

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

XAVIER A. HARRISON,\*† TOM TREGENZA,\* RICHARD INGER,\* KENDREW COLHOUN,‡  
DEBORAH A. DAWSON,† GUDMUNDUR A. GUDMUNDSSON,§ DAVID J. HODGSON,\* GAVIN J.  
HORSBURGH,† GRAHAM McELWAIN¶ and STUART BEARHOP\*

\*Centre for Ecology and Conservation, University of Exeter, Tremough Campus, Penryn, Cornwall TR10 9EZ, UK, †NERC Biomolecular Analysis Facility – Sheffield, Department of Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Western Bank, Sheffield, South Yorkshire S10 2TN, UK, ‡Wildfowl and Wetlands Trust, Castle Espie, Ballydrain Road, Comber, County Down, Northern Ireland BT23 6EA, UK, §Icelandic Institute of Natural History, PO Box 5320, IS-125 Reykjavik, Iceland, ¶100 Strangford Road, Downpatrick, Co. Down BT30 7JD, UK

## 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

Received 18 May 2010; revision received 15 August 2010; accepted 17 August 2010

## 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 under-

standing 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

Correspondence: Xavier Harrison and Stuart Bearhop, Fax: +44(0) 1326253638; E-mails: xavierh22@gmail.com and s.bearhop@ex.ac.uk

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 migrate 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 tibial 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. Repeatability 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

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

Locus	EMBL accession	A	N	H <sub>O</sub>	H <sub>E</sub>
	number				
Bbh011	FN691790	5	1104	0.609	0.625
Bbh021	FN691800	7	1024	0.701	0.705
Bbh027	FN691806	10	1105	0.748	0.768
Bbh029	FN691808	72	1016	0.962	0.968
Bbh043	FN691822	7	1104	0.344	0.347
Bbh064	FN691843	18	1022	0.828	0.861
Bbh070	FN691849	12	1117	0.861	0.838
Bbh080	FN691859	30	1021	0.849	0.858
Bbh089	FN691868	94	1091	0.946	0.975
Bbh112	FN691891	63	1103	0.938	0.95
Bbh113	FN691892	13	1021	0.786	0.791
Bbh120	FN691899	37	1109	0.902	0.907
Bbh123	FN691902	52	1109	0.936	0.947
Bbh135	FN812696	8	1019	0.634	0.738
Bbh136	FN812697	11	1021	0.726	0.719
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<sub>O</sub>, observed heterozygosity; H<sub>E</sub>, expected heterozygosity.

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

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 geese, *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 allow us to take into account the fact that birds may use several neighbouring sites but spend the majority of their time in only a subset of these. Whilst we acknowledge that this does increase the risk that bias in observer effort among sites will affect centroid calculation, it is unlikely to artificially inflate any signal by placing centroids of related birds closer than if midpoints were used. This is a conservative approach as it will tend to increase distances between related birds because parent–offspring pairs are unlikely to have the same number of observations at the same sites. Only data from the first adult year of life (>1 year old) and above were used to avoid bias caused by families travelling as a group and therefore using the same sites. Depending on the frequency of observation of each individual, data for between 1 and 4 years of life were available in both Ireland and Iceland, but only one centroid per individ-

ual was calculated for each country. If birds are highly site-faithful between years, then the centroid calculated using multiple years of data should be similar to centroids calculated for each individual year. Using only one centroid per individual has the advantage of making the analysis both more robust and simpler to perform. To test that centroids were temporally stable (between years), we used data from the individuals with multiple years of observations and calculated a separate centroid for each year and then calculated displacement between centroids for each year in both countries. Thirty-three individuals comprising four consecutive years of data were used in Ireland, and 12 individuals comprising 3 years of consecutive data were used in Iceland. We calculated a repeated-measures ANOVA for each country, with individual bird ID as a random error term to investigate the temporal stability of centroid location. To estimate fidelity to parental sites, pairwise distance between centroids was calculated for each parent–offspring pair using the 'haversine' function (Loehrke 2008) in R, which calculates the distance between points whilst taking into account the curvature of the earth's surface.

