal swab following protocols described in Yannic et al. (2011) (see also Supplementary material 1). Previously optimized microsatellite markers were used in four polymerase chain reaction (PCR) multiplexes, totaling 22 markers (Yannic et al. 2011). For samples obtained from shed feathers, we performed three independent PCR replicates of each locus to obtain reliable genotypes (see Yannic et al. 2011). The microsatellite amplicons were loaded on an ABI PRISM 3100 (Applied Biosystems Foster City, CA, USA) automated DNA sequencer. Microsatellite alleles were detected, scored and manually verified using GENEMAPPER 3.7 (Applied Biosystems).

Genetic structure

All loci were found to be independent of one another (linkage disequilibrium test performed in FSTAT 2.9.4 (Goudet 2005), using 10,000 permutations and p values adjusted for multiple comparisons using the Benjamini and Yekutieli false discovery rate procedure with initial α = 0.05). We used two sets of loci depending on downstream analyses. All 22 loci were used for the parentage analyses because: (1) all genetic data from the juveniles came from good quality samples (tissue and buccal swab) and (2) genotyping errors or null alleles can be identified and taken into account (see below). For the analysis of spatial genetic structure, some data come from “low-quality” samples (shed feathers, Table 1). Hence, for these analyses, we used a subset of 13 loci (listed in Table 2) chosen for their polymorphism and reliability as reported in Yannic et al. (2011).

We investigated the differentiation among ivory gulls sampling sites by estimating $F_{ST}$ (Weir and Cockerham 1984). We ran some of the analyses using only the samples with >10 adults. Global $F_{ST}$ was computed with FSTAT for different combinations of samples: overall adults ($n = 15$ localities), over sites with >10 adults ($n = 9$ localities) and among breeders only ($n = 6$ localities). The significance of the differentiation was tested using two approaches. First, we used the log-likelihood $G$ statistic calculated for observed data and compared to that of 10,000 randomized datasets obtained through permutation of individuals among samples (as implemented in FSTAT; Goudet et al. 1996; Goudet 2005). Second, for a strict comparison with results from our evaluation of power (see below), we also used Fishers’ exact test as implemented in GENEPOP. In that case, the distribution of alleles within individuals is ignored and thus genic rather than genetic differentiation among samples is tested. Furthermore, the null distribution is obtained using a Markov chain algorithm rather than permutations, performed here with defaults GENEPOP parameters. Pairwise $F_{ST}$ among all samples were also calculated with FSTAT.

The statistical power to detect a significant genetic heterogeneity at various true levels of differentiation for the present set of samples, number of loci and allele frequencies was evaluated using POWSIM 4.1 (Ryman and Palm 2006). POWSIM simulates samples of genes from a specified number of populations that have drifted to an expected predefined level of differentiation (measured as $F_{ST}$). These samples are then used for testing genetic homogeneity using Fisher’s exact test. With this procedure,
we estimated the power that we had when looking for genetic differentiation using all adults and breeders only (see Table 1). Estimates of power were given by the proportion of significant outcomes when repeating the simulations 1000 times for each level of simulated \( F_{ST} \). The use of post hoc power analyses should, however, be used with caution as stressed by Hoenig and Heisey (2001). But here our goal is not to modify a hypothesis test a posteriori (the problematic situation identified by Hoenig and Heisey (2001)) but rather to give an idea of the degree to which our data are informative.

**Reproductive success and effective number of breeders**

To interpret our observations of genetic structure across colonies, we needed an estimate of effective colony sizes. This can be approximated using the effective number of breeders \( (N_b) \) \((N_b; \text{Waples and Teel 1990})\), a parameter that depends on the census number of adults in a colony (here noted \( N_c \)) and the distribution of reproductive success among individuals within colonies following (Kimura and Crow 1963): \( N_b = (N_c k - 1)/[k( k - 1 + (V_k/k))] \), where \( k \) is the mean and \( V_k \) the variance in reproductive success among individuals. As a first approximation, we estimated these figures from field observations of the number of juveniles per nest in colonies Amdrup Land and Station Nord, considering that there are two and only two adults associated with a given nest.

