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FAST TRACK

Tug of war between continental gene flow and rearing site philopatry in a migratory bird: the sex-biased dispersal paradigm reconsidered

NICOLAS LECOMTE,*† GILLES GAUTHIER,* JEAN-FRANÇOIS GIROUX,‡ EMMANUEL MILOT† and LOUIS BERNATCHEZ†

**Département de Biologie and Centre d'Études Nordiques, Université Laval, Québec, QC, Canada G1V 0A6, †Département de Biologie and Québec-Océan, Université Laval, Québec, QC, Canada G1V 0A6, ‡Groupe de Recherche en Écologie Comportementale et Animale, Département des Sciences Biologiques, Université du Québec à Montréal, PO Box 8888, Stn Centre-Ville, Montréal, QC, Canada H3C 3P8*

Abstract

Nonrandom dispersal has been recently advanced as a mechanism promoting fine-scale genetic differentiation in resident populations, yet how this applies to species with high rates of dispersal is still unclear. Using a migratory species considered a classical example of male-biased dispersal (the greater snow goose, *Chen caerulescens atlantica*), we documented a temporally stable fine-scale genetic clustering between spatially distinct rearing sites (5–30 km apart), where family aggregates shortly after hatching. Such genetic differentiation can only arise if, in both sexes, dispersal is restricted and nonrandom, a surprising result considering that pairing occurs among mixed flocks of birds more than 3000 km away from the breeding grounds. Fine-scale genetic structure may thus occur even in migratory species with high gene flow. We further show that looking for genetic structure based on nesting sites only may be misleading. Genetically distinct individuals that segregated into different rearing sites were in fact spatially mixed during nesting. These findings provide new, scale-dependent links between genetic structure, pairing, and dispersal and show the importance of sampling different stages of the breeding cycle in order to detect a spatial genetic structure.

Keywords: fine-scale structure, goose, migration, pairing, sex-biased dispersal

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Introduction

The spatial structure of natural populations has major consequences both for contemporary population dynamics and long-term evolutionary changes. Dynamically, dispersal, defined as the movement of individuals from one genetic population to another (Clobert *et al*. 2001), will determine to what extent local populations may fluctuate independently (Hanski & Gaggiotti 2004). Evolutionarily, the level of gene flow will determine how local populations are bound together as cohesive units, and at what scale evolutionary trajectories may diverge (Waples & Gaggiotti 2006). Weak genetic structure is usually considered a consequence of high dispersal rates and gene flow in systems at dispersal–drift equilibrium (Bohonak 1999). However, recent studies in resident species have challenged this idea by empirically showing that, when dispersal is directional, neutral and adaptive genetic differentiation can occur at a fine spatial scale (1–8 km), even under a regime of frequent and constant gene flow (Garant *et al*. 2005; Postma & vanNoordwijk 2005; Garant *et al*. 2007), a pattern that was only theoretically anticipated (e.g. Barton & Whitlock 1997). The generality of these results nonetheless remains an open question, especially in migratory species [migration being the regular annual movements of individuals between breeding and wintering grounds (Clobert *et al*. 2001)] where dispersal (hence the potential for gene flow) is typically high (Rockwell & Cooke 1977; Paradis *et al*. 1998) or in species with weakly developed social systems (Coltman *et al*. 2003). Our goal was thus to examine for possible fine-scale genetic structuring in a migratory species.

In birds, female-biased dispersal and male philopatry to the breeding territory, defined as the fidelity of an individual

Correspondence: Nicolas Lecomte, Department of Biology, University of Tromsø, N-9037 Tromsø, Norway. Fax: +4777646333; E-mail: nicolas.lecomte@ib.uit.no

to its natal site, is common (Greenwood 1980) except in waterfowl, which exhibit male-biased dispersal and female philopatry. Mate choice in waterfowl is thought to occur in mixed flocks during winter or spring migration, away from the breeding ground, and can result in permanent pair bonds in geese (Ganter *et al*. 2005). Consequently, gene flow in these species is expected to be high and mostly male-mediated, as mated males follow their female returning to its natal site. Indeed, a lack of large-scale genetic structure has been documented in several waterfowl species (Avise *et al*. 1992; Ely & Scribner 1994). Nonetheless, more recent studies using different molecular markers have detected nonrandom pattern of genetic relatedness among neighbouring nests in colonies of some species of geese and ducks as a result of female philopatry (van der Jeugd *et al*. 2002; Fowler *et al*. 2004; Fowler 2005; McKinnon *et al*. 2006; Waldeck *et al*. 2008). These results suggest the possible existence of fine-scale kin structure.

