TO WINTER EAST OR WEST? HETEROGENEITY IN WINTER PHILOPATRY IN A CENTRAL-ARCTIC POPULATION OF KING EIDERS

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Abstract. We used banding data from King Eiders (*Somateria spectabilis*) at Karrak Lake, Nunavut, Canada, during 2001 and 2002 in conjunction with analysis of naturally occurring stable isotopes (^{13}C, ^{15}N) from feathers to connect winter and breeding areas of individuals. We also investigated the occurrence of winter philopatry among nesting females, and examined cross-seasonal effects of wintering area on subsequent breeding. Isotopic data suggested that 66–73% of this central-arctic breeding population wintered to the west (i.e., Bering Sea and North Pacific) and the remaining 24–37% wintered to the east (i.e., west Greenland, northwest Atlantic). In contrast, limited band recoveries from hunter-killed King Eiders marked at the same breeding location suggested that about 56% of individuals were shot in eastern wintering areas. These differences likely reflect stronger hunting pressures along the coast of Greenland, which result in more band recoveries for this area. Our results suggest that female King Eiders were not strongly philopatric to wintering areas among years. Individuals that wintered in western seas initiated nests 1.9 days earlier and had slightly larger clutches during early initiation relative to females that wintered in the east. Nest parasitism appeared to be biased toward earlier nesters, many of which wintered in the west. Female condition during incubation did not vary by wintering area. Our results have important implications for gene flow and for potentially associating wintering-area conditions with overall demography and individual fitness of King Eiders.

Key words: carbon-13, King Eider, nitrogen-15, Somateria spectabilis*, stable isotopes, winter philopatry.*

¿Pasar el Invierno en el Este o en el Oeste? Heterogeneidad en la Filopatría al Sitio de Invernada en una Población de *Somateria spectabilis* del Ártico Central

Resumen. Para conectar las áreas de invernada con las de reproducción en la especie *Somateria spectabilis*, utilizamos datos de aves anilladas durante 2001 y 2002 en Karrak Lake, Nunavut, Canadá, junto con análisis de isotópos estables que se encuentran en la naturaleza y en las plumas (^{13}C, ^{15}N). También investigamos la existencia de filopatría al sitio de invernada entre hembras nidificantes, y examinamos los efectos del área de invernada sobre la reproducción subsiguiente. Los datos isotópicos sugirieron que el 66–73% de los individuos de esta población que nidifica en el Ártico central pasa el invierno al oeste (i.e., Mar de Bering, Pacífico Norte) y que el 24–37% restante lo hace al este (i.e., oeste de Groenlandia, noroeste del Atlántico). En contraste, los pocos anillos puestos en la misma localidad reproductiva que fueron recobrados por cazadores, mostraron que alrededor del 56% de los individuos fueron cazados en áreas de invernada ubicadas al este. Estas diferencias probablemente reflejan que las presiones de cacería son más fuertes a lo largo de la costa de Groenlandia, lo que conlleva a que se recobren más anillos en esta área. Nuestros resultados sugieren que las hembras de *S. spectabilis* no son fuertemente filopátricas a sus sitios de invernada entre años. Los individuos que invernaron en los mares del oeste iniciaron sus nidos 1.9 días más temprano y tuvieron nidadas ligeramente más grandes durante la etapa temprana de iniciación en comparación con las hembras que invernaron al este. El parasitismo de nidos pareció estar sesgado hacia las aves que nidificaron temprano, muchas de las cuales invernaron en el oeste. La condición de las hembras durante la incubación no

varió entre áreas de invernada. Nuestros resultados tienen implicaciones importantes en términos de flujo génico y potencialmente para asociar las condiciones de las áreas de invernada con la demografía en general y con la adecuación biológica de los individuos de esta especie.

