Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant

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Abstract

Cultural transmission is thought to be a mechanism by which migratory animals settle into habitats, but little evidence exists in wild populations because of the difficulty of following individuals over successive generations and wide geographical distances. Cultural inheritance of migration routes represents a mechanism whereby geographical isolation can arise between separate groups and could constrain individuals to potentially suboptimal sites within their range. Conversely, adopting the parental migratory route in adult life, rather than dispersing randomly, may increase an individual’s reproductive success because that strategy has already been proven to allow successful breeding. We combined a pedigree of related light-bellied Brent geese (*Branta bernicla hrota*) with 6 years of observations of marked birds to calculate the dispersal distances of adult offspring from their parents in both Ireland and Iceland. In both countries, the majority of offspring were found to recruit into or near their parental sites, indicating migratory connectivity in the flyway. Despite this kin structure, we found no evidence of genetic differentiation using genotype data from 1127 individuals across 15 microsatellite loci. We suggest that the existence of migratory connectivity of subpopulations is far more common than previous research indicates and that cultural information may play an important role in structuring reproductive isolation among them.

Keywords: *Branta bernicla hrota*, Brent goose, centroid, culture, genetic structure

Introduction

Choosing where to settle as an adult is a key decision in the life cycle of many animals. Such decisions underpin the genetic and demographic structure of populations and have important implications for conservation, ecology and evolutionary processes such as speciation (Clobert *et al.* 2001; Clark *et al.* 2004). However, despite a general appreciation of its importance, our understanding of dispersal and settlement in highly vagile groups remains limited because of the difficulty in tracking individuals throughout their early lives. This remains most problematic for long-distance migratory species where dispersal rates are generally high (Lecomte *et al.* 2009), and the impact that site choice has on demographic or genetic composition varies across the season. For example, if young animals show fidelity to wintering sites but disperse randomly among sites at other times of year, the effect on the genetic structure would be much less than if site fidelity persisted throughout the annual cycle. The extent to which site fidelity persists across the annual cycle and the linkages...
between different stages (known as migratory connectivity: Webster et al. 2002) is therefore a vital component in the understanding of the consequences of dispersal decisions in migratory species. From here on we shall refer to non-breeding season sites visited in the first year of life (while moving with the family group) as ‘parental sites’ to draw the distinction from the term ‘natal site’ that tends to refer to the area where an individual was born. Consequently, we refer to ‘dispersal’ in the non-breeding period as the distance between an individual’s parental site and the site it chooses in adulthood.

While fidelity to natal sites has been demonstrated in a diverse range of vertebrate taxa, including whales (e.g. Hoelzel 1998), lizards (e.g. Stow & Sunnucks 2004) turtles (e.g. Kamel & Mrosovsky 2006) and birds (e.g. Larsson & Forslund 1992; Van Der Jeugd et al. 2002; Alcaide et al. 2009; Lecomte et al. 2009), high levels of fidelity and migratory connectivity among parental sites (which would tend to strengthen the demographic and genetic effects associated with dispersal decisions) are rare in the literature (e.g. Valenzuela et al. 2009).

In animals where the young spend extended periods of their early life with parents, there also exists the possibility of a cultural basis to the selection of sites. There are few examples of social information transfer structuring site fidelity in migratory animals in addition to those described in the cetacean literature, where cultural inheritance has been shown to play an important role in determining feeding site fidelity (Valenzuela et al. 2009). In systems such as these where there is an extended period of parental care of juveniles (Connor et al. 1998), there seems to be ample opportunity for vertical information transfer from parents that can subsequently structure the adult life of offspring (Berthold 1996; Sutherland 1998). Importantly, cultural inheritance has been shown to drive fitness asymmetries in sperm whales (Physeter macrocephalus) where it influences both clan membership and foraging strategies, with differential feeding success among clans (Whitehead & Rendell 2004). Thus, it is clear that the use of information gained from social transmission as a juvenile can be immensely influential on choice of site and habitat in adult life, which for migratory animals can have large implications for individual performance (e.g. Gill et al. 2001; Norris et al. 2004; Gunnarsson et al. 2005; Inger et al. 2008; Harrison et al. 2010a). Moreover given its potential to propagate allopatry among groups occupying different sites, site fidelity arising from cultural inheritance has considerable power to shape genetic divergence within a species (Greenwood 1980; Hoelzel 1998). However, it is important to recognize that site fidelity could itself have a genetic basis and be heritable (Kamel & Mrosovsky 2006), because certain beneficial mutations may have habitat-specific effects that constrain individuals to particular sites at which they can forage most efficiently (Hoelzel 1998).