#### 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 reshuffled into new family clusters. One bird was randomly assigned as the 'parent' goose, and distance between reshuffled '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 reshuffled 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. 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 dif-

ferent 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

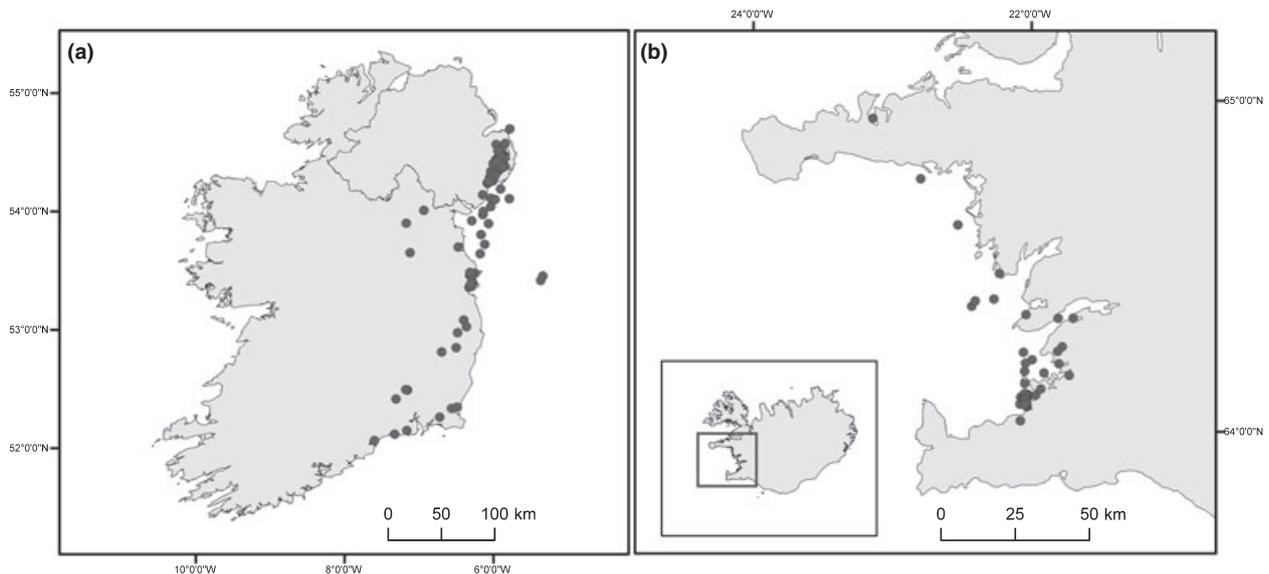
Mean centroid offset between parent and offspring in Ireland was 36.2 km with a median of 9.2 km (86 offspring). The Iceland mean was 13.6 km with a median of 3.4 km (36 offspring) (Figs 1 and 2).