The snow goose (*Chen caerulescens*) is a classical example of contemporary male-biased dispersal in birds (Greenwood 1980). Previous genetic investigations have nourished the view of a poor concordance between genetic structure and spatially segregated colonies at the scale of North America (Quinn *et al*. 1987; Avise *et al*. 1992; and references therein; Quinn 1992). Using a larger number of polymorphic markers, we revisited this idea by testing the hypothesis that, even at a small spatial scale (tens of kilometres), fidelity to specific areas during the reproductive cycle can promote concordance between genetic and spatial structuring of geese and a higher relatedness within, as opposed to among, sites in a local breeding population.

In bird species where young individuals leave the nest shortly after hatching (precocial birds), there is often a spatial segregation between nesting and rearing sites. Nesting site refers to the area where nests are built and eggs incubated and rearing site to the area used by parents to rear their young. For instance, goose families can travel several kilometres away from nesting colonies shortly after hatching to reach rearing sites with high-quality resources where young grow before their migration to the wintering area (Mainguy *et al*. 2006). Although these sites are physically segregated, individuals show some fidelity to both their nesting and rearing sites (Lindberg & Sedinger 1998 and references therein), which raises the possibility that genetic structuring may occur according to the nesting site, the rearing site, or both.

Materials and methods

Study population and sampling procedures

The study was conducted on Bylot Island, Nunavut, Canada (72°53′N, 79°54′W), where about 20 000 breeding pairs of greater snow geese (*Chen caerulescens atlantica*) breed each year (Reed *et al*. 2002). The local breeding population was defined as birds nesting and rearing their brood over an area of *c*. 800 km^2, which included the largest goose colony and the best rearing habitats on the island (Fig. 1). Within this area, there is one large colony, where most (> 95%) of the birds nest, the remaining birds nesting in small, loose colonies in various areas. In years when lemming abundance is high, snowy owls (*Bubo scandiacus*) breed and many geese will nest in small colonies around owl nests in a protective association against egg predators. Good rearing areas are centred on dense patches of wetlands and occur at several sites within the study area (Fig. 1). Samples were collected in 2003, 2004, and 2005 over a short period of time each year to avoid any possible confusion between spatial and temporal genetic changes.

To sample rearing sites, we captured moulting adults with their young when birds are flightless in several catches of a few hundred birds each. In 2004, we randomly sampled adult females in one to eight catches/site at three distinct rearing sites (Qarlikturvik valley, main colony and Dufour; Fig. 1). In 2005, we sampled both females and males at the same three sites and at a fourth site (Camp 3 site; Fig. 1) to increase the spatial coverage. Overall, 241 females (99 in 2004 and 142 in 2005) and 139 adult males were sampled for genetic analyses. We only sampled adults in the rearing sites to prevent the risk of biased sampling due to brood mixing, which sometimes occurs. All sampled individuals were banded before release and no individual was sampled twice in different years.

For the nesting sites, we sampled embryos in eggs during hatching because adults are difficult to catch at the nest (Lecomte *et al*. 2006). In 2003, we sampled 140 embryos in nests (1 per nest) at the main goose colony. Samples were about equally split among three clusters of nests located as far apart as possible within the colony (average distance between clusters: 4.27 km; average diameter of clusters: 0.38 km). These nest clusters will be hereafter referred to as nesting sites. In 2004, due to the presence of snowy owls, a few hundred goose nests were distributed in small colonies around owls in the Qarlikturvik valley area, *c*. 30 km away from the main colony (Fig. 1), which allowed us to compare birds that nested inside and outside the main colony. Thus, in that year we sampled 150 hatchlings randomly located within the main colony and 32 in the Qarlikturvik valley.

For adults captured on rearing sites, we collected blood from the quill of a growing secondary flight feather, whereas for embryos, blood sampling followed the procedure of Lecomte *et al*. (2006). Blood samples collected in the field were stored in Queen's lysis buffer and kept at cool temperature for 2 to 9 weeks before long-term storage at –20 °C in the laboratory.