Here, we use a pedigree-based approach to investigate the role of cultural information transfer in structuring site fidelity across two stages of the annual cycle in a long-distance migrant and discuss its implications for demography and genetic structure. The East Canadian High Arctic (ECHA) light-bellied Brent goose (Branta bernicla hrota) winters annually around the coast of Ireland from late September to April (Inger et al. 2006a,b) and stages for a month and a half in Iceland in April–May to replenish endogenous fat reserves (Inger et al. 2008) before heading into the Canadian Arctic to breed (Gudmundsson et al. 1995). Most importantly, fledged juvenile Brent geese spend the wintering and staging periods of their first year shadowing the migratory movements of their parents, travelling and feeding in distinct family groups (Inger et al. 2010). As a result, juveniles gain information about the quality of only a subset of sites from the total available to them at a particular stage of the annual cycle. If individuals stay faithful throughout adult life to the migration routes they learned from their parents as juveniles, this represents a mechanism whereby cultural information transfer can structure site fidelity across multiple generations. Moreover, if this pattern persists over multiple stages of the annual cycle, it suggests the existence of migratory connectivity (Webster et al. 2002), where distinct genetic lineages of geese use the same sets of sites along the migratory route and in doing so remain separate from other lineages.

**Methods**

**Study population and sample collection**

The majority of the ECHA light-bellied Brent goose population migrates to Strangford Lough, Northern Ireland (54.5°N, 5.7°W), at the beginning of winter to make use of abundant marine resources such as Zostera spp., before dispersing around the entire coast of Ireland for the core winter period (Robinson et al. 2004). The Irish Brent Goose Research Group (IBGRG) and collaborators have marked >3500 light-bellied Brent geese to date across the entire range (Ireland, Iceland and Canada) since 2001. Geese were caught in cannon nets in Ireland and Iceland, and closures during moult in Canada, fitted with individually coded coloured leg rings, had morphometric data taken and were sexed by cloacal examination. Blood samples were collected from the caudal caudal vein and stored in absolute ethanol at room temperature in screw-topped rubber sealed microfuge tubes at a blood to alcohol volume–volume ratio of
1 to 20. Over 60 000 observations of colour-marked birds from this population have been accumulated in a database since 2001 from throughout their range in Ireland and Iceland, many of which include information on family groups and associations.

Genotyping and parentage assignments

We genotyped 1127 geese in two PCR multiplex sets using 15 unique autosomal light-bellied Brent geese (Branta bernicla hrota) microsatellite loci (Table 1, Harrison et al. 2010b) and sex-typed individuals using the marker Z002A (Dawson 2007). All samples were genotyped using an ABI 3730 DNA Sequencer (Applied Biosystems, USA) and allele sizes assigned using GeneMapper software v3.7. Genotyping error rates were calculated by repeating the typing of 50 randomly selected individuals including the initial stage of the DNA extraction from blood. This process involved rescoring alleles in a blind fashion and then comparing the rescored genotypes with those obtained originally across all 15 sets of the microsatellite loci. Repetability was calculated to be over 99% using these markers, which is high (e.g. Bonin et al. 2004). Despite high polymorphism at some loci (Table 1), all showed high repeatability and were not systematically responsible for errors. We then used the program COLONY v2.0 (Wang 2004) to assign parentage. All 1127 geese were placed in the candidate offspring section, with 581 males and 546 females placed in the candidate father and mother categories, respectively. Light-bellied Brent geese are highly faithful to mates between years (IBGRG, unpublished data) and so monogamy was assumed for both males and females. Three iterations of a ‘long’ simulation were carried out to check for concordance between runs. We accepted only parental assignments with an assignment probability of 0.95 or greater. In total, these simulations identified 60 families containing at least one parent and between 1 and 4 juveniles to be used in subsequent analyses.

