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Limited genetic differentiation among breeding, molting, and wintering groups of the threatened Steller's eider: the role of historic and contemporary factors

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Abstract

Due to declines in the Alaska breeding population, the Steller's eider (*Polysticta stelleri*) was listed as threatened in North America in 1997. Periodic non-breeding in Russia and Alaska has hampered field-based assessments of behavioral patterns critical to recovery plans, such as levels of breeding site fidelity and movements among three regional populations: Atlantic-Russia, Pacific-Russia and Alaska. Therefore, we analyzed samples from across the species range with seven nuclear microsatellite DNA loci and cytochrome *b* mitochondrial (mt)DNA sequence data to infer levels of interchange among sampling areas and patterns of site fidelity. Results demonstrated low levels of population differentiation within Atlantic and Pacific nesting areas, with higher levels observed between these regions, but only for mtDNA. Bayesian analysis of microsatellite data from wintering and molting birds showed no signs of sub-population structure, even though band-recovery data suggests multiple breeding areas are present. We observed higher estimates of *F*-statistics for female mtDNA data versus male data, suggesting female-biased natal site fidelity. Summary statistics for mtDNA were consistent with models of historic population expansion. Lack of spatial structure in Steller's eiders may result largely from insufficient time since historic population expansions for behaviors, such as natal site fidelity, to isolate breeding areas genetically. However, other behaviors such as the periodic non-breeding observed in Steller's eiders may also play a more contemporary role in genetic homogeneity, especially for microsatellite loci.

Introduction

Conservation and management plans often seek to delineate geographic or taxonomic units as distinct population segments (e.g., US Fish and Wildlife Service and National Marine Fisheries Service 1996) to effectively monitor status and trends. Defining such units relies upon a wide array of criteria and for migratory birds may include morphological or plumage characteristics, behavioral patterns quantified by banding or radio telemetry, or geographic separation of population segments during all or part of the annual cycle. Genetic markers are now widely used to quantify population divergence, identify or clarify management and taxonomic units, and offer insights into both historical and more contemporary processes involved in levels of divergence (e.g., Congdon et al. 2000; Scribner et al. 2003; Spruell et al. 2003; Gay et al. 2004). Yet for many migratory species, historical processes (e.g., Pleistocene ice movements) have substantially

influenced gene flow and contemporary geographic distribution (Hewitt 2000), resulting in disparities between behavioral patterns, such as site fidelity or philopatry, and range-wide genetic characteristics. Sex-biased behaviors, such as philopatry should lead to genetic divergence among populations provided that sufficient time has elapsed since dispersal from ancestral areas. However, a number of species considered to be highly philopatric, demonstrate little or no genetic structure across multiple sampling areas (e.g., Avise et al. 1992; Lanctot et al. 1999; Haavie et al. 2000; Roeder et al. 2001; Pearce et al. 2004). Such findings suggest that: (1) historical events may still dominate more contemporary behavioral patterns, (2) large effective population sizes may limit genetic drift, or (3) previously unrecognized gene flow exists. Thus, an accurate assessment of intrapopulation patterns, especially for delineating population segments for conservation, relies upon multiple markers (genetic and non-genetic) capable of probing both historic and contemporary time scales.

The Steller's eider (*Polysticta stelleri*) is the smallest of the four eider duck species and breeds in coastal tundra of arctic Russia and Alaska (Fredrickson 2001). Although the world population estimate is near 200,000 (Fredrickson 2001), only a small number breed in Alaska in two disjunct areas (Figure 1). One area is along the coastal fringe of Western Alaska on the Yukon-Kuskokwim Delta, where only eight nests have been found since 1994 (Kertell 1991; Flint and Herzog 1999). The second area is along the western North Slope of Alaska, primarily near Barrow, with an estimated population size between 176 and 2543 (Mallek 2002). Following breeding, birds undergo a flightless molt along the Alaska Peninsula and then winter throughout the Aleutian Islands and east to Cook Inlet (Fredrickson 2001). Prompted by an apparent contraction in the species' breeding range, reduced numbers of nesting birds, and geographic isolation from the more numerous Russian breeding population (Kertell 1991; Quakenbush et al. 2002), the Alaska population of Steller's eiders was listed as threatened under provisions of the US Endangered Species Act (Anonymous 1997).

Outside Alaska, two additional breeding populations are recognized (Solovieva et al. 1998; Fredrickson 2001). The Atlantic-Russian population is comprised of approximately 40,000 birds that nest in northern Norway and east to the Taimyr Peninsula, Russia and winter in the Barents and Baltic seas (Nygård et al. 1988, 1995). The Pacific-Russian population nests in scattered locations east of the Taimyr Peninsula and spends winters in the southern Bering Sea and northern Pacific Ocean (Figure 1). Aerial surveys indicate that the number of birds breeding in eastern Russia is approximately 129,000 (Hodges and Eldridge 2001). Each autumn, birds from Pacific and Alaskan breeding populations congregate in coastal lagoons of the Alaska Peninsula to undergo a flightless molt (Petersen 1981). Analysis of banding data from these molting flocks has provided the bulk of current knowledge about

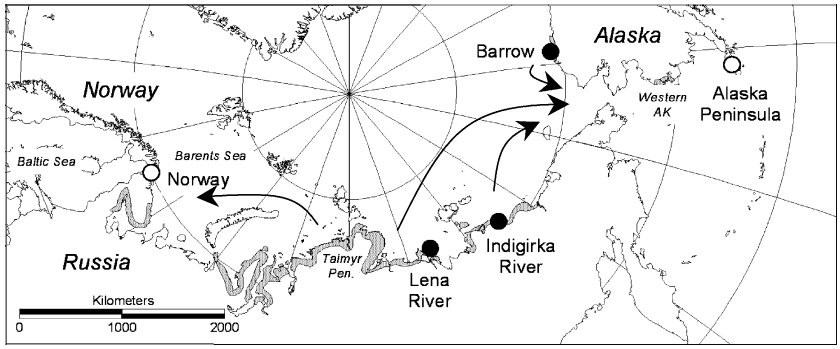

Figure 1. Nesting range (shaded area) and sampling locations of breeding (closed circles) and molting or wintering (open circles) areas of Steller's eiders. The Taimyr Peninsula is the hypothesized boundary between the Atlantic and Pacific breeding populations (Nygård et al. 1995). Arrows show post-breeding movements of birds as inferred from banding and radio telemetry studies (Dau et al. 2000; Petersen et al. 2005).

migratory movements and demographic ecology of the Pacific population (Jones 1965; Flint et al. 2000; Dau et al. 2000), while recent satellite telemetry work on wintering birds in Norway describes movements of the Atlantic population (Petersen et al. 2005). These studies confirm the general distributions of Atlantic and Pacific populations, demonstrate that these two regional populations overlap during the breeding season along the Taimyr Peninsula (Figure 1), and show that birds from multiple breeding sites are present in Norway during winter (Petersen et al. 2005) and along the Alaska Peninsula during molt (Dau et al. 2000).

