MOLECULAR ECOLOGY

Molecular Ecology (2013) **22**, 5835–5847 doi: 10.1111/mec.12548

Genetic consequences of breaking migratory traditions in barnacle geese *Branta leucopsis*

R. M. JONKER,*† R. H. S. KRAUS,*‡ Q. ZHANG,*§ P. VAN HOOFT,* K. LARSSON,¶ H. P. VAN DER JEUGD,** R. H. J. M. KURVERS,*†† S. E. VAN WIEREN,* M. J. J. E. LOONEN,‡‡ R. P. M. A. CROOIJMANS,§§ R. C. YDENBERG,*¶¶ M. A. M. GROENEN§§ and H. H. T. PRINS*

**Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands, †Department of Animal Behaviour, University of Bielefeld, Morgenbreede 45, 33615 Bielefeld, Germany, ‡Conservation Genetics Group, Senckenberg Research Institute and Natural History Museum, Clamecystraße 12, 63571 Gelnhausen, Germany, §Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101 China, ¶Kalmar Maritime Academy, Linnaeus University, 391 82 Kalmar, Sweden, **Dutch Centre for Avian Migration and Demography, NIOO-KNAW, Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands, ††Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany, ‡‡Arctic Centre, University of Groningen, Aweg 30, 9718 CW Groningen, The Netherlands, §§Animal Breeding and Genomics Centre, Wageningen University, P.O. Box 338, 6700 AH Wageningen, The Netherlands, ¶¶Department of Biological Sciences, Centre for Wildlife Ecology, Simon Fraser University, Burnaby, BC, Canada V5A 1S6*

Abstract

Cultural transmission of migratory traditions enables species to deal with their environment based on experiences from earlier generations. Also, it allows a more adequate and rapid response to rapidly changing environments. When individuals break with their migratory traditions, new population structures can emerge that may affect gene flow. Recently, the migratory traditions of the Barnacle Goose *Branta leucopsis* changed, and new populations differing in migratory distance emerged. Here, we investigate the population genetic structure of the Barnacle Goose to evaluate the consequences of altered migratory traditions. We used a set of 358 single nucleotide polymorphism (SNP) markers to genotype 418 individuals from breeding populations in Greenland, Spitsbergen, Russia, Sweden and the Netherlands, the latter two being newly emerged populations. We used discriminant analysis of principal components, F_{ST}, linkage disequilibrium and a comparison of geneflow models using MIGRATE-N to show that there is significant population structure, but that relatively many pairs of SNPs are in linkage disequilibrium, suggesting recent admixture between these populations. Despite the assumed traditions of migration within populations, we also show that genetic exchange occurs between all populations. The newly established nonmigratory population in the Netherlands is characterized by high emigration into other populations, which suggests more exploratory behaviour, possibly as a result of shortened parental care. These results suggest that migratory traditions in populations are subject to change in geese and that such changes have population genetic consequences. We argue that the emergence of nonmigration probably resulted from developmental plasticity.

Keywords: admixture, cultural evolution, migration modelling, population genetics, SNP, speciation

Received 27 March 2013; revision received 18 September 2013; accepted 20 September 2013

Introduction

Long-distance migration, in which individuals travel seasonally between breeding and nonbreeding locations, is a widespread phenomenon (Milner-Gulland *et al.*

Correspondence: Rudy M. Jonker,
E-mail: mrjonker@gmail.com

2011) and can be found in species ranging from insects to birds to mammals. The mode of transmission of migratory behaviour plays a crucial role in the evolution of migration and in how migration changes in response to environmental change. Generally, there are two distinct modes of transmission of migration (Sutherland 1988), genetic (e.g. Helbig 1991; Pulido & Berthold 2010) and cultural (Sutherland 1998; Guttal & Couzin 2010).

In the case of culturally transmitted migration, social or kin groups follow a migratory route acquired by tradition (Raveling 1979; Nelson 1995; Palacín *et al.* 2011) or selected by majority decisions (Prins 1996). Offspring generally travel where their parents have travelled and breed where they were born (Van der Jeugd *et al.* 2002). Traditions and natal philopatry can limit gene flow between colonies or populations, thereby increasing the rate of divergence (Friesen *et al.* 2007; Riesch *et al.* 2012). Culturally transmitted migration is widespread and is especially prominent in long-lived species because longevity allows an individual to profit from acquired information. Learning from parents is especially beneficial, as their behaviour demonstrably produced offspring and was thus successful. Overlapping generations and a relatively stable environment (McNamara & Dall 2011) are a prerequisite for cultural transmission. The more generations overlap, the greater the benefit for individuals that learn migration (or any other behaviour) culturally as compared to individuals that do not, because there are more informed generations available for naive individuals.

Migratory routes or schedules are, however, by no means fixed/unalterable across generations (Berthold & Helbig 1992; Pulido 2007), and in both genetic and cultural transmissions, mechanisms have evolved that allow for changes in migratory behaviour. Interestingly, those species able to adjust their migratory behaviour rapidly are the 'cultural' migrants (Sutherland 1998) as traditions change more quickly than genes. A change in migratory tradition can result in the emergence of new migratory routes or new populations, and the question arises how a change in migration tradition affects the population genetic structure of a species. We expect that the discovery of novel breeding areas or migratory routes (and subsequent establishment of new breeding populations) may lead to genetic differentiation due to subsequent natal philopatry, whereas the mixing of previously (culturally) separated breeding areas or flyways may lead to population admixture. Here we study how a change in migratory traditions affected the population genetic structure of a long-distance migrant, the Barnacle Goose *Branta leucopsis*, which has gone through several major changes in migration.

In geese, parental care extends up to nearly a year. These close family bonds and cultural inheritance of migratory behaviour are assumed to have caused '*the closest kind of inbreeding*' (Mayr 1942 p.242) among Arctic or sub-Arctic birds, with the emergence of many different races as a result (Mayr 1942; Hochbaum 1955; Kear 1970; Baker 1978; Owen 1980). An example of this mechanism of cultural transmission is that of the lesser white-fronted goose *Anser erythropus*. Eggs of this species were placed in nests of barnacle geese upon which the young adopted the migration strategy of their foster parents (Von Essen 1991). Recently, the migration system of the Barnacle Goose has gone through a number of striking changes. In the middle of the twentieth century, there were three Arctic breeding populations (Greenland, Spitsbergen and Russia) with distinct flyways (Fig. 1). The Arctic populations have rapidly increased and expanded their breeding ranges within the Arctic over the past few decades (Fox *et al.* 2010). New breeding colonies established on Gotland, Sweden, in the 1970s (Larsson *et al.* 1988). Later in the 1980s and 1990s, the number of colonies increased in the Baltic region as well as in the southwest of the Netherlands in the 1980s. The populations breeding in Russia, Sweden and the Netherlands all winter mainly in the Netherlands. Additionally, the barnacle geese migrating from the Netherlands to Russia have since the 1990s delayed their commencement of spring migration by approximately one month, although there was considerable variation in commencement of migration before the 1990s already. The cause of this delay is subject to debate as both competition for food (Eichhorn *et al.* 2008) and predation danger (Jonker *et al.* 2010) are proposed. Recently, the population wintering in Scotland and breeding on Spitsbergen have also started to delay the commencement of spring migration (Loonen *et al.* unpublished data). This delay in migration has the potential to affect the cultural transmission of migratory behaviour, possibly causing the establishment of new migration routes or breeding areas. Here, we study the consequences of these dramatic changes in migratory behaviour on the population genetic structure of the Barnacle Goose. We use genetic samples from the five main global populations, and we make use of the availability of a new set of 358 single nucleotide polymorphism (SNP) markers with genomewide coverage (Jonker *et al.* 2012b).