DNA extraction and AFLP procedures

We developed amplified fragment length polymorphism (AFLP) markers from the blood samples to document the

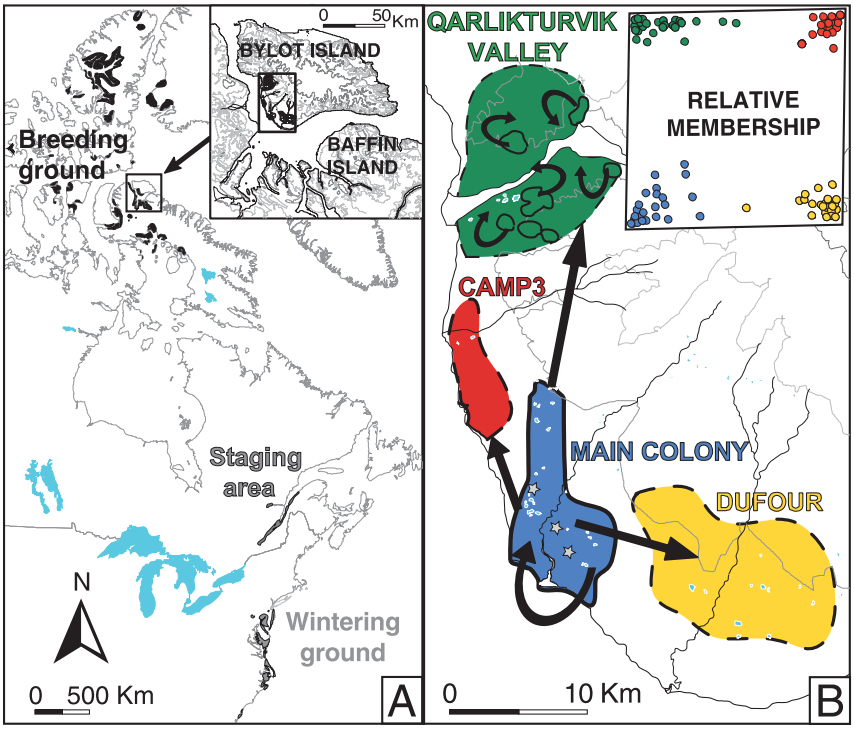

Fig. 1 (A) Geographical locations of the wintering, staging, and breeding areas of greater snow geese (*Chen caerulescens atlantica*) in North America. (B) Location of major nesting (heavy, continuous line) and rearing (dotted line) sites with their relative genetic membership based on 701 greater snow geese sampled on Bylot Island. Site limits were drawn from information in Reed *et al*. (2002) and G. Gauthier, unpublished data. The main colony is also used as a rearing site by some birds. Geese nesting in the Qarlikturvik valley typically nest in association with snowy owls (*Bubo scandiacus*) only in years of peak lemming abundance (Lecomte *et al*. 2008a). Black arrows show movements of birds between their nesting and rearing sites as inferred by our genetic analyses of birds sampled both on the nesting and rearing sites (see Results). Stars indicate locations of the three sampling sites within the main nesting colony. The upper right inset shows the membership (each colour corresponds to a different rearing area) of individual birds within the four genetic groups inferred by the shareware Structure. Each point is a sampled individual but not all individuals are shown because of overlapping points.

fine-scale genetic structure. We chose to use AFLPs because they are efficient in discriminating weakly differentiated populations (Campbell *et al*. 2003). The general mode of inheritance of AFLPs is biparental and dominant. Our procedure was based on the protocol of Vos *et al*. (1995). We extracted DNA using the QIAamp Mini kit for blood samples (QIAGEN). The diluted DNA samples were then run on 2% agarose gels to determine the DNA quality and quantity. We digested 15 ng of high molecular weight DNA with restriction enzymes *Eco*RI and *Mse*I and we ligated the resulting fragments with adaptors. Using the pre-selective primers *Eco*RI-A and *Mse*I-C, we amplified through polymerase chain reaction (PCR) the ligated fragments and then re-amplified a subset of the preselected fragments with six combinations of selective primers (Table S1, Supporting Information), which provided clear and variable profiles in preliminary tests on 18 different individuals. The fragments were then denaturated and separated on an ABI 3100 DNA sequencer using a ROX (red) labelled size standard. The digital gel data was processed in the Applied Biosystems GeneScan analysis software (version 3.7). Each lane file was scored by eye for the presence and absence of AFLP fragments at approximately 1-bp intervals using Applied Biosystems Genotyper software (version 3.7).