### 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

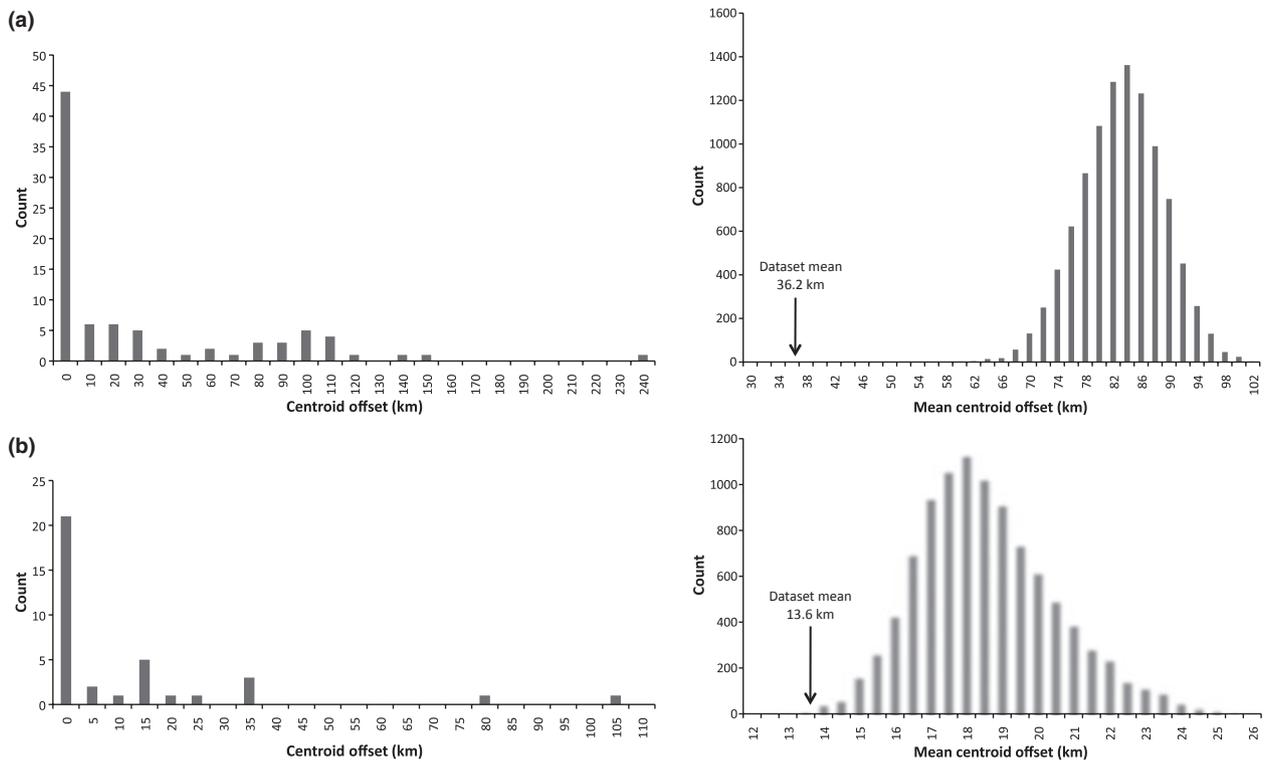


**Fig. 1** Map showing centroid locations of individuals in Ireland (Panel a) and W-Iceland (Panel b) Ireland data set: 138 individuals in 51 families Iceland data set: 59 individuals in 23 families.

**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)

	<i>n</i>	Dublin	Dundrum	Dungarvan	Kerry	Galway	Sligo	Strangford
Dublin	68	–						
Dundrum	38	0	–					
Dungarvan	37	0.002	0	–				
Kerry	14	0	0	0	–			
Galway	15	0.002	0	0	0	–		
Sligo	14	0	0	0	0	0.001	–	
Strangford	95	0	0	0.005	0	0.003	0	–
Wexford	26	0	0	0	0	0	0	0

Values computed using the software Arlequin v3.0 (Excoffier *et al.* 2005). *n*, is number of birds assigned to each site.



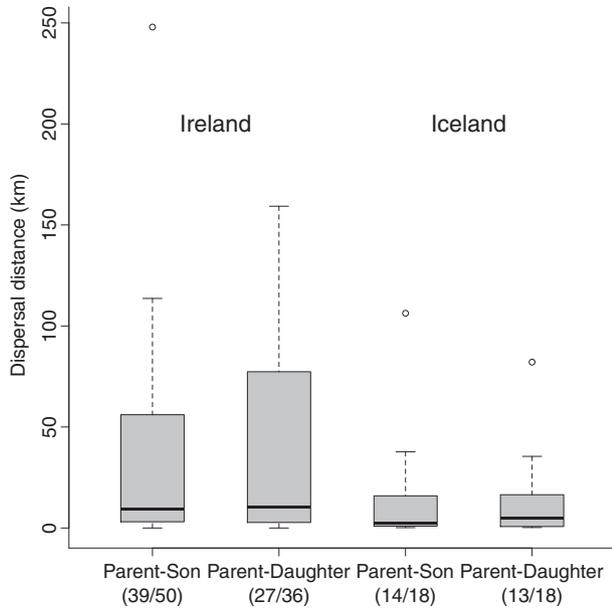
**Fig. 2** Histogram of centroid offsets (km) of offspring from parents in Ireland (Panel a, 86 offspring) and Iceland (Panel b, 36 offspring). Means of each data set are compared to the distributions of means from 10 000 randomizations of family groups where offspring are randomly reassigned to parents.