Materials and methods

Study populations and sampling

We used previously collected samples of the five main populations of the Barnacle Goose: Greenland (GL),

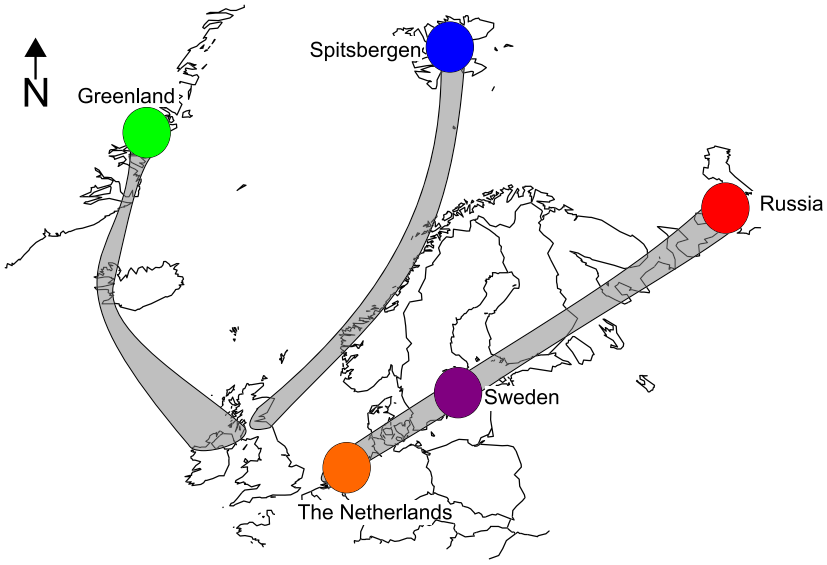

Fig. 1 Map of Barnacle Goose populations. Colours correspond with the colours in the other figures. The separate migratory flyways are indicated in grey.

Spitsbergen (SP), Russia (RU), Sweden (SE) and the Netherlands (NL). The Swedish and Russian populations use the Netherlands as wintering area, but mainly use the north of the Netherlands for wintering, whereas the Dutch population mainly uses the southwest of the Netherlands as breeding area. All samples were collected at the breeding site during the moult after breeding, and the vast majority of individuals were sampled as adult (388 of 418). For Greenland, tissue samples collected from the foot sole were used. These were collected in the 1970s and were obtained from the collection of the Zoological Museum in Amsterdam. For all other populations, we used ethanol-preserved whole-blood samples.

Samples from Spitsbergen were collected in 2007 from the colonies near Nordenskioldkysten, Ny-Ålesund and Longyearbyen. Russian samples originated from the colony of the Kolokolkova Bay near Tobseda (Van der Jeugd *et al.* 2003) and were collected in 2007 and 2008. Swedish samples were collected from the Gotland population (Larsson *et al.* 1988) in 2009. Samples from the Netherlands were collected in the Krammersche Slikken in 2007 and 2008 (Table 1). All samples were collected following national and institutional rules. Because barnacle geese have an average life expectancy of 8–15 years (depending on population), the collected samples represent a cross-section from these populations covering up to one decade *before* the moment of sampling. We isolated DNA using Proteinase-K and the Gentra Systems Puregene DNA purification kit, described in detail elsewhere (Kraus *et al.* 2011a; Jonker *et al.* 2012b).

We used the Illumina Golden Gate® genotyping assay on an Illumina® BeadXpress with VeraCode™ technology to genotype each individual for 384 single nucleotide polymorphisms (SNPs) (Jonker *et al.* 2012b) and the program Genome Studio (Illumina Inc.) for allele calling (clustering) for each SNP individually.

Table 1 Overview of origin of samples of individuals

Location	Lat/lon	Number of individuals
Greenland	70.4° N/22.3° W	5
Spitsbergen	78° N/12° E	117
Russia	70° N/50° E	107
Sweden	57.27° N/18.45° E	55
The Netherlands	51.6° N/4.2° E	134

General population genetic analyses

We tested all SNP markers for deviation from Hardy–Weinberg equilibrium (HWE) in each population separately using the package *Adegenet 1.2-8* (Jombart 2008) in *R* (R Development Core Team 2013). We calculated pairwise F_{ST} for all populations with *pp.fst* from the package *hierfstat* (Goudet 2005) in *R*. We tested the significance of these observed F_{ST} values using a bootstrap procedure using 100 000 bootstraps using *boot.ppfst* from the same package and calculated 95% confidence intervals of these F_{ST} values.

Discriminant analysis of principal components

We used discriminant analysis of principal components (DAPC$_S$) (Jombart *et al.* 2010) to analyse the population structure. This method allows identification of genetic clusters and unravelling complex population

structures. Because DAPC is not sensitive to underlying family structures, we did not remove related individuals from the analysis. We used the percentage of successful assignment as a measure of group differentiation, corrected for the number of retained principal components (function *a.score* in *R*-package *Adegenet* version 1.3-5). Because using too many principal components leads to overfitting of the model, the successful assignment is corrected for the number of principal components. We determined the optimal number of retained principal components using the function *optim.a.score* (with 20 simulations per principal component). In our study, we retained 50 principal components cumulatively explaining 45% of the variance.

We ran two DAPC analyses. First, we assigned each individual *a priori* to its population of origin (*a priori* population assignment) and obtained for each individual the probability of assignment to their populations of sampling. This allowed us to test which of the prior populations an individual could be assigned to best and showed us whether individuals recently moved from one population to another, indicating admixture. Thereafter, we used the *find.clusters* function, to determine the number of clusters and assign each individual to a cluster without providing any *a priori* population assignment. Similar to the *a priori* population assignment, we then obtained a probability of assignment to each cluster for each individual *a posteriori* (*a posteriori* population assignment). This removes the effect of assigning populations *a priori* on the eventual assignment to clusters and offers an unbiased interpretation of population structure.

Linkage disequilibrium

We used COANCESTRY (Wang 2011), with standard settings unless mentioned differently, to calculate relatedness between all individuals in our data set. Of the pairs that had relatedness higher than 0.2, we randomly removed one individual to remove possible family substructure from the data set. Then we tested for each pair of SNPs whether there was significant linkage disequilibrium using *LD* from the *R*-package *Genetics* (Warner & Leisch 2002) to estimate '*D*'. Only those markers polymorphic within each population were tested. Bonferroni correction for multiple pairwise comparisons thus resulted in a different *P*-value threshold $\left(0.05/\left(\frac{n*(n-1)}{2}\right)\right)$, with n being the number of polymorphic loci) per population because in some populations, more SNPs were polymorphic than in others. To test for physical linkage as explanation for linkage disequilibrium, we have mapped the LD pairs on the genome (SNP positions as inferred from comparisons with the chicken genome, for details see Jonker *et al.* (2012b)) to see how many of the LD pairs were within and between chromosomes. To test for inbreeding as a cause for LD, we calculated the average inbreeding coefficient using dyadic maximum-likelihood estimator (DyadML) (Milligan 2003) using COANCESTRY, which was lower than 0.06 for all populations.

GeneFlow model selection

We used the program MIGRATE-N (Beerli 2009) to compare different models of gene flow among the populations (Beerli 2012) to test different scenarios on the evolution of migratory flyways of the Barnacle Goose and obtain insight into whether some populations have stronger traditions (i.e. lower relative emigration) or are difficult to immigrate into because of differences in life history. We excluded samples from Greenland in these analyses because they were collected before the Swedish and Dutch populations emerged, which makes inference of gene flow between these populations from present-day data questionable.