INTRODUCTION

Extent of dispersal defines the spatial boundaries of a population (Berryman 2002). Therefore, estimates of philopatry, or the probability that individuals use the same area in sequential years, are necessary to understand population boundaries. When pairs form on breeding areas alone, the amount of emigration influences estimates of breeding philopatry. However, pair formation by waterfowl occurs on wintering areas (Rohwer and Anderson 1988), so philopatry to both breeding and wintering areas can influence mixing between areas (Cooke et al. 1975, 2000, Rockwell and Barrowclough 1987). Shifts in areas used by birds can have profound effects on interpretations about population trends and overall demography because changes in area use could be misinterpreted as changes in population size if inferences are drawn from unmarked birds (Mosbech and Boertmann 1999, Suydam et al. 2000).

Linkage between breeding and wintering areas is also important for understanding population dynamics because weather and habitat conditions encountered by birds during the winter can cause severe mortality (Fournier and Hines 1994, Dierschke 1998) or influence subsequent breeding success (Alisauskas 2002). Individuals from the same breeding area often share wintering areas, so entire cohorts could be affected by ecological factors on either of these areas (Esler 2000). Thus, knowledge of linkages between wintering and breeding areas will improve understanding of population biology over a species' annual cycle (Webster et al. 2002).

King Eider (*Somateria spectabilis*) populations in North America are presumably of two distinct groups that winter in either Northern Atlantic or Northern Pacific regions (Suydam 2000). Lack of genetic differentiation between these eastern and western populations suggests that these populations may interbreed (Pearce et al. 2004). Band recoveries from hunter-killed birds indicate that individuals from the Pacific and Atlantic populations share the same breeding grounds within the central Arctic (Bird Banding Laboratory, Canadian Wildlife Service, Quebec, Canada, unpubl. data). However, the extent and timing of population mixing remain unknown.

Previous isotopic analyses of zooplankton indicated an east-west gradient in the incidence of ^{15}N and ^{13}C in the arctic marine environment of North America, with the Bering and Chukchi Seas more enriched relative to the arctic waters of eastern North America (Dunton et al. 1989, Schell et al. 1998). Because eiders grow body feathers on their wintering areas (Suydam 2000), and isotopic ratios within feathers reflect the food webs where they were grown (Hobson 1999), stable-isotope ratios are useful in identifying the wintering locations of King Eiders. Naturally occurring stable isotopes from King Eider head feathers have proven successful in stratifying western and eastern winter King Eider populations based on known winter origin (99% and 94% correct classification for western and eastern seas, respectively; Mehl et al. 2004). Head feathers provided the best discrimination over other feather tracts (Mehl et al. 2004). The objective of the present study was to use naturally occurring stable isotope values from head feathers of individually marked female King Eiders to evaluate extent of winter philopatry. Secondly, to understand whether choice of wintering area influences breeding biology, we tested whether nest initiation date, clutch size, and body condition differed for individuals that wintered in Pacific compared to Atlantic waters. Our study was motivated by apparent declines in King Eider populations (Suydam et al. 2000) and the need for a better understanding of linkages between breeding and wintering areas.

METHODS

During 2001 and 2002, we systematically searched for King Eider nests on islands in Karrak and Adventure Lakes (67°14′N, 100°15′W; Fig. 1), about 60 km south of Queen Maud Gulf, Nunavut, Canada. These islands support one of the highest known densities of breeding King Eiders (Kellett et al. 2003; see Kellett 1999 for detailed descriptions of the study area). We began nest searches in mid-June and revisited nests every 4 to 7 days to determine clutch size, egg attrition rate, and nest fate. We calculated nest
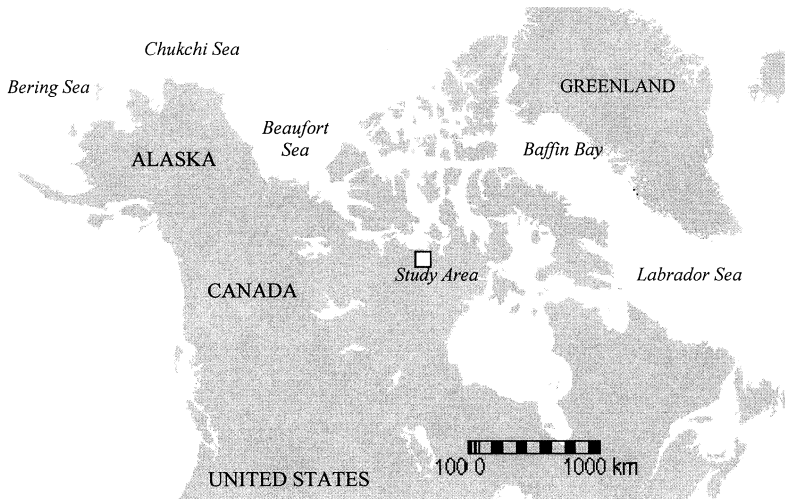
FIGURE 1.   Study area of Karrak Lake and Adventure Lakes, Nunavut, Canada, where incubating female King Eider feathers were collected for stable isotope analysis during 2001 and 2002. King Eiders wintered in either the northern Pacific (Chukchi or Bering Sea) or northern Atlantic, including the Labrador Sea.