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

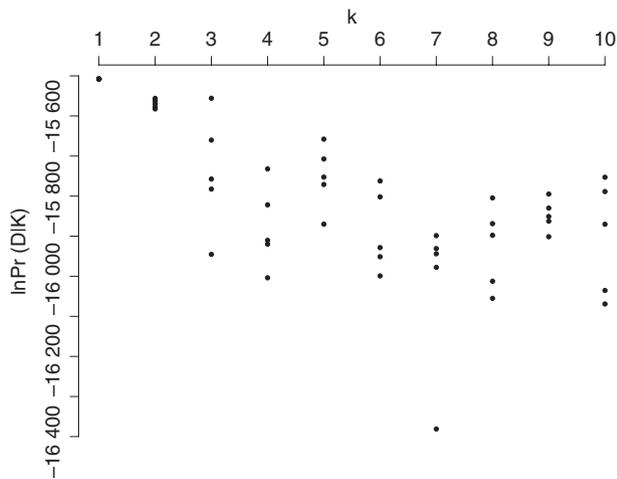
either Ireland ( $\chi^2_{1,86} = 0.46, P = 0.49$ ) or Iceland ( $\chi^2_{1,36} = 0.45, P = 0.5$ ).

*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

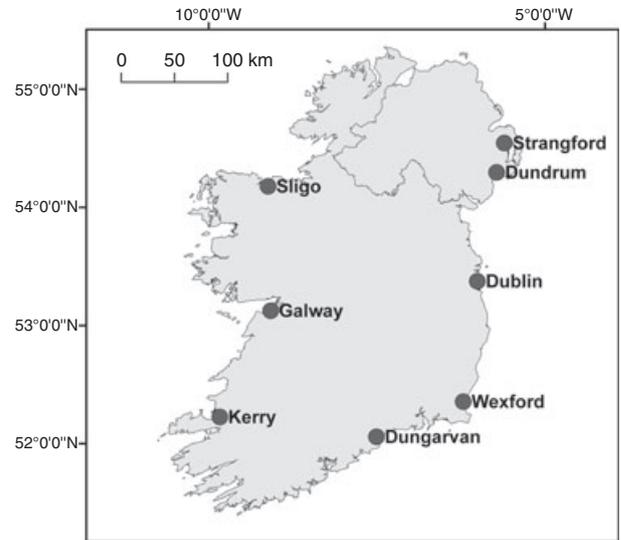


**Fig. 3** Boxplots of pairwise centroid offsets of parent-son and parent-daughter pairs in Ireland and Iceland. Numbers in parentheses are (no. of families/no. of pairwise distances). Solid black lines are the median dispersal Parental Brent geese always travel as a pair, so we do not differentiate between them for the purpose of calculating distance.



**Fig. 4** Output from Bayesian clustering analysis of 470 unrelated light-bellied Brent geese sampled from throughout the range (Ireland/Iceland/Canadian Arctic). Five iterations were carried out for each value of 'k' (the number of potential clusters being tested) to test the probability of the data under each scenario.

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



**Fig. 5** Locations of eight sites assigned comprising 307 birds used for pairwise  $F_{ST}$  comparisons (Table 2). Number of birds at each location: Dublin (68), Dundrum (38), Dungarvan (37), Sligo (14), Kerry (14), Galway (15), Strangford Lough (95), Wexford (26).

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 novaengliae*) 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 (*B. 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 comparably 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 structure, 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 Ireland 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 using 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.

