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TIMING AND DISTANCE OF KING EIDER MIGRATION AND WINTER MOVEMENTS

STEFFEN OPPEL[1,4], ABBY N. POWELL[2], AND D. LYNNE DICKSON[3]

[1]*Department of Biology and Wildlife, 211 Irving 1, University of Alaska, Fairbanks, AK 99775-6100*
[2]*U.S. Geological Survey, Alaska Cooperative Fish & Wildlife Research Unit, and Institute of Arctic Biology, 209 Irving 1, University of Alaska, Fairbanks, AK 99775-7020*
[3]*Canadian Wildlife Service, Room 200, 4999 98th Avenue, Edmonton, AB T6B 2X3, Canada*

Abstract. Understanding the patterns, extent, and phenology of migration is important for estimating potential influences of habitat or climate changes on populations of migratory birds. We used satellite telemetry of >100 individual King Eiders (*Somateria spectabilis*) tagged in northwestern North America in 2002–2006 to describe the timing and extent of their migration and winter movements in the Bering Sea. We found high variability in timing of migration events and distances flown. Arrival on breeding grounds and onset of molt migration were the least variable events in duration. Fall migration was extremely variable, ranging from less than a week to several months. More than a third of King Eiders did not migrate after wing molt and wintered on or near wing-molting areas. We found diffuse migratory connectivity between breeding and wintering areas, and low intrayear fidelity to 25 km radius wintering sites. More than half of the King Eiders used several wintering sites in a given year, and their winter ranges were considerably larger than those of other sea duck species. We identified three distinct wintering regions in the Bering Sea that were several hundred km apart, among which no movements occurred from late December until April. The onset of spring migration was earlier for birds wintering farther south, but arrival time on breeding grounds was not correlated with wintering latitude. We conclude that high phenotypic plasticity in migratory traits may render King Eiders more likely to respond to environmental shifts than sea duck species that show stronger migratory connectivity.

Key words: King Eider, migration, migratory connectivity, satellite telemetry, Somateria spectabilis.

Fenología y Distancia de la Migración y Movimientos Invernales de *Somateria spectabilis*

Resumen. Para estimar la influencia potencial de cambios climáticos, o de hábitat, en las poblaciones de aves migratorias, es importante comprender los patrones, la extensión y la fenología de su migración. Nuestro estudio utilizó telemetría satelital de >100 individuos de *Somateria spectabilis*, marcados con transmisores en el noroeste de América del Norte (2002–2006), para describir la extensión de la migración y los movimientos invernales de estas aves en el Mar de Bering. Encontramos un alto nivel de variación respecto a la sincronía y a las distancias de vuelo de los movimientos migratorios. El arribo a las zonas de apareamiento y el inicio de la muda de migración fueron los eventos menos variables. La migración otoñal fue altamente variable, con una variación desde menos de una semana, hasta varios meses. Más de un tercio de los individuos de *S. spectabilis* no migraron después de la muda en las alas, pasando el invierno en, o cerca de, la zona de muda. Encontramos una conectividad migratoria difusa entre las áreas de apareamiento y las de invernada, y baja fidelidad a sitios de invernada de 25 km de radio en un mismo invierno. Más de la mitad de los individuos de *S. spectabilis* utilizaron varios sitios de invernada durante cada año, y las áreas de invernada fueron considerablemente más amplias que las de otras especies de patos marinos. Identificamos tres regiones distintas de invernada en el Mar de Bering separadas por varios cientos de kilómetros. Entre éstas, no ocurrieron movimientos desde fines de diciembre hasta abril. El inicio de la migración de primavera fue más temprano para las aves que invernaron más al sur, pero el tiempo de arribo a las áreas de apareamiento no resultó estar correlacionado con la latitud de la invernada. Concluimos que, en *S. spectabilis*, una alta plasticidad fenotípica en los rasgos migratorios puede hacer más probable que estas aves respondan a cambios ambientales, en comparación a aquellas especies de patos marinos que muestran una mayor conectividad migratoria.

INTRODUCTION

King Eiders (*Somateria spectabilis*) are migratory sea ducks that breed in the circumpolar Arctic and winter at sea (Madge and Burn 1988). In fall, the birds from northwestern North America migrate into the Bering Sea (Suydam 2000) to several known molting and wintering areas (Phillips et al. 2006). Detailed information about the timing, extent, and variability of migratory routes is currently lacking.