initiation dates by backdating from known laying dates, or from incubation stages estimated by candling eggs (Weller 1956), assuming an incubation length of 23 days (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973). We captured nesting female King Eiders during late incubation ($\geq$16 days incubation) using either mist nets placed over nesting females or with self-triggered bow nets. We marked females with standard Canadian Wildlife Service-U.S. Fish and Wildlife Service leg bands and weighed each with a Pesola spring scale to the nearest 10 g. We also recorded the following measurements (twice for each female): head and tarsus length using dial calipers to the nearest 0.1 mm, and flattened wing chord using a flat ruler (Dzubin and Cooch 1993). Means were used to obtain indices of size. We also collected 3–10 feathers from the crown, and stored feathers from each bird in separate paper envelopes.

We rinsed feathers in a 2:1 chloroform:methanol solution and allowed samples to air dry. We placed weighed, dry feather samples (1 mg) into tin cups and combusted each in a RoboPrep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific, Crewe, UK; Hobson and Schell 1998). We report all stable isotope values in δ notation relative to Pee Dee Belemnite (PDB) and atmospheric air standards for δ^{13}C

and δ^{15}N measurements, respectively. Measurement precision, based on thousands of measurements of our albumen lab standard, is estimated to be $\pm$0.1‰ for δ^{13}C measurements and $\pm$0.3‰ for δ^{15}N measurements.

STATISTICAL ANALYSES

We classified individuals as wintering in eastern or western areas using predictive equations derived from quadratic discriminant function analysis (QDFA) based on isotope-ratios of eider feathers of known winter origin (Mehl et al. 2004). Using chi-square analysis, we investigated possible local breeding segregation by testing if observed nesting locations (islands and lakes) of King Eiders that wintered in eastern and western seas differed from expected ratios. We grouped individuals by year and assessed the proportion of individuals that were estimated to have wintered in eastern or western seas during the preceding winter. We then compared those results with the proportion of individuals that wintered in eastern and western seas, as indicated by band recoveries (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data), to determine possible differences in hunting pressure between wintering areas. We calculated 95% CI for wintering-area classifications based on random binomial variance (Zar 1999). We assessed the proportion of individuals that returned to the same area during consecutive winters

based on breeding females captured in both 2001 and 2002, and from band recoveries for birds whose previous year's wintering area we had inferred from stable-isotope analysis. Estimates of philopatry were contingent upon classification probabilities in both 2001 and 2002. When an individual was judged to have switched to an alternate wintering site during the second year, we calculated a classification probability for the switch among wintering areas as the product of both annual winter-area classification probabilities for that individual.

We estimated body condition during incubation, nest initiation date, and clutch size for females classified as having wintered in eastern compared to western seas during the preceding winter. We used principal components analysis (PCA) with mean body measurements to establish an index of female size (Rising and Somers 1989, Alisauskas and Ankney 1990). We then regressed eider mass on the size index (PC1), incubation stage at capture, and nest initiation date to adjust these parameters (Kellett and Alisauskas 2000) and then used residuals as an index of body condition (Weatherhead and Brown 1996). We tested for differences in female condition and nest initiation date using separate ANOVAs, by comparing models with single effects of year and wintering area, an additive model with year and area effects, and a global model that included the year * wintering area interaction. We confirmed that variances associated with nest initiation dates and body condition were normally distributed, based on the most saturated model using the Shapiro-Wilk statistic (Zar 1999). We chose the most parsimonious of four candidate models for each response variable using Akaike's Information Criterion corrected for sample size (AIC_c; Akaike 1985, Burnham and Anderson 1992). We did not correct for overdispersion as each observation was based on a separate individual female and therefore not likely affected by overdispersion (Burnham and Anderson 2002). We estimated mean condition and nest initiation date, along with associated 95% CI adjusted for year and wintering area, using least-squared means in PROC GLM (SAS Institute 1996).