Genotyping error and repeatability

The amplification of AFLP fragments was highly repeatable as 99.2% of them ($n = 191$) were identical in replicate DNA samples (30% of our samples). Hence, scoring error was lower than reported in previous studies with values ranging from 1.9 to 2.5% (Busch *et al*. 2000; Miller *et al*. 2002; Mock *et al*. 2002). Nonrepeatable bands were mainly faint bands that showed up in some PCRs but not in others.

Homoplasy

We tested for size homoplasy, i.e. the occurrence of nonhomologous loci of identical size, in our AFLP data set with the AFLP-SURV shareware (Vekemans *et al*. 2002). If size homoplasy occurs, a negative and significant correlation between fragment size and frequency should be observed, with the probability to detect homoplasy being the highest for smaller fragments (Vekemans *et al*. 2002). We rejected the hypothesis of a size homoplasy bias in our data since fragment size was not correlated with its frequency ($r = –0.09$; $P = 0.61$, $n = 44$ loci). We have thus confidently computed AFLP score in a data matrix assuming one locus for each amplified band (Wang *et al*. 2003).

Genetic diversity

Genetic diversity was first determined as the percentage of polymorphic loci, excluding loci shared by less than 5% or by more than 95% of all individuals (95% criterion). Second, we calculated nearly unbiased estimates of heterozygosity using the method of Zhivotovsky (1999) with non-uniform prior allelic distribution. The genetic diversity

for each primer combination and each rearing site sampled is summarized in Table S1. In the size range of 50 to 500 bp, the six primer combinations generated a total of 191 clear and reproducible bands across the 701 individuals analysed (Table S1A). The primer pair ACA/CCC generated the largest number of polymorphic bands ($n = 15$), whereas the primer pair AAC/CGC generated the smallest ($n = 2$). Average heterozygosity was relatively similar among rearing sites, ranging from 0.08 to 0.11 (Table S1B).

Population structure and relatedness

To increase the robustness of our analyses, we used four complementary methods to detect the presence of genetic structuring in the samples collected at the goose nesting and rearing sites. First, we applied the Bayesian approach of Structure version 2.2 shareware to infer population structure patterns and to assign individuals to specific clusters (Pritchard *et al*. 2000; Falush *et al*. 2007). As with other likelihood-based approaches, cluster inference is subject to convergence and local minima problems. We therefore ran 20 independent simulations, averaged the resulting values and checked for slope variations in the log-likelihood function. For each simulation, we used 30 000 iterations of burn-in periods without prior information on the origin of individuals and then collected data after 10^6 iterations.

Second, we determined the origin of nesting individuals among putative rearing site groups in 2004 with the allocation procedure of AFLPOP version 1.1 shareware (Duchesne & Bernatchez 2002). We defined a minimal log-likelihood difference threshold value of 1.3 for assignment, which means that an individual was assigned to a site only if its genotype was at least 20 times more likely in that site than in any other ones.

Third, we performed an analysis of molecular variance (AMOVA) with Arlequin version 3.0 shareware (Excoffier *et al*. 2005) to apportion the total genetic variance into hierarchical components (within and among groups) and computed Φ_{ST}. The significance of the overall Φ-statistic was derived from null distributions generated from 5000 random permutations among breeding groups. To verify these results, we ran more permutation tests (50 000) with the Genetix shareware (Belkhir *et al*. 2004).

Finally, the degree of relatedness (r) between birds within and among sites was calculated using the unbiased estimators implemented in MER shareware using 1000 bootstraps over loci (Wang 2004). Due to the interdependence of pairwise estimates, mean r comparisons among groups cannot be analysed using standard parametric statistics but require permutation approaches. Consequently, we performed two-tailed distribution-free permutation tests with 1000 repetitions using an SAS macro.

Simulations and dispersal values

We performed individual-based simulations to distinguish between possible demographic causes for the patterns of genetic differentiation observed among sites on Bylot Island. Using the shareware EASYPOP (Balloux 2001), we defined the following five distinct scenarios, with the first used as a null model and the others as tests of specific hypotheses: (1) random dispersal for both sexes; (2) random male dispersal and no dispersal for female; (3) no dispersal for male and random female dispersal; (4) limited dispersal for both sexes using an island model of dispersal where among-site dispersal is equal; (5) limited dispersal for both sexes using a stepping-stone model of dispersal, where only neighbouring populations exchange dispersers. This model predicts that neighbouring populations would be less differentiated than non-neighbouring ones contrary to this island-model.