Family reconstruction

Parentage assignment with COLONY v2.0 (Wang 2004) showed high levels of agreement with the field observations of family groups of marked individuals taken from a 6-year database of resightings on the Irish wintering and Icelandic staging grounds. Families of parental and juvenile Brent geese feed as a cohesive unit, and ringed groups are easily identified by observation using a spotting scope. Of 60 families identified by COLONY, 40 of these had multiple corresponding observations of the same family groups in the database. Of the remaining 20, offspring from nine families were all ringed as adults and so would not have corresponding family observations. These results suggest that these field observations are a reliable way to identify related first-order relatives. Families ringed in the Canadian Arctic during the breeding season were also resighted multiple times as a cohesive family unit on the wintering grounds following migration. This allowed us to increase our sample size by identifying further families from the database by looking for associated groups of adults and juveniles. Whilst we acknowledge that conspecific brood parasitism (e.g. Weigmann & Lamprecht 1991; Waldeck et al. 2007; Anderholm et al. 2009), extra-pair copulation (e.g. Dunn et al. 1999) and adoption of extra-pair young (Choudhury et al. 1993) have all been observed in species of Anatidae, we found no disagreement between field observations of family groups and genetically assigned families, suggesting that if present the frequency of non-kin in family groups is low.

Centroid calculation

In Ireland, only families containing at least one parent, where there were at least five observations per family member, were used in the analyses. The threshold of five observations was chosen to maximize the data

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**Table 1** Microsatellite polymorphism and summary statistics for 15 loci for light-bellied Brent geese (Branta bernicla hrota)

<table>
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<tr>
<th>Locus</th>
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Max 94 1117 0.96 0.98
Min 5 1016 0.34 0.35
Mean 29.27 1065.63 0.78 0.80
SD 28.23 44.07 0.17 0.16

Summary statistics at foot of table: max, maximum; min, minimum; sd, standard deviation. A, number of alleles; N, sample size; H_0, observed heterozygosity; H_E, expected heterozygosity.
available to us and provide a minimum level of coverage. Data for Iceland were more limited because of the much shorter time frame of staging (1 month compared to 4 months in the core wintering areas), and so a minimum of three observations were chosen to provide an adequate sample size. If sufficient data were available for both parents, then one was chosen at random. From the combined 160 families from the ‘Genetics’ and ‘Database’ data set, 53 families comprising 138 individuals in Ireland and 23 families comprising 59 individuals in Iceland satisfied these criteria. In Ireland, only records from November–February were considered to avoid noise associated with early-season dispersal at Strangford Lough. Similarly in Iceland, only records from 7th to 20th May were used because of similar patterns associated with early (as some birds move through southerly sites to settle in northerly staging areas) and late-season movements (as birds move northwards prior to crossing the Denmark Strait on the next stage of their migration). We regularly observe intact family groups during this period, suggesting that parental care persists throughout staging in a similar fashion to other goose species, where parents remain associated with their brood even after 9–10 months (e.g. Barnacle goose, Branta leucopsis; Black & Owen 1989).