We compared clutch size between years and wintering areas using an analysis of covariance (ANCOVA), with nest initiation date as a continuous covariate. We tested for normal distribution of variances associated with clutch size using the most saturated model with the Shapiro-Wilk statistic (Zar 1999). Log-transformed clutch size resulted in normally distributed variances and was used for all clutch size analyses. Clutches with more than six eggs are likely the result of nest parasitism (Anderson 2000), so we considered two sets of ANCOVA models each with eight candidate models: one set that included all clutch sizes and another that included only clutches of less than seven eggs. Candidate models included interactions of nest initiation date * year, wintering area * year, and nest initiation date * wintering area. We chose the most parsimonious models using AIC_c (Akaike 1985, Burnham and Anderson 1992), and estimated 95% CI of mean clutch size adjusted for nest initiation date, year, and wintering area during early, middle, and late nest initiation dates using the ESTIMATE option in PROC GLM (SAS 1996). Estimates of early, middle, and late nest initiation date included only those dates when individuals that wintered in both areas nested simultaneously. We did not compare estimates of nest success for birds between wintering areas because capture of individuals and subsequent acquisition of feather samples was only possible in late incubation periods, after which most nest failures had already occurred (Kellett et al. 2003).

RESULTS

We collected feathers from 85 and 82 female King Eiders during 2001 and 2002, respectively. Based on QDFA classification, about 69% (117 of 167; 95% CI = 63–77%) of these individuals wintered to the west, in Pacific waters, and 31% (51 of 167; 95% CI = 24–38%) wintered to the east, in Atlantic waters. The estimated proportion of individuals wintering to the west was slightly higher during 2002 (73%; 60 of 82; 95% CI = 52–82%), relative to 2001 (66%; 56 of 85; 95% CI = 56–77%). Precision around the classification estimates was greater during 2002, with 87% (71 of 82) of all individuals having >90% probability of wintering in the respective eastern or western areas, compared with 71% (60 of 85) of individuals with >90% probabilities during 2001 (Fig. 2). In contrast, only about half (56%, 5 of 9) of hunter-killed King Eiders (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data) marked at Karrak Lake were recovered in eastern wintering areas. Wintering area did not appear to influence local
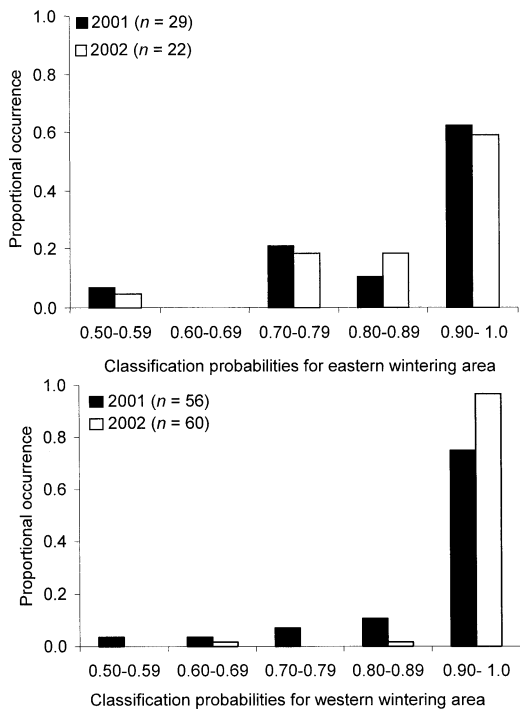
FIGURE 2. Proportional occurrence of classification probabilities for adult female King Eiders breeding at Karrak and Adventure Lakes, Nunavut, Canada, and wintering in the eastern and western seas during 2001 and 2002. Classification probabilities were based on predictive equations derived from Mehl et al. (2004) and reflect the probability that an individual King Eider wintered in that region.

breeding locations, as King Eiders at Karrak Lake nested among islands ($\chi^2_{25} = 23.0$, $P = 0.58$) and lakes ($\chi^2_1 = 0.9$, $P = 0.35$) independently of wintering area.

