Do common eiders nest in kin groups? Microgeographic genetic structure in a philopatric sea duck

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Abstract

We investigated local genetic associations among female Pacific common eiders (*Somateria mollissima v-nigrum*) nesting in a stochastic Arctic environment within two groups of barrier islands (Simpson Lagoon and Mikkelsen Bay) in the Beaufort Sea, Alaska. Nonrandom genetic associations were observed among nesting females using regional spatial autocorrelation analyses for distance classes up to 1000 m in Simpson Lagoon. Nearest-neighbour analyses identified clusters of genetically related females with positive *lr* values observed for 0–13% and 0–7% of the comparisons in Simpson Lagoon and Mikkelsen Bay, respectively, across years. These results indicate that a proportion of females are nesting in close proximity to more genetically related individuals, albeit at low frequency. Such kin groupings may form through active association between relatives or through natal philopatry and breeding site fidelity. Eiders nest in close association with driftwood, which is redistributed annually by seasonal storms. Yet, genetic associations were still observed. Microgeographic structure may thus be more attributable to kin association than natal philopatry and site fidelity. However, habitat availability may also influence the level of structure observed. Regional structure was present only within Simpson Lagoon and this island group includes at least three islands with sufficient driftwood for colonies, whereas only one island at Mikkelsen Bay has these features. A long-term demographic study is needed to understand more fully the mechanisms that lead to fine-scale genetic structure observed in common eiders breeding in the Beaufort Sea.

Keywords: common eider, environmental variation, habitat stability, kin association, site fidelity, *Somateria mollissima v-nigrum*

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Philopatry can lead to strong patterns of spatial genetic subdivision among populations (Tiedemann *et al.* 1999; Scribner *et al.* 2001; Avise 2004), and numerous studies have documented examples of kin structure (Lambin & Krebs 1993; Andersson & Åhlund 2000; MacColl *et al.* 2000; Fowler *et al.* 2004; Double *et al.* 2005; Støen *et al.* 2005; McKinnon *et al.* 2006; Zeyl *et al.* 2009). Possible mechanisms that promote such behaviour include: selective advantages of increased assistance from relatives during the breeding season (Lessells *et al.* 1994),

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decreased competition and aggression between related or familiar neighbours (Greenwood *et al.* 1979; Waldman 1988; Eason & Hannon 1994) or a variety of benefits associated with site familiarity (Anderson *et al.* 1992). However, philopatry and kin association may have different effects on spatial genetic structure at the interindividual scale. Individuals preferentially breeding near more genetically related individuals might create clusters of nonrandom genetic associations among individuals at fine-spatial scales (Fowler *et al.* 2004; Double *et al.* 2005). Conversely, if individuals are philopatric to an area alone, fine-scale genetic similarities between individuals may not be observed depend-

ing on the extent of philopatric behaviour, where individuals acquire mates, spatial contiguity of breeding habitat and the size and density of the population (see Öst *et al.* 2005; McKinnon *et al.* 2006). Furthermore, positive genetic associations are thought to reduce competition among individuals (Hamilton 1964) and enhance advantages of sociality (Waldman 1988). Variability in resources (habitat and foraging) probably influences the degree of unselfish behaviour that individuals exhibit. Only a few studies, however, have investigated social organization of taxa in Arctic environments, which are characterized by high levels of stochasticity (e.g. polar bears, *Ursus maritimus*; Zeyl *et al.* 2009). Such studies can provide valuable insight on the plasticity of kin associations in this spatially and temporally variable environment.

Here we investigate microgeographic genetic structure of female Pacific common eiders (*Somateria mollissima v-nigrum*) breeding in the Beaufort Sea of Alaska. Females nest in either dense colonies or scattered locations on islands, and the distribution of nest sites is influenced annually by the availability (i.e. distribution and density) of driftwood (Goudie *et al.* 2000). Similar to other waterfowl, female common eiders exhibit high natal philopatry and breeding site fidelity (Goudie *et al.* 2000), which promotes high levels of genetic partitioning among populations (Tiedemann *et al.* 1999, 2004; Sonsthagen *et al.* 2007, 2009). In Hudson Bay, for example, Schmutz *et al.* (1983) hypothesized that groups of common eiders (*Somateria mollissima sedentaria*) were composed of extended families; within these groups, females exhibited greater nesting synchrony and lower variance in egg shape than expected by chance. Numerous clutches in this colony also contained eggs from two or more closely related individuals (Robertson 1998; Waldeck & Andersson 2006; Andersson & Waldeck 2007). In addition, molecular data indicate that common eiders (*Somateria mollissima borealis*) breeding in colonies on tundra habitats on Southampton Island in Hudson Bay arrive at the colony, nest and raise broods in female kin-based social groups (McKinnon *et al.* 2006).