Behavioral traits of many waterfowl species lead to various hypotheses about the location and degree of population genetic structure. First, both sexes may exhibit winter philopatry, possibly to reform breeding pairs since mate choice is thought to occur on the wintering grounds (reviewed by Robertson and Cooke 1999). Thus, philopatry to isolated wintering areas (after the flightless molt period), followed by pair formation, may lead to accrual of population genetic structure among birds of different wintering areas rather than among nesting areas. Second, most waterfowl species exhibit female-biased natal and breeding site fidelity (Anderson et al. 1992). Over sufficient periods of time, such behaviors should lead to genetic differentiation among breeding sites, especially for maternally inherited molecular markers such as mtDNA. In Steller's eiders, levels of molt site fidelity are high (Flint et al. 2000), but levels winter and nest site fidelity are poorly known and no information is available regarding natal philopatry (Fredrickson 2001). While only a very limited number of breeding females have been marked – 17 near Barrow (Quakenbush et al. 2004) and one on the Yukon Delta (Flint and Herzog 1999) – some of these banded birds have been resighted in subsequent years, suggesting some female fidelity. On the Yukon Delta, the inter-annual nest distance for one marked female was 123 meters (Flint and Herzog 1999).

We used seven nuclear microsatellite DNA loci and cytochrome *b* mtDNA sequence data to address the following objectives: (1) examine levels of population differentiation among breeding areas across Russia and in Alaska, (2) further examine breeding area differentiation by testing for admixture within wintering and molting samples, (3) evaluate levels of differentiation between islotated wintering areas in the Atlantic and Pacific regions, and (4) compare female and male mtDNA data to make inferences about levels of breeding site fidelity. Because the population genetic structure of many species has been influenced by Pleistocene environmental events, such as isolated refugia and subsequent deglaciation (Hewitt 2000), we also use analytical methods that examine the impact of historical demographic patterns on contemporary species distributions and population genetics.

Methods

Sampling

We analyzed feather, blood quill, tissue, and blood samples collected from five locations across the species' range in Alaska, Russia, and Norway (Figure 1) that included birds sampled during breeding (Lena R., Indigirka R., and Barrow), the flightless molt period (Alaska Peninsula), and winter (Norway). Feathers were collected from within nest bowls, whereas blood and feather quills came from trapped birds and tissue was from hunter shot specimens. The types and numbers of samples from each area are as follows: Norway (46 blood), Lena R. (25 blood), Indigirka R. (6 blood, 8 tissue, 8 feather), Barrow (16 blood, 37 feather), and the Alaska Peninsula (51 blood quill). Periodic non-breeding by Steller's eiders resulted in low sample sizes for some years. Therefore, we used samples collected in muliple years on the Lena and Indigirka rivers (4 years between 1988 and 1996) and at Barrow (6 years between 1993 and 2001) to increase sample sizes within each location. To reduce the chance of double-sampling individuals, we used mtDNA haplotype designations and multilocus microsatellite genotypes (see below) to identify matches across years. No matches were observed and based on microsatellite allele frequencies across these breeding areas, the probability of a random match was low (6.8×10^{-6} or 1 in 147,000 individuals). Low sample sizes within years limited the use of genotype matches across years as a method of quantifying levels of female breeding philopatry.

DNA extraction, amplification, and visualization

Extraction of DNA followed methods described elsewhere (Pearce et al. 2004). We used the polymerase chain reaction (PCR) and a Li-Cor 4200 DNA system (Lincoln, Nebraska) to screen 19 available waterfowl microsatellite loci for allele variation in Steller's eiders. Primers were tested across a gradient of annealing temperatures (50–60 °C) to optimize product yield. From this initial screening, eight loci yielded non-monomorphic allelic patterns: Sfiμ3 and Sfiμ4 (1B8 and 1D8, respectively; Fields and Scribner 1997), Alaμ1 (Fields and Scribner 1997), Sfiμ9, Sfiμ10, and Sfiμ11 (Libants et al. unpublished data, GenBank accession numbers AF180499–AF180501), and Bcaμ10 and Bcaμ11 (Buchholz et al. 1998). During initial screening of locus Aalμ1, we consistently observed a band within the allele range of Steller's eiders that we presumed was a co-amplified product and not a true allele. To test this possibility, we selected and sequenced eight Steller's eiders homozygous for this band. Only one of eight samples contained the expected repeat sequence pattern characteristic of microsatellites. The remaining samples contained flanking sequence identical to the Alaμ1 locus, but not the repeat. A similar pattern was also observed when individuals homozygous for a different "allele" were also sequenced. Based on these results, we excluded locus Alaμ1 from analyses and used a total of seven loci to generate individual genotypes for all Steller's eider samples. Genotypes at each locus were generated with a Li-Cor 4200 DNA system using methods described in Pearce et al. (2004). PCR amplification of microsatellite loci was conducted on a Stratagene 96 Robocycler (La Jolla, California). Reagents were heated to 94 °C for 2 min, then cycled 35–40 times through the following temperatures: 94 °C for 2 min, locus-specific annealing temperatures (47 °C for Sfiμ9 and Sfiμ11, 50 °C for Sfiμ3, Sfiμ4, and Bcaμ10, and 54 °C for Bcaμ1 and Bcaμ11) for 1 min, and 72 °C for 1 min.

We amplified and sequenced a 519-base pair fragment within the cytochrome *b* gene of mtDNA using PCR primers HCB652 (5′-ATTGAGCGTA GGATGGCA-3′) and LCB28 (5′-GTAGCGAAC ACATGCCGA-3′) for each of 192 Steller's eider samples. PCR primers were designed to specifically avoid nuclear pseudogenes observed in Steller's eiders (Pearce and Talbot, unpublished data) after an initial amplification with the universal primers of Sorenson et al. (1999) for cytochrome *b*. Methods of amplification and visualization are described in Pearce et al. (2004). Due to the common occurrence of nuclear pseudogenes in avian species (Lopez et al. 1994; Sorenson and Quinn 1998), we verified that amplified sequences were of mtDNA origin by comparing sequences obtained from heart, blood, and muscle samples from the same individual. PCR primers were redesigned until all tissues yield identical sequences. Sequences were also compared to homologous mtDNA regions for king eider (*Somateria spectabilis*; Pearce et al. 2004) and common eider (*S. mollissima*; Donne-Gousse et al. 2002) to ensure similarity.

Genetic variation and tests of disequilibrium and heterogeneity

For each microsatellite locus, we calculated allele frequencies, number of alleles per locus (A), observed (H_O), and expected (H_E) heterozygosity using GENEPOP Version 3.2a (Raymond and Rousset 1995). GENEPOP was also used to conduct exact probability tests for deviations from Hardy–Weinberg equilibrium in each sampling area using the method of Guo and Thompson (1992) and to test genotypic linkage disequilibrium for each pair of loci in each sampling area. Deviations from Hardy–Weinberg were also assessed using Wright's F_{IS} indices estimated in GENEPOP according to Weir and Cockerham (1984). These indices were also used for evidence of population admixture (Wahlund effect) in Norway and along the Alaska Peninsula where birds from multiple breeding areas were sampled (see also below). The programme ARLEQUIN Version 2.0 (Schneider et al. 2000) was used to estimate mtDNA haplotype diversity (*h*; Nei 1987), nucleotide diversity (π; Nei and Tajima 1983), and examine the selective neutrality of mtDNA by generating values for Tajima's D (Tajima 1989).