We defined seven candidate models constraining the presence and directionality of gene flow between the four populations: Spitsbergen, Russia, Sweden and the Netherlands. Model 1 allowed gene flow between all possible population pairs (full island model). In model 2, there was no gene flow between Spitsbergen and any other population, except to and from the Netherlands. Two-way gene flow was possible among Russia, Sweden and the Netherlands. Model 3 was similar to model 2, but did not allow gene flow from Spitsbergen to the Netherlands. Model 4 reflects the situation before the emergence of the additional populations in the 1970s. At that time, only the Russian and Spitsbergen (and Greenland) populations were present, which are assumed to have had some exchange. From the Russian population, the Swedish and Dutch populations emerged, which is reflected in our model by allowing gene flow between these populations. Model 5 is different from model 4 in that there is no direct gene flow from Russia to the Netherlands. This model represents the situation that there is gene flow between Russia and Sweden, and between Sweden and the Netherlands. Model 6 reflects gene flow between Russia and the Netherlands and Sweden, without allowing any gene flow between Sweden and the Netherlands. In model 7, one-way gene flow from the Netherlands to Sweden is added to those possible in model 6 (Table 4 and Fig. S1 (Supporting information) for a visual representation of the seven models).

We compared the models using Bayes factors (Beerli & Palczewski 2010; Beerli 2012), which are marginal likelihoods over the complete parameter range (Newton & Raftery 1994). We ranked the Bayes factors of all

models using:

$$\mathrm{BF} = e^{\left(\mathrm{HM}_{\mathrm{model}_i} - \mathrm{HM}_{\mathrm{model}_j}\right)}$$

in which model i is the model with the lowest harmonic mean (HM) of the marginal likelihood and model j is each of the other models. This difference between two harmonic means is denoted as dHM (Table 4). Subsequently, we calculated the probability of each model using

$$\mathrm{Prob}_{\mathrm{model}_i} = \frac{\mathrm{mL}_{\mathrm{model}_i}}{\sum_j^n \mathrm{mL}_{\mathrm{model}_j}}$$

in which $\mathrm{mL}_{\mathrm{model}_i}$ is the maximum likelihood of model_i and $\sum_j^n \mathrm{mL}_{\mathrm{model}_j}$ is the sum of the maximum likelihoods of all the other models.

Results

The number of polymorphic SNPs for the entire sample (all populations combined) was 358. In the Greenland samples, only 282 SNPs were polymorphic, whereas the other populations had more than 350 polymorphic SNPs. The vast majority of polymorphic SNPs did not deviate significantly from Hardy–Weinberg equilibrium (GL: 100%, SP: 96%, RU: 95%, SV: 98%, NL: 95%, $\alpha = 0.05$). Calculations of pairwise F_{ST} values reveal significant population structure. Although the F_{ST} values are low (between 0.006 and 0.035), they are significantly different from 0 (Table 2). The F_{ST} analyses show that Greenland is most separated from the other populations with values ranging from 0.028 to 0.034. However, the confidence intervals of these estimates are much larger compared with those from other populations, so we need to be cautious with such conclusions because of the low sample size of this population. The Spitsbergen population is least differentiated from the Russian population (Fig. 2, $F_{ST} = 0.020$) and equally differentiated from the Swedish and Dutch populations (Fig. 2, F_{ST}, respectively, 0.026 and 0.027). The Swedish population and the Russian population are the two least differentiated populations with an F_{ST} of 0.006. The F_{ST} values from the Dutch population indicate that the Russian and Dutch populations are similarly differentiated ($F_{ST} = 0.015$) compared with the Dutch and Swedish populations ($F_{ST} = 0.018$).

Discriminant analysis of principal components

The DAPC analysis, which explained 45% of the variance in our data of prior clusters, confirms the presence of the genetic structure as indicated by the F_{ST} analysis. Both the F_{ST} values and the PCA plot indicate that Spitsbergen is relatively differentiated from the other populations. Furthermore, these results show that Sweden and Russia are closer to each other than to the Dutch cluster (Fig. 3A). The probability of assignment of individuals to their original sampling locality (Fig. 4A) shows that the individuals from Greenland were all assigned to the Greenland clusters with probabilities close to 1. For Spitsbergen, most individuals (113 of 117) were assigned to the Spitsbergen cluster, but some individuals had a high probability of being assigned to the Russian genetic cluster (3 of 117). In the Russian population, most individuals had the highest probability of being assigned to the Russian cluster (93 of 107), but a relatively large proportion of individuals show a substantial probability (>0.3) of assignment to the Dutch (5 of 107) and Swedish clusters (8 of 107). The results for the Swedish population show that most were assigned to Sweden (42 of 55), and many of the individuals were assigned to the Russian (8 of 55). Also, there were a number of individuals for which the probability of assignment to Sweden and Russia differed little (3 of 55). Only few Swedish individuals had high probabilities of assignment to the Dutch cluster (2 of 55). Of the Dutch population, most individuals (124 of 134) were assigned with high probabilities to the Dutch cluster, and number of individuals had high assignment probabilities to the Russian cluster (10 of 134). Only very few individuals (2 of 134) had some assignment probability (>0.3) to the Swedish genetic cluster.

The *a posteriori* DAPC analysis (Fig. 3B and 4B) shows that most individuals (111 of 117) of the Spitsbergen population were assigned to the same cluster (cluster 2), where the ones assigned to other clusters were also

Table 2 F_{ST} values between population pairs. All calculated F_{ST} values were significant at the $P < 0.0001$ threshold. Values in between brackets indicate the lower and upper 95% confidence limits

	Greenland	Spitsbergen	Russia	Sweden
Greenland	—			
Spitsbergen	0.029 (0.016–0.043)	—		
Russia	0.028 (0.015–0.043)	0.020 (0.016–0.023)	—	
Sweden	0.035 (0.020–0.051)	0.026 (0.021–0.031)	0.006 (0.004–0.008)	—
Netherlands	0.035 (0.021–0.049)	0.027 (0.022–0.031)	0.015 (0.012–0.017)	0.018 (0.014–0.021)

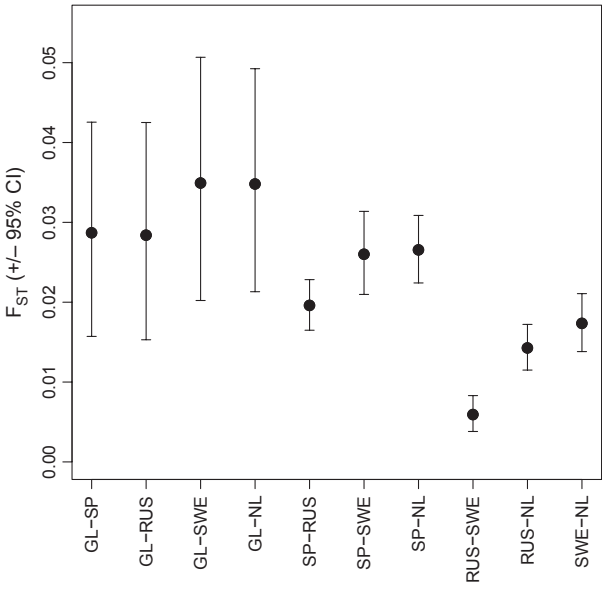

Fig. 2 F_{ST} statistics between all population pairs with 95% confidence intervals. GL = Greenland, SP = Spitsbergen, RUS = Russia, SWE = Sweden, NL = The Netherlands.

assigned to other populations in the a priori assignment procedure. The individuals of the Russian and Swedish population were also assigned mostly to one cluster (cluster 1, 147 of 162). Cluster 6 consists of individuals originating from Russia (4), Sweden (7) and the Netherlands (69). Most remaining individuals (45) from the Netherlands are assigned to clusters 3, 4 and 5. These clusters contain, except for one Swedish individual, no individuals from other populations than the Dutch population.