We used a multivariate autocorrelation analyses developed by Peakall & Smouse (2006) to investigate local genetic associations among eiders nesting in driftwood on two barrier island groups (Simpson Lagoon and Mikkelsen Bay) composed of 12 islands in the Beaufort Sea. Genetic data were used as a partial proxy for the Beaufort Sea population as detailed demographic data are difficult to collect in this area. Given evidence from previous studies of common eiders that demonstrated high philopatry to natal breeding sites, we predicted that common eiders nesting in close proximity would be more genetically related than expected by chance. Differences in the stability of nesting habitat and the availability of driftwood should result in less pronounced spatial genetic associations in the Beaufort Sea barrier islands relative to Hudson Bay colonies. Specifically, seasonal Arctic storms in the Beaufort Sea dramatically modify island topology and redistribute driftwood, changing the location and quality of nesting habitat annually (Noel *et al.* 2005). In contrast, Hudson Bay common eiders nest on coastal wetland tundra habitat (Goudie *et al.* 2000) that remains relatively unchanged across consecutive breeding seasons. The lack of predictable nesting sites at the Beaufort Sea might thus limit individuals from nesting at or near their natal or previous breeding site. Furthermore, we expected to observe differences in the occurrence of microgeographic structuring among islands within the Beaufort Sea. Specifically, we hypothesized that Simpson Lagoon would exhibit more spatial genetic associations than Mikkelsen Bay because of differences in the distribution and availability of nesting habitat. Simpson Lagoon contains three high-density nesting colonies. In contrast, Mikkelsen Bay has only one island with a colony and therefore eiders typically nest in low densities on the other islands. Previous research in Hudson Bay has shown that eiders nesting in dense colonies had higher levels of relatedness among a focal female and her nearest neighbours than in low-density areas (McKinnon *et al.* 2006). The relatively low nesting density of female eiders in Mikkelsen Bay may thus limit the occurrence of genetic associations among females.

Methods

Sample collection

Blood or feather samples were collected from breeding female common eiders during mark–recapture and monitoring efforts on barrier islands in the Beaufort Sea, Alaska, between 2000 and 2003 (Flint *et al.* 2003). Samples were collected from two island groups, consisting of 12 islands in total (Fig. 1). The Simpson Lagoon group consists of five islands: Stump, 'Wannabe', Egg, Long and Spy islands (Fig. 1a). The Mikkelsen Bay group consists of seven islands: 'Camp', Point Thomson, Mary Saches, North Star, Duchess, Alaska and Challenge islands (Fig. 1b). Distances between islands within each of the two island groups ranged from 1.2 to 49.2 km, and distances between islands located in Simpson and Mikkelsen Bay ranged from 78.1 to 143.1 km. Genetic material was collected from 0% to 53% of nests found in a given year, with no nests sampled in 2001 at Mikkelsen Bay and few nests sampled (13%) in Simpson Lagoon in 2002 because of high predation.
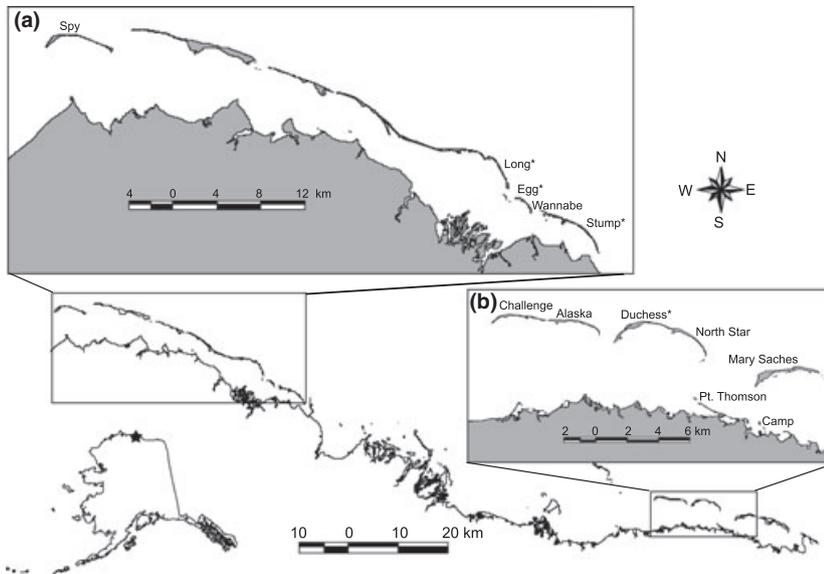
Fig. 1 Beaufort Sea barrier islands located in (a) Simpson Lagoon and (b) Mikkelsen Bay. The enlarged area is indicated with a star near the map of Alaska. Islands containing colonies are marked with an asterisk. 'Wannabe' and 'Camp' islands are designations used by the authors and are not official names of islands. Islands are shaded in gray.

Females were captured on nests using a dip net during initial searching efforts, or with a bow net during late incubation (Sayler 1962). Blood was collected from the tarsal, brachial or jugular veins and placed in lysis buffer (Longmire et al. 1988). Feather samples were collected from nest bowls of females that were not captured and stored in silica gel desiccant at room temperature. After returning from the field, samples were archived at −80 °C at the US Geological Survey Molecular Ecology Laboratory, Anchorage, Alaska. Genomic DNAs were extracted using either a 'salting out' protocol described in Medrano et al. (1990) with modifications described in Sonsthagen et al. (2004), or a QIAGEN DNeasy Tissue Kit. Concentrations of genomic DNA extracts were quantified using fluorometry and diluted to 50 ng/μL working solutions.