Population genetic differentiation

Genetic distance, based on variances in microsatellite allele frequencies (F_{ST}) was measured among breeding areas (Norway, Lena R., Indigirka R., and Barrow) and between Atlantic wintering (Norway)

and Pacific molting (Alaska Peninsula) areas with *F*-statistics as implemented in ARLEQUIN Version 2.0 (Schneider et al. 2000). We assume that the Norway birds breed within the Atlantic region based on satellite telemetry data of Petersen et al. (2005), which found that all marked birds ($n = 20$) remained west of the Lena River, Russia, throughout the breeding period. Overall significance levels for *F*-statistics were determined through 1000 permutations of individuals between populations. To further examine subpopulation structure, we examined nuclear microsatellite data from breeding, molting, and wintering samples using the Bayesian clustering method of Pritchard et al. (2000), implemented in the programme STRUCTURE Version 2.0 (Pritchard et al. 2000). Molting samples comprise birds from throughout the Pacific-Russian area, as well as small numbers of Alaska breeders (Dau et al. 2000). Wintering samples were obtained from birds captured within Varangerfjord of northern Norway, the primary wintering location for Steller's eiders in Europe (Nygård et al. 1995). We excluded population information from the analysis and assessed the likelihood that the entire data set was composed of individuals from $K = 1$ to 5 populations (using the admixture model), each of which may be characterized by a unique set of multilocus allele frequencies. Five independent runs for each value of K were conducted. The average log likelihood value across five runs was used to calculate Akaike's Information Criterion adjusted for sample size (AIC_c) and used AIC_c weights (w_i) to determine the strength of support for a particular value of K (Burnham and Anderson 1998). Results are based on 30,000 Markov Chain Monte Carlo iterations following a burn-in period of 30,000 iterations.

ARLEQUIN was used to generate estimates of intra-population variance in mtDNA haplotype frequency (Φ_{ST}) in two separate analyses: (1) among breeding areas (Norway, Lena R., Indigirka R., and Barrow) and (2) between Atlantic (Norway) and Pacific (Alaska Peninsula) populations. Estimates of Φ_{ST} were generated using molecular information according to the Tamura and Nei (1993) model of nucleotide evolution as identified by MODELTEST (Posada and Crandall 1998). Estimates of population differentiation (Φ_{ST}) were tested for statistical significance using 1000 randomizations of the data. Samples came predominantly from females, but male samples were obtained in all areas. Therefore, we compared estimates of Φ_{ST} from female and male mtDNA haplotypes to examine levels of female natal site fidelity. We predicted that levels of Φ_{ST} would be higher for female than male samples, under the waterfowl model of female-biased philopatry (Anderson et al. 1992), which should decrease the among-population genetic variance. Finally, we evaluated the mtDNA haplotype genealogy of all Steller's eider samples by generating an unrooted haplotype network using a statistical parsimony criterion (Templeton et al. 1992) in the programme TCS (version 1.13, Clement et al. 2000), which graphically displays the substitutional relationships among haplotypes.

Population demographics

Values of Tajima's D (Tajima 1989) and Fu's F_s (Fu 1997) were used to infer patterns of variation in population size because, they are sensitive to departures from demographic equilibrium (Aris-Brosou and Excoffier 1996; Fu 1997). Significantly large negative F_s values can be interpreted as evidence for population expansion. Evidence for population expansion was also examined by deriving the mismatch distribution of pairwise genetic differences in the programme DNASP Version 3.5 (Rozas and Rozas 1999). The distribution tends to be multimodal when populations are at equilibrium and uni-modal in cases of recent demographic expansion (Rogers and Harpending 1992). To graphically display the observed mismatch distribution compared to the expected distributions for populations in equilibrium and expansion, we used Roger's method of moments (Rogers 1995) as calculated in DNASP.

Results

Genetic variation

Allelic variation for the seven nuclear microsatellite loci ranged between three (Bcaμ10) to 16 (Sfiμ10) alleles (Table 1) with one to three common alleles that occurred in similar frequency across sampling areas. Significant deviations from Hardy–Weinberg proportions ($P < 0.05$) were detected for four of the 35 area-locus combinations and these were distributed across two (Bcaμ10 and Sfiμ9) of the

seven loci (Table 1). Wright's F_{IS} indices revealed four significantly positive values out of the 35 area-locus combinations (Table 1). Mean F_{IS} values across all loci were not significantly positive, except for the Indigirka River ($F_{IS} = 0.15$, $P = 0.001$), indicating an excess of homozygote genotypes in this area. Genotypic linkage disequilibrium exact tests showed significant values ($P < 0.05$) at 5 of 105 comparisons (per locus and per population). With 105 tests, 5 tests are expected to give significant deviations by chance alone at the 5% level. The fact that two tests involved the Sfiμ9 locus raises suspicions about the independence between this and other loci (see Discussion). Mean levels of F_{IS} were not greater in Norway or Alaska Peninsula samples than in breeding areas (Table 1), suggesting these samples did not comprise genetically distinct subpopulations.

Table 1. Summary statistics for seven microsatellite loci including: the number of individuals (n), the number of alleles (A), proportions of expected (H_E) and observed (H_O) heterozygosities for each sample, probability tests of Hardy–Weinberg Equlibrium (HWE; * $P < 0.05$, ns = not significant), the inbreeding coefficient (F_{IS}), and estimates of genetic distance (F_{ST})

Area	Locus							
	Sfiμ3	Sfiμ4	Sfiμ9	Sfiμ10	Sfiμ11	Bcaμ10	Bcaμ11	Mean over loci
Norway (wintering)[a]								
n	43	43	43	42	43	38	39	43
A	7	7	6	13	4	4	6	6.7
H_E	0.69	0.65	0.42	0.69	0.63	0.70	0.56	0.62
H_O	0.62	0.62	0.23	0.62	0.65	0.81	0.64	0.60
HWE deviation	ns	ns	*	ns	ns	ns	ns	ns
F_{IS}	0.09	0.04	0.45*	0.09	−0.02	−0.15	−0.05	0.03
Lena R. (breeding)								
n	20	25	25	24	25	25	23	25
A	7	6	5	9	4	3	8	5.7
H_E	0.69	0.52	0.29	0.67	0.47	0.65	0.57	0.55
H_O	0.75	0.56	0.32	0.70	0.48	0.52	0.56	0.55
HWE deviation	ns	ns	ns	ns	ns	*	ns	ns
F_{IS}	−0.08	−0.07	−0.10	−0.04	−0.01	0.20*	0.02	0.01
Indigirka R. (breeding)								
n	22	22	20	21	21	19	22	22
A	6	5	5	13	6	5	6	6.8
H_E	0.66	0.45	0.59	0.85	0.64	0.75	0.68	0.66
H_O	0.59	0.40	0.50	0.81	0.71	0.42	0.50	0.56
HWE deviation	ns	ns	ns	ns	ns	*	ns	*
F_{IS}	0.11	0.11	0.16	−0.05	−0.10	0.44*	0.27	0.15*
Barrow (breeding)								
N	49	47	36	48	49	47	47	49
A	8	6	6	14	4	5	7	7.1
H_E	0.67	0.63	0.50	0.76	0.54	0.69	0.53	0.61
H_O	0.69	0.55	0.38	0.72	0.53	0.55	0.61	0.58
HWE deviation	ns	ns	*	ns	ns	ns	ns	ns
F_{IS}	−0.02	0.12	0.20*	0.04	0.02	0.19	−0.15	0.05
Alaska Peninsula (molting)								
n	45	45	45	43	44	45	45	45
A	7	6	5	16	5	4	10	7.4
H_E	0.66	0.53	0.44	0.82	0.56	0.66	0.58	0.61
H_O	0.62	0.55	0.44	0.73	0.54	0.60	0.60	0.58
HWE deviation	ns	ns	ns	ns	ns	ns	ns	ns
F_{IS}	0.05	−0.03	−0.01	0.10	0.03	0.09	−0.02	0.04
F_{ST}	0.008*	0.006*	0.004	0.006	0.008	0.001	−0.002	0.005*

[a]Also a breeding area in population genetic analyses (see Methods).