Over the past 30 years, King Eider numbers surveyed on breeding (Dickson et al. 1997, Gratto-Trevor et al. 1998, Raven and Dickson 2006), molting, and wintering grounds (Frimer

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Manuscript received 23 October 2007; accepted 4 June 2008.
[4]E-mail: steffen.oppel@gmail.com

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1995, Mosbech and Boertmann 1999), and during migration have declined substantially (Suydam et al. 2000, Dickson and Gilchrist 2001). The causes of these declines are poorly understood. Global climatic changes can affect environmental conditions along migratory flyways and on wintering areas, which could result in demographic effects on King Eiders. To better understand how future environmental changes may affect King Eiders, more information on the behavior and phenotypic plasticity during migration and winter is needed.

In this study, we describe and quantify migration and wintering movements of King Eiders breeding in northwestern North America to examine their vulnerability to environmental changes. We further examine the degree to which birds from different breeding regions migrate to the same nonbreeding regions, a concept known as migratory connectivity (Webster et al. 2002, Webster and Marra 2005). By tracking individual birds with satellite transmitters, we estimate: (1) the minimal distance flown during outward and return migration; (2) time spent on migration as well as arrival times at molting, wintering, and breeding grounds; (3) the number of wintering sites used by individual birds and the number of movements among wintering sites; and (4) winter range size and the minimal distance flown during the winter period. The results provide a better understanding of the variability of migratory events and will yield hypotheses for changes that may occur under predicted climate scenarios.

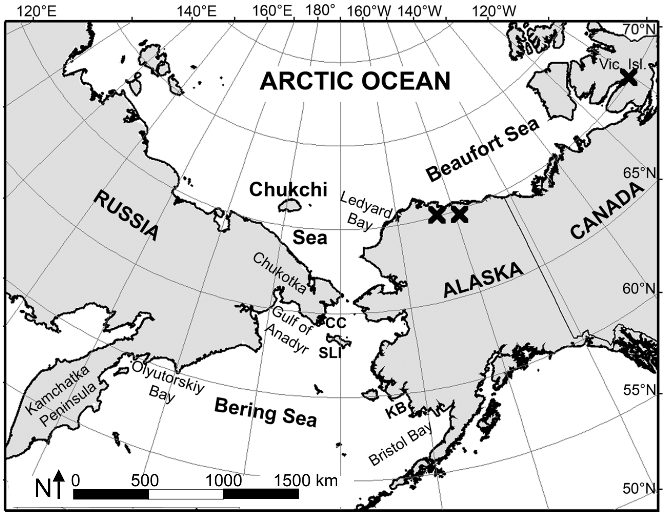

FIGURE 1. Map of northwestern North America and eastern Russia where King Eiders were tracked with satellite transmitters between 2002 and 2006. Capture locations are indicated by crosses. Illustrated in a Lamberth Azimuthal map projection centered on 65°N and 170°W. Vic. Isl. = Victoria Island, CC = Cape Chukotskiy, SLI = St. Lawrence Island, KB = Kuskokwim Bay.

METHODS

SATELLITE TELEMETRY

We trapped 80 (32 females, 48 males) adult King Eiders in Alaska, and 23 (10 females, 13 males) in the Northwest Territories, Canada, and equipped each bird with an intra-abdominal satellite transmitter (38 g platform terminal transmitter with external whip antenna; Microwave Telemetry Inc., Columbia, Maryland). We captured birds with mist nets on tundra ponds shortly after their arrival on breeding grounds but prior to nesting, following the methods described by Phillips et al. (2006). We caught birds in early June 2003–2005 near Teshekpuk Lake, Alaska (70°26′N, 153°08′W); in June 2002–2005 in the Kuparuk Oilfield, Alaska (70°20′N, 149°45′W); and in June 2003–2004 on Victoria Island, Northwest Territories (70°21′N, 110°30′W; Fig. 1). The transmitters were implanted by following standard surgical methods (Korschgen et al. 1996, Mulcahy and Esler 1999). We released the birds where they were caught, 2 hr after surgery. Transmitters were programmed to different duty cycles throughout the year, with shorter duty cycles (4–6 hr of transmission every one to four days) from June through November and longer duty cycles (6 hr every six to seven days) from December through March.