For each simulation scenario, we defined the following rules. The number of populations was fixed to four virtual sites. We specified a 1:1 operational sex ratio with a monogamous mating system but allowing a 2% rate of extra-pair copulations (Dunn *et al*. 1999). We set a mutation rate compatible with AFLP loci, i.e. 10^{-4} per generation (Campbell & Bernatchez 2004), following a random model of mutation for unlinked loci. The number of possible allelic states was restricted to 2 (with AFLP, state 1 for presence and state 0 for absence). We replicated each scenario 100 times and analysed genotypes after 100 generations, computing the mean and the upper and lower quartiles of the 100 replicates. For each replication in each scenario, reference samples of $n = 30$ genotypes were randomly picked in each of the four sites. We then used Arlequin version 3.0 (Excoffier *et al*. 2005) to estimate Φ_{ST} values and P values.

To determine values of dispersal rate per generation to be included in the model, we needed to differentiate between natal and breeding dispersal (respectively, the movement of individuals between their natal and breeding population or between breeding populations after the first breeding event (Greenwood 1980; Greenwood & Harvey 1982). As recruitment of geese starts at 2 years and is completed at 4 years (Reed *et al*. 2003), we assumed that natal dispersal occurred at 2–3 years and breeding dispersal at 4+ years of age. According to the model of Gauthier & Brault (1998), the approximate stable age distribution in the population should be 37.7% for the first age class, 13.1% for the second and third age classes and 49.2% for the 4+ age class. Because individuals of the first age class do not breed, the 2–3 and 4+ year-old individuals composed 21% and 79% of the potentially dispersing population, respectively. In addition, given a similar and high annual adult survival probability for both sexes (83%: Gauthier *et al*. 2001) and monogamous long-term pair bonds (Cooke *et al*. 1981), breeding dispersal of males should be low and driven

either by dispersal of its own mate or by repairing following death of its mate. Based on these rules, we used values of dispersal rate per generation ranging from 0 to 0.5 for males and from 0.04 to 0.08 for females. These ranges include the values previously estimated for dispersal across distant colonies of lesser snow geese, i.e. 30 to 50% for males and 4 to 5% for females (Rockwell & Cooke 1977). Finally, 100 model replications were run to determine the variance around Φ_{ST} estimates measured as a function of different values of dispersal.

Results

Population structure and relatedness

Without using prior information on the geographical origin of individuals, the model-based Bayesian approach of the Structure indicated that greater snow geese breeding on Bylot Island (Fig. 1) are most likely composed of four genetically distinct groups (Table S2, Supporting Information), with different geographical distribution depending on the breeding stage. For instance, while 90.4% of geese ($n = 380$) were correctly assigned to their respective rearing sites (Fig. 1; difference from random sampling expectation $\chi^2_7 = 21.4$; $P = 0.003$), no such relationship was found for the three nesting sites sampled in the main colony ($\chi^2_6 = 5.7$; $n = 140$; $P = 0.44$). Interestingly, 96.8% ($n = 31$) of nests sampled around snowy owls in the Qarlikturvik valley (30 km away from the main nesting colony; Fig. 1) were allocated to the population using the same valley during the rearing period, a pattern that differed from random expectation ($\chi^2_3 = 18.9$; $P < 0.001$). Conversely, individual nests located in each sampled site of the main colony were assigned to each of the four rearing sites with equal probability ($\chi^2_3 = 2.6$; $P = 0.45$).