Geographical centroids were calculated for each individual using the package ‘PBSMapping’ (Schnute et al. 2004) in the statistical package R v2.10 (R Development Core Team 2009). We chose centroids because they provide a weighted estimate of the centre of an animal’s home range and therefore allow point-to-point distance calculations between individuals to be made. The mean number of location fixes per bird for the calculation of centroids was 19.5 in Ireland and 11.4 in Iceland. Similarly, we did not have sufficient data to calculate reliable kernel density estimates for every individual (see Hemson et al. 2005). We chose centroids over midpoints to avoid noise associated with early-season dispersal at Strangford Lough. Similarly in Iceland, only records from November–February were considered to avoid noise associated with early-season dispersal at Strangford Lough. Similarly in Iceland, only records from 7th to 20th May were used because of similar patterns associated with early (as some birds move through southerly sites to settle in northerly staging areas) and late-season movements (as birds move northwards prior to crossing the Denmark Strait on the next stage of their migration). We regularly observe intact family groups during this period, suggesting that parental care persists throughout staging in a similar fashion to other goose species, where parents remain associated with their brood even after 9–10 months (e.g. Barnacle goose, Branta leucopsis; Black & Owen 1989).

Randomizations

To test the probability of the observed displacement between parental and offspring centroids arising by chance, two types of randomization were performed for each country. First, all individuals were randomly re-shuffled into new family clusters. One bird was randomly assigned as the ‘parent’ goose, and distance between re-shuffled ‘progeny’ was calculated. A mean of all distances was calculated, and the process was carried out 10 000 times in total to build a probability distribution. In the second randomization, all parents remained as in the original data set, but offspring were randomly reassigned among the family clusters, again 10 000 times in total. All randomizations were programmed in R v2.10 and followed the structure of the original data (i.e. 138 geese re-shuffled into 53 families in Ireland, 59 geese into 23 families in Iceland). For each country, the mean of the data was compared to the frequency histogram of means from 10 000 randomizations to derive a P-value.

Sex bias

To test for sex bias in dispersal, data from each country were separated into dispersal by males and females, respectively. Sex of offspring was assigned using either molecular sex typing data using the Z002A marker (Dawson 2007) for families from the ‘Genetics’ data set or from cloacal sexing of birds from the ‘Database’ data set.
set. We used a general linear mixed model with dispersal distance as the dependent variable, sex as the explanatory variable and family as random factor to account for the fact that dispersal distances of siblings are calculated from the same parent and therefore not independent. Dispersal data for each country were Box-Cox transformed to approximate normality prior to model fitting. Tests were performed in R v2.10 (R Development Core Team 2009).

Genetic structure

We used the program Structure v.2.3.1 (Pritchard et al. 2000) to investigate possible genetic differentiation in the migratory flyway. We used genotypes across all 15 loci of 470 unrelated individuals sampled from the multiple locations across the entire distribution (Ireland, Iceland and the Canadian Arctic). We tested for \( k \) (the number of potential distinct genetic clusters) from 1 to 10, assuming an admixture model and correlated allele frequencies and using no prior location information. Five iterations for each \( k \) were performed with 200 000 iterations after a burn-in of 100 000 iterations. Owing to the high polymorphism of some loci (Table 1), we repeated the analysis using the 10 and 5 least polymorphic loci, respectively. In a separate analysis, we used the IBGRG database to assign birds to distinct wintering sites to give a priori locations for testing population genetic structure. Birds were assigned to a site only if they had been seen at a site three times within the core period (November–March) of a single winter over a period of at least 2 months or for two consecutive winters. Three hundred and seven birds could be assigned to eight different wintering sites using this method (Fig. 5). We then used Arlequin v.3.0 (Excoffier et al. 2005) to look for genetic differentiation among sites (Table 2).

Results

Offspring dispersal

Mean centroid offset between parent and offspring in Ireland was 36.2 km with a median of 9.2 km (86 offspring). The Iceland mean was 13.6 km with a median of 3.4 km (36 offspring) (Figs 1 and 2).

Randomizations

Ten thousand randomizations revealed that the centroids of related birds were significantly closer than would be expected by chance in Ireland both when all birds were reassigned among clusters (\( P < 0.001 \), randomization mean = 83.2 km) and when only offspring were reassigned (\( P < 0.001 \), randomization mean = 85.2 km). Randomizations of all birds (\( P < 0.01 \), randomization mean = 17.7 km) and offspring only (\( P < 0.001 \), randomization mean 18.8 km) in Iceland were also both significant. These results suggest a kin structure both in Iceland and in Ireland, whereby substantial numbers of offspring remain closer to the parental sites than would be expected by chance.