Linkage disequilibrium

We detected linkage disequilibrium between SNPs in all but the Greenland population. The absence of LD in the Greenland population is probably due to low sample size. In the Spitsbergen population, 63 pairs of SNPs (0.05%) showed linkage disequilibrium. Also in the Russian population (40 pairs, 0.03%), the Swedish population (33 pairs, 0.03%) and the Dutch population (130 pairs, 0.10%), a higher proportion of SNPs than would be expected by chance were in linkage disequilibrium (Table 3). Of the 247 unique LD pairs, 45 were within

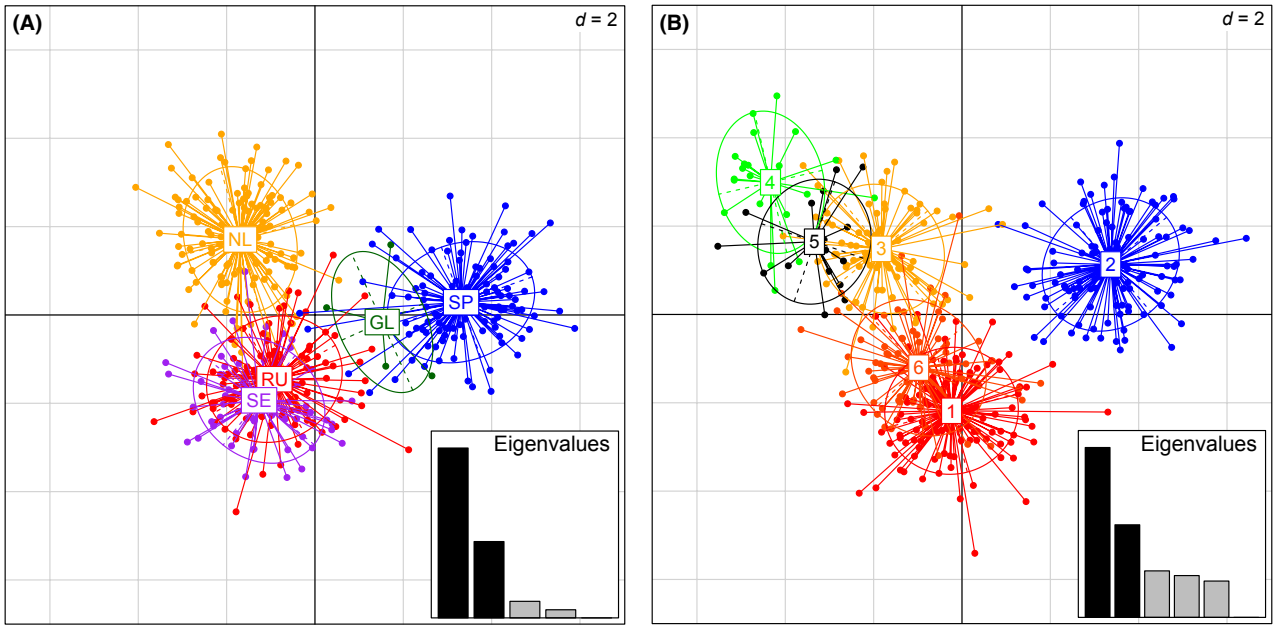

Fig. 3 Scatter plot of prior and posterior clusters. In the left panel (3A), the individuals are plotted with *a priori*-defined populations (GL: Greenland, SP: Spitsbergen, RU: Russia, SE: Sweden, NL: The Netherlands). In the right panel (3B), the individuals are assigned to populations *a posteriori*, that is, after determining the number of clusters by the program, instead of forcing into known populations. Cluster 2 corresponds largely with Spitsbergen and cluster 1 corresponds to Russia and Sweden together. In cluster 6, individuals from all populations are present, but mainly from the Netherlands; clusters 3, 4 and 5 almost completely consist of individuals from the Netherlands. The colours in Fig. 3A correspond with the colours in Fig. 4A, and the colours of Fig. 3B correspond with the colours of Fig. 4B. The bar graph insets indicate the amount of variance explained by the two discriminant eigenvalues used for plotting. Both plots have the same scale on both axes, as indicated by the d = 2 in both graphs. Ellipses are inertia ellipses calculated by the variance of both pc-axes and represent 67% of the variance.

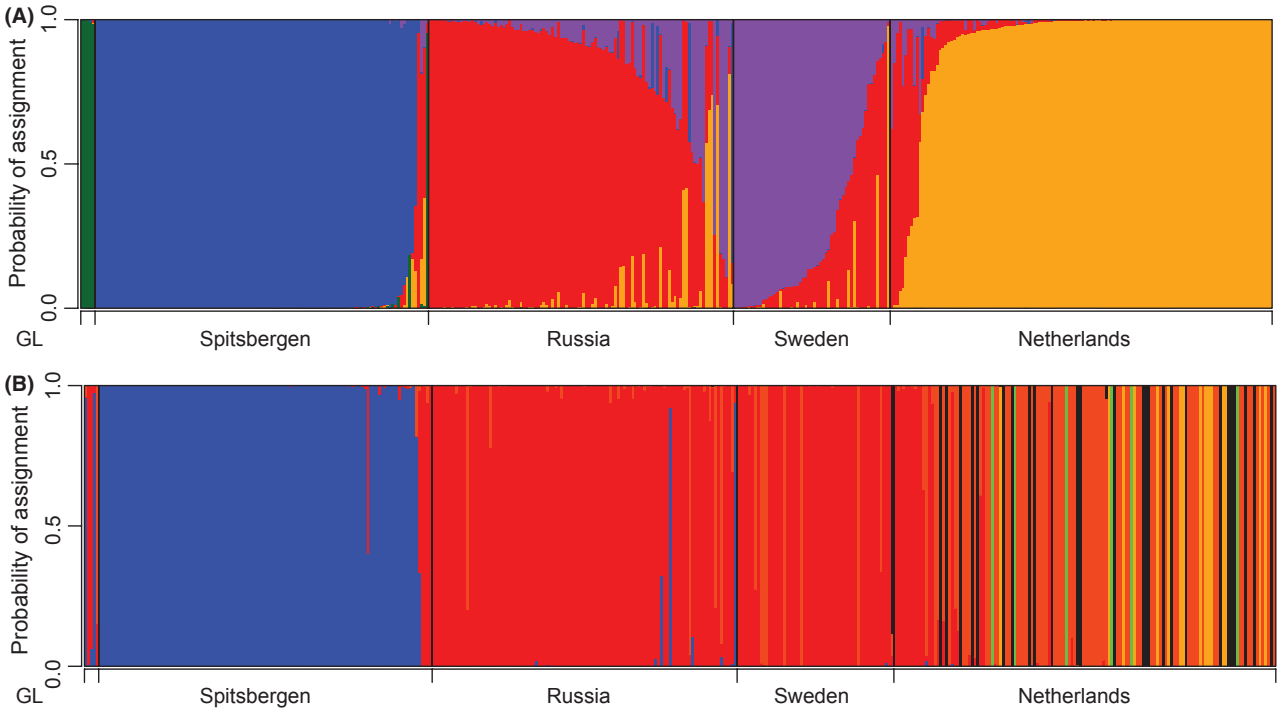

Fig. 4 Stacked bar graph of assignment probabilities per individual. In the upper panel (Fig. 4A), populations of the individuals were defined *a priori*. The probability of assignment indicates the probability that each individual was assigned to its *a priori* set population. In the lower panel (Fig. 4B), no populations were defined *a priori*. Instead individuals were assigned to one of the clusters that were detected by the software. Both Fig. 4A,B consist of 418 stacked bars, in which each bar is one individual and the order of the individuals is the same in both graphs. If an individual was assigned to multiple clusters, bars were stacked.