The low but significant genetic structure depicted among rearing sites for females was stable over the two sampling years (Table 1A). This stability could not be an artefact of sampling the same individuals because different individuals were sampled each year. The molecular variance attributed to divergence between rearing sites was 1.4%, a value 28 times higher than variance between years within site (Table 1A; $\Phi_{ST} = 0.014$, $P < 0.001$). An independent Φ_{ST} estimate obtained from a permutation procedure was essentially identical ($\Phi_{ST} = 0.016$). The mean estimate of females' pairwise relatedness on rearing sites was greater

Table 1 Hierarchical partitioning of the genetic variance (AMOVA — Arlequin software version 3.0) based on 44 AFLP (amplified fragment length polymorphism) loci showing percentage of total variance (%V) depending on the grouping in greater snow geese

A. Comparison among three rearing sites, Qarlikturvik valley (QV), main colony (MC) and Dufour, adult females only, 2004–2005

Variance component	d.f.			%V			*P*		
Among sites	2			1.42			< 0.0001		
Between 2004–2005 within sites	1			0.05			0.41		
Within sites in each year	208			98.53			< 0.001		
Rearing sites	QV			MC			Dufour		
Variance component	d.f.	%V	*P*	d.f.	%V	*P*	d.f.	%V	*P*
2004–2005	1	0.26	0.29	1	0.24	0.26	1	0.50	0.23
Within each year	92	99.74	< 0.001	59	99.16	< 0.001	57	99.50	< 0.001

B. Comparison among four rearing sites, QV, MC, Dufour and Camp 3, adult females and males, 2005

	Females			Males		
Variance component	d.f.	%V	*P*	d.f.	%V	*P*
Among sites	3	1.2	0.001	3	0.8	0.04
Within sites	138	98.8	< 0.001	135	99.2	< 0.001

C. Hatchlings in nests, 2003–2004

	Within main colony*			Among QV–MC		
Variance component	d.f.	%V	*P*	d.f.	%V	*P*
Among sites	2	0.01	0.95	1	0.8	0.12
Within sites	137	99.99	< 0.001	180	99.2	< 0.001

*three clusters of nests spaced out within the colony (see Fig. 1).

within (r = 0.013; SE = 0.002) than among rearing sites (r = –0.015; SE = 0.004; n = 1000 permutations; P = 0.04). We also found a significant structure among rearing sites for males, although the mean Φ_{ST} value (0.008) was about half of the mean value detected in females (Table 1A–B). However, males showed similar pairwise relatedness values within (r = –0.015; SE = 0.002) and among rearing sites (r = –0.016; SE = 0.003; n = 1000 permutations; P = 0.66). In contrast, we observed no concordance between the genetic structure and the three geographic sites sampled within the main nesting colony (Φ_{ST} = 0.001, d.f. = 2, P = 0.95; Table 1C). Finally, Φ_{ST} between birds nesting in the main colony and those nesting outside was not significant (Table 1C).

Simulations and dispersal values

Scenarios where one or both sexes dispersed randomly (scenarios 1 to 3) never yielded Φ_{ST} significantly different from 0, regardless of the values used for the other parameters. Significant Φ_{ST} values, however, were obtained for a range of limited dispersal values for both sexes, using isolation model with or without distance (scenarios 4 and 5). Φ_{ST} values similar to those measured in our system were only obtained when male dispersal rates ranged between 0.10 and 0.18 per generation and those of females between 0.04 and 0.08 (Fig. 2). Therefore, results of the EASYPOP simulations clearly show that significant genetic structure can occur only if dispersal of both sexes is restricted. These results, however, were conditional upon using an effective population size (N_e) below or equal to 1500, as simulations did not yield significant Φ_{ST} above this value.

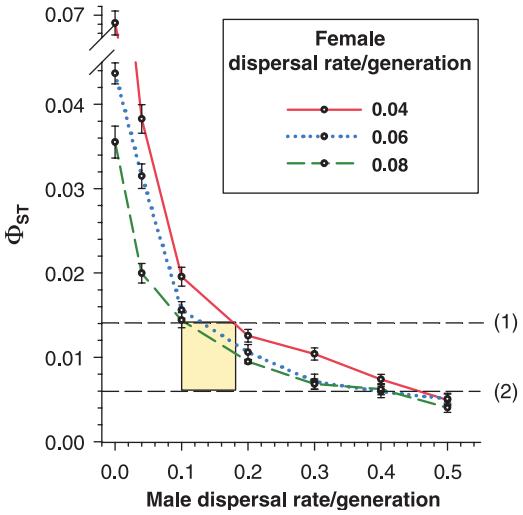

Fig. 2 Φ_{ST} variation as a function of simulated dispersal rates in both sexes. Mean values of $\Phi_{ST} \pm$ SE were obtained after 100 simulations using the shareware EASYPOP. The dotted line (1) indicates the level of Φ_{ST} measured for greater snow goose females on Bylot Island and (2) the level where Φ_{ST} is not significantly different from 0 with an alpha threshold of 5%. The yellow-shaded area represents the range of dispersal values for greater snow goose males required to obtain Φ_{ST} similar to those measured in our study. Comparable results were obtained using either a stepping-stone or an island model of dispersal in both sexes (scenarios 4 and 5 described in the Methods).