MtDNA cytochrome *b* sequences across the 519-bp region were identical for different tissue types within the same individual and similar to homologous cytochrome *b* regions for king eider (Pearce et al. 2004) and common eider (Donne-Gousse et al. 2002), indicating that DNA fragments amplified in this study represent mtDNA sequences and not nuclear pseudogenes. Seventeen unique cytochrome *b* haplotypes (GenBank accession numbers AY351682 – AY351683, AY351685 – AY351696, AY737679 – AY737681) defined by 19 variable sites were identified among 192 Steller's eiders (Table 2). Variable sites included two non-synonymous second position transitions (Haplotypes Q and R) and 17 synonymous third position transitions. Several mtDNA haplotypes were shared among areas and levels of haplotype and nucleotide diversity were consistent across all areas (Table 3). The highest level of haplotype diversity was in the Alaska Peninsula sample (Table 3), an area with the highest concentration of molting Steller's eiders in the world. Statistical tests of the neutral mutation hypothesis for mtDNA were negative (Tajima's D = −1.09, Fu's F_s = −16.8), but only Fu's F_s was significantly different from zero ($P < 0.01$). The haplotype network (Figure 2) involved several common haplotypes from which other, less frequent sequence types radiated. Haplotype distribution around the network was not clustered according to the geographic locale of sampling and common haplotypes were observed within both Atlantic and Pacific areas.

Population genetic differentiation

We observed a statistically significant level of differentiation ($F_{ST} = 0.006$, $P = 0.02$) among the four breeding areas (Norway, Lena R., Indigirka R., Barrow) for nuclear microsatellite loci, although the overall estimate was very low, suggesting gene flow. Significant pairwise estimates among breeding areas suggested differentiation between Norway and Barrow and a possible boundary between Atlantic and Pacific populations, with the largest estimate occurring between the Lena and Indigirka rivers (Table 4). A significant difference was noted between Barrow and the Lena River, but not between Barrow and the Indigirka River. Using only female mtDNA data ($n = 99$, Table 3), we observed no significant difference in the spatial distribution of mtDNA haplotype frequencies among all breeding areas ($\Phi_{ST} = 0.054$, $P = 0.21$) or when Norway was excluded and only Pacific breeding areas were considered ($\Phi_{ST} = 0.114$, $P = 0.13$).

The low level of differentiation among some breeding areas for microsatellite loci, was not detected by programme STRUCTURE. The model likelihood of the microsatellite data for all breeding areas was at a maximum when *K* equaled a single population (Table 5), suggesting genetic homoge-

Table 2. Variable sites among 17 haplotypes, labeled A through U, observed for 519 bp of cytochrome *b* mtDNA in Steller's eiders (GenBank accession AY351682 – AY351683, AY351685 – AY351696, AY737679 – AY737681)

A	C	T	A	G	A	A	G	C	C	G	C	A	C	A	C	A	G	A	A
B	.	.	.	A	.	.	.	T	T	.	.	T	.	.	.	G	.	.	.
D	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	G	.	.	.
E	.	.	.	.	.	.	.	T	.	.	.	.	.	C	.	G	.	.	G
F	.	.	.	.	.	.	.	T	.	.	.	.	.	C	.	G	.	.	.
G	.	.	.	.	.	.	.	T	.	A	.	.	.	C	.	G	.	.	.
I	?	.	G	.	G	.	.	.	.	.	.	.	.	.	.	.	.	G	.
J	.	.	.	.	.	.	A	T	.	.	.	.	.	C	.	G	.	.	.
L	.	.	G	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M	.	.	.	.	.	.	.	T	.	.	.	.	.	C	.	G	A	.	.
N	.	.	.	.	.	.	.	T	.	.	A		.	C	.	G	.	.	.
O	.	.	.	A	.	.	.	T	.	.	.	T	.	.	.	G	.	.	.
P	.	C	.	A	.	.	.	T	.	.	.	T	.	.	.	G	.	.	.
Q	T	.	.	A	.	.	.	T	.	.	.	T		.	.	G	.	.	.
R	.	.	.	.	.	.	.	T	.	.	.	.	T	C	T	G	.	.	.
S	.	.	G	A	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.
U	.	.	.	.	.	G	.	T	.	.	.	.	.	.	.	G	.	.	.

Periods denote sequence similarity with haplotype A.

Table 3. Numbers and diversity indices of cytochrome *b* mtDNA haplotypes observed in 192 Steller's eiders across the five sampling areas

Haplotype	Norway (wintering)[a]	Lena R. (breeding)	Indigirka R. (breeding)	Barrow (breeding)	AK Peninsula (molting)
A	–	1	1	1	1
B	1	1	–	–	–
D	7	5	5	6	3
E	6	2	1	5	9
F	6	7	6	14	15
G	2	4	5	16	6
I	–	–	1	1	–
J	–	1	–	–	–
L	14	1	–	7	6
M	7	–	–	–	–
N	2	–	–	–	–
O	–	1	–	1	2
P	–	–	1	–	4
Q	–	–	–	–	4
R	–	–	–	–	1
S	–	–	–	1	–
U	1	–	–	–	–
Females	30	10	13	47	37
Males	16	13	7	6	14
Total	46	23	20	53	51
Haplotype diversity (h)	0.833	0.849	0.815	0.812	0.856
Nucleotide diversity (π)	0.005	0.003	0.003	0.004	0.005

[a]Also a breeding area in population genetic analyses (see Methods).

neity. In addition, mean levels of F_{IS} were not greater among Norway or Alaska Peninsula samples than in breeding areas (Table 1) and AIC_c values were the lowest with a model of one population ($K=1$). Thus, there is little evidence of subpopulation structuring among birds within the Norway wintering populations, or among birds within the Alaska Peninsula molting populations, although banding and telemetry data demonstrate that these areas are used by birds from multiple breeding areas. We did observe a significant level of differentiation between Norway and the Alaska Peninsula with mtDNA ($\Phi_{ST} = 0.078$, $P=0.02$) using only female samples, but not with the seven microsatellite loci examined through *F*-statistics ($F_{ST}=0.001$, $P=0.13$) or with the clustering method in programme STRUCTURE (AIC_c $w_i=1.0$ when $K=1$; Table 5).

Female fidelity

Estimates of Φ_{ST} were higher for female than male mtDNA samples among breeding areas and between Atlantic (Norway) and Pacific (Alaska Peninsula) populations. When only male mtDNA haplotypes were analyzed for these comparisons, estimates of population differentiation decreased significantly among breeding areas to $\Phi_{ST} = 0.033$ (one-tailed variance ratio test, $F_{100,42}=1.63$, $P< 0.05$) and to $\Phi_{ST} = 0.019$ between Atlantic and Pacific populations (one-tailed variance ratio test, $F_{67,30}=4.10$, $P< 0.01$), suggesting a greater level of dispersal by males than females.