Table 3 Number of pairs of markers in linkage disequilibrium (LD) and associated *P*-value thresholds (0.05/((n*n-1)/2)) for LD. The number of polymorphic SNPs in each population is n. The number of individuals is the number that remained in the analysis after removing the closely related individuals

	Nr of pairs in LD	*P*-value threshold	n (SNPs)	# of individuals
Greenland	0	1.262E-06	282	5
Spitsbergen	63	8.048E-07	353	112
Russia	40	8.002E-07	354	103
Sweden	33	8.140E-07	351	49
Netherlands	130	8.094E-07	351	79

chromosomes. The median distance between these within chromosome LD pairs was 2.7 Mb (Fig. S2–S6, Supporting information).

Migration rate model comparison

Our comparison of candidate models of gene flow between populations showed that the full geneflow model (model 1) fitted our data best (Table 4). The large difference in harmonic mean of the marginal likelihood between the models results in a probability of 1 (1–0.1*10^{-27}) for this model. Hence, we further only report results for model 1. For convenience, we scaled all geneflow measures relative to the smallest, which is $M_{SE\rightarrow SP}$ (Migration from Sweden (SE) to Spitsbergen (SP), unscaled M: 922). Consequently, all further conclusions from this analysis are based on relative differences in gene flow. A number of patterns become clear from these geneflow measures (Fig. 5). The geneflow measures to Sweden ($M_{SP\rightarrow SE}$, $M_{RU\rightarrow SE}$, $M_{NL\rightarrow SE}$) are all relatively high (average: 2.08), whereas the geneflow measures from Sweden are relatively low (average: 1.17). For the Netherlands, the pattern is the opposite. The geneflow measures to the Netherlands ($M_{SP\rightarrow NL}$, $M_{RU\rightarrow NL}$, $M_{SE\rightarrow NL}$) are relatively low (average: 1.30), whereas the geneflow measures from the Netherlands are relatively high (average: 1.93). The geneflow measures from Spitsbergen ($M_{SP\rightarrow RU}$, $M_{SP\rightarrow SE}$, $M_{SP\rightarrow NL}$) are relatively higher (average: 1.75) than geneflow measures to Spitsbergen (average: 1.43). Finally, the geneflow measures from Russia ($M_{RU\rightarrow SP}$, $M_{RU\rightarrow SE}$, $M_{RU\rightarrow NL}$) are similar (average 1.53) to the geneflow measures to Russia (average: 1.57).

Discussion

Our F_{ST} analysis and the structure analysis of the DAPC show that the five populations of barnacle geese are

Table 4 Bayes factors model comparison of migration models

Model	Model parameters	Harmonic mean (HM)	dHM	Probability
Model 1	**** **** **** ****	−5899	0	1
Model 2	*00* 0*** 0*** ****	−7428	−1530	0
Model 3	*00* 0*** 0*** 0***	−6537	−639	0
Model 4	**00 **** 0*** 0***	−7076	−1177	0
Model 5	**00 ***0 0*** 00**	−8178	−2279	0
Model 6	**00 **** 0**0 0*0*	−8191	−2293	0
Model 7	**00 **** 0*** 0*0*	−7819	−1920	0

In this model comparison, four populations were used: (i) Spitsbergen, (ii) Russia, (iii) Sweden, (iv) the Netherlands. Model parameters code as follows: the first four signs indicate migration to the first population from populations 1, 2, 3 and 4. The second four signs indicate migration to the second population from 1,2,3 and 4. The first sign of the first quartet and the second of the second quartet indicate estimation of theta for populations 1, 2, etc. An asterisk indicates that that particular migration rate was estimated by the model, and a 0 indicates that no migration was allowed. For example, for model 2: no migration from Russia and Sweden to Spitsbergen was estimated, and no migration from Spitsbergen to Russia and Sweden was estimated. For each model, we used 4 heated chains with 1, 1.5, 3, 1 000 000 heating scheme. The sampling increment in the prior was set to 20, the number of steps discarded (burn-in) was 2.000.000, and the number of steps analysed was 5.000. Prior thetas were generated from a uniform distribution ranging from 0 to 15, and prior migration rates were generated from a uniform distribution ranging from 0 to 4000. These settings resulted in converged posterior distributions with a clear maximum for each estimate (Supplementary File 1 for model 1).

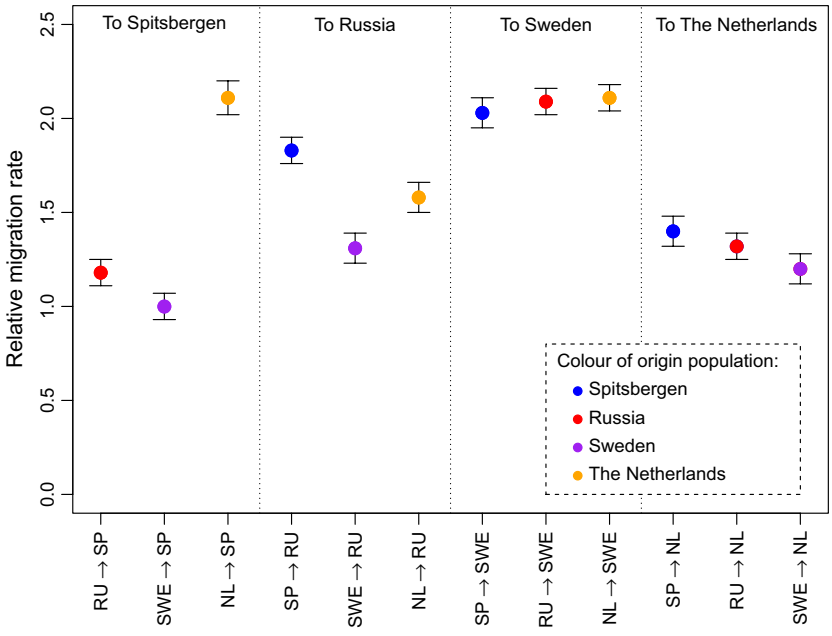

Fig. 5 Migration rates with confidence intervals. The modes of the scaled migration rates with 95% confidence intervals are shown. Colours represent the source population. Dashed lines separate the populations of destination.

differentiated populations. However, the presence of linkage disequilibrium among a number of the SNPs suggests admixture (Hartl & Clark 2007) between the populations. The alternative explanations for linkage disequilibrium, physical linkage, low recombination rate or selection for particular SNPs, are unlikely to explain this. Because the minimum physical distance between the SNPs ranged from a 100–200 kb (Jonker *et al.* 2012b), it is unlikely this could have caused linkage disequilibrium, which is also shown by the distance between LD pairs within chromosomes (Fig. S6, Supporting information). Differences in recombination rates between the populations are unlikely, and linkage disequilibrium caused by selective sweeps would have resulted in a nonrandom pattern of distribution of LD pairs over the genome, which is not the case (Fig. S2–S5, Supporting information). Linkage disequilibrium in the Spitsbergen population could potentially have been caused by small population size in the past, while linkage disequilibrium in the Dutch and Swedish populations could have been caused by small populations of founders. In the Russian population, such a cause is

unlikely because of the large population size in the past. However, our explanation of admixture is consistent with the assignment probabilities in the DAPC analysis that showed that in most populations a considerable number of individuals have a high assignment probability to a population different from their sampling population and with the gene flow estimated by MIGRATE-N.