Discussion

Detecting evidence of genetic clustering among spatially distinct rearing sites located only ~10 km apart was unexpected because previous studies on geese suggested a high regime of dispersal and gene flow at large spatial scales (Avise *et al*. 1992; Ely & Scribner 1994). Such structure was supported by four different genetic approaches and our Φ_{ST} values, although low, were in the range reported by studies showing biologically meaningful fine-scale genetic structure (e.g. Coltman *et al*. 2003; Lampert *et al*. 2003; Nussey *et al*. 2005; Keyghobadi *et al*. 2006). Wide-ranging male dispersal has been proposed as the primary vector of genetic mixing because pairing occurs on the wintering ground, far away from the breeding colonies. Females could also play a role in long-term gene exchange among colonies when bottlenecks occur (Fig. 2), such as during glacial episodes (Avise *et al*. 1992) or after major perturbations, such as habitat degradation (Jefferies *et al*. 2004). Contrary to these arguments, our results imply that the classic paradigm of large and widespread genetic mixing in migratory species should be reconsidered, especially by taking into account the role of philopatry in both sexes. In addition, we showed that a concordance between genetic and spatial structuring may be present at some stages of the breeding cycle (e.g. rearing) but not at others (e.g. nesting). Such discrepancy calls for caution when examining individual assortment in natural populations, especially considering that the nesting stage is commonly used for sampling populations in the field (e.g. Fowler 2005; McKinnon *et al*. 2006).

The critical role of genetic drift in generating differentiation among rearing sites was emphasized by the effective population size required to obtain patterns compatible with those observed ($N_e \leq 1500$). This represents about 6% of the estimated current population size of greater snow geese breeding on Bylot Island (Reed *et al*. 2002). This ratio of effective vs. total size is also in the range reported for many animal species including birds (Frankham 1995) and is compatible with the occurrence of a recent bottleneck for this population. Indeed, 100 years ago the entire population of this subspecies may have been as low as 4000 individuals (Gauthier *et al*. 2005), which is indicative of a much-reduced effective population size in the recent past.

In sex-biased dispersal systems, social associations among single-sex groups can drive the formation of genetic clusters (Coltman *et al*. 2003 and references therein). In our study, the adequacy between spatial and genetic structure

is likely driven by high female philopatry to the rearing site, increasing the probability of kin structure. Under this scenario, females recruiting into the breeding population should rear their goslings where they were reared themselves, which could allow differential selective pressure to emerge if rearing sites differ in quality, a pattern observed in other studies where habitat and predation pressure differ at small spatial scales (e.g. Slabbekoorn & Smith 2002; Saint-Laurent *et al*. 2003; Smith *et al*. 2005). Although males demonstrated significant clustering during rearing, their genetic differentiation was less than that for females. While this result is consistent with the general pattern of male-biased dispersal (Greenwood 1980), our simulations suggested that the fine-scale population structuring observed here can only occur if males also show some philopatry and have a lower rate of dispersal than previously reported (Rockwell & Cooke 1977) (Fig. 2).

Until now, male philopatry in long-distant migrants such as geese was thought to be negligible because pairing occurs mainly on wintering grounds where birds from distant colonies are extensively mixed (Robertson & Cooke 1999). With long-term pair bonds and high adult survival, natal dispersal should play a more important role in genetic structure through first-time pairing than through breeding dispersal. Thus, our results can only arise if individuals reared in the same site preferentially pair together later in life. Unfortunately, little is known about the wintering structure and pairing mechanisms in waterfowl. However, several lines of evidence suggest that pairing in geese is assortative and could contribute to reduce gene flow among colonies. First, hitherto unrecognized aggregations of birds born on the same rearing sites may persist away from the breeding ground, including on the wintering or staging areas. For instance, spatially distinct breeding groups of Pacific white-fronted goose (*Chen albifrons frontalis*) use exactly the same wintering grounds, although not at the same time (Ely & Takekawa 1996). Second, individual recognition may allow preferential mating of individuals born in the same area (van der Jeugd *et al*. 2002). Such assortative pairing is likely based on individual characteristics, such as plumage colour (Cooke *et al*. 1995), size (Choudhury & Black 1993) and familiarity (i.e. individuals paired with whom they have associated intermittently during early life: Choudhury & Black 1994). Despite such evidence for assortative mating, the exact mechanism involved in the reduction of gene flow among colonies remains to be elucidated.