We pooled migration data from the two trapping sites in Alaska because the two sites were close enough (~130 km) that we did not expect different migratory behavior, and migration data were not statistically different. Because the Alaskan and Canadian sites were >1000 km apart, we analyzed migration distances and winter movements separately for birds from Alaskan and Canadian breeding grounds. Migration schedules that are not related to the onset and termination of the winter period for Canadian birds are being analyzed for Beaufort Sea management issues and will be presented elsewhere.

Based on the time of departure from nesting areas, we assumed that no females equipped with satellite transmitters in June raised offspring that year. Therefore, the migration timing we report includes unsuccessful or nonbreeding females only. In most years, however, ~80% of females seen on the nesting grounds in Alaska are either unsuccessful or nonbreeding (SO and R. L. Bentzen, unpubl. data), so we are confident that our data are representative of a large portion of the population.

We received location data from Argos (CLS America, Inc., Largo, Maryland) and filtered them for unreasonable locations by using the Douglas Argos filter algorithm (Douglas 2006). This algorithm selected the best location per duty cycle, based on location quality class and the distance, angle, and rate to previous and subsequent locations (Kenow et al. 2002). The filter program also provided the distance between subsequent locations calculated as great circle routes (Imboden and Imboden 1972). We began data collection two weeks after implanting transmitters to minimize bias caused by effects of capture and surgery (Esler et al. 2000).

Of the 80 Alaskan birds equipped with satellite transmitters, 2 males (3% of all birds marked) died within three weeks of surgery, and 7 more birds (9%) died in spring or summer the year after they were equipped with transmitters. In 6 birds (7%), signals were lost for unknown reasons, and in the remaining 65 birds (81%) transmitter batteries lost power while the birds were still alive. Of the 23 birds marked in Canada, 1 disappeared within 10 months for unknown reasons, but no mortality was evident. In the remaining 22 birds, batteries lost power while the birds were still alive. On average, transmitter life was 385 days and allowed tracking of approximately half of the birds for a complete annual migration cycle.

DEFINITION OF SEASONS

Most King Eiders molt their flight feathers in late summer, generally at locations intermediate to their breeding and wintering areas (Suydam 2000). The annual cycle of adult King Eiders therefore can be characterized by the following seasons: breeding, molt migration, wing molt, fall migration, winter period, and spring migration. We used distance and rate measurements provided by the satellite locations to define seasons for each bird.

We defined the onset of molt migration as the first long (>120 km) movement in a westerly direction that was followed by another movement in the same direction. This definition was based on the distance between capture sites and known staging areas (Phillips et al. 2007) and on the assumption that birds would molt west of the Beaufort Sea (Suydam 2000). We defined the beginning of the molt period as the last location of long-distance directional movement, followed by locations <15 km apart over a period of >20 days (Guillemette et al. 2007).

We defined fall migration as movement >500 km that was initiated before January, because it is the approximate distance between primary molting and wintering areas identified by Phillips et al. (2006). This definition also was chosen to exclude shorter movements that were partially reversed within three weeks and thus did not qualify as migration. Shorter movements of 190–500 km also were considered to be fall migration if they originated from areas that were vacated in winter by all birds in this study. We used the beginning of January as a cutoff for the latest date for fall migration because decreasing day length generally is considered its trigger (Berthold 1996). We defined the arrival on the wintering grounds by the timing of the first of a series of locations <50 km apart. If a fall migration was not evident, the start of the winter period was defined as the end of molt migration.

The winter period lasted until the onset of spring migration, which was defined as the first unreversed displacement in a northerly direction at a rate of 50 km day^{-1}. This velocity was chosen based on general information of spring-migrating waterfowl (Hedenström and Alerstam 1998, Arzel et al. 2006). We defined the completion of spring migration as the timing of the northernmost terrestrial location reached by an individual between late May and early July, if two subsequent locations were within 10 km of each other. If the last locations recorded of an individual were outside of the known breeding range of King Eiders or did not indicate a reduction of travel rate (e.g., battery failure or the bird died on spring migration), spring migration was considered incomplete, and the data were not included in analyses.

DEFINITION OF WINTER MOVEMENTS AND SITES

We defined a wintering site for each bird as an area with at least two consecutive locations ≤50 km apart during the winter period defined above. This definition was based on available location accuracy from satellite transmitters and on prior information on predicted daily movements of a related species (Spectacled Eider [*S. fischeri*]; Bump and Lovvorn 2004).