This approach assumes that juveniles within a nest descend from the adult pair providing parental care to these offspring. This is a weak assumption since extra-pair paternity is frequent in socially monogamous birds (Westneat and Stewart 2003), meaning that some males may not have sired the juveniles they are taking care of, while other males may have parented offspring with more than one female. Hence, males may have a slightly higher variance in reproductive success than those calculated from field observations. To check whether social monogamy reflects the actual breeding system, we performed genetic parentage assignments in colony Station Nord, where we had DNA samples from a number of juveniles (\( n = 20 \)) and presumed parents (\( n = 24 \)), that is, adults seen hatching eggs or raising chicks. Details of the parentage analysis, performed with the method implemented in COLONY 2.0.4.5 (Jones and Wang 2009; Wang 2012), are described fully in Electronic Supplementary Material (Supplementary material 1). We repeated these analyses in the colony of Amdrup Land, where 45 juveniles (but no parents) were sampled.

**Model of genetic structure: overlapping generations, natal and breeding dispersal**

Interpreting genetic differentiation in terms of connectivity and dispersal behavior is not trivial given that it requires some knowledge of the effective number of breeders within colonies \( (N_b; \text{which we investigated in this study}) \) and the effect of life history traits such as longevity and the potential movement behavior of juveniles (natal dispersal) and adults between breeding seasons (breeding dispersal). We therefore used a two-sample coalescent approach to

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**Table 2** \( F_{ST} \) and exact G-test probability values obtained for each autosomal microsatellite and over all loci for two different datasets of ivory gull \((\text{Pagophila eburnea})\)

<table>
<thead>
<tr>
<th>Loci</th>
<th>All adults sites ((n = 15))</th>
<th>Breeding colonies ((n = 6))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( F_{ST} )</td>
<td>( p ) value</td>
</tr>
<tr>
<td>A111</td>
<td>0.005</td>
<td>0.78</td>
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<tr>
<td>B125</td>
<td>0.002</td>
<td>0.32</td>
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<tr>
<td>C7</td>
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<td>0.83</td>
</tr>
<tr>
<td>D126</td>
<td>0.004</td>
<td>0.27</td>
</tr>
<tr>
<td>D5</td>
<td>0.004</td>
<td>0.17</td>
</tr>
<tr>
<td>D9</td>
<td>0.008</td>
<td>0.76</td>
</tr>
<tr>
<td>A112</td>
<td>0.003</td>
<td>0.65</td>
</tr>
<tr>
<td>A132</td>
<td>0.010</td>
<td>0.37</td>
</tr>
<tr>
<td>B114</td>
<td>0.009</td>
<td>0.76</td>
</tr>
<tr>
<td>D103</td>
<td>0.006</td>
<td>0.11</td>
</tr>
<tr>
<td>C6</td>
<td>0.002</td>
<td>0.20</td>
</tr>
<tr>
<td>B103</td>
<td>0.008</td>
<td>0.62</td>
</tr>
<tr>
<td>D1</td>
<td>0.007</td>
<td>0.04</td>
</tr>
<tr>
<td>Over all loci</td>
<td>0.001</td>
<td>0.09</td>
</tr>
<tr>
<td>Jackknifing over loci</td>
<td>0.001</td>
<td>0.003</td>
</tr>
<tr>
<td>Bootstrapping 95 % CI</td>
<td>-0.002; 0.005</td>
<td>-0.006; 0.005</td>
</tr>
</tbody>
</table>
describe an island model, with overlapping generations and both natal and breeding dispersal. The model is used to explore the dispersal scenarios that are consistent with the observed level of population differentiation (global \( F_{ST} \)) among Arctic-wide populations of ivory gulls.

The model builds upon Yearsley et al. (2013) to introduce overlapping generations following the general approach laid out by Laporte and Charlesworth (2002). Each deme contains \( N \) diploid non-selfing individuals, of which \( N_a = vN \) are adults who have survived at least one breeding cycle and \( N_j = (1 - v)N \) are first-year juveniles (\( v \) is the adult survival probability per breeding cycle). One breeding cycle going forward in time represents a unit time step and is composed of reproduction, mutation, dispersal, adult mortality, juveniles either mature into adults or die, population regulation (i.e., the population size remains constant at every breeding cycle). The model simplifies certain aspects of the ivory gull’s life history. Maturation for ivory gulls is known to be longer than one year, whereas our model, to enable an analytical solution, assumes that a maximum juvenile period of one year. From numerical simulations (results not shown), the effect of a prolonged juvenile stage on \( F_{ST} \) is small when adult mortality is low (as for the ivory gull). All adults in the model are assumed to have equal reproductive success. Individual variation in reproductive success and non-breeding adults must be accounted for by the effective population size, \( N \). The model also does not describe sex-linked differences in life history, such as dispersal or survival. At present, we do not have sufficient sex-specific data for the ivory gull to know whether such differences exist for this species.