Demographic inferences

We observed the mismatch distribution among pairs of haplotypes to be multi-modal (not shown), but this pattern was not significantly different from a uni-modal distribution (Harpending's raggedness index = 0.026, $P=0.63$). There was no difference between the observed data and a simulated model of sudden population growth (sum of squared deviations = 0.005, $P=0.55$). A uni-modal mismatch distribution can

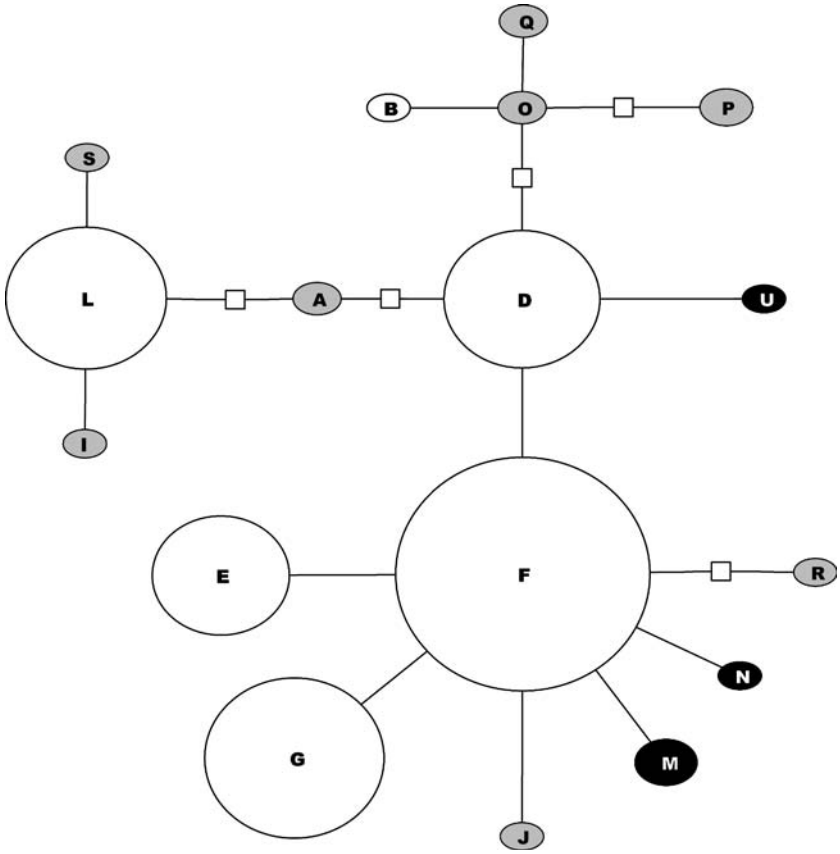

Figure 2. MtDNA haplotype network for sampling areas of Steller's eider. Circle size represents the frequency of each haplotype and connecting lines reflect a single mutation. Black circles = haplotypes observed only in Atlantic sampling area (Norway), gray circles = haplotypes observed only in Pacific sampling areas, and white circles = haplotypes observed in both Atlantic and Pacific sampling areas. White squares represent unsampled haplotypes.

Table 4. Pairwise estimates of *F*-statistics for Steller's eider breeding areas based seven nuclear microsatellite loci. Analysis includes both male and female samples

	Norway[a]	Lena R.	Indigirka R.
Lena R.	−0.001	–	–
Indigirka R.	0.001	0.007*	–
Barrow	0.002*	0.005*	−0.001

[a]Also a breeding area in population genetic analyses (see Methods).
* $P < 0.05$.

result from selection acting on mtDNA, but Tajima's D statistic was negative, (−1.09, $P = 0.15$), but only Fu's F_s was significantly different from zero ($F_s = -16.8$, $P < 0.01$). A negative Tajima's D and rejection of Fu's F_s for population stasis indicates an excess of recent mutations and thus population increase (Aris-Brosou and Excoffier 1996).

Discussion

We observed little evidence for genetic divergence among breeding of Steller's eiders using both traditional *F*-statistics and a Bayesian clustering method. Low but significant pairwise estimates among breeding areas suggested differentiation between Norway and Barrow and a possible boundary between Atlantic and Pacific populations. While a significant difference was noted between Barrow and the Lena River, the estimate between Barrow and the Indigirka River was lower and non-significant. These subtle patterns of variation between Atlantic and Pacific breeding areas were not detected using the Bayesian clustering method (Table 5). Additional evidence for genetic homogeneity among breeding areas is the similar levels of F_{IS} within wintering (Norway) and molting (Alaska Peninsula) samples (i.e., lack of a

Table 5. Competing models of hypothetical population structure among sampling areas of Steller's eiders using seven nuclear microsatellite loci. Akaike's Information Criterion (AIC_c) values and model selection statistics are based on log-likelihood (log*P*) estimates averaged over five runs using programme STRUCTURE (Pritchard et al. 2000). Each model consists of a different number of hypothetical populations (*K*)

K	log*P*	AIC_c	Δ AIC_c[a]	AIC_c w_i[b]
Breeding (Norway, Lena R., Indigirka R., Barrow)				
1	−2515.2	5032.5	0.0	1.0
2	−2550.2	5104.6	72.1	0.0
3	−2611.8	5229.9	197.3	0.0
4	−2654.3	5317.0	284.4	0.0
5	−3012.8	6036.0	1003.5	0.0
Wintering (Norway)				
1	−760.7	1523.6	0.0	1.0
2	−771.4	1547.2	23.6	0.0
4	−770.9	1550.9	27.3	0.0
5	−771.7	1555.0	31.4	0.0
3	−777.2	1561.0	37.4	0.0
Molting (Alaska Peninsula)				
1	−831.5	1665.0	0.0	0.92
5	−829.7	1671.6	5.9	0.04
4	−831.7	1672.4	7.3	0.02
2	−840.9	1686.1	21.0	0.0
3	−841.0	1688.5	23.4	0.0
Atlantic vs. Pacific (Norway, Alaska Peninsula)				
1	−1605.0	3210.1	0.0	1.0
3	−1618.2	3236.5	30.6	0.0
2	−1620.4	3240.9	32.8	0.0
4	−1691.3	3382.6	178.8	0.0
5	−1692.3	3384.7	183.2	0.0

[a]Defined as the difference in −2log(Likelihood) of the current model and the saturated model (Burnham and Anderson 1998). Models $> \Delta AIC_c = 2.0$ from the top suggest that the model is not well supported by the data.
[b]AIC_c weight or approximate probability that model *i* is the best model (Burnham and Anderson 1998).

Wahlund effect) and the fact that the lowest AIC_c scores for wintering and molting birds were with models of a single population rather than a multi-population admixture (Table 5). Therefore, even though banding (Dau et al. 2000) and radio telemetry (Petersen et al. 2005) data have shown that birds from multiple breeding areas are represented in molting and wintering groups, these areas cannot be distinguished with the genetic markers used here.

The increase in the estimate of Φ_{ST} when mtDNA sequences from males were excluded suggests that gene flow is predominantly male-mediated. Male-biased dispersal and female-biased fidelity are common among waterfowl species (Anderson et al. 1992), but very little is known about the levels of these behaviors in Steller's eiders. Additionally, periodic non-breeding has been observed in Steller's eiders near Barrow (Quakenbush et al. 2004) and on the Lena River (Solovieva 1999) across multiple years. For example, Steller's eiders have not nested near Barrow since 2000, although variable numbers of birds are present during each breeding season (N. Rojek, U.S. Fish and Wildlife Service, pers. comm.). Whether birds forgo nesting in non-breeding years or attempt to breed elsewhere remains unknown, but the periodic non-breeding may lead to higher levels of dispersal by both males and females in some years (see below).