Based on stable isotope values from feathers of individuals captured during both 2001 and 2002 ($n = 20$), we calculated that six females may have switched between eastern and western wintering areas among years, and that at least four females probably did so (Table 1). Classification probabilities for wintering area varied among years and individuals (Table 1). We collected feather samples from four of eight King Eiders banded at Karrak Lake that were eventually shot by hunters. Based on classification results from isotope data, three of these individuals were shot in the same wintering area as we predicted them to have wintered during the previous year. The remaining individual was classified as wintering in the west during 2001 (91% classification probability) but was shot near the Greenland coast the following winter. Collectively, these two data sets indicated that up to 29% (7 of 24; 95% CI = 11–47%) of King Eiders switched among wintering areas. Only 13% (3 of 24; 95% CI = 0–26%) of females had >80% classification probability of having switched between western and eastern wintering areas. We collected feather samples from only one mother-daughter pair and both individuals were classified as having wintered in the east during the previous winter (79% and 91% classification probability, respectively).

PC1 accounted for 51% of variation in structural size, with loadings of 0.76, 0.52, and 0.43 for head, tarsus, and wing lengths, respectively. Size accounted for half of the variation in body mass ($F_{3,168} = 76.7$, $r^2 = 0.50$, $P < 0.01$). AIC_c model weight (0.53) suggested that female condition varied more between years than between

TABLE 1. Based on 20 female King Eiders analyzed in both 2001 and 2002, six were classified as wintering in different areas between years. Differing degrees of classification probability among individuals yielded variable confidence, but at least four eiders had a high likelihood of switching wintering areas between years. Classification was based on quadratic discriminant function analysis of stable-isotope ratios for female eiders nesting at Karrak Lake, Nunavut, Canada. Classification probability of switching among wintering areas was defined as the product of annual winter classification probabilities.

Individual	2001		2002		Classification probability of switching among winter areas
	Classification probability	Winter location	Classification probability	Winter location	
1	0.93	East	0.95	West	0.88
2	0.88	West	0.94	East	0.83
3	0.78	East	0.87	West	0.68
4	0.66	West	0.89	East	0.59
5	0.56	West	0.73	East	0.41
6	0.76	West	0.51	East	0.39

TABLE 2. Akaike's Information Criterion (AIC$_c$) values for all candidate models explaining condition of incubating female King Eiders. Models are based on ANOVA with female condition as the dependent variable and winter location (determined from stable-isotope analysis) and year as independent variables. Values are based on 163 females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC$_c$ weight reflects the relative support of each model given the model set, and sums to one; k is the number of parameters.

Model	RSS[a]	k	ΔAIC$_c$[b]	AIC$_c$ weight
Year	922 143	3	0.00	0.53
Location Year	918 748	4	1.84	0.21
Location	950 778	3	2.19	0.18
Location Year Location∗Year	917 396	5	3.86	0.08

[a] Residual sums of squares.
[b] Lowest AIC$_c$ value = 624.46.

wintering areas (Table 2) but the 95% CI of all four estimates of relative size overlapped (mean PC1 scores [95% CI]: 2001, western area: −5.1 [−25.2 to 15.1]; eastern area: −8.2 [−36.5 to 20.1]; 2002, western area: −11.6 [95% CI = −27.3 to 7.8]; eastern area: −1.8 [−39.7 to 24.1]).