Sex bias

Mean dispersal was 34 km for males and 39 km for females in Ireland and 13.1 km for males and 13.8 km

Fig. 1 Map showing centroid locations of individuals in Ireland (Panel a) and W-Iceland (Panel b) Ireland data set: 138 individuals in 51 families Iceland data set: 59 individuals in 23 families.
for females in Iceland. Median dispersal was 9.13 km for males and 10.35 km for females in Ireland and 4.8 and 2.5 km in Iceland, respectively (Fig. 3). Data points were not independent as some family clusters contained multiple offspring, and therefore their dispersal was calculated from the same parent. We used a general linear model to test for differences between sexes in dispersal whilst controlling family as a random factor. There was no significant difference between sexes in either Ireland ($\chi^2_{1,86} = 0.46, P = 0.49$) or Iceland ($\chi^2_{1,36} = 0.45, P = 0.5$).

**Temporal stability**

A repeated-measures ANOVA showed that centroid location did not change significantly between years in either Ireland ($F_{3,32} = 1.68, P = 0.19$) or Iceland ($F_{2,11} = 0.98, P = 0.34$), indicating that one centroid calculated from

### Table 2

Slatkin’s linearized $F_{ST}$ (Slatkin 1995) data for pairwise comparisons between birds assigned to eight different locations around the coast of Ireland (Fig. 5)

<table>
<thead>
<tr>
<th>n</th>
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Values computed using the software Arlequin v3.0 (Excoffier et al. 2005).

$n$, is number of birds assigned to each site.

![Fig. 2](image-url)
data from multiple years is a good proxy of centroids calculated for separate years. Mean change in individual centroid between years was 25 km in Ireland and 7.6 km in Iceland. However, these values are heavily skewed by one individual in each data set that moved a long distance in one of the years. A more accurate reflection of the magnitude of change between years is the median, which was 6.3 km in Ireland and 1.2 km in Iceland, respectively. This shows that parental centroids are likely to be similar both in the first year of their offspring’s life and in subsequent years, so that comparison of offspring’s centroids to that of parents in any given year is likely to represent what the offspring experienced during first year of life.

Genetic structure

We found no evidence to suggest genetic differentiation within a sample of 470 unrelated geese using the program Structure v3.2 (Pritchard et al. 2000). The mean log-likelihood was highest when assuming one cluster (k = 1), compared to values assuming a k of 2–10 (Fig. 4). We also found no significant differentiation between a sample of 307 geese (Table 2) assigned among eight Irish wintering sites (Fig. 5) using the resighting database (All \( F_{ST} \) values <0.005, \( P \) values >0.05). Both samples of 470 and 307 geese, respectively, also conformed to expectations of Hardy–Weinberg equilibrium (Bonferroni-corrected \( P \) values >0.05) suggesting a single panmictic assortment of birds.

Discussion

Our results are consistent with the notion that information gained in the first year of life exerts a strong
influence on adult dispersal in two stages of the annual cycle in light-bellied Brent geese. Most offspring chose staging and wintering sites in adulthood that were identical or very near to those of their parents. It seems highly unlikely that such fine-scale migratory patterns and site selection could have a purely genetic basis. If this was under genetic control alone, the mechanism would have to be more complex than anything yet described for migration, because it would have to enable birds to hit different targets a few tens of km in diameter at multiple stages of the annual cycle. This mechanism would also have to allow the birds to account for environmental variables such as wind, which are known to cause large deviations in migratory trajectory (e.g. Erni et al. 2005; Akesson & Hedenström 2007). Thus, it is highly feasible that the fine-scale patterns of site selection we observe in this study have been learned from parents (e.g. Morton et al. 1991), rather than be controlled by purely genetic mechanisms. This emphasizes the important role that culturally inherited information can play in structuring site choice and dispersal in migratory animals. Moreover, such fine-scale connectivity in a migratory species could have implications for our understanding of the importance of culture as a mechanism driving reproductive isolation. Further experimental work would be required to fully elucidate the relative roles of cultural vs. genetic determination of migration, using cross-fostering experiments, but would be logistically difficult to achieve because of the remote nature of, and low nesting densities within, the Arctic breeding grounds.