The model estimate expected coalescence times, genetic diversities and \( F \)-statistics for a DNA sequence under the infinite-sites model (Kimura 1969) with a mutation rate \( \mu / \)generation/sequence. For our model parameterizations, the force of mutation upon genetic diversity is weak compared to the forces of genetic drift and gene flow. Our model considers the coalescent for a sample of two DNA sequences that are randomly sampled just prior to population regulation. We define three states for a pair of DNA sequences: two sequences in the same diploid individual, two sequences in different individuals in the same deme and two sequences in different individuals in different demes (states 1, 2 and 3, respectively).

The ancestral history of a pair of sequences can be defined by a transition matrix, \( G \), where an element, \( G_{ij} \), gives the probability that a pair of sequences in state \( i \) had ancestors from the previous generation in state \( j \) (the rate of coalescence per generation for a pair of sequences in state \( i \) is then given by \( G_{i0} = 1 - \sum_j G_{ij} \)). Using first-step analysis (Wakeley 2009), the expected times to coalescence of two lineages in state \( i \), \( T_i \), can be calculated by solving

\[
T_i = 1 + \sum_{j=1}^{3} G_{ij} T_j
\]

This equation is analogous to equation 8 in Laporte and Charlesworth (2002), and details of the approach used to derive Eq. 1 are given in Yearsley et al. (2013). Using Slatkin’s approximation (Slatkin 1991), these coalescence times can be used to approximate \( F \)-statistics in the small mutation limit as

\[
F_{IS} = \frac{T_2 - T_1}{T_2}
\]

\[
F_{ST} = \frac{T_3 - T_2}{T_3}
\]

Alternatively, mutations can be included in the matrix \( G \) and \( F \)-statistics calculated from recurrence relationships for identity by descent.

We specified the transition matrix, \( G \), by identifying three types of sequence pair: sequences from two juveniles (i.e., newly born in the current breeding cycle), sequences from two adults (i.e., individuals surviving from the previous breeding cycle) and sequences from one juvenile and one adult (these types are labeled \(-, +, \pm \), respectively). The transition matrix can be written as \( G = G^- + G^+ + G^0 \) where

\[
G^- = (1 - v)^2 \begin{pmatrix}
0 & 1/(1-v) & 0 \\
\alpha^-/2N & \alpha^-(N-1)/N & 1-\alpha^- \\
\beta^-/2N & \beta^-(N-1)/N & 1-\beta^-
\end{pmatrix}
\]

\[
G^0 = 2v(1-v) \begin{pmatrix}
0 & 0 & 0 \\
\alpha^+/2N & \alpha^+(N-1)/N & 1-\alpha^+ \\
\beta^+/2N & \beta^+(N-1)/N & 1-\beta^+
\end{pmatrix}
\]

\[
G^+ = v^2 \begin{pmatrix}
1/v & 0 & 0 \\
0 & \alpha^+ & 1-\alpha^+ \\
0 & \beta^+ & 1-\beta^+
\end{pmatrix}
\]
Substituting Eq. 3a–c into Eq. 1 and solving and taking the many-deme limit gives

\[ T_1 = T_2 = 2N_aD/(1 - \nu^2) \]  
\[ T_3 = T_2 + D(1 - m_j)/(1 + p)M/[(1 - M^2)(1 + \nu)] \]

where \( M = (1 - \nu) (1 - m_j) + \nu (1 - m_a), \) \( p = \nu (1 - m_a)/M \) and time units are in breeding cycles. To express these coalescence times in numbers of generations, they should be divided by generation time [equal to \( 1/(1 - \nu) \)].

Substituting Eqs. 4 into Eqs. 2 gives the \( F \)-statistics, \( F_{IS} = 0 \) and an expression for \( F_{ST} \) in the small mutation limit of

\[ \frac{1 - F_{ST}}{F_{ST}} = 2N_a \frac{1 - M^2}{M^2} \frac{1}{1 - p^2} \]

(5)

For non-overlapping generations \( (\nu = 0) \) and small migration rates, Eq. 5 gives the classic result \( (1 - F_{ST})/F_{ST} = 4N_a m_j \) (Wright 1931). The model also correctly predicts the inbreeding effective population size \( N_e = N_d/(1 + \nu) \) for a single isolated population with overlapping generations (Felsenstein 1971; Hill 1972), equivalent to the case when \( m_j = m_a = 0 \).