These findings suggest that over the past few generations, individuals have moved from one population to another, which implies that a number of individuals broke with their migratory traditions. We argue that this is a recent event, because otherwise linkage disequilibrium would already have disappeared. Evidence for recent population exchange via dispersal also comes from (sparse) data of ring recoveries. Based on ring recoveries, exchange rates between the Spitsbergen and Greenland populations were estimated at (0.0010 and 0.0011 (probability of dispersal to destination population, taking into account source population specific survival and recapture probabilities, see for more details Black *et al.* 2007), but most individuals that dispersed (40–90%) returned to their population of origin after one or several years (Black *et al.* 2007). The probability for a Russian individual immigrating into the Spitsbergen population was much lower at 0.00014 and 0.0008 in the other direction, with fewer birds returning (9–39%). No evidence for exchange between the Russian and Greenland populations based on resightings was found (Black *et al.* 2007). These data illustrate that dispersal events occur, creating opportunities for interpopulation breeding pairs to establish. Our genetic analysis allow for much more fine-grained analysis of exchange rates between populations than based on ring resightings and suggest that exchange rates are generally higher than previously assumed.

Both the DAPC analysis and the F_{ST} analysis showed that the genetic distance between the Spitsbergen population and the Russian, Swedish and Dutch populations is larger than among the last three populations, with the Russian population being closest to Spitsbergen of these three. This suggests that the Swedish and Dutch population recently diverged from the Russian population. Moreover, the result that the F_{ST} between Russia and Sweden is the smallest of all pairwise comparisons indicates that most exchange of individuals occurs between Russia and Sweden. This is also supported by the DAPC analysis, which shows that many birds sampled in Sweden have a high probability of being assigned to the Russian population. During wintering in the Netherlands, individuals from the Russian and Swedish populations mainly reside in the north of the Netherlands, while individuals from the Dutch population mainly reside in the south as indicated from the ring recoveries (Jonker *et al.* 2012a). This could explain the strong connection between the Swedish and Russian populations. Van Der Jeugd & Litvin (2006) documented long-distance dispersal from the Baltic based on ring resightings and recoveries and estimated that 6.6% of all Baltic juveniles dispersed over long distances, mainly to the Russian population.

At the same time, the three identified groups of Dutch barnacle geese in the *a posteriori* DAPC analysis may lead one to believe that minor mixing with individuals of a captive origin (Lensink 1996), or possibly hybridisation with cackling geese *Branta hutchinsi* (HvdJ pers obs) have occurred. If this were the case, however, the F_{ST} between the Dutch population and the other populations would be expected to be higher than F_{ST} values among the other populations. In either case, this population structure within the Dutch population is an interesting observation that warrants further research in the future.

Additionally, our MIGRATE-N analysis indicates that a full island model (bidirectional gene flow between all populations) is best supported, while dispersal between all populations, and especially between the three flyways, is very unlike traditionally inherited migration systems (Mayr 1942; Anderson *et al.* 1992). The exchange between the flyways could in time lead to a pattern of general lack in flyway structure already present in Mallard *Anas platyrhynchos* (Kraus *et al.* 2011b, 2013) depending on overall migration rates. The relatively large emigration from and low immigration to the Netherlands suggests high exploration rates for individuals from this population and a certain constraint to immigrate into this population. Potentially, the difference in seasonally migratory behaviour of the Dutch population, as compared to all the others (the Dutch population is the only nonmigratory population), reduces the chance of settling permanently in the Dutch population, because adults who already adopted a migratory tradition may not be likely to lose it. Further, population differences in the timing of breeding and moult (Van der Jeugd *et al.* 2009) may reduce the fitness of individuals that settle into a new population because these events can have strong fitness consequences (Prop *et al.* 2003), and individuals have shown to not easily adjust the timing of moult (Loonen & Follestad 1997).

The seemingly high emigration rate from the Dutch population could be caused by the very short duration of parental care in this nonmigratory population (Jonker *et al.* 2012a). Whereas parents in the (migratory) Russian population provide parental care until approximately early March, the parents in the (nonmigratory) Dutch population provide parental care only until the end of November. As juveniles are suggested to venture on exploratory trips after being released from the family (Baker 1978), this increases the exploratory potential for

the Dutch population. Because linkage disequilibrium due to admixture disappears very rapidly (halving each generation), our results suggest that this mixing did not start longer than a few generations ago, which fits the timescale of the behavioural changes in migration and parental care duration (Jonker *et al.* 2010, 2011). Moreover, the convergence of populations, resulting from the reduced cultural transmission of migration, probably reversed the ongoing differentiation of populations caused by the strong natal philopatry and conservatism of migratory traditions in populations. This race-forming is thought to be exceptionally high in geese (Mayr 1942), although the genetic consequences of migratory traditions have been rarely studied in detail and on the large spatial scale as in our study. Harrison *et al.* (2010) studied whether the strong natal philopatry affected the dispersal distance between parents and offspring within one flyway of the light-bellied brent geese *Branta bernicla hrota*. They show that dispersal distances were indeed smaller than expected based on random dispersal distances, confirming natal philopatry. Subsequently, among 1127 individuals, there was no apparent population structure, in contrast to what they expected based on natal philopatry and dispersal distances. Although a large part of their individuals studied hardly dispersed from the natal area, there was a long tail in the distribution of dispersal distances, which would explain the lack of population structure in their analysis. This suggests that only few broken traditions can make a population appear panmictic, a phenomenon compatible with the often quoted 'one migrant per generation' rule (Mills & Allendorf 1996). Similarly, a study on lesser kestrels *Falco naumanni* that combined capture–recapture and genetic analysis using microsatellites showed that very small-scale natal philopatry (<100 km) did not lead to genetic differentiation (Alcaide *et al.* 2009). Contrastingly, in greater snow geese *Chen caerulescens atlantica,* it was shown, using AFLP markers, that even on this small spatial scale, genetic differentiation occurred as a result of natal philopatry (Lecomte *et al.* 2009).

An important aspect in understanding gene flow between goose populations is the pair formation in winter. As the individuals in our study from the Russian, Swedish and Dutch populations winter in the Netherlands, there is considerable potential for exchange between these populations. Pairs between individuals from the same population will be most common as barnacle geese prefer to mate with individuals familiar from earlier in life (Choudhury & Black 1994). However, pair formation with unfamiliar mates can and does occur (Kurvers *et al.* 2013). Because of the strong female natal philopatry in geese (Van der Jeugd *et al.* 2002), a male from another population is most likely to accompany its new mate to her population. Interestingly, Lecomte *et al.* (2009) showed that in greater snow geese, distances of 10–30 km at the rearing site resulted in differentiation even though the pairing took place almost 3000 km away, indicating that pairing mostly occurred between individuals of the same rearing site.

Changes of traditions in populations have been reported before, but not always have population genetic consequences. In herring *Clupea harengus,* the removal of adult individuals as a result of overfishing caused young individuals to explore new spawning grounds, whereas they would normally spawn at the traditional locations used by the older individuals (Corten 2002). The spawning ground was the tradition, and hatched larvae disperse easily, after which young herring join existing schools (McQuinn 1997). Consequently, the loss or acquisition of traditions would not likely have population genetic consequences. Also, in Canada geese *Branta canadensis,* nonmigratory populations have emerged. In some cases, this can be attributed to the re-introduction programmes from captive bred geese, which lacked traditions of migration (Mowbray *et al.* 2002). It has also been shown that young Canada geese made so-called reversal migration, which could play an important role in exchange between populations (Raveling 1976). Some populations of Pacific flyway brant geese *Branta bernicla nigricans* also lost their migratory behaviour. Unlike the Dutch population of barnacle geese that remain year-round in their traditional wintering habitat, they remain in their breeding area year-round (Ward *et al.* 2009), most likely because of increasing temperatures in the breeding area in winter. Thus, despite long-standing ideas of strong natal philopatry and high winter site fidelity in geese, in recent years, a variety of dramatic changes in migratory behaviour have been witnessed in several species of geese. Studying the population genetic consequences in these systems with migratory change, as well as in systems without much migration changes have taken place (Humphries *et al.* 2009), may provide insights into the generality of our findings.