Several factors may affect our ability to detect fine-scale genetic structure in wild populations. For instance, Nussey *et al*. (2005) recently showed that such structure may change rapidly over time. Our study shows that fine-scale genetic structure may also differ markedly depending on the stage of the breeding cycle that is sampled. Most studies looking for genetic structure in breeding bird populations have focused on nesting sites where birds are spatially confined to the vicinity of their nest (e.g. Fowler *et al*. 2004; McKinnon *et al*. 2006; Andersson & Waldeck 2007). We have shown that in a precocial bird, this may be misleading as we found no concordance between genetic and geographical structure within a large nesting colony. Yet, a concordance emerged when the same individuals segregated according to their rearing sites. Our findings call for an evolutionary explanation as to why a population may be structured more according to specific parts of its breeding cycle than others. In the Arctic, the availability of nesting sites is often more temporally variable than that of rearing sites (Lecomte *et al*. 2008b), possibly contributing to reduced nest site fidelity and promoting the evolution of structure based on rearing sites. Furthermore, as families leave their nesting site shortly after hatching, the environment experienced by young birds are primarily their rearing site and not the nesting site of their parents. The primary mechanism of philopatry in a precocial bird like geese may then be fidelity to a familiar rearing site, with fidelity to a specific nesting site a by-product of the latter (Abraham 1980). If the cost of movements to rearing sites after hatching is low (Mainguy *et al*. 2006), benefits associated with colonial nesting (e.g. reduced predation) may promote the mixing of nesting birds, which later segregate in genetically distinct rearing sites.

Such mechanism is supported by the occasional protective nesting associations between geese and snowy owls (Fig. 1). We found that geese that take advantage of owls are not a random sample of individuals but are primarily birds using the nearby rearing site. These birds have the double benefit of nesting in a safe site and avoiding any potential cost associated with movements to a rearing site. In this context, we propose that nest site fidelity may be a more flexible strategy than rearing site fidelity, a mechanism likely to drive fine-scale genetic clustering. It is therefore possible that studies, which limited their investigation only to the nesting period, may have missed the fine-scale genetic structure present in some species at other period of their life cycle.

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Nicolas Lecomte is currently a post-doctoral researcher at the University of Tromsø, where he is investigating trophic interactions in the Arctic terrestrial ecosystems (project 'Arctic Predators': http://www.arctic-predators.uit.no). The present study is part of his PhD thesis linking predation risk, habitat heterogeneity and nesting fidelity. Gilles Gauthier is a Professor of animal ecology at the Université Laval (CA) and was the main supervisor of Nicolas Lecomte's thesis. His research focuses on the population dynamic and trophic interactions, using High-Arctic tundra and migratory birds as model systems. Jean-François Giroux is a Professor of ecology at the Université du Québec à Montréal (UQAM, CA) and was the co-supervisor of Nicolas Lecomte for his PhD. His current work centres on the ecology and integrated management of several waterfowl species. Emmanuel Milot is finishing a PhD work on dispersal, genetic structure and population dynamic of wandering albatrosses. Louis Bernatchez is a Professor of molecular ecology at the Université Laval. His major interests are in the understanding of patterns and processes of molecular and organismal evolution and their relevance to conservation.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of amplified fragment length polymorphisms according to primer combination (A) or rearing sites (B) for 701 greater snow geese sampled in the breeding population of Bylot Island (NU, CA)

Table S2. Mean likelihood of data [ln Pr(X | K)] and posterior probabilities [P (K | X)] for different numbers of genetic clusters

(K) for 701 greater snow geese sampled in the breeding population of Bylot Island (NU, CA). The number of genetic clusters corresponds to the number of groups estimated by the Structure shareware (Pritchard *et al.*, 2000) without using any a priori information about potential population structure. Note that ~0 and ~1 refer to probability < 0.001 and > 0.999, respectively