Equation 5 shows how the genetic differentiation among ivory gull colonies depends upon adult survival \( (\nu) \), effective colony size \( (N_a) \), natal dispersal \( (m_j) \) and breeding dispersal \( (m_a) \).

Adult annual survival rate was estimated to \( \nu = 0.86 \pm 0.04 \) (95 % CI 0.75; 0.91) (Stenhouse et al. 2004). We used our model with the mean annual survival rate \( \nu = 0.86 \) and the upper limit of the confidence interval \( \nu = 0.91 \). Using a higher survival value will tend to underestimate migration rates, making our interpretation more conservative. Effective colony size \( N_a \) cannot be precisely parameterized because contrary to our model's assumptions, the number of breeding adults is variable across colonies. Known colony sizes (reviewed in Table 3) show a skewed distribution, with a few large colonies (in the order of 100–2000 breeding pairs) and many smaller ones (below 100 pairs). Furthermore, we did not know the prevalence and year-to-year behavior of adults that are apparently non-breeding at some observation time point. Such individuals can inflate \( N_a \) if they have or will enter reproduction at some other breeding season. Based upon (1) field observations of colony sizes (Table 3), (2) the fact that low variance in reproductive success should inflate local effective numbers of breeders (see results for \( N_d/N_e \) in colonies Amdrup Land and Station Nord), and (3) remaining uncertainties about the resulting parameter \( N_a \), we explored the model behavior for \( N_a \) ranging 50–1000. Using Eq. 5, we then worked out the conditions of juvenile and adult migration that would result in a \( F_{ST} \) value equal to the observed global \( F_{ST} = 0.001 \). This allows us to estimate and discuss the lower bound on migration rates for ivory gulls.

Results

Genetic structure

Number of alleles observed and expected heterozygosity in each sample and for each of the 13-microsatellite loci are shown in Table 1 and in Electronic Supplementary Material (Table S1 in Supplementary material 1), respectively. With 13 loci examined in 15 samples, nine locus/site combinations showed a significant deficit in heterozygotes. There was no consistent pattern across samples or loci, and only one locus in one sample (B125, Schmidt Island, Russia) remains significant if one corrects for multiple testing. Yet it is plausible that a small number of allelic dropouts remained undetected in genotypes obtained from shed feathers despite marker selection and genotyping repetitions. The number of genotyping repetitions that we used is based upon average error rates reported in Yannic et al. (2011), but individual shed feathers may happen to be unusually poor sometimes (Yannic et al. 2011). For this reason, we reported differentiation statistics with and without data from shed feathers. The mean observed heterozygosity (0.63–0.85) and mean expected heterozygosity (0.73–0.82) across loci are shown in Table 1.

No genetic differentiation was observed among breeding samples \( (n = 6, F_{ST} = 0.000, 95 \% CI \pm 0.006; 0.005; \) \( G \) statistic permutation test \( p = 0.61, \) Fisher’s exact test \( p = 0.40; \) Table 2) or among samples containing more than ten individuals \( (n = 9, F_{ST} = 0.000, 95 \% CI \pm 0.002; 0.003; \) \( G \) statistic permutation test \( p = 0.15, \) Fisher’s exact test \( p = 0.14; \) Table S2 in Supplementary material 1), while very low and nonsignificant differentiation was found overall adult samples \( (n = 15, F_{ST} = 0.001, 95 \% CI \pm 0.002; 0.005; \) \( G \) statistic permutation test \( p = 0.09, \) Fisher’s exact test \( p = 0.09; \) Table 2). This figure was unaffected when removing all shed feather samples \( (n = 8, F_{ST} = 0.000). \) Pairwise \( F_{ST} \) values were also very low, ranging from \(-0.032 \) to \( 0.043, \) and none of these pairwise values was significant after correction for multiple testing (Benjamini–Yekutieli correction; Table S3 in Supplementary material 1). There was no significant difference in relatedness among breeders versus among unknown birds sampled the same year in the same colony (i.e., Station Nord in 2009: “Effect of transient individuals on genetic structure” section in Supplementary material 1), suggesting that breeders and unknown birds belong to a homogeneous pool. These results were further confirmed by model-based clustering that suggests that our ivory gulls most likely form
one worldwide population (“Model-based clustering” section in Supplementary material 1) and by the absence of isolation by distance over long distance (“Isolation by distance” section in Supplementary material 1).