We hypothesize that our results provide an elegant example of the emergence of novelty as a result of developmental plasticity as proposed by West-Eberhard (2003, 2005). Developmental plasticity means that the phenotype of individuals develops during their lifetime as a result of a particular sensitivity to their environment. Our results are comparable with Kondo *et al.* (2008) who compared two recently diverged long-distance and short-distance migrant Neotropical species to test which of these two species was the ancestral type, that is, whether short-distance migration emerged from long-distance migration as a result of a loss of

migration or *vice versa*. Their analysis suggested that the short-distance migrants recently diverged from the long-distance migrant via a founder event (although Jacobsen & Omland (2011) note that the species tree in this genus is not yet completely understood). They argued that the difference in the experienced year-round environment of the short-distance migrant led to altered natural selection, resulting in divergence between the two species, which supported the theory of speciation by developmental plasticity. In our case, we argue for the opposite effect of this developmental plasticity, that is, because of the reduced transmission of migratory traditions and the increased exploration, possibly leading to increased gene flow between populations, the likely ongoing differentiation between the different populations of barnacle geese might have been reversed.

Finally, cultural transmission mechanisms are most likely to evolve in occasionally fluctuating environments in which changes persist for a number of generations (Feldman *et al*. 1996). This suggests that geese, which primarily transmit migration strategy culturally, have evolved in an environment that has frequently changed before with intermediate periods of stability, bringing 'new' traditions into populations following events of environmental change. Following this argumentation, we hypothesize that the loss and acquisition of migration behaviour in geese has occurred before. In the Netherlands, there is currently a debate about the status of nonmigratory geese because geese are not 'supposed' to be nonmigratory with consequent persecution measures. We show that traditions in populations are not fixed and loss of traditions may lead to gene flow between traditional migration routes or lead to the emergence of nonmigration. We argue that this is not probably the result of a newly evolved trait, but of developmental plasticity. It is hoped that this insight will lead to a less conservative attitude towards wild populations in a rapidly changing environment.

Acknowledgements

Many thanks to Bert Dibbits, whose assistance was invaluable in the laboratory. Blood samples were collected as part of project BIRDHEALTH, funded by the Netherlands Organization for Scientific Research (NWO) on the occasion of the International Polar Year. Jouke Prop, Götz Eichhorn, Helmut Kruckenberg, Alexander Kondratyev and several students assisted in sample collection. We thank Kees Roselaar for access to the museum samples from the Zoological Museum Amsterdam. This work was financially supported by the KNJV (Royal Netherlands Hunting association), the Faunafonds and the Stichting de Eik Trust. We thank Staffan Bensch and the anonymous reviewers for their comments on the manuscript. This is publication 5517 of the Netherlands Institute of Ecology (NIOO-KNAW).

References

Alcaide M, Serrano D, Tella JL, Negro JJ (2009) Strong philopatry derived from capture-recapture records does not lead to fine-scale genetic differentiation in lesser kestrels. *Journal Of Animal Ecology*, **78**, 468–475.

Anderson MG, Rhymer JM, Rohwer FC (1992) Philopatry, dispersal, and the genetic structure of waterfowl populations. In: *Ecology and Management of Breeding Waterfowl* (eds Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL), pp. 365–395. University of Minnesota Press, Minneapolis, US.

Baker RR (1978) *The Evolutionary Ecology of Animal Migration*. Holmes & Meier Publishers, New York.

Beerli P (2009) How to use migrate or why are markov chain monte carlo programs difficult to use?. In: *Population Genetics for Animal Conservation* (eds Bertorelle G, Bruford MW, Hauffe HC, Vernesi C, Rizzoli A), pp. 42–79. Cambridge University Press, Cambridge UK.

Beerli P (2012) *Tutorial: Comparison of Gene Flow Models Using Bayes Factors*. Comparison of gene flow models using Bayes Factors, Tutorial.

Beerli P, Palczewski M (2010) Unified framework to evaluate panmixia and migration direction among multiple sampling locations. *Genetics*, **185**, 313–326.

Berthold P, Helbig AJ (1992) The genetics of bird migration: stimulus, timing, and direction. *Ibis*, **134**, 35–40.

Black JM, Prop J, Larsson K (2007) *Wild Goose Dilemmas*. Branta Press, Groningen, The Netherlands.

Choudhury S, Black JM (1994) Barnacle geese preferentially pair with familiar associates from early life. *Animal Behaviour*, **48**, 81–88.

Corten A (2002) The role of "conservatism" in herring migrations. *Reviews in Fish Biology and Fisheries*, **11**, 339–361.

Eichhorn G, Drent RH, Stahl J, Leito A, Alerstam T (2008) Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology*, **78**, 63–72.

Feldman M, Aoki K, Kumm J (1996) Individual versus social learning: evolutionary analysis in a fluctuating environment. *Anthropological Science*, **104**, 209–232.

Fox AD, Ebbinge BS, Mitchell C *et al*. (2010) Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. *Ornis Svecica*, **20**, 115–127.

Friesen VL, Burg TM, McCoy KD (2007) Mechanisms of population differentiation in seabirds. *Molecular Ecology*, **16**, 1765–1785.

Goudet J (2005) HIERFSTAT, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes*, **5**, 184–186.

Guttal V, Couzin ID (2010) Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences*, **107**, 16172–16177.

Harrison XA, Tregenza T, Inger R *et al*. (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Molecular Ecology*, **19**, 5484–5496.

Hartl DL, Clark AG (2007) *Principles of Population Genetics*. Sinauer Associates, Sunderland, MA.

Helbig AJ (1991) Inheritance of migratory direction in a bird species - a cross-breeding experiment with Se-migrating and Sw-migrating blackcaps (Sylvia-Atricapilla). *Behavioral Ecology and Sociobiology*, **28**, 9–12.

Hochbaum HA (1955) *Travels and Traditions of Waterfowl*. University of Minnesota Press, Minneapolis.

Humphries EM, Peters JL, Jónsson JE *et al.* (2009) Genetic differentiation between sympatric and allopatric wintering populations of snow geese. *The Wilson Journal of Ornithology*, **121**, 730–738.

Jacobsen F, Omland KE (2011) Species tree inference in a recent radiation of orioles (Genus Icterus): multiple markers and methods reveal cytonuclear discordance in the northern oriole group. *Molecular phylogenetics and evolution*, **61**, 460–469.

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

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics*, **11**, 1–15.

Jonker RM, Eichhorn G, van Langevelde F, Bauer S (2010) Predation danger can explain changes in timing of migration: the case of the barnacle goose. *PLoS ONE*, **5**, e11369.

Jonker RM, Kuiper MW, Snijders L *et al.* (2011) Divergence in timing of parental care and migration in barnacle geese. *Behavioral Ecology*, **22**, 326–331.

Jonker RM, Kurvers R, van de Bilt A *et al.* (2012a) Rapid adaptive adjustment of parental care coincident with altered migratory behaviour. *Evolutionary Ecology*, **26**, 657–667.