Microsatellite genotyping

Primers used for microsatellite genotyping were obtained via cross-species screening of microsatellite primers developed for other waterfowl. We screened 12 common eiders at 50 microsatellite loci reported to be variable for other waterfowl species and selected 14 microsatellite loci found to be polymorphic: *Aph*02, *Aph*08, *Aph*20, *Aph*23 (Maak et al. 2003); *Bca*μ1, *Bca*μ11, *Hhi*μ3 (Buchholz et al. 1998); *Cm*09 (Maak et al. 2000); *Sfi*μ10 (S. Libants, K. Oswald, E. Olle, and K. Scribner, GenBank accession: AF180500); *Smo*4, *Smo*7, *Smo*08, *Smo*10 and *Smo*12 (Paulus & Tiedemann 2003). Microsatellites were amplified using the polymerase chain reaction (PCR), and products were electrophoresed following protocols described in Sonsthagen et al. (2004) for tailed primers (*Aph*02, *Aph*08, *Aph*20, *Aph*23, *Cm*09, *Smo*4, *Smo*7, *Smo*08,

*Smo*10 and *Smo*12) and Pearce et al. (2005) for direct-labelled primers (*Bca*μ1, *Bca*μ11, *Hhi*μ3 and *Sfi*μ10). For quality control, 10% of the samples were randomly selected, reamplified and genotyped in duplicate.

Analysis of genetic diversity

Allelic frequencies and the expected and observed heterozygosities for each microsatellite locus were calculated in Genepop 3.1 (Raymond & Rouset 1995) and FSTAT 2.9.3 (Goudet 1995, 2001). Hardy–Weinberg equilibrium and linkage disequilibrium were tested in Genepop using the default parameters (Markov chain parameters: dememorization number 1000, number of batches 100 and number of iterations per batch 10 000), adjusting for multiple comparisons using Bonferroni corrections ($\alpha = 0.05$). To determine if we could accurately identify individuals, and therefore assess levels of relatedness among individuals, probabilities of identity for a randomly mating population (P_{ID}) and among siblings ($P_{ID_{sib}}$) were calculated in Gimlet 1.3.3 (Valière 2002) using genotypes from the 14 microsatellite loci.

Queller & Goodnight's (1989) index of relatedness (r_{xy}) was calculated among pairs of individuals breeding on each island group and averaged across all individuals within a group in a given year using Identix 1.1 (Belkhir et al. 2002). Relatedness values range from −1 to 1, where r_{xy} equals 0.5 for first-order (i.e. full-sibling, mother–daughter) relationships, 0.25 for second-order (i.e. half-sibling) relationships, 0 for unrelated individuals and −1 for outbred individuals. Genetic discordance among sampled areas may cause incorrect relatedness values, as r_{xy} values measure genetic differences in overall allelic frequency (Queller & Goodnight 1989).

Therefore, spatial analyses of individuals were partitioned by island groups because significant genetic differentiation was observed at both mitochondrial and nuclear genomes between Mikkelsen Bay and Simpson Lagoon (see Sonsthagen et al. 2009). Significant pairwise comparisons at 14 microsatellite loci were observed between Spy and Long ($F_{ST} = 0.009$), Spy and Egg ($F_{ST} = 0.010$) and Camp and Mary Saches ($F_{ST} = 0.020$; Sonsthagen et al. 2009) islands. Variance estimates are low but may influence background allelic frequencies. However, F_{ST} estimates were calculated from samples pooled across years, and population comparisons were not significant when F_{ST} was calculated within years. This nonsignificance is probably a result of low sample size among islands within years. Squared genetic distance (Smouse & Peakall 1999) were calculated between pairs of individuals within each island group using GenAlEx 6 (Peakall & Smouse 2006); an analysis of a single microsatellite locus with ith, jth, kth and lth different alleles, a set of squared distances is defined as $d^2(ii, ii) = 0$, $d^2(ij, ij) = 0$, $d^2(ii, ij) = 1$, $d^2(ij, ik) = 1$, $d^2(ij, kl) = 2$, $d^2(ii, jk) = 3$ and $d^2(ii, jj) = 4$ (Peakall et al. 2003). Genetic distances for each locus are summed across loci for each individual in the matrix under the assumption of statistical independence. Geographic distances among sampled nests were calculated in GenAlEx using Universal Transverse Mercator (UTM) coordinates.

Analysis of regional spatial genetic structure

We use the term regional to describe genetic structure within island groups (i.e. Mikkelsen Bay and Simpson Lagoon) and local to describe the presence of nonrandom genetic associations among female common eiders nesting within a single island. Fine-scale genetic associations may or may not be observed in the absence of significant regional genetic structure (Sokal et al. 1998).