Simulations demonstrated that our sample sizes and genetic markers provided sufficient power to detect weak population structure. Population structure was found significant for all simulated populations (i.e., power = 100 %) with an $F_{ST}$ of 0.006 when using all adult sampling sites ($n = 17$; Fig. 2). Even when $F_{ST}$ was reduced to 0.0035, structure was correctly detected in 90 % of the simulations. For $F_{ST}$ values as low as or lower than the observed value (i.e., global $F_{ST}$ among all adults = 0.001), power drops to 25 %. When using only breeders sampling sites ($n = 6$ sites), the sample sizes and the genetic markers contain sufficient power to detect population structure with 90 % accuracy for simulated populations with $F_{ST}$ values $\geq 0.007$ (Fig. 2).

### Table 3: Census colony size across the breeding distribution of ivory gull (*Pagophila eburnea*)

<table>
<thead>
<tr>
<th>Country</th>
<th>Number of ivory gulls</th>
<th>Number of colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greenlanda</td>
<td>Records between 1854 and 2009</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;5</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>5–24</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>25–99</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>100–300</td>
<td>5</td>
</tr>
<tr>
<td>Norwayb</td>
<td>Maximum records</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;5</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>4–10</td>
<td>5</td>
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<tr>
<td></td>
<td>11–30</td>
<td>19</td>
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<td></td>
<td>31–60</td>
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<td></td>
<td>61–100</td>
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<td></td>
<td>101–135</td>
<td>1</td>
</tr>
<tr>
<td>Russiac</td>
<td>Historically maximum records</td>
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<td></td>
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<td>&gt;10</td>
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<tr>
<td></td>
<td>2000+</td>
<td>3</td>
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<tr>
<td>Canadae</td>
<td>Historically records</td>
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<tr>
<td></td>
<td>Between 1976 and 1992</td>
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<tr>
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<td>5–24</td>
<td>3</td>
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<tr>
<td></td>
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<td></td>
<td>Recent time records between 2001 and 2003</td>
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<td>10</td>
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<td>25–50</td>
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<td>50–99</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>100–300</td>
<td>0</td>
</tr>
</tbody>
</table>

* Gilg et al. (2009); b Norwegian Polar Institute; c Maria Gavrilo, unpublished data; d Gilchrist and Mallory (2005)
Reproductive success and effective number of breeders

In the colony Amdrup Land, we counted 98 adults (49 nests) with one offspring, 82 adults (41 nests) with two offspring and 12 adults (6 nests) with an unknown number of offspring (Yannic et al. 2014a). Assuming that the latter show the same distribution of reproductive success than all other adults, this gives $k \approx 1.46$, $V_k \approx 0.25$ and $N_k \approx 445$. In Station Nord, we observed 24 adults with one offspring and 48 adults with two, which gives $k \approx 1.67$, $V_k \approx 0.23$ and $N_k \approx 148$.

Genetic parentage assignment at Station Nord identified the two parents (from our sample of adults) for 6 juveniles out of 20. Twelve additional juveniles had one of their parents identified from the candidate adults. The “second parents” of these juveniles and the two parents of the remaining juveniles ($n = 2$) were not identified from the adult samples, but their genotype was reconstructed by the software COLONY, meaning that these adults could still be used to check for extra-pair paternity (e.g., if one unsampled male had sired three of our offspring with different unsampled females, this would be visible in the data). As it turned out, the parental–offspring relationships observed in the field were all confirmed by the genetic assignment (that is, for all the individuals with a DNA sample available), with one exception: One adult that was observed caring for a juvenile did not appear to be its genetic parent. Moreover, this true parent was identified from our sample of adults and it was found to have a second offspring with a different mating partner (field observation, independently confirmed by the genetic data). This suggests one plausible event of extra-pair paternity.

We repeated these analyses in the colony of Amdrup Land, where 45 juveniles (but no parents) were sampled. But with such small clutch size (one or two offspring in general) and without any actual parent genotyped, we did not succeed to recover reliable sibship information in this colony (data not shown).

In summary, observable parental behavior seems a reliable indicator of parentage, and field observations suggest that the effective breeding size $N_b$ is approximately twice the census colony size $N_c$. This figure results from the near-zero variance in breeding success among birds seen in colonies. This variance could be slightly inflated by extra-pair paternity, but with very little consequences for the $N_b/N_c$ ratio (e.g., $N_b$ decreases from 148 to 142 in colony Station Nord if one considers one event of extra-pair paternity where one bird has no success and another one has fathered three offspring).

Model of genetic structure: natal versus breeding dispersal

We explored the conditions of natal dispersal (dispersal of juveniles) and breeding dispersal (movement of adults among colonies across breeding seasons) that would be consistent with the low level of observed genetic structure.