### Acknowledgements

We are grateful to three anonymous reviewers whose comments improved an earlier version of this manuscript. Genotyping and DNA sex typing were performed at the Biomolecular Analysis Facility at Sheffield supported by the Natural Environment Research Council (NERC). We thank Terry Burke for advice and guidance during the genotyping at the NBAF. We thank the Irish Brent Goose Research Group and the Icelandic Ringing Group for invaluable assistance with catching birds and providing observations of marked individuals. We thank Kerry Mackie and Alyn Walsh for leading cannon net catches in Ireland and Olafur Torfason and Jon Gunnar Johannsson for their invaluable help in catching geese in Iceland. Austin Reed and Alyn Walsh assisted with captures of geese in Canada. XAH is grateful to Laurène Gay and Alain Frantz for advice interpreting Structure results and Ross Dwyer for advice about methods of spatial analysis in R. XAH was supported by NERC grant (NE/F008058/1) with a Wildfowl

and Wetlands Trust CASE partnership, and RI was supported by NERC grant (NE/F021690/1), both awarded to SB. Elements of this work have been funded by the National Parks & Wildlife Service, the Northern Ireland Environment Agency and the Heritage Council. Work in Canada was undertaken via the support of Polar Continental Shelf.

## References

- Akesson S, Hedenström A (2007) How migrants get there: migratory performance and orientation. *BioScience*, **57**, 123–133.
- 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.
- Anderholm S, Waldeck P, Van J (2009) Colony kin structure and host-parasite relatedness in the barnacle goose. *Molecular Ecology*, **18**, 4955–4963.
- Baker CS, Medrano-Gonzalez I, Calambokidis J *et al.* (1998) Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. *Molecular Ecology*, **7**, 695–707.
- Berthold P (1996) *Control of Bird Migration*, pp. 158–160. Chapman & Hall, London, UK.
- BirdLife International (2004) *Birds in Europe: population estimates, trends and conservation status* Cambridge, UK BirdLife Conservation Series No 12.
- Black J, Owen M (1989) Parent-offspring relationships in wintering barnacle geese. *Animal Behaviour*, **37**, 187–198.
- Bonin A, Bellemain E, Bronken Eidesen P, Pompanon F, Brochmann C, Taberlet P (2004) How to track and assess genotyping errors in population genetics studies. *Molecular Ecology*, **13**, 3261–3273.
- Carter AJ, Macdonald SL, Thomson VA, Goldizen AW (2009) Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. *Animal Behaviour*, **77**, 839–846.
- Choudhury S, Jones C, Black J, Prop J (1993) Adoption of young and intraspecific nest parasitism in barnacle geese. *The Condor*, **95**, 860–868.
- Clark RG, Hobson KA, Nichols JD, Bearhop S (2004) Avian dispersal and demography scaling up to the landscape and beyond. *The Condor*, **106**, 717–719.
- Clarke AL, Sæther B, Røskaft E (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**, 429–438.
- Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) *Dispersal*. Oxford University Press, New York.
- Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales. *Trends in Ecology and Evolution*, **13**, 228–232.
- Davis JM, Stamps JA (2004) The effect of natal experience on habitat preferences. *Trends in Ecology and Evolution*, **19**, 411–416.
- Dawson D (2007) *Genomic analysis of passerine birds using conserved microsatellite loci*. PhD Thesis, University of Sheffield, Sheffield, UK.
- Dunn P, Afton A, Gloutney M, Alisauskas R (1999) Forced copulation results in few extrapair fertilizations in Ross's and lesser snow geese. *Animal Behaviour*, **57**, 1071–1081.
- Erni B, Liechti F, Bruderer B (2005) The role of wind in passerine autumn migration between Europe and Africa. *Behavioural Ecology*, **16**, 732–740.
- Excoffier L, Laval G, Schneider S (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.
- Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WJ (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature*, **412**, 436–438.
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Gudmundsson GA, Benvenuti S, Alerstam T, Papi F, Lilliendahl K, Akesson S (1995) Examining the limits of flight orientation and performance – satellite tracking of Brent geese migrating over the Greenland ice cap. *Proceedings the Royal Society Series B: Biological Sciences*, **261**, 73–79.
- Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ (2005) Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2319–2323.
- Handley LJ, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, **16**, 1559–1578.
- Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2010a) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, DOI: 10.1111/j.1365-2656.2010.01740.x.
- Harrison XA, Dawson DA, Horsburgh GJ, Tregenza T, Bearhop S (2010b) Isolation, characterisation and predicted genome locations of Light-bellied Brent goose (*Branta bernicla hrota*) microsatellite loci (Anatidae, AVES). *Conservation Genetics Resources*, **2**, 365–371.
- Hatchwell B (2010) Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology*, **116**, 203–216.
- Hemson G, Johnson P, South A, Kenward R, Ripley R, McDonald D (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology*, **74**, 455–463.
- Hoelzel A (1998) Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. *Journal of Heredity*, **89**, 451–458.
- Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. *The Ibis*, **150**, 447–461.
- Inger R, Bearhop S, Robinson JA, Ruxton G (2006b) Prey choice affects the trade-off balance between predation and starvation in an avian herbivore. *Animal Behaviour*, **71**, 1335–1341.
- Inger R, Ruxton G, Newton J *et al.* (2006a) Using daily ration models and stable isotope analysis to predict biomass depletion by herbivores. *Journal of Applied Ecology*, **43**, 1022–1030.
- Inger R, Gudmundsson GA, Ruxton GD *et al.* (2008) Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla hrota*: potential impacts on fitness? *Journal of Avian Biology*, **39**, 704–708.
- Inger R, Harrison XA, Ruxton GD *et al.* (2010) Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, **79**, 974–982.