Nest initiation date varied by both winter location and year (Table 3). During 2002, nest initiation date was 3.4 days earlier for females that wintered to the west (95% CI [Julian dates]: western area: 169.3–171.7; eastern area: 171.9–175.9), with overlapping confidence intervals during 2001 (western area: 169.3–171.8; eastern area: 168.8–172.4). When we included all clutches in analyses, models showed support for clutch-size variation among wintering area, timing of nest initiation, and years (Table 4). Clutch size was greater for females that wintered in the west, but these differences existed only during the early initiation period when nest parasitism (i.e., clutches with >6 eggs) was more frequent (Fig. 3). Estimated mean clutch size and associated 95% CI adjusted for nest initiation date

during early, middle, and late nest initiation dates are shown in Figure 3. When considering only clutch sizes with <7 eggs, clutch size models supported similar effects of year, timing of nest initiation, and wintering area, with support for nest initiation * year and nest initiation date * winter location (ΔAIC$_c$ < 2; Burnham and Anderson 1992; Table 5). Estimated mean clutch sizes and 95% CI for clutches smaller than 7 eggs, adjusted for nest initiation date, are shown in Figure 3 for each of the three nest initiation categories.

DISCUSSION

Use of stable-isotopic measurements from head feathers of King Eiders offered a useful method of distinguishing wintering areas. When combined with local banding efforts, this technique provided insight into winter philopatry not otherwise possible by more conventional approaches. Alternative methods, such as resighting color-marked individuals on wintering areas, is difficult because King Eiders winter at sea several kilometers from shore (Mosbech and Johnson

TABLE 3. Akaike's Information Criterion (AIC$_c$) values for all candidate models explaining nest initiation dates for King Eiders. Models are based on ANOVA with nest initiation date as the dependent variable and winter location (determined from stable-isotope analysis) and year as independent variables. Values are based on 165 females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC$_c$ weight represents the relative support of each model given the model set, and sums to one; k is the number of parameters.

Model	RSS[a]	k	ΔAIC$_c$[b]	AIC$_c$ weight
Location	3851	3	0.00	0.45
Location Year	3815	4	1.42	0.22
Location Year Location∗Year	3719	5	1.73	0.19
Year	3983	3	2.42	0.14

[a] Residual sums of squares.
[b] Lowest AIC$_c$ value = 231.90.

TABLE 4.   Akaike's Information Criterion (AIC$_c$) values for all candidate models explaining King Eider clutch size, including all clutch sizes. Models are based on analysis of covariance with clutch size as the dependent variable adjusted for nest initiation date, winter location (determined from stable-isotope analysis), and year. Values are based on 165 clutches for females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC$_c$ weight represents relative support of each model given the model set, and sums to one; k is the number of parameters.

Model	RSS[a]	k	ΔAIC$_c$[b]	AIC$_c$ weight
Initiation, Location, Year, Initiation*Location, Initiation*Year	11.6	7	0.00	0.39
Initiation, Location, Initiation*Location	12.2	6	1.65	0.17
Initiation, Year, Initiation*Year	12.2	6	1.65	0.17
Initiation, Location, Year, Initiation*Location, Initiation*Year, Location*Year	11.6	8	2.20	0.13
Initiation, Location	13.4	4	3.25	0.08
Initiation, Location, Year	13.2	5	5.25	0.03
Initiation, Year	13.8	4	5.96	0.02
Initiation, Location, Year, Location*Year	13.2	6	7.33	0.01

[a] Residual sums of squares.
[b] Lowest AIC$_c$ value = −175.63.