A general result obtained with the model is that breeding dispersal is very effective at homogenizing the distribution of the genetic variation across populations in long-lived species with overlapping generations. For instance with the ivory gulls, with $v = 0.91$ (Fig. 3b) and $N_a = 1000$ and no natal dispersal (that is, perfect philopatry), a breeding dispersal of only 4.6% is required to yield an $F_{ST}$ as low as 0.001. By contrast, above 30% natal dispersal would be required in the absence of breeding dispersal.

The above scenario is conservative, providing lower bounds on dispersal rates because we used our highest observation of global $F_{ST}$ ($F_{ST} = 0.001$; see Table 2), large colony size and high survival. A slightly less conservative scenario ($F_{ST} = 0.001, N_a = 500, v = 0.86$, visible in Fig. 3a) gives 14% breeding dispersal or 48% natal dispersal (or any combination along the $F_{ST} = 0.001$ contour line in Fig. 3a). Any smaller (i.e., less conservative) value for $N_a$ or $F_{ST}$ will increase the minimum level of dispersal. As expected, predictions of genetic structure were highly sensitive to effective colony size (as shown by the different contour lines within Fig. 3a, b) and survival (compare Fig. 3a against b).

![Fig. 2](image-url) Statistical power for obtaining significant outcomes in tests of genetic differentiation involving the specific marker characteristics and sample sizes of ivory gull for (1) all adult localities and (2) breeding colonies only. Simulations were performed using POWSIM version 4.1 (Ryman and Palm 2006). The dotted lines indicate the level of genetic differentiation that can be detected with 90% statistical power for the two datasets.
Discussion

The key finding from this research is the striking genetic homogeneity of the ivory gull across its entire distribution range. Even with conservative assumptions for local effective breeding numbers and survival rate, this suggests that gene flow regularly occurs among distant regions in order for populations to become, and remain, genetically homogenous. We develop below the interpretation of these results indicating genetic homogeneity among populations separated by up to 2800 km.

A single Arctic-wide population

Information retrieved from microsatellites suggests that the ivory gull represents a single, Arctic-wide metapopulation. We found no significant genetic differentiation among breeding colonies of ivory gull ($F_{ST} = 0.000$, 95 % CI −0.006; 0.005) or among overall adult samples ($F_{ST} = 0.001$, 95 % CI −0.002; 0.005). We did not observe significant isolation by distance among breeding colonies and among overall adult samples across the range of the species (“Isolation by distance” section in Supplementary material 1). These results agree with the weak differentiation found using mitochondrial data (Royston and Carr 2014 and this study; Supplementary material 1).

This absence of genetic structure is a priori not surprising for a species capable of traveling thousands of kilometers either on single foraging trips or to reach its wintering grounds (Gilg et al. 2010). Genetic homogeneity is, however, not the rule in seabird species with similar flying capability. Out of forty-seven seabird species reviewed by (Friesen et al. 2007), only few were reported to have as little genetic structure as the ivory gull. The grey-faced petrel Pterodroma macroptera gouldi (Lawrence et al. 2014), the little auk Alle alle (Wojczulanis-Jakubas et al. 2014) and the wandering albatross Diomedea exulans (Milot et al. 2008) are examples of seabird that present weak genetic structure throughout their distribution. But the vast majority of seabird species rather seem to show a stronger level of genetic divergence, even among geographically proximate colonies (e.g., the Hawaiian petrel Pterodroma sandwichensis (Welch et al. 2012) or Cory’s shearwater Calonectris diomedea (Genovart et al. 2013). Genetic divergence among seabird populations inhabiting the polar regions seems then to be generally lower in comparison with those breeding at lower latitudes.

Patterns of genetic structuring in species capable of long-distance dispersal may be driven by multiple mechanisms, including restricted gene flow as a result of high natal philopatry, cryptic barriers to dispersal or behavioral mechanisms (Friesen et al. 2007). In addition, local adaptation to differing ecological conditions and strong selective pressures may promote geographic patterns of differentiation. Our results show that such gene flow limiting processes are not at work in the ivory gull population and high intercolony dispersal genetically homogenizes the populations. It is, however, worth noting that our results are based on neutral genetic loci (i.e., microsatellite loci) and adaptive differences could exist among colonies.