- Kamel S, Mrosovsky N (2006) Inter-seasonal maintenance of individual nest site preferences in hawksbill sea turtles. *Ecology*, **87**, 2947–2952.
- Larsson K, Forslund P (1992) Genetic and social inheritance of body and egg size in the Barnacle goose (*Branta leucopsis*). *Ecology*, **46**, 235–244.
- Le Galliard J (2006) Natal dispersal, interactions among siblings and intrasexual competition. *Behavioural Ecology*, **17**, 733–740.
- Lecomte N, Gauthier G, Giroux J, 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.
- Loehrke J (2008) Haversine function for calculating distance between two points. Available from <http://r.789695.n4.nabble.com/How-to-calculate-the-linear-distance-between-2-points-tid874352.html>.
- Malik S, Brown MW, Kraus SD, Knowlton AR, Hamilton PK, White BN (1999) Assessment of mitochondrial DNA structuring and nursery use in the North Atlantic right whale (*Eubalaena glacialis*). *Canadian Journal of Zoology*, **77**, 1217–1222.
- Merom K, Yom-Tov Y, McClery R (2000) Philopatry to stopover site and body condition of transient reed warblers during Autumn migration through Israel. *The Condor*, **102**, 441–444.
- Morton ML, Wakamatsu MW, Pereyra ME, Morton GA (1991) Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scandinavica*, **22**, 98–106.
- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 59–64.
- Patenaude NJ, Portway VA, Schaeff CM *et al.* (2007) Mitochondrial DNA diversity and population structure among southern right whales (*Eubalaena australis*). *Journal of Heredity*, **98**, 147–157.
- Perez-Gonzalez J, Carranza J (2009) Female-biased dispersal under conditions of low male mating competition in a polygynous mammal. *Molecular Ecology*, **18**, 4617–4630.
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945.
- R Development Core Team (2009) R: a language and environment for statistical computing. Available from <http://www.R-project.org>.
- Robinson J, Colhoun K, Gudmundsson G *et al.* (2004) *Light-bellied Brent Goose (Branta bernicla hrota) (East Canadian High Arctic Population) in Canada, Ireland, Iceland, France, Greenland, Scotland, Wales, England, the Channel Islands and Spain*. 1960/61–1999/2000 Waterbird Review Series. The Wildfowl & Wetlands Trust/Joint Nature Conservation Committee, Slimbridge.
- Salomonsen F, Johansen PG, Hedtoft H (1950) *The Birds of Greenland*. Ejnar Munksgaard, Copenhagen.
- Schnute JT, Boers NM, Haigh R (2004) PBS Mapping 2: user's guide. *Canadian Technical Report of Fisheries and Aquatic Science*, **2549**.
- Slatkin M (1995) A Measure of Population Subdivision Based on Microsatellite Allele Frequencies. *Genetics*, **139**, 457–462.
- Sonsthagen SA, Talbot SL, Lanctot RB, McCracken KG (2010) Do common eiders nest in kin groups? Microgeographic genetic structure in a philopatric sea duck. *Molecular Molecular Ecology*, **9**, 647–657.
- Stow A, Sunnucks P (2004) High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology*, **13**, 419–430.
- Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441–446.
- Toth Z, Bokony V, Lendvai A, Szabo K, Penzes Z, Liker A (2009a) Effects of relatedness on social-foraging tactic use in house sparrows. *Animal Behavior*, **77**, 337–342.
- Toth Z, Bokony V, Lendvai A, Szabo K, Penzes Z, Liker A (2009b) Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, **82**, 173–177.
- Valenzuela L, Sironi M, Rowntree V, Seger J (2009) Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology*, **18**, 782–791.
- Van Der Jeugd H, Van Der Veen I, Larsson K (2002) Kin clustering in barnacle geese: familiarity or phenotype matching? *Behavioral Ecology*, **13**, 786–790.
- Waldeck P, Andersson M, Kilpi M, Ost M (2007) Spatial relatedness and brood parasitism in a female-philopatric bird population. *Behavioral Ecology*, **19**, 67–73.
- Wang J (2004) Sibship reconstruction from genetic data with typing errors. *Genetics*, **166**, 1963–1979.
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, **17**, 76–83.
- Weigmann C, Lamprecht J (1991) Intraspecific nest parasitism in bar-headed geese, *Anser indicus*. *Animal Behaviour*, **41**, 677–688.
- Whitehead H, Rendell L (2004) Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, **73**, 190–196.
- Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation*, **120**, 427–437.
- Zeyl E, Aars J, Ehrlich D, Wiig Ø (2009) Families in space: relatedness in the Barents Sea population of polar bears (*Ursus maritimus*). *Molecular Ecology*, **18**, 735–749.
- Zink R, Barrowclough G (2008) Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, **17**, 2107–2121.