1999, Suydam 2000), battery lifespan for satellite transmitters is too short to allow for estimates of philopatry among years, and differential hunting pressures among regions can bias band recovery data (Robertson and Cooke 1999). Our results suggested that inference about winter distributions based on band recoveries from hunters was biased for King Eiders. Isotope analyses showed that most King Eiders at Karrak Lake wintered in the Pacific (66–
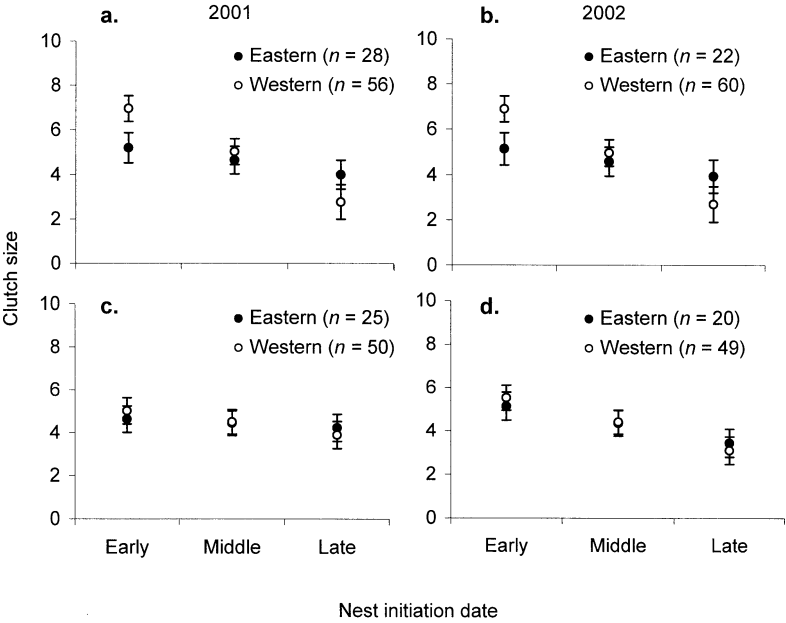

FIGURE 3.   ANCOVA estimates of mean (95% CI) clutch size scaled to midpoints of the early (14 June), middle (20 June), and late (27 June) incubation periods for female King Eiders that nested at Karrak and Adventure Lakes during 2001 and 2002 and were predicted to have wintered within western (Pacific) or eastern (Atlantic) seas during the winter preceding that breeding season. Estimates are for nests of all clutch sizes, including those where (a–b) more than one female likely contributed to the overall clutch size and (c–d) for only those clutches with <7 eggs.

TABLE 5. Akaike's Information Criterion (AIC$_c$) values for all candidate models explaining King Eider clutch size, including only clutch sizes with <7 eggs (i.e., nests in which brood parasitism was unlikely). Models are based on analysis of covariance with clutch size as the dependent variable adjusted for nest initiation date, winter-site location (determined from stable-isotope analysis), and year. Values are based on 143 clutches for females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC$_c$ weight represents relative support of each model given the model set, and sums to one; k is the number of parameters.

Model	RSS[a]	k	ΔAIC$_c$[b]	AIC$_c$ weight
Initiation, Location, Year, Initiation*Year	6.9	6	0.00	0.45
Initiation, Location, Year, Initiation*Location, Initiation*Year	6.9	7	1.35	0.23
Initiation, Location	7.9	4	3.35	0.08
Initiation, Location, Year, Initiation*Location, Initiation*Year, Location*Year	6.8	8	3.49	0.08
Initiation, Location, Year, Initiation*Location	7.4	6	3.89	0.06
Initiation, Location, Year	7.7	5	4.33	0.05
Initiation, Location, Year, Location*Year	7.7	6	6.38	0.02
Initiation, Year	8.3	4	6.42	0.02

[a] Residual sums of squares.
[b] Lowest AIC$_c$ value = −175.27.

73%), whereas limited band recoveries for the same breeding population suggested that only about 44% wintered there. We suggest that intensive hunting along the coast of Greenland (Christensen and Falk 2001) resulted in more band recoveries for that area.

Some female King Eiders switched between wintering areas, and must have used completely different migration pathways among years. This suggests that winter philopatry among King Eiders is weak, despite high rates of philopatry to breeding areas (Kellett 1999). Benefits and consequences of philopatry and dispersal are generally assessed relative to breeding areas (Greenwood 1980, Rohwer and Anderson 1988). Unlike most birds, waterfowl are thought to exhibit female-biased breeding philopatry (Greenwood 1980, Rohwer and Anderson 1988, but see Doherty et al. 2002). Robertson and Cooke (1999) suggested that in waterfowl, the normal avian pattern of male-biased philopatry was likely selected for on wintering, as opposed to breeding areas, due to the tendency for waterfowl to form pairs during winter. However, there have been few studies of winter philopatry in waterfowl, leaving hypotheses largely untested (Robertson et al. 1999). Nevertheless, low philopatry to wintering areas leads to increased gene flow (Cooke et al. 1975, 2000), and even if male King Eiders exhibit high winter philopatry (Robertson et al. 1999), winter dispersal by females alone would provide ample gene flow for population mixing to occur (see Slatkin 1987). This may

explain lack of phylogeographic structure among eastern and western populations (Pearce et al. 2004).