The role of culture in structuring populations has been explored in cetaceans. Baker et al. (1998) used both mitochondrial and nuclear DNA markers to show that genetic lineages of Humpback whales (Megaptera novaeangliae) are faithful to the same feeding and nursery grounds. Similarly, Valenzuela et al. (2009) showed that adult Southern Right whales (Eubalaena australis) were probably returning to the same feeding grounds that they visited with their mothers as juveniles. However, there is no consensus in the literature about whether this pattern persists at multiple stages of the annual cycle for all whales (e.g. North Atlantic Right whales (Eubalaena glacialis) Malik et al. 1999; Southern Right whales, Patenaude et al. 2007), which is vital for our understanding of the extent to which culture might underpin genetic and large-scale demographic variation. Likewise, fine-scale spatial structuring of distinct lineages has been described in polar bears (Ursus maritimus) during the mating season, but it is unclear whether this kin structure persists throughout the annual cycle (Zeyl et al. 2009). As in the present study, attempting to track species with high dispersal capabilities such as polar bears (Zeyl et al. 2009) and whales (Valenzuela et al. 2009) at multiple stages throughout the annual cycle can present enormous difficulties and thus prevent inferences about cross-seasonal migratory patterns being made. We make a significant advance using the ‘pedigree’ approach to show that familial structures persist at two separate stages of the annual cycle, and although we have not yet managed to access enough individuals from the breeding grounds, they are strongly suggestive that the observed kin structure may in fact persist throughout the entire annual cycle. Indeed, research in other Anatidae had demonstrated evidence of offspring remaining highly faithful to their natal sites, returning to raise offspring in the same areas that they were raised (e.g. Barnacle geese (Branta leucopsis), Larsson & Forslund 1992; Van Der Jeugd et al. 2002; greater Snow geese (Chen caerulescens atlantica), Lecomte et al. 2009; Pacific common Eiders (Somateria mollissima v-nigrum), Sonsthagen et al. 2010).

Whilst it is clear from our results that some light-bellied Brent geese do disperse away from parental areas on the wintering and staging grounds, the majority of birds within our sample remained on or near their parental sites. An important consequence of such a pattern is that individuals may be constrained to suboptimal sites within their range. For example, if there is a large asymmetry in quality among sites, then cultural inheritance of migration route as demonstrated in this study could lead to individuals settling in sites of comparatively poor quality, which would likely have downstream consequences for fitness (see Whitehead et al. 2004). However, Sutherland (1998) suggested that species with culturally determined migration routes might be more plastic in their ability to respond to environmental change than species with genetically determined migration, subsequently changing their route should conditions at a particular site deteriorate. Moreover, fidelity to the parental migratory route represents inheritance of a strategy that has already been proven to allow successful reproduction and therefore should be a more successful strategy than random dispersal, as this carries an increased risk of adopting lower quality sites that may negatively affect individual performance. Thus, one might expect that individuals adhering to cultural migratory routes would, on average, be more successful than those whose migration is largely genetically determined (making them less able to respond to environmental change; Sutherland 1998) or those dispersing randomly. Future directions for research might focus on whether probability of dispersal is related to the quality of parental site, although admittedly it will be difficult to disentangle the relative effects of site quality (e.g. food availability), individual quality and density dependence.
The reduction in centroid offset observed in Iceland (mean 13.6 vs. 36.2 km in Ireland) is largely because of the range of Brent geese being highly compressed in the former, and as a result the population occupies sites that are spread within a much smaller total area during staging. The fact that we have been able to detect the limited dispersal of kin despite the smaller range of birds in Iceland suggests that in many families of birds, fidelity to parental sites is operating at extremely fine scales. Small-scale centroid offsets of the magnitude observed in our study (<50 km in Ireland and <20 km in Iceland) may represent the displacement of individuals seeking to avoid inbreeding by moving to neighbouring coastal sites, or simply be the result of density-dependence forcing individuals out of heavily populated areas. We also cannot discount the possibility that small-scale ‘dispersal’ events may simply be an artefact of our sampling, whereby the home ranges of a parent–offspring pair overlap significantly but we have merely recorded them occupying different sites.