We observed a significant level of divergence between Norway and the Alaska Peninsula, but only for mtDNA. We also observed singleton and multiples of unique mtDNA haplotypes in these areas that suggest additional variation across the range of the species. The lower Φ_{ST} among breeding areas for mtDNA does not necessarily suggest that Steller's eider exhibit higher levels of site fidelity to

wintering rather than breeding areas. Although Steller's eiders along the Alaska Peninsula demonstrate high annual fidelity to certain lagoon areas (Flint et al. 2000), molting birds are still in basic, non-breeding plumage and have not yet formed mating pairs. This is important, since it is both fidelity and pairing among the same group of wintering birds that should eventually lead substructuring (see Robertson and Cooke 1999). It thus seems unlikely that mate choice would take place during molt when birds are in non-breeding plumage. Additionally, our Norway sample comes from a single area, rather than multiple wintering sites, which would be a more effective method for evaluating sea duck population structure during winter. Pearce et al. (2004) found no evidence for spatial genetic structure among two Pacific and one Atlantic sampling areas for king eiders. However, the highly migratory nature of king eiders may contribute to the lack of structure observed (see Mehl et al. 2004). The hypothesis of winter area population structure deserves further examination because, anthropogenic impacts to sea duck populations are increasing on the wintering grounds (Flint et al. 1999; Lanctot et al. 1999; Camphuysen et al. 2002).

Heterozygote deficiency

We observed significant levels of the inbreeding coefficient, F_{IS}, due to greater than expected frequencies of homozygotes at locus Sfiμ9 in Norway and Barrow at locus Bcaμ10 on the Lena and Indigirka rivers (Table 1). Significant levels of heterozygote deficit have been reported in several avian genetic studies involving microsatellite loci (Nesje et al. 2000; Eggert et al. 2004; Gay et al. 2004; Tiedemann et al. 2004) and can result from the presence of non-amplifying alleles (null alleles), allelic dropout, a Wahlund effect (Wahlund 1928), or from processes such as inbreeding and selection. Null alleles arise when one allele is not amplified due to mutations in PCR primer sequences, whereas allelic dropout occurs when sample quality or laboratory methods influence the scoring of genotypes. A large proportion of samples that do not produce amplified product during PCR is one indication of null alleles, but generally null alleles affect F_{IS} values only at the affected locus (Callen et al. 1993) and should not influence all loci in a multi-locus genotype. Several lines of evidence argue against null alleles at the Sfiμ9 locus in this study. We observed a relatively continuous distribution of allele sizes across all areas (not shown) and there was no indication of heterozygote deficit across all sampling areas or across loci (Table 1). For the same reason, inbreeding and selection seem unlikely causes of heterozygote deficiency in Steller's eider, particularly given the large estimated census sizes for the Atlantic and Pacific populations and the highly migratory nature of the species. A Wahlund effect, which occurs when two or more subpopulations are inadvertently sampled as a single population, also appears unlikely because of the general lack of population divergence among sampling areas and lack of evidence for admixture using programme STRUCTURE.

Across all samples, the proportion of missing data was highest for the Sfiμ9 locus (13 of 184), but this occurred only among Barrow samples, many of which contained low amounts of DNA obtained from nest feathers. Sefc et al. (2003) found that low amounts of DNA obtained from one to two feathers can lead to allele dropout and incorrect genotypes for microsatellite loci, especially when allele sizes are greater than 200 base pairs. However, alleles at the Sfiμ9 locus ranged from 148 to 162 and two to three additional amplifications of 11 homozygous individuals from Barrow produced identical genotypes for this locus. Thus, we are unable to conclusively determine origins of heterozygote deficiency at Sfiμ9. The exclusion of Sfiμ9 from analyses did not alter estimates of population divergence or their statistical significance, either across breeding areas ($F_{ST} = 0.005$) or in pairwise comparisons (not shown). For Bcaμ10, we suspect that low sample size at the Lena and Indigirka rivers contributes to the significant estimates of F_{IS} for this locus.

Historic determinants of population structure

Demographic analyses of mtDNA cytochrome *b* sequences suggest that one or more historic population expansions, following deglaciation of the arctic, may play a major role in shaping contemporary genetic characteristics of Steller's eiders. The mtDNA haplotype network (Figure 2) is star-like, the mismatch distribution is generally uni-modal and similar to a simulated model of population expansion, both Fu's F_s and Tajima's D are negative, and consistently high and low

levels of haplotype (h) and nucleotide (π) diversity, respectively are observed across the range of the species. High h and low π are indicative of population growth and expected if time was sufficient for recovery of haplotype variation via mutation, but too short for the accumulation of large sequence differences (Avise 2000). All of these indices are expected under a scenario of historic demographic expansion (Aris-Brosou and Excoffier 1996; Fu 1997; Avise 2000). Several recent studies of avian species have also attributed the lack of intra-specific phylogeographic divergence to recent population growth following Pleistocene deglaciation, these species include the great tit (*Parus major*; Kvist et al. 1999), marbled murrelet (*Brachyrampus marmoratus*; Congdon et al. 2000), lesser black-backed gull (*Larus fuscus*; Liebers and Helbig 2002), and the great-spotted woodpecker (*Dendrocopus major*; Zink et al. 2002).

The shallow level of population genetic structure observed in Steller's eiders has also been documented in other sexually dimorphic waterfowl species. Pearce et al. (2004) observed genetic homogeneity across much of the holarctic distribution of the king eider with both nuclear microsatellite loci and mtDNA. Similar patterns are also observed in long-tailed ducks (*Clangula hyemalis*) sampled from Alaska, Canada, and Russia (Talbot and Gust, unpublished data) and in the Northern pintail (*Anas acuta*) across much of North America (Cronin et al. 1996). However, Scribner et al. (2001) observed higher levels of differentiation among isolated breeding areas of spectacled eiders (*S. fischeri*) for mtDNA. To date, intra-specific population genetic structure has only been observed in waterfowl species with one or more of the following traits: sexual monomorphism (McCracken et al. 2001); intra-specific variation in vocalizations (McCracken and Sheldon 1997) or morphology (Pearce et al. 2000; Gay et al. 2004; Tiedemann et al. 2004); and seasonal monogamy, with both parents rearing young after hatch (Scribner et al. 2003). Snow geese (*Chen caerulescens*; Avise et al. 1992) are, however, an exception to this general pattern.