The overall correlation between genetic similarity (r_{xy}) and geographic distance across island groups was assessed using Mantel tests implemented in the software zt 1.0 (Bonnet & Van de Peer 2002). Significance of Pearson correlation coefficients were assessed using a randomization procedure, where the original value of the statistic was compared with 10 000 values calculated from random reallocations of the distance value matrices.

Regional spatial autocorrelation analyses were conducted in GenAlEx to further investigate spatial partitioning of individuals within an island group in a given year, as weak or scattered patterns may not be detected using a simple Mantel analysis (Double et al. 2005). Genetic and geographic matrices calculated in GenAlEx were used to determine spatial autocorrelation of common eider nests with increasing distance class intervals ranging from 4 m to 1 km (4, 6, 8, 10, 25, 50, 100, 250, 500 and 1000 m). Distance classes were used to determine the spatial scale at which genetic structure was detected. Distance intervals larger than actual spatial genetic structure would lead to failure to detect structure, whereas distance classes smaller than actual genetic structure would result in increased interindividual variance and decrease the probability of detecting structure. Distance classes were selected using nearest-neighbour distances calculated in GenAlEx for a given year and island group in an attempt to account for differences in nest density of common eiders breeding in the Beaufort Sea, as well as to account for different nesting strategies among eider females (i.e. colonial vs. dispersed). Because common eiders either nest in dense colonies or are dispersed throughout the islands, median nearest-neighbour values ranged from 14 to 128 m across island groups and years, with a minimum observed distance of <1 m and a maximum distance of 6.4 km (Table 2). There were seven instances where pairs of sampled nests were located within centimetres of each other. Genetic correlation coefficient (r) was estimated using two approaches: permutation and 1000 bootstrap replicates (Peakall & Smouse 2006).

Local spatial genetic structure

A two-dimensional local spatial analysis was implemented in GenAlEx as described by Double et al. (2005) to assess fine-scale nonrandom patterns in genetic structure. Social structure and barriers to dispersal, such as female natal philopatry and breeding site fidelity, can create nonrandom genetic patterns. If females preferentially nested closer to relatives, we would expect to observe a significant correlation at finer spatial scales. In contrast, if females are faithful to a particular island/group but not to a nest site, then more genetically related females would not nest in close association with each other. Local autocorrelation (lr) was estimated based on n pairwise comparisons for a focal individual and its n nearest neighbours using genetic and geographic distances calculated in GenAlEx. This analysis was repeated for all individuals in the data set using two-dimensional local spatial analysis for four, six, eight and ten nearest neighbours (10 000 permutations). Geographic distances calculated in GenAlEx, as described before, were used to determine the four, six, eight and ten nearest neighbours. Significant comparisons among a focal female and her n nearest neighbours with geographic distances greater than 1 km were not presented as these probably do not present biologically meaningful interactions. Because the results for the six, eight and ten nearest neighbours did not differ from the four nearest neighbours, we present only the latter

here. The output of the two-dimensional spatial analysis was converted to bubble plots across the landscape (e.g. Double *et al.* 2005).

Results

Genetic diversity

Multi-locus genotypes were obtained for 317 individuals. The number of alleles per locus for the 14 polymorphic microsatellite loci ranged from 3 to 44 (Table 1), with an average of 11.3 alleles per locus. The average number of alleles across all loci per island group in a given year ranged from 6.21 to 8.79 (Table 2). The observed heterozygosity for each area in

Table 1 Number of alleles, fragment length, observed heterozygosity (H_O) and probability of identity among common eider individuals (P_{ID}), and siblings ($P_{ID_{sib}}$) breeding in the Beaufort Sea, Alaska, for 14 microsatellite loci used in this study

Locus	Number of alleles	Fragment length	H_O	P_{ID}	$P_{ID_{sib}}$
*Aph*02	4	110–116	0.516	2.84×10^{-1}	5.49×10^{-1}
*Aph*08	3	138–142	0.459	3.95×10^{-1}	6.21×10^{-1}
*Aph*20	9	162–184	0.645	1.69×10^{-1}	4.54×10^{-1}
*Aph*23	7	206–218	0.599	1.96×10^{-1}	3.84×10^{-1}
*Cm*09	9	102–124	0.599	2.04×10^{-1}	5.03×10^{-1}
*Bca*μ1	4	108–114	0.451	3.37×10^{-1}	6.29×10^{-1}
*Bca*μ11	7	135–147	0.395	3.94×10^{-1}	6.49×10^{-1}
*Hhi*μ3	3	110–114	0.119	6.21×10^{-1}	7.94×10^{-1}
*Sfi*μ10	19	129–181	0.875	2.57×10^{-2}	3.19×10^{-1}
*Smo*4	44	155–257	0.918	3.98×10^{-3}	2.75×10^{-1}
*Smo*7	6	197–213	0.362	3.89×10^{-1}	6.45×10^{-1}
*Smo*8	7	115–127	0.625	2.04×10^{-1}	5.00×10^{-1}
*Smo*10	21	115–163	0.782	6.72×10^{-2}	3.81×10^{-1}
*Smo*12	15	100–117	0.729	8.45×10^{-2}	4.00×10^{-1}
Total loci	—	—	0.577	3.21×10^{-12}	5.34×10^{-5}

a given year ranged from 56.1% to 60.6% with an overall value of 57.7% (Table 2). None of the loci deviated significantly from Hardy–Weinberg equilibrium, and none were found to be in linkage disequilibrium.