Our interpretation of the data assumes that the $F_{ST}$ is at migration-drift equilibrium. With small deme size and large migration rates, $F_{ST}$ reaches equilibrium very rapidly [i.e., in the order of a few dozen of generations, Rousset (2004)], contrary to gene diversity which may take a much longer time to reach equilibrium (Crow and Aoki 1984). The hypothesis that we believe to be most parsimonious in the case of ivory gulls is that $F_{ST}$ has long been equilibrated and there is large-scale genetic exchange between colonies, most likely due to a combination of natal and breeding dispersal. An alternative hypothesis may be that the worldwide population is substructured into poorly connected demes and the genetic homogeneity observed in ivory gull today is a consequence of the evolutionary history of the species, i.e., a northward expansion of population from a single homogeneous refugia after the deglaciation of the Arctic region (e.g., Wojczulanis-Jakubas et al. 2014). However, while it is widely accepted that temperate species were restricted to refugial area during glacial stages, taxa found in more northern latitudes today are known to have had greater distributions during the glacial phases (e.g., Lorenzen et al. 2011; Yannic et al. 2014b). This suggests that colder adapted species were in more restricted areas during interglacial and not during glacial stages (Stewart and Lister 2001; Stewart and Dalen 2008). From this perspective, ivory gulls could be said to be in “refugia” today and not necessarily in the Late Pleistocene.

Natal versus breeding dispersal

To disentangle the respective role of natal dispersal, i.e., the movement from the natal site to the site of first reproduction (Greenwood and Harvey 1982), and breeding dispersal, i.e., movement between successive breeding attempts in the ivory gull, we developed a infinite island model with overlapping generations that we used to calculate the expected global $F_{ST}$ at equilibrium for a range of adult and juvenile migration rate scenarios. Our results show that breeding dispersal is very effective at reducing genetic differentiation across populations in long-lived seabird with overlapping generations. We used this model here in an attempt to better understand the demo-genetics of a featured high-Arctic seabird species, but the modeling framework that we presented here is very general. Our model could be used further to look at the effect of...
overlapping generations and variations in natal versus breeding dispersal, two aspects that have largely been ignored from empirical molecular ecology research so far.

Long-term field data are lacking for the ivory gull (see next section below), but breeding dispersal is thought to be less than natal dispersal for seabirds in general (e.g., Gauthier et al. 2010). In many long-lived seabird species with low reproductive rate, breeding philopatry is believed to be very high, although actual dispersal rates have been rigorously quantified for a few species only: roseate tern Sterna dougallii \( (m_a = 0.00-0.09 \text{ year}^{-1}; \text{Lebreton et al. 2003}) \), common tern Sterna hirundo \( (m_a = 0.04-0.08 - \text{year}^{-1}; \text{Nisbet and Cam 2002}) \), wandering albatross \( (m_a = 0.00-0.30 \text{ year}^{-1}; \text{Gauthier et al. 2010}) \) or Adélie penguin Pygoscelis adeliae \( (m_a < 0.01 \text{ year}^{-1}; \text{Dugger et al. 2010}) \). In these species, breeding dispersal rates appear to be very low and strongly limited by the distance among colonies, although dispersal could vary with ice conditions (e.g., Dugger et al. 2010). These observations suggest that there are behavioral constraints on adult movement among breeding colonies (Friesen et al. 2007).

Many seabirds have an extraordinary ability to travel long distances and yet show evidence of restricted gene flow and exhibit high levels of philopatry, sometimes returning to breed within a few meters of their natal nest (Friesen et al. 2007). The ultimate causes for such philopatric behavior are not known, although familiarity with natal and/or previous breeding habitats (Friesen et al. 2007) and fitness costs incurred by dispersal itself (Clobert et al. 2001) seem likely to be involved.

Our results contradict in some ways the general pattern found in the literature (Friesen et al. 2007). According to our models (and recalling that we are considering lower bounds on migration rates), it seems unlikely that the low breeding dispersal rates reported above for seabirds are compatible with the genetic pattern observed here for the ivory gull, even if natal dispersal is strong. To be compatible with our observations, a level of breeding dispersal below 0.1 would have to be associated with extremely frequent natal dispersal (that is, a complete mixture of young adults, see Fig. 3 with \( m_a \) in 0–0.1). Demographic data from the field will be very important to test this suggestion. Information on the movement behavior of juvenile birds and additional estimates of adult survival would be particularly valuable.