---

XAH is a PhD student at the Centre for Ecology and Conservation, University of Exeter, where he studies aspects of site fidelity and its consequences in light-bellied Brent geese. TT is a Professor of evolutionary ecology at the CEC and studies taxa from insects to vertebrates in the hope of improving our understanding of speciation and the evolutionary consequences of sexual reproduction. RI is a postdoc interested in the trophic ecology of vertebrates, with particular focus on the use of stable isotopes. KC was formerly a research biologist at the Wildfowl and Wetlands Trust (WWT) and currently works as a conservation biologist for the Royal Society for the Protection of Birds (RSPB). His research focuses on the conservation and management of Brent geese and other priority species. DAD is the coordinator of the NERC Biomolecular Analysis Facility

(NBAF) at Sheffield. Her research interests include conservation genetics, parentage and populations studies and developing enhanced genetic markers suitable for comparing species. GAG is a senior researcher at the Icelandic Institute of Natural History, still focused on the subject of his Ph.D. thesis – migration strategies of birds breeding in the High Arctic. DJH is a senior lecturer in population ecology in the Centre for Ecology and Conservation. He has key interests in the maintenance of biodiversity, empirical modeling of population dynamics, and ecological statistics. GJH is a member of the NBAF where he develops novel genetic markers for use in population genetic

and behavioural ecology studies, with a particular focus on enrichment methods for microsatellite genotyping. GMcE is the administrator of the Irish Brent Goose Research Group database, and maintains active research interests in a number of Anatidae species, including Brent and Greenland White-fronted Geese, and Whooper swans. SB is a Senior Lecturer in Conservation Biology at the Centre for Ecology and Conservation. His research interests centres on the causes and consequences of individual variation in behaviour with a particular focus on foraging and migration ecology.

---