Regional spatial genetic structure

We calculated an overall P_{ID} of 3.2×10^{-12} for a population composed of randomly mating individuals and 5.3×10^{-5} for siblings using genotypes collected from 14 microsatellite loci (Table 1). These P_{ID} denominator values are much larger than the number of birds breeding on the western Beaufort Sea (~660 nests found on the islands; Noel *et al.* 2005), which gave us confidence in identifying individuals correctly among years. A comparison of individual genotypes obtained from blood and feathers indicated that no individual was sampled repeatedly within a given year. A total of 34 females were detected nesting in multiple years based on mark–recapture banding data and genetic techniques (Sonsthagen *et al.* 2009). Overall r_{xy} values from Mikkelsen Bay and Simpson Lagoon in any given year ranged from −0.037 to −0.008, and −0.063 to −0.014 and did not significantly differ from zero, respectively (Table 2).

We did not observe any significant correlations between genetic distance and geographic distance or between r_{xy} values and geographic distance among years at Mikklesen Bay or Simpson Lagoon island groups (Table 2). No correlation would be expected, however, unless spatial structure extended over the full geographic range of the data set (Peakall *et al.* 2003). Fine-scale spatial structure was observed in Simpson Lagoon but not at Mikkelsen Bay. Common eiders nesting at Simpson Lagoon had significantly different genetic correlation (r) than the mean permutated r during the following years and distance classes: (i) in 2000 at 0–50 m ($r = 0.099$, $n = 9$) distance class interval; (ii) in

Table 2 Average number of alleles, observed and expected heterozygosities (H_O/H_E), overall relatedness values (r_{xy}; Queller & Goodnight 1989) with 95% confidence intervals in parentheses, geographic distance between a female and her nearest neighbour (NN) with the median in parentheses, Pearson correlation coefficients between genetic similarity (r_{xy}) and geographic distance and sample sizes (n) for common eiders breeding on Simpson Lagoon and Mikkelsen Bay island groups in the Beaufort Sea, Alaska, between 2000 and 2003. Zero in the NN distance column indicates that females were nesting <1 m apart

	Number of alleles	H_O/H_E	r_{xy}	NN distance (m)	r	n
Simpson Lagoon						
2000	7.36	59.5/59.5	−0.026 (−0.389, 0.337)	26–3814 (101)	−0.006	40
2001	7.29	60.1/60.3	−0.033 (−0.374, 0.308)	0–6412 (84)	0.088	31
2002	6.21	60.6/58.3	−0.063 (−0.458, 0.332)	1–2975 (84)	0.027	17
2003	8.64	56.1/59.3	−0.014 (−0.399, 0.371)	1–1072 (23)	0.018	69
Mikkelsen Bay						
2000	6.64	58.2/58.5	−0.037 (−0.416, 0.342)	13.6–692 (88)	−0.048	28
2002	8.00	57.3/59.8	−0.021 (−0.431, 0.389)	0–1502 (29)	0.094	43
2003	8.79	56.1/58.6	−0.008 (−0.393, 0.377)	0–804 (14)	0.028	89

2002 at 0–250 ($r = 0.091$, $n = 9$) and 0–500 m ($r = 0.079$, $n = 9$) distance class intervals; and (iii) in 2003 at 0–4 ($r = 0.103$, $n = 8$), 0–8 ($r = 0.098$, $n = 14$), 0–10 ($r = 0.118$, $n = 18$), 0–25 ($r = 0.061$, $n = 43$), 0–500 ($r = 0.016$, $n = 398$) and 0–1000 m ($r = 0.011$, $n = 525$) distance class intervals.

Local spatial genetic structure

Within Simpson Lagoon, nonrandom genetic associations, based on local autocorrelation among a focal female and her four nearest neighbours (i.e. *lr* values), were observed for 0–13% of the comparisons among females nesting in 2000 and 2003 ($P < 0.05$; Table 3). Positive *lr* values were observed for females nesting on Egg and Long islands in 2000 and Long, Stump and Spy islands in 2003 (Fig. 2; see Fig. 1a for location of islands). Negative *lr* values were estimated for females nesting on Stump Island in 2003 (Fig. 2; see Fig. 1a for location of island). The composition of genetic associations illustrated in Fig. 2 is as follows. In 2000, two focal females were positively associated but did not share their nearest neighbours. In 2003, two focal females had the same individuals in their positive cluster but were not associated with each other; four focal females were positively associated with each other and their nearest neighbours; and two focal females were negatively associated with each other and had the same two individuals in their clusters.