We found no evidence of a sex bias to dispersal in light-bellied Brent geese and no evidence that age affected likelihood of dispersal. Whilst it is possible that we lacked sufficient power to detect a difference between sexes, we argue that with a sample of 86 geese (50 male/36 female) in Ireland, we should have sufficient power to detect the magnitude of effect reported in other studies (e.g. Greenwood 1980; Clarke et al. 1997 and references therein). If a sex bias in dispersal is present in our study population, then it is likely to be a small effect (i.e. both sexes dispersing large distances, but one sex to a slightly lesser degree) and not comparable to fine-scale philopatry observed in other goose species (e.g. Lecomte et al. 2009). Greenwood (1980) argued that prevalent sex biases in dispersal tend to arise as a consequence of territoriality or limited access to mates. For example, mate competition has been suggested to be one of the strongest forces driving male-biased dispersal in mammals (see Handley & Perrin 2007 for a review), but red deer (Cervus elaphus) have been shown to switch from male- to female-biased dispersal under the conditions of relaxed mate competition among males (Perez-Gonzalez & Carranza 2009). Evidently, dispersal is not a fixed but a plastic trait in some species (Le Galliard 2006), and indeed, the observed bias in dispersal (or lack thereof) in an animal system is likely the product of the balance of selective pressures acting upon it (Handley & Perrin 2007). For example, lack of dispersal in the light of the apparent costs of philopatry (such as increased inbreeding risk) can be explained if those costs are offset by benefits of remaining in parental areas. Experience of the conditions in a particular habitat is thought to be beneficial (Merom et al. 2000; Davis & Stamps 2004), and remaining at a site where there is prior knowledge of predation/disturbance risk and spatial variation in food supply could be adaptive because residents may have an advantage over immigrants when competing for resources (Handley & Perrin 2007). More importantly for migratory animals, use of familiar sites along the migration route may permit shorter residence times at staging sites and promote earlier departure for breeding because knowledge of local resource heterogeneity allows them to increase body condition faster (e.g. Merom et al. 2000).

Perhaps one of the greatest potential benefits of philopatry is the possibility of cooperation among kin within a site, which can impart a competitive advantage that would not be present if individuals dispersed (Handley & Perrin 2007). Indeed, there is a wealth of research from multiple taxa that suggests the existence of social structure in animals traditionally thought to be non-cooperative (e.g. Carter et al. 2009), which would consequently permit the evolution of kin-selective behaviours (see Hatchwell 2010 for a review). For example, Le Galliard (2006) found that root voles (Microtus oeconomus) did not moderate dispersal rates to reduce inbreeding risk, but that related females clustered together to collectively defend territories from unfamiliar males. Similarly, extended kin structure outside the breeding period can be adaptive because individuals may suffer fewer aggressive interactions from kin, consequently allowing more efficient foraging. Toth et al. (2009a) found that House sparrows (Passer domesticus) were able to recognize close kin within winter feeding flocks and subsequently reduce kin-exploitation behaviour such as aggressive scrounging. Interestingly, this effect was most pronounced for males and dominants, indicating that position in social hierarchy may modify the extent to which individuals exploit close relatives (Toth et al. 2009a). Research on captive individuals also suggests that sparrows preferentially affiliate with siblings over unrelated individuals during social behaviours (e.g. roosting, dust bathing) (Toth et al. 2009b). Collectively, these results demonstrate that kin-biased behavioural strategies are likely to exist in groups that are not thought to demonstrate any form of kin selection (Hatchwell 2010). Whilst cultural information transfer may inform juveniles of fine-scale migratory routes in the first year, it is possible that birds may use them perpetually between years because of the advantages of associating with close kin. The dispersal of some individuals away from parental sites that we observed may be attributed to a complex interaction between dominance (Toth et al. 2009a), density dependence and environmental factors (Greenwood 1980) that we do not fully understand.
Genetic structure