**Movement of adult ivory gulls inferred from ecological data**

Ring recoveries are in line with large-scale movement in ivory gulls and suggest long-distance travel events (>3400 km; Lyngs 2003; Gaston et al. 2008). However, it is often not known whether recovered birds were actually breeding in the areas where they were found, making inferences about the frequency of effective dispersal at large spatial scales difficult. Recent advances in movement ecology using satellite transmitters indicated similar post-breeding flyways over long distance for ivory gulls breeding in the northeast Atlantic, i.e., for birds breeding in north Greenland, Svalbard and Franz Josef Land, Russia.
Wintering grounds were reached in December, in southeast Greenland and along the Labrador Sea ice edge, where Canadian birds also overwinter or in the Bering Strait region (Mallory et al. 2008; Gilg et al. 2010). Data also indicate that birds from different colonies, however, migrate eastwards toward wintering area in the Bering Strait region, hence demonstrating a bidirectional migration pattern (Fig. 1).

Similar flyways and wintering area for birds from different colonies over the entire species range may result in the recruitment of birds to distant colonies after the overwinter period (i.e., birds never return to the natal colony). Such movement events may be accidental (i.e., birds are unable to return to the natal area) or may reflect behavioral variation in philopatry among individuals (Weatherhead and Forbes 1994). The tendency for birds to disperse may also be linked to the conditions in the natal colony the year they were born and to the local dynamics of the colonies that they recruit to. Such long-distance dispersal events or reshuffling of individuals on the pre-breeding flyways may be sufficient to eliminate the traces of regional structure among populations. The fidelity of ivory gulls to the breeding site is unknown but at least some marked individuals return to the same breeding colony from one year to the next (MacDonald 1976), and an example of extreme breeding site fidelity has been reported (Mallory et al. 2012). Populations that breed on flat land of Russia, where the highest census population size are observed (Table 3), are often prone to move from site to site (de Korte and Volkov 1993).

Dispersal and connectivity under climate change

Climate change is geographically shifting the climatic envelope of many species, and this is predicted to occur rapidly in the Arctic (up to ~0.40 km year$^{-1}$; Loarie et al. 2009). The capacity of populations to respond to climate change will depend of evolutionary and demographic processes (i.e., plasticity, adaptation or migration) (Bourne et al. 2014). Specifically, level of additive genetic variance within population can directly influence evolutionary outcomes in response to environmental change by providing the necessary genetic variation upon which selection can act (Lande and Shannon 1996; Bourne et al. 2014). Now, our genetic results suggest high connectivity and gene flow among populations that furthermore still maintain high level of genetic diversity and higher evolutionary potential within each population, despite recent declines in population census size in some regions (e.g., Canada).

Following these results, two important points call, however, for further investigations. First, the very high level of genetic connectivity revealed by this study remains difficult to translate into an estimate of demographic connectivity. We have made some efforts to disentangle the effects of dispersal from local population size, but there remains too much uncertainty in our estimates to determine whether the extent of dispersal that ensures genetic homogeneity is enough to have an effect on local demography (a relevant issue in high gene flow species; Waples 1998; Waples and Gaggiotti 2006). Information on the behavior of first- and second-year ivory gulls and adult survival estimates will be key to reduce the space of dispersal parameters that are compatible with our genetic findings. We need to know more about the movement of birds between their natal site and first breeding attempt. Second, while our findings show that the genetic diversity within colonies is currently high, further studies will have to determine whether this state is stable or show signs of disequilibrium (e.g., in line with findings from demographic surveys that show a strong decline in colony numbers and size). The effects of overlapping generations and metapopulation functioning will have to be taken into account when looking for genetic signatures of demographic stability or decline (Leblois et al. 2006; Broquet et al. 2010; Chikhi et al. 2010).

Conservation implications

Resources for conservation management of endangered species are always limited, and therefore, an understanding of population differentiation and connectivity can help identify conservation priorities and inform management decisions. Here our results indicate that the ivory gull should be considered a wide-range, genetically homogeneous metapopulation. The lack of population genetic structure found among colonies, in tandem with independent evidence of movement among colonies, suggests that ongoing effective dispersal is occurring across ocean basins. This intercolony movement over large spatial scales can potentially enhance the persistence of highly fragmented seabird colonies. The generally large nonbreeding component of populations may also play an important role on the structure, dynamics and persistence of populations in buffering the effects of mortality with compensatory recruitment (Votier et al. 2008; although it may also hide a recent population decline, Penteriani et al. 2011). Our study suggests immigrant recruitment from distant populations could have similar effects. Understanding patterns of connectivity among disjunct populations of highly vagile colonial seabirds is vital to appropriately manage their populations and help predict the effect of future environmental change.

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