Within Mikkelsen Bay, 0–7% of the *lr* values were positive and 3–7% of the *lr* values were negative in a given year ($P < 0.05$; Table 3). Positive *lr* values were found for females nesting on Camp and Duchess islands in 2002 and 2003, and for Challenge island in 2003 (Fig. 2; see Fig. 1b for location of islands), indicating female eiders are nesting in close association with more genetically related individuals on these islands. Negative *lr* values were found for females nesting on North Star Island in 2000; Duchess and Pt. Thomson islands in 2002; and Alaska, Camp, Challenge and Duchess islands in 2003 (Fig. 2; see Fig. 1b for location of islands). The composition of genetic associations illustrated in Fig. 2 is as follows. In 2002, two sets of two focal females were positively associated with each other and their nearest neighbours. In 2003, three focal females were positively associated with each other and shared a majority of their nearest neighbours, and two focal females had the same three individuals in their negative associations but were not associated with each other.

Only 8 of 32 (24%) females with multiple-year breeding data were involved in genetic associations with their neighbours, six were positive and two were negative and these associations were observed in only 1 year. In the year that genetic associations were not observed, no close neighbours of focal females were sampled (i.e. nearest neighbours were >1 km).

Discussion

Regional and local autocorrelation analyses revealed fine-scale genetic structure among a small proportion of

Table 3 Nonrandom ($P < 0.05$) local autocorrelation (*lr*) values and their proportions (%) and geographic distance among a focal female and her four nearest neighbours (median in parentheses), for common eiders nesting on Simpson Lagoon and Mikkelsen Bay between 2000 and 2003. Dashes indicate that correlations were not observed for that year

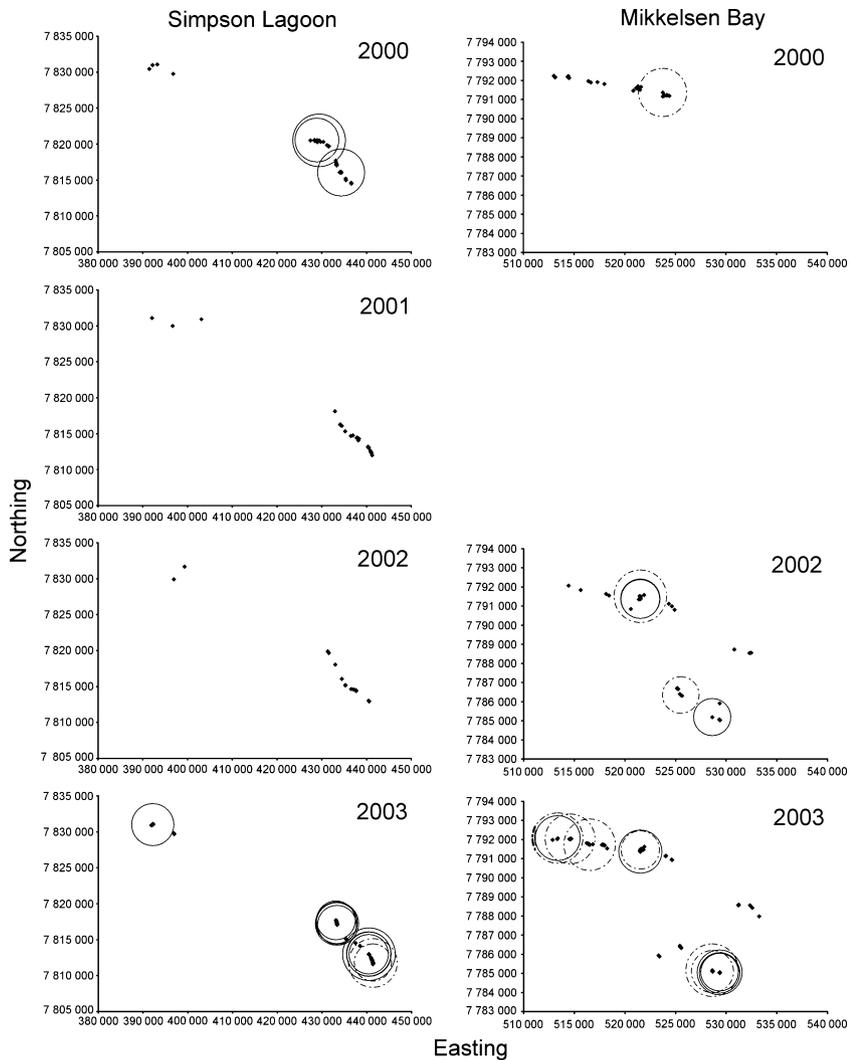|	2000	2001	2002	2003
Simpson Lagoon				
Positive *lr*	0.123–0.177	—	—	0.137–0.250
	8% ($n = 3/40$)	0% ($n = 0/31$)	0% ($n = 0/17$)	13% ($n = 9/69$)
Distance (m)	28–959	—	—	2–190
	(435)			(22)
Negative *lr*	—	—	—	−0.128 to −0.214
	0% ($n = 0/40$)	0% ($n = 0/31$)	0% ($n = 0/17$)	3% ($n = 2/69$)
Distance (m)	—	—	—	47–110
				(66)
Mikkelsen Bay				
Positive *lr*	—	No data	0.139–0.155	0.125–0.180
	0% ($n = 0/31$)		7% ($n = 3/43$)	6% ($n = 5/89$)
Distance (m)	—		0–777	0–63
			(6)	(18)
Negative *lr*	−0.164	No data	−0.134 to −0.271	−0.132 to −0.242
	3% ($n = 1/31$)		5% ($n = 2/43$)	7% ($n = 6/89$)
Distance (m)	200–412		1–447	0–78
	(300)		(98)	(38)