Despite the fact that there is strong evidence of familial genetic divergence, we found no evidence of genetic divergence within our sample using both the program Structure (Pritchard et al. 2000) (Fig. 4) or looking for differences in $F_{ST}$ using Arlequin (Excoffier et al. 2005) (Fig. 5, Table 2). Although work on breeding greater snow geese has reported genetic structure at similar sorts of spatial scales to those we investigated (Lecomte et al. 2009), Alcaide et al. (2009) found no evidence of fine-scale genetic differentiation in lesser kestrels (Falco naumanni) despite the fact that most individuals were highly philopatric and bred within 10 km of their parental sites. This suggests that populations can still appear panmictic under the conditions of limited dispersal (Alcaide et al. 2009). We suggest two possible explanations for the lack of genetic structure observed in this study. First, although dispersal certainly appears to be restricted in Brent geese, the small proportion of individuals that do disperse probably represent a level of gene flow between groups that prevents genetic differentiation, as observed in the lesser kestrels (Alcaide et al. 2009). Second, the ECHA population of light-bellied Brent geese, currently numbering around 40,000 individuals, passed through a population bottleneck in the 1930s following a crash in their main food resource (marine eelgrass, Zostera spp; Salomonsen et al. 1950). As the population has increased, so has their range around the coast of Iceland as competition has forced birds to move to new sites. Therefore, whilst cultural inheritance appears to be driving fidelity of genetic lineages to specific sites, occupancy of those sites has conceivably only occurred for <50 years, which may not be sufficient time for genetic differentiation to have occurred. Generation length for Brent geese has been estimated at 7 years (BirdLife International 2004), and thus, the fidelity we observe may conceivably have persisted for <7 generations. This is arguably too short a period to expect to detect a signal of genetic divergence among molecular markers, particularly nuclear markers such as our microsatellites. Nuclear markers have longer coalescence times than markers with lower effective population sizes (e.g. mitochondrial DNA, see Zink & Barrowclough 2008), so future work using mtDNA might prove informative. However, similar studies using nuclear markers have shown evidence of genetic structure such as work on greater snow geese using AFLPs (Lecomte et al. 2009), suggesting it would not be unreasonable to expect that we would also observe a comparable signal using microsatellites. However, if the timescale of range expansion is truly in the region of 40 years, then it is probably that no genetic marker would allow us to detect structure so early after it has arisen.

Conclusion

Our study highlights the advantages of combining genetic approaches with long-term data sets of field observations. The field observations not only allowed us to increase our sample of related individuals but allowed a much more detailed knowledge of animal movements and site choice beyond simply using the sampling location. Moreover, collecting long-term data from marked individuals is one of few ways to accurately quantify such patterns across several points of the annual cycle, the exception being forensic techniques such as stable isotope analysis (e.g. Valenzuela et al. 2009). By using a pedigree approach, we have been able to demonstrate an extended kin structure at two stages of the annual cycle in an Arctic migrant. This suggests that social information transfer has the ability to structure site fidelity at multiple points in an animal’s range and annual cycle, thus driving migratory connectivity. It also represents a mechanism whereby behaviour learned from parents could generate reproductive isolation through allopatry. Cultural inheritance in migratory animals may in fact be more prevalent than the literature currently suggests, as many studies have identified kin structure at one stage of the annual cycle but have been unable to study the animals at other times (e.g. Alcaide et al. 2009). More importantly, kin structure of the nature described in this study raises the possibility of the occurrence of kin-selective behaviour, as described in previous studies in winter feeding aggregations of birds (Toth et al. 2009a). Understanding the driving forces behind individual site choice is crucial to our ability to predict changes at the population level, in terms of both short-term fluctuations owing to changes in food supply and long-term genetic divergence owing to spatial separation and migratory connectivity.

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