Dispersal by female King Eiders among wintering areas may be facilitated by gregarious behavior and group migration. Females congregate on breeding areas before fall migration; we observed such flocks of up to 46 females at Karrak Lake during late summer. King Eiders migrate in groups (Suydam 2000), so individuals from one wintering area may follow those of another to an alternate wintering site. Potential benefits of philopatry include familiarity with local food resources and predators (Anderson et al. 1992). Winter philopatry may be less important to female King Eiders if flocking during winter (Suydam 2000) allows for information exchange on productive foraging areas (Brown 1988) and if lack of predators in open oceanic waters lessens the need for familiarity with local predators (Rohwer and Anderson 1988).

Dispersal among areas is most likely if movement is favorable in both directions (Bull et al. 1987); otherwise, geographic variation in selection can partially block gene flow (Barton 1983). Although our results show benefits in the form of earlier nest initiation and larger clutches for females that wintered in the west, these benefits are likely not consistent among years and thus may not constitute a strong force of selection. For instance, differences in nest initiation dates likely reflect differential spring conditions among western and eastern seas and the avail-

ability of open water along migration routes (Abraham and Finney 1986, Suydam 2000). Late springs generally result in lower nest densities (Coulson 1984), and we suspect that a later eastern spring during 2002 may have delayed spring migration and hence nesting attempts and decreased breeding probability for eastern birds, compared to 2001. If so, western seas are also likely to experience late seasons, as trends in diminished sea ice indicate similar long-term (18-year) trends for both eastern (Labrador Sea, Davis Strait) and western (Bering and Chukchi Seas) wintering areas (Parkinson 2000).

Females that wintered in the Pacific appeared to reap increased benefits with larger clutch sizes, but they also showed a greater prevalence for apparent nest parasitism compared to females from the Atlantic. However, high frequency of apparent nest parasitism during early nest initiation may counter these benefits if parasitism leads to decreased egg success or offspring survival (Eadie and Anstey 1999). Unfortunately, we were unable to test for differences in nest success with respect to preceding wintering area. Assuming that lack of winter philopatry by female King Eiders results in population mixing between eastern and western populations, increased nest parasitism by individuals that wintered in the west should not reflect genetic differences between these local populations. Without genetic analysis of young, identification of parasitic females, and hence their winter origin (west or east) remains unknown.

Despite apparent differences in clutch size and nest initiation date, female condition of breeders was similar among individuals that wintered in eastern and western areas. We suggest that these similarities were related to a minimum threshold of endogenous nutrients, which females must exceed as a precondition for breeding (Kellett and Alisauskas 2000). Adult survival may also differ among wintering areas due to differential hunting pressures. However, longer-term data that incorporate isotope analysis with mark-recapture methods are needed before movement and subsequent survival probabilities can be estimated directly (Lindberg et al. 1995).

Collection and isotopic analysis of feathers has recently gained the attention of many ecologists (Webster et al. 2002, Smith et al. 2003). Our results show that isotope analysis of feathers can be of further use when combined with local

banding efforts and that these data allow for broad-scale inferences useful for modeling demography. Our method also offers a means of monitoring gene flow directly through dispersal and subsequent breeding success. Evidence for movement among wintering areas and lack of segregation on the breeding area according to winter distribution suggest that King Eiders wintering in Atlantic and Pacific seas may behave as one population rather than two (see Berryman 2002). These data also emphasize the need to use caution when interpreting band recoveries for purposes of movement and dispersal due to differences in hunting pressures among areas. Finally, we hope that this study will encourage researchers to incorporate, where appropriate, stable-isotope analysis with local banding efforts. Future work should focus on long-term research throughout the breeding and wintering range of the species.

ACKNOWLEDGMENTS

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