Jonker RM, Zhang Q, Van Hooft P *et al.* (2012b) The development of a genome wide SNP set for the barnacle goose *Branta leucopsis*. *PLoS ONE*, **7**, e38412.

Kear J (1970) The Adaptive Radiation of Parental Care in Waterfowl. In: *Social Behavior in Birds and Mammals* (ed. Crook JH), pp. 492. Academic Press, London.

Kondo B, Peters JL, Rosensteel BB, Omland KE (2008) Coalescent analysis of multiple loci support a new route to speciation in birds. *Evolution*, **62**, 1182–1191.

Kraus RHS, Kerstens HHD, Van Hooft P *et al.* (2011a) Genome wide SNP discovery, analysis and evaluation in mallard (*Anas platyrhynchos*). *BMC Genomics*, **12**, 1–11.

Kraus RHS, Zeddeman A, van Hooft P *et al.* (2011b) Evolution and connectivity in the world-wide migration system of the mallard: inferences from mitochondrial DNA. *BMC Genetics*, **12**, 99.

Kraus RHS, van Hooft P, Megens H-J *et al.* (2013) Global lack of flyway structure in a cosmopolitan bird revealed by a genome wide survey of single nucleotide polymorphisms. *Molecular Ecology*, **22**, 41–55.

Kurvers RHJM, Adamczyk VMAP, Kraus RHS *et al.* (2013) Contrasting context-dependence of familiarity and kinship in animal social networks. *Animal Behaviour*. doi: 10.1016/j.anbehav.2013.09.001.

Larsson K, Forslund P, Gustafsson L, Ebbinge BS (1988) From the high Arctic to the Baltic: the successful establishment of a Barnacle Goose *Branta leucopsis* population on Gotland, Sweden. *Ornis Scandinavica*, **19**, 182–189.

Lecomte N, Gauthier G, Giroux JF, Milot E, Bernatchez L (2009) Tug of war between continental gene flow and rearing site philopatry in a migratory bird: the sex-biased dispersal paradigm reconsidered. *Molecular Ecology*, **18**, 593–602.

Lensink R (1996) De opkomst van exoten in de Nederlandse Avifauna: verleden, heden en toekomst. (in Dutch, translated as: the emergence of exots in the Netherlands avifauna: past, present and future.). *Limosa*, **69**, 103–130.

Loonen MJJE, Follestad A (1997) Geographical variation in the timing of wing moult in Greylag Geese Anser anser. In: *Goose breeding ecology. Overcoming successive hurdles to raise goslings*. PhD Thesis Maarten Loonen.

Mayr E (1942) *Systematics and the Origin of Species, From the Viewpoint of a Zoologist*. Columbia University Press, New York.

McNamara JM, Dall SRX (2011) The evolution of unconditional strategies via the "multiplier effect". *Ecology Letters*, **14**, 237–243.

McQuinn IH (1997) Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, **7**, 297–329.

Milligan BG (2003) Maximum-likelihood estimation of relatedness. *Genetics*, **163**, 1153–1167.

Mills LS, Allendorf FW (1996) La regla de Un-Migrante-Por-Generación en Conservación y Manejo. *Conservation Biology*, **10**, 1509–1518.

Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) *Animal Migration: A Synthesis*. Oxford University Press, USA.

Mowbray TB, Ely CR, Sedinger JS, Trost RE (2002) Canada Goose (Branta canadensis). In: *The Birds of North America Online* (ed. Poole A), Cornell Lab of Ornithology, Ithaca. Available from: http://bna.birds.cornell.edu/bna/species/682.

Nelson ME (1995) Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Canadian Journal of Zoology*, **73**, 1069–1076.

Newton MA, Raftery AE (1994) Approximate Bayesian inference with the weighted likelihood bootstrap. *Journal of the Royal Statistical Society. Series B (Methodological)*, **56**, 3–48.

Owen M (1980) *Wild Geese of the World - Their Life History and Ecology*. B T Batsford Ltd., London.

Palacín C, Alonso JC, Alonso JA, Magaña M, Martín CA (2011) Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard Otis tarda. *Journal of Avian Biology*, **42**, 301–308.

Prins HHT (1996) *Ecology and Behaviour of the African Buffalo*. Chapman & Hall, London, UK.

Prop J, Black JM, Shimmings P (2003) Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, **103**, 403–414.

Pulido F (2007) The genetics and evolution of avian migration. *BioScience*, **57**, 165–174.

Pulido F, Berthold P (2010) Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 7341–7346.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org.

Raveling DG (1976) Migration reversal: a regular phenomenon of Canada geese. *Science*, **193**, 153–154.

Raveling DG (1979) Traditional use of migration and winter roost sites by Canada geese. *Journal of Wildlife Management*, **43**, 229–235.

Riesch R, Barrett-Lennard LG, Ellis GM, Ford JKB, Deecke VB (2012) Cultural traditions and the evolution of reproductive

isolation: ecological speciation in killer whales? *Biological Journal of the Linnean Society*, **106**, 1–17.
Sutherland WJ (1988) The heritability of migration. *Nature*, **334**, 471–472.
Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441–446.
Van Der Jeugd HP, Litvin KY (2006) Travels and traditions: long-distance dispersal in the Barnacle Goose *Branta leucopsis* based on individual case histories. *Ardea*, **94**, 421–432.
Van der Jeugd HP, van der Veen IT, Larsson K (2002) Kin clustering in barnacle geese: familiarity or phenotype matching? *Behavioral Ecology*, **13**, 786–790.
Van der Jeugd HP, Gurtovaya E, Eichhorn G *et al.* (2003) Breeding barnacle geese in Kolokolkova Bay, Russia: number of breeding pairs, reproductive success and morphology. *Polar Biology*, **26**, 700–706.
Van der Jeugd HP, Eichhorn G, Litvin KE *et al.* (2009) Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology*, **15**, 1057–1071.
Von Essen L (1991) A note on the Lesser White-Fronted Goose *Anser erythropus* in Sweden and the result of a re-introduction scheme. *Ardea*, **79**, 305–306.
Wang J (2011) Coancestry: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, **11**, 141–145.
Ward DH, Dau CP, Tibbitts TL *et al.* (2009) Change in abundance of Pacific Brant wintering in Alaska : evidence of a climate warming effect? *Arctic*, **62**, 301–311.
Warner GE, Leisch F (2002) *"Genetics'', a Package for Handling Marker-Based Genetic Data within the Open-Source Statistical Package R*. Available from: http://cran.r-project.org.
West-Eberhard MJ (2003) *Developmental Plasticity and Evolution*. Oxford University Press, Oxford, UK.
West-Eberhard MJ (2005) Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences*, **102**, 6543–6549.

R.M.J. designed the study, coordinated sample collection, prepared DNA, analysed and interpreted data, and wrote the manuscript. R.H.S.K. designed the study, analysed and interpreted data, revised the manuscript. Q.Z. prepared DNA, revised the manuscript. P.v.H. co-designed the study, interpreted data, revised the manuscript. K.L. contributed samples, interpreted data, revised the manuscript. H.P.V.D.J. contributed samples, revised the manuscript. R.H.J.M.K., S.V.W., R.P.M.A.C., R.C.Y., M.A.M.G., H.H.T.P. co-designed the study, revised the manuscript. M.J.J.E.L. coordinated sample collection, contributed samples, revised the manuscript.

Data accessibility

All the details of the SNPs are already publicly available and are described in Jonker *et al.* (2012b). All data and R-scripts are deposited in Dryad at http://doi:10.5061/dryad.mf3gd.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 A geographical representation of the 7 gene-flow models.

Fig. S2–S5 Schematic map of LD pairs across the 374 SNPs.

Fig. S6 Distribution of within chromosome LD pairs.