Fig. 2 Bubble plots of two-dimensional local spatial autocorrelation analysis of common eider nesting in Simpson Lagoon and Mikkelsen Bay between 2000 and 2003. Each plot shows the study area with squares indicating the nest location. Bubbles surround the nests with positive *lr* values (solid lines) and negative *lr* values (dashed lines) within the 5% tails of the permutated distribution, based on the association between a focal female and her four nearest neighbors. The size of the circle is proportional to the magnitude of *lr*.

nesting females in the Beaufort Sea, indicating that genetically related individuals nested closer to each other more frequently than expected by chance. However, this pattern varied among island groups. Low, albeit significant, *r* values were observed for Simpson Lagoon in 2000, 2002 and 2003, whereas females nesting in Mikkelsen Bay did not deviate from a random distribution. Microgeographic genetic structure was uncovered by the two-dimensional local spatial autocorrelation analysis in both Simpson Lagoon (2000 and 2003) and Mikkelsen Bay (2002 and 2003), suggesting that some females nested in association with more genetically related individuals. Positive associations occurred among a small component of the breeding population, with positive *lr* values observed at 0–13% and 0–7% of the comparisons for Simpson Lagoon and Mikkelsen Bay, respectively, across years. Negative autocorrelation values (*lr* values) were also

observed; however, negative autocorrelations are expected if discrete kin-based clusters are in close geographic proximity or related individuals are overdispersed (see next).

Mechanisms promoting genetic structure

There are several plausible scenarios for why fine-scale spatial genetic structure is present on some, but not all, of the islands within Simpson Lagoon and Mikkelsen Bay. First, limited suitable nesting areas may increase fine-scale genetic structure. Storms in the Arctic Ocean constantly augment and redistribute driftwood across the islands in our study site, and this driftwood provides essential nesting cover for common eiders (Noel *et al.* 2005). This process has led to large accumulations of driftwood on several islands where common eiders nest in colonies, whereas the remaining islands have far

less driftwood and eiders tend to nest solitarily. Constrained habitat availability may therefore be an important component in promoting genetic structuring of eider populations (Sonsthagen et al. 2009), as we found stronger evidence for microgeographic genetic structure at Simpson Lagoon, which has three islands with considerable amounts of driftwood (and three eider colonies), than Mikkelsen Bay, which has only one island with large amounts of driftwood and hence one colony (Flint et al. 2003; see Fig. 1). McKinnon et al. (2006) also found that female common eiders nesting in high densities had higher levels of relatedness among focal females and her nearest neighbours than those nesting in low-density areas.

Second, the presence of high female philopatry and breeding site fidelity may lead to population structure. Females of other common eider subspecies have been reported to be philopatric to natal sites (Swennen 1990), areas within colonies (Cooch 1965) and to exhibit fidelity to specific nest bowls among years (Bustnes & Erikstad 1993). Double et al. (2005) hypothesized that clusters of local positive genetic autocorrelation may exist because some individuals are more successful reproductively. In highly philopatric species, progeny from successful lineages might cluster around natal sites. Therefore, clusters of related females may result from extreme natal philopatry and breeding site fidelity coupled with high reproductive output.

Third, it is possible that females are actively selecting to nest near more genetically related individuals because of increased assistance from relatives during the breeding season (Lessells et al. 1994) or reduced aggression among kin (Greenwood et al. 1979; Waldman 1988; Eason & Hannon 1994). In contrast, females nesting in low densities, owing to lack of suitable habitat, may not have an advantage to nest in close association with kin because of presumably fewer interactions among neighbours. Female eiders might benefit from nesting near kin if they collectively defend nests and offspring from glaucous gulls (Larus hyperboreus), which nest colonially with eiders and frequently depredate eggs and chicks (Noel et al. 2005). Competition for favourable nest sites in high-density driftwood sites might also be reduced if females nest near relatives, especially as females that nest solitarily or on the edges of colonies frequently lose their nests to predators or have them inundated with water during storm surges (R. Lanctot & S. Sonsthagen, unpublished). Kin-based clusters have been postulated to occur among nesting female common eiders at La Perouse Bay in Hudson Bay (Schmutz et al. 1983), and female eiders breeding on Southampton Island, Hudson Bay, have been shown to form kin-based social groups when arriving at colonies, during nesting, and at colony departure (McKinnon et al. 2006).