We defined a winter movement as any movement >50 km during the winter period. We considered sequential displacements of >50 km each in the same direction as one winter movement. If the intermittent stop involved two locations, we counted these as a wintering site and two movements leading to and away from that site. If the direction of the second movement step was reversed from the first step, and if both step lengths were >50 km, the two segments were counted as two winter movements.

We classified winter movements into random movements (50–150 km) and those with migratory character (>150 km). We defined winter movements with migratory character as directional movements of at least 150 km in a southerly (extension or substitution of fall migration) or a northerly (precursor of spring migration) direction. A prerequisite of a winter movement as extension or substitution of fall migration was that the bird used the destination site for at least two weeks.

CALCULATION OF TIME PERIODS, DISTANCES, AND RANGES

We calculated the duration of every season as the difference in days between the first and last location of a season defined above. For stationary seasons (wing molt and winter), this calculation included the two days of the first and last location and yielded a minimal estimate of the season duration. For migratory seasons (molt, fall, and spring migration), the days defining the onset and end of the respective season were excluded, and the period between those dates yielded a maximal estimate of the duration of migration. We calculated the total distance moved for each season as the sum of distances between all successive locations within that season. These distances assume a straight-line travel between successive locations and therefore are minimal estimates of distance traveled. We calculated travel rates for migratory seasons as the total distance flown divided by the total time spent on migration. These estimates thus include staging times within a migratory period, because staging is a key component of migration (Hedenström and Alerstam 1998).

To compare the winter movement ranges of King Eiders with results from other sea duck studies, we calculated 95%

minimum convex polygons for each individual based on all the locations within the winter period with the software Home Range Tools (HRT) for ArcGIS (Rodgers et al. 2005). We consider the minimum convex polygon as a "movement range" and do not assume usage of the entire area covered by the polygon. We chose a minimum convex polygon approach over kernel-based home-range estimators, as the latter did not adequately reflect distances between discrete wintering sites for birds using more than one site. We were primarily interested in comparing the range of movements with other studies, which did not report details of movements or home-range estimation parameters, rendering equivalent analysis impossible (Laver and Kelly 2008). We realize that comparisons of movement ranges across studies using different sampling regimes and range estimation techniques require caution (Börger et al. 2006), but this approach nonetheless allows a qualitative comparison across sea duck species.

STATISTICAL ANALYSES

Because most of our data were not normally distributed, we compared distance, rate, and time measures of migrating and wintering King Eiders with nonparametric Mann-Whitney *U*-tests between sexes and capture locations, and Kruskal-Wallis tests among years and wintering areas. Correlations between variables were tested with a Spearman rank-correlation test. We used $\alpha = 0.05$ for all tests and report results as mean ± SD and range.

RESULTS

MOLT MIGRATION

Male King Eiders started the molt migration on average 32 days earlier than females ($U = 32.5$, $P < 0.001$) and arrived at molting areas 24 days earlier ($U = 89$, $P < 0.001$, $n = 89$; Table 1). Most birds molted along the Chukotka Peninsula, and the distance of the molt migration was similar between males and females (Table 2). Birds marked in Canada also migrated to Chukotka and had a molt migration that was on average 1600 km longer than did birds marked in Alaska ($U = 56$, $P < 0.001$; Table 2).

Travel speed during molt migration was significantly greater for females (122 ± 82 km day^{-1}, $n = 33$) than for males (77 ± 35 km day^{-1}, $n = 56$; $U = 516$; $P = 0.001$). On average, males spent more days (89 ± 24, $n = 37$) on molting areas than did females (70 ± 16, $n = 16$; $U = 166$, $P = 0.01$). Despite different arrival times at molting areas (Table 1), the departure time for fall migration did not differ between males and females ($U = 214$, $n = 51$, $P = 0.25$). A single female stayed in the Beaufort Sea until October before migrating to Chukotka for the winter. Her movement was classified as fall migration because some females are assumed to molt near breeding areas (Knoche 2004).

FALL MIGRATION

Fall migration from molting to wintering areas was extremely variable and did not differ between birds from Alaska and Canada (males: $U = 111$, $P = 0.78$; females: $U = 20.0$, $P = 0.10$; Table 2). Fall migration lasted 3–105 days. Fewer than a third of the males (24%, $n = 55$) and more than half of the females (53%, $n = 40$) did not initiate fall migration consistent with our definition and wintered on or near their molting areas. Among the Alaskan birds having a fall migration, 32% ($n = 47$) completed the journey in less than two weeks, whereas 60% spent three weeks or more en route, interrupted by several stopovers lasting up to six weeks. Consequently, the travel speed during fall migration ranged from 11 to 218 km day^{-1} (mean: 50 ± 39 km day^{-1}). Important fall staging areas were in the southern Bering Strait east of St Lawrence Island, in Kuskokwim Bay, as well as along the Russian coastline from the Gulf of Anadyr to Olyutorskiy Bay (Fig. 1).