Conservation implications and additional research needs

The US Endangered Species Act dictates that populations or groups of populations are protected as "distinct population segments", based on the "discreteness of the population segment in relation to the remainder of the species to which it belongs" (US Fish and Wildlife Service and National Marine Fisheries Service 1996). Steller's eiders in Alaska are discrete geographically from other breeding populations in their range, but little evidence for genetic differentiation between Alaska and Russian breeding areas was observed in this study. We find evidence for female natal site fidelity through comparisons of male and female mtDNA haplotype variance among sampling areas. However, these levels do not appear to be sufficient to cause genetic differentiation between Alaskan and Russian areas or insufficient time has elapsed since de-glaciation and colonization of the current breeding range. Additional sampling throughout the Russian breeding range of Steller's eiders would help to clarify any boundary between Atlantic and Pacific populations along the Taimyr Peninsula of Russia. However, this division may be an emerging pattern and ephemeral depending upon arctic breeding conditions that dictate whether Steller's eiders nest in a given year. The periodic non-nesting of Steller's eiders deserves further investigation so as to identify possible factors involved. For example, the densities and distributions of waterbird species, including the northern pintail, tend to shift in response to water availability in some regions of North America (Niemuth and Solberg 2003) and these movements may influence population genetic structure (Cronin et al. 1996). For Steller's eiders, internal physiological constraints, external environmental factors, and fluctuating densities of brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*) and associated avian predators are currently hypothesized to explain the annual breeding biology of Steller's eiders (Kertell 1991; Quakenbush et al. 2004), yet these factors remain poorly quantified.

Genetic data are not the sole measure for discreteness and offer only one perspective on population divergence. In their examination of the lesser snow goose, a waterfowl species that exhibits high female breeding site fidelity, Avise et al. (1992) demonstrated how the historical perspective of mtDNA can mask contemporary behavioral patterns. Although more recent periods of gene flow can be inferred with nuclear microsatellite data, the bi-parental inheritance pattern of these

loci can reduce the power to detect population structure in the presence of high levels of male-biased dispersal (e.g., Scribner et al. 2001). We agree with the conclusion of Avise et al. (1992) that both historic and contemporary perspectives from genetic and non-genetic markers are needed for a complete understanding of current population patterns, especially when levels of movement among different areas influence the delineation of conservation units.

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References

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

Anonymous (1997) Endangered and threatened wildlife and plants: threatened status for the Alaska breeding population of the Steller's eider. *US Federal Register*, **62**(112) 31748–31757.

Aris-Brosou S, Excoffier L (1996) The impact of population expansion and mutation rate heterogeneity on DNA sequence polymorphism. *Mol. Biol. Evol.*, **13**, 494–504.

Avise JC, Alisauskas RT, Nelson WS, Ankney CD (1992) Matriarchal population genetic structure in an avian species with female natal philopatry. *Evolution*, **46**, 1804–1096.

Avise JC (2000) *Phylogeography: The History and Formation of Species*, Harvard University Press, Cambridge, Massachusetts.

Buchholz WG, Pearce JM, Pierson BJ, Scribner KT (1998) Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): characterization of a sex-linked (Z-specific) and 14 bi-parentally inherited loci. *J. Anim. Genet.*, **29**, 323–325.

Burnham KP, Anderson DR (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*, Springer-Verlag, New York, New York.

Callen DF, Thompson AD, Shen Y, Phillips HA, Richards RI, Mulley JC, Sutherland GR (1993) Incidence and origin of "null" alleles in the (AC)n microsatellite markers. *Am. J. Hum. Genet.*, **52**, 922–927.

Camphuysen CJ, Berrevoets CM, Cremers HJ, Dekinga A, Dekker R, Ens BJ, van der Have TM, Kats RK, Kuiken T, Leopold MF (2002) Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biol. Conserv.*, **106**, 303–317.

Clement M, Posada D, Crandall D (2000) TCS: a computer programme to estimate gene genealogies. *Mol. Ecol.*,, **9**, 1657.

Congdon BC, Piatt JH, Martin K, Friesen VL (2000) Mechanisms of population differentiation in marbled murrelets: historical versus contemporary processes. *Evolution*, **54**, 974–986.

Cronin MA, Grand JB, Esler D, Derksen DV, Scribner KT (1996) Breeding populations of northern pintails have similar mitochondrial DNA. *Can. J. Zool.*, **74**, 992–999.

Dau CP, Flint PL, Petersen MR (2000) Distribution of recoveries of Steller's eiders banded on the lower Alaska Peninsula, Alaska. *J. Field Ornith.*, **71**, 541–548.

Donne-Gousse C, Laudet V, Hanni C (2002) A molecular phylogeny of Anseriformes based on mitochondrial DNA analysis. *Mol. Phylogen. Evol.*, **23**, 339–356.

Eggert LS, Mundy NI, Woodruff DS (2004) Population structure of loggerhead shrikes in the California Channel Islands. *Mol. Ecol.*, **13**, 2121–2133.

Fields R, Scribner KT (1997) Isolation and characterization of novel waterfowl microsatellite loci, cross-species comparisons and research applications. *Mol. Ecol.*, **6**, 160–164.

Flint PL, Herzog MP (1999) Breeding of Steller's eiders, *Polysticta stelleri*, on the Yukon-Kuskokwim Delta, Alaska. *Can. Field Nat.*, **113**, 306–308.

Flint PL, Fowler AC, Rockwell RF (1999) Modeling bird mortality associated with the M/V Citrus oil spill off St. Paul Island, Alaska. *Ecol. Model.*, **117**, 261–267.

Flint PL, Petersen MR, Dau CP, Hines JE, Nichols JD (2000) Annual survival and site fidelity of Steller's eiders molting along the Alaska Peninsula. *J. Wild. Manag.*, **64**, 261–268.

Fredrickson LH (2001) Steller's eider (*Polysticta stelleri*) In: The Birds of North America, No. 571. (eds. Poole A, Gill F), The Academy of Natural Sciences, Philadelphia Pennsylvania.

Fu YX (1997) Statistical tests on neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, **147**, 915–925.

Gay L, DefosDu Ray P, Mondain-Monval JY, Crochet PA (2004) Phylogeography of a game species: the red-crested