Mechanisms diluting genetic structure

Perhaps equally important as knowing how genetic structure might develop is understanding why significant population genetic structure was not observed across all years and island groups. Lack of genetic structure may be a function of how and when common eiders recognize kin, differences in movement patterns among island groups or an artefact of sampling limitations. A variety of mechanisms enabling individuals to discriminate kin have been identified (Komdeur & Hatchwell 1999); one possible mechanism could be achieved indirectly though association (Hatchwell et al. 2001; Komdeur et al. 2004; Waldeck et al. 2008). If recognition among common eiders occurs while chicks are in brood amalgamations, it is possible that they form associations both with birds that are, and are not, genetically related to them (as brood amalgamations are made up of many broods that are frequently not kin-based; Öst et al. 2005). In the highly philopatric barnacle goose (Branta leucopsis), females preferentially nested in kin groups that were based on kin recognition rather than extreme natal philopatry; females that dispersed from their natal sites still nested in close geographic proximity to sisters that they were familiar with as brood mates (van der Jeugd et al. 2002). If recognition among female common eiders influences nest site selection, this may explain, in part, why only some females nest in kin groups. Therefore, some common eiders may nest in close proximity to brood mates, independently of their genetic relatedness, because of decreased competition and aggression among related or familiar neighbours (Greenwood et al. 1979; Waldman 1988; Eason & Hannon 1994).

Dispersal and gene flow between Mikkelsen Bay and Simpson Lagoon may explain, in part, differences in the degree of genetic structuring between island groups. Gene flow estimates, based on multiple marker classes, indicate that more individuals have dispersed from Mikkelsen Bay to Simpson Lagoon (Sonsthagen et al. 2009). Asymmetrical gene flow between island groups could generate a pattern of lower genetic structure in the 'source' (Mikkelsen Bay) population and clusters of more genetically related individuals in the 'receiving' (Simpson Lagoon) population. In the source population, females may be less able to nest in close proximity to kin because genetically related individuals may have dispersed to the other island group. In the 'receiving' population, females may nest in close proximity to kin, creating clusters of positive genetic autocorrelations. However, fewer clusters of positive autocorrelation may be observed owing to nest site competition created by the influx of 'source' population females.

Differences in genetic structure observed for Mikkelsen Bay between regional distance class sampling and local autocorrelation analyses may be attributable to the spatial scale at which analyses were conducted. For example, we may not have selected distance classes at intervals sufficient to detect structure among females (see 'Methods'). Local autocorrelation analyses, however, were conducted among focal females and her four nearest neighbours, irrespective of distance, and therefore, may be more biologically significant as analyses reflect genetic associations among females that are potentially interacting with each other during nesting. In addition, we were unable to sample all individuals that nested in our study site. In some cases, we may not have detected structure because what we considered as the female's nearest neighbours may not be the nearest individuals that a female interacted with during nest site selection.

Evolutionary impact of kin associations

It remains unknown whether there is an increase in the inclusive fitness of common eider females that nest in close proximity to relatives. Kin associations among individuals have been shown to be positively correlated with increased survivorship (Lambin & Krebs 1993), increased recruitment (MacColl *et al.* 2000; Støen *et al.* 2005; Zeyl *et al.* 2009), and increased reproductive success via conspecific brood parasitism (Andersson & Åhlund 2000). However, proximity of kin (or any other female) may also lead to competition among relatives for limited resources. Stochasticity in the temporal availability of resources probably influences the frequency of kin-based associations. In years when resources are scarce, kin-based unselfish behaviours may not occur presumably because of reduced fitness. Variability in habitat and food resources may explain why positive genetic associations among nesting eiders were not observed in all years. Therefore, these data illustrate the importance of sampling across years to determine the extent and strength of kin associations within a species.

Conclusion

A small but significant proportion of female common eiders nesting on the coastal barrier islands in the Beaufort Sea nested in close proximity to more genetically related individuals, creating clusters of nonrandom associations among individuals. Female-based kin associations among nesting eiders may reduce the overall genetic diversity on a given island, as islands are composed of family clusters rather than random assortment of individuals. Therefore, a larger geo-

graphic area may be needed to observe similar levels of genetic diversity relative to an island composed of a random distribution of nesting females. Finally, we cannot completely exclude the possibility that common eiders are nesting in close proximity to kin because of extreme natal (nest site) philopatry rather than preferentially nesting close to kin. However, driftwood nest sites are regularly disrupted and redistributed, and genetic associations among nesting females were still observed. A close association with habitat and not kin would thus be expected to randomize nearest neighbours across years. We therefore contend that the observed genetic structure may be more attributable to kin association than site fidelity, as kin associations are present *despite* habitat restructuring that alters nest sites from year to year. Nevertheless, an understanding of why fine-scale genetic structuring in common eiders exists can only be answered by collecting long-term demographic data coupled with molecular techniques. Such data will help determine whether the fine-scale genetic structure observed in Beaufort Sea common eiders is a result of extreme philopatry and breeding site fidelity, female kin association, brood amalgamation or some other mechanism not identified to date.

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