Because of the high variation in both onset and duration of fall migration, King Eiders arrived on their wintering grounds between late July and mid-January, with the mean arrival date being about three weeks later for males than females (Table 1). Excluding birds wintering on molting areas, the mean arrival time on wintering areas was 4 December (males: ± 23 days,

TABLE 1. Range and average timing of migration events for adult male and female King Eiders tracked with satellite telemetry from breeding areas in northern Alaska and the western Canadian Arctic (winter arrival and start spring migration only), 2002–2006. Note that sample size depends on how many birds initiated a migration and thus may not add up to the total number of tagged birds.

	Male				Female			
Migration Event	*n*	Mean	Minimum	Maximum	*n*	Mean	Minimum	Maximum
Start molt migration	57	4 July	17 June	26 July	33	5 August	7 July	27 August
Arrival wing molt area	57	2 August	18 July	20 August	37	26 August	10 August	18 September
Start fall migration	36	28 October	26 September	18 December	15	2 November	8 October	28 November
Arrival wintering area	55	4 November	20 July	12 January	40	14 October	10 August	10 January
Start spring migration	49	2 April	3 February	9 May	37	5 April	1 March	28 May
Arrival breeding grounds	26	9 June	25 May	24 June	16	10 June	27 May	25 June

TABLE 2. Minimal travel distance (km) for King Eiders tracked with satellite telemetry from breeding areas in northern Alaska and the western Canadian Arctic, 2002–2006. Distances are estimates of straight-line travel along great circle routes. Note that sample size depends on how many birds initiated a migration and thus may not add up to the total number of tagged birds.

Season	Male					Female				
Origin of birds	*n*	Mean	SD	Minimum	Maximum	*n*	Mean	SD	Minimum	Maximum
Molt migration										
Alaska	56	1820	661	951	4395	33	1710	756	1043	4727
Canada	9	3378	565	2701	4145	8	3392	431	2751	4202
Fall migration										
Alaska	34	1067	500	207	2163	13	1225	493	437	2127
Canada	7	1027	563	211	1970	6	785	578	193	1600
Wintering period										
Alaska	41	634	413	46	1499	29	639	402	74	1478
Canada	9	648	397	77	1462	9	404	372	77	1197
Spring migration										
Alaska	26	3701	1131	1936	5950	16	2273	739	1187	3834
Canada	8	3859	931	2787	5366	6	3322	460	2485	3736

18 October–12 January, $n = 42$; females: ± 26 days, 9 September–10 January, $n = 24$).

WINTER PERIOD

King Eiders from Alaska and Canada wintered in the northern, eastern, and western Bering Sea, as well as in adjacent areas of the Sea of Okhotsk and the Gulf of Alaska; however, there was little relationship between specific breeding and wintering areas. We identified three distinct wintering regions. Winter movements occurred frequently within these regions, but there was no recorded winter movement or migration event between any two regions from late December until April. These regions were: (1) the northern Bering Sea, with the main wintering site around Cape Chukotskiy, (2) southwestern Alaska, with the main wintering sites in the inner Bristol Bay area, and (3) the Kamchatka peninsula, with major wintering sites in Olyutorskiy Bay, as well as near the southern tip and southwestern coast of the peninsula (Fig. 2).

On average, the winter period for adult King Eiders lasted 160 ± 68 days (54–294, $n = 88$). During this time, 55% of tracked individuals each used more than one wintering site, whereas 13% performed circular winter movements without using a second wintering site, and 32% did not perform any winter movements. The mean distance traveled during the winter period was 614 ± 403 km (46–1499 km, $n = 88$) and did not differ between birds from Alaska and Canada (males: $U = 184$, $P = 0.99$; females: $U = 84$, $P = 0.11$). The winter travel distance represented on average approximately 11% of the total annual migration distance of Alaskan individuals, and 7% of Canadian individuals ($U = 190$, $P = 0.05$, $n