pochard (*Netta rufina*) and consequences for its management. *Mol. Ecol.*, **13**, 1035–1045.
Guo SW, Thompson EA (1992) Performing the exact test of Hardy–Weinberg proportion for multiple alleles. *Biometrics*, **48**, 361–372.
Haavie J, Saetre GP, Moum T (2000) Discrepancies in population differentiation at microsatellites, mitochondrial DNA and plumage colour in the pied flycatcher – inferring evolutionary processes. *Mol. Ecol.*, **9**, 1137–1148.
Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.
Hodges JI, Eldridge WD (2001) Aerial surveys of eiders and other waterbirds on the eastern Arctic coast of Russia. *Wildfowl*, **52**, 127–142.
Jones RD (1965) Returns from Steller's eiders banded at Izembek Bay, Alaska. *The Wildfowl Trust*, **16**, 83–85.
Kertell K (1991) Disappearance of the Steller's eider from the Yukon-Kuskokwim Delta, Alaska. *Arctic*, **44**, 177–187.
Kvist L, Ruokonen M, Lumme J, Orell M (1999) The colonization history and present-day population structure of the European great tit (*Parus major major*). *Heredity*, **82**, 495–502.
Lanctot RB, Goatcher B, Scribner KT, Talbot S, Pierson B, Esler D, Zwiefelhofer D (1999) Harlequin duck recovery from the Exxon Valdez oil spill: A population genetics perspective. *Auk*, **116**, 781–791.
Liebers D, Helbig AJ (2002) Phylogeography and colonization history of lesser black-backed gulls (*Larus fuscus*) as revealed by mtDNA sequences. *J. Evol. Bio.*, **15**, 1021–1033.
Lopez JV, Yuhki N, Masuda R, Modi M, O'Brien SJ (1994) Numt, a recent transfer and tandem amplification of mitochondrial DNA to the nuclear genome of the domestic cat. *J. Mol. Evol.*, **39**, 174–190.
Mallek EJ (2002) Aerial breeding pair surveys of the Arctic Coastal Plain of Alaska, 2001. Unpubl. report. US Fish and Wildlife Service, Fairbanks, Alaska.
McCracken KG, Sheldon FH (1997) Avian vocalizations and phylogenetic signal. *Proc. Natl. Acad. Sci. USA*, **94**, 3833–3836.
McCracken KG, Johnson WP, Sheldon FH (2001) Molecular population genetics, phylogeography, and conservation biology of the mottled duck (*Anas fulvigula*). *Conserv. Genet.*, **2**, 87–102.
Mehl KR, Alisauskas RT, Hobson KA, Kellett DK (2004) To winter east or west? Heterogeneity in winter philopatry in a central-arctic population of King Eiders. *Condor*, **106**, 241–251.
Nei M (1987) *Molecular Evolutionary Genetics*, Columbia University Press, New York, New York.
Nei M, Tajima F (1983) Maximum likelihood estimation of the number of nucleotide substitutions from restriction site data. *Genetics*, **105**, 207–217.
Nesje M, Røed KH, Lifjeld JT, Lindberg P, Steen OF (2000) Genetic relationships in the peregrine falcon (*Falco peregrinus*) analyzed by microsatellite DNA markers. *Mol. Ecol.*, **9**, 53–60.
Niemuth ND, Solberg JW (2003) Response of waterbirds to number of wetlands in the Prairie Pothole region of North Dakota, USA. *Waterbirds*, **26**, 233–238.
Nygård TB, Larsen BH, Follestad A, Strann KB (1988) Numbers and distribution of wintering waterfowl in Norway. *Wildfowl*, **39**, 164–176.
Nygård TB, Frantzen B, Svazas S (1995) Steller's eiders *Polysticta stelleri* wintering in Europe: numbers, distribution, and origin. *Wildfowl*, **46**, 140–155.
Pearce JM, Pierson BJ, Talbot SL, Derksen DV, Kraege D, Scribner KT (2000) A genetic evaluation of morphology used to identify harvested Canada geese. *J. Wild. Manag.*, **64**, 863–874.
Pearce JM, Talbot SL, Pierson BJ, Scribner KT, Dickson DL, Mosbech A (2004) Lack of spatial genetic structure among nesting and wintering king eiders. *Condor*, **106**, 229–240.
Petersen MR (1981) Populations, feeding ecology and molt of Steller's eiders. *Condor*, **83**, 256–262.
Petersen MR, Bustnes JO, Systad GH (2005) Distribution patterns of Steller's eiders *Polysticta stelleri* in northern Norway and northwest Russia. J. Avian Bio., **37**, In Press.
Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.
Pritchard JK, Stephens M, Donnelly PJ (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.
Quakenbush LT, Day RH, Anderson BA, Pitelka FA, McCaffery BJ (2002) Historical and present breeding season distribution of Steller's eiders in Alaska. *West. Birds*, **33**, 99–120.
Quakenbush LT, Suydam R, Obritschkewitsch T, Deering M (2004) Breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991–1999. *Arctic*, **57**, 166–182.
Raymond M, Rousset F (1995) GENEPOP Version 3.2a: Population genetics software for exact tests and ecumenicism. *J. Hered.*, **86**, 248–249.
Robertson GJ, Cooke F (1999) Winter philopatry in migratory waterfowl. *Auk*, **116**, 20–34.
Roeder AD, Marshall RK, Mitchelson AJ, Visagathilagar T, Ritchie PA, Love DR, Pakai TJ, McPartlan HC, Murray ND, Robinson NA, Kerry KR, Lambert DM (2001) Gene flow on the ice: genetic differentiation among Adelie penguin colonies around Antarctica. *Mol. Ecol.*, **10**, 1645–1656.
Rogers AR (1995) Genetic evidence for a Pleistocene population explosion. *Evolution*, **49**, 608–615.
Rogers AA, Harpending HC (1992) Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol. Evol.*, **9**, 552–569.
Rozas J, Rozas R (1999) DNASP, version 3.1. An integrated programme for molecular population genetics and molecular evolution analysis. *Bioinformatics*, **15**, 174–175.
Schneider S, Roessli D, Excoffier L (2000) *Arlequin Version 2.0: A Software for Population Genetics Data Analysis*, Genetics and Biometry Laboratory, Department of Anthropology, University of Geneva, Switzerland.
Scribner KT, Petersen MR, Fields RL, Talbot SL, Pearce JM, Chesser RK (2001) Sex-biased gene flow in spectacled eiders (Anatidae): inferences from molecular markers with contrasting modes of inheritance. *Evolution*, **55**, 2105–2115.
Scribner KT, Talbot SL, Pearce JM, Pierson BJ, Bollinger KS, Derksen DV (2003) Phylogeography of Canada geese (*Branta canadensis*) in Western North America. *Auk*, **120**, 889–907.

Sefc KM, Payne RB, Sorenson MD (2003) Microsatellite amplification from museum feather samples: effects of fragment size and template concentration on genotyping errors. *Auk*, **120**, 982–989.

Solovieva DV, Phil S, Fox AD, Bustnes JO (1998) Steller's eider (*Polysticta stelleri*). In: *The Birds of the Western Palearctic* (eds. Perrins CM, Snow DW). Oxford University Press.

Solovieva DV (1999) Biology and Bioenergetics of the Steller's Eide (*Polysticta stelleri*). Ph.D. dissertation, Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia.

Sorenson MD, Quinn TW (1998) Numts: a challenge for avian systematics and population biology. *Auk*, **115**, 214–221.

Sorenson MD, Ast JC, Dimcheff DE, Yuri T, Mindell DP (1999) Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Mol. Phylogen. Evol.*, **12**, 105–114.

Spruell P, Hemmingsen AR, Howell PJ, Kanada N, Allendorf FW (2003) Conservation genetics of bull trout: Geographic distribution of variation at microsatellite loci. *Conserv. Genet.*, **4**, 17–29.

Tajima F (1989) The amount of DNA polymorphism maintained in a finite population when the neutral mutation rate varies among sites. *Genetics*, **143**, 1457–1465.

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.*, **10**, 512–526.

Templeton AR, Crandall KA, Sing CF (1992) A cladistic analysis of phenotypic association with haplotypes inferred from restriction endonuclease mapping. III. Cladogram estimation. *Genetics*, **132**, 619–633.

Tiedemann R, Paulus KB, Scheer M, Von Kistowski KG, Skirnisson K, Bloch D, Dam M (2004) Mitochondrial DNA and microsatellite variation in the eider duck (*Somateria mollissima*) indicate stepwise postglacial colonization of Europe and limited current long-distance dispersal. *Mol. Ecol.*, **13**, 1481–1494.

US Fish and Wildlife Service and National Marine Fisheries Service (1996) Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. *US Federal Register*, **61**, 4721–4725.

Wahlund S (1928) Composition of populations from the perspective of the theory of heredity. *Hereditas*, **11**, 65–105.

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

Zink RM, Drovetski SV, Rohwer S (2002) Phylogeographic patterns in the great spotted woodpecker *Dendrocopos major* across Eurasia. *J. Avian Biol.*, **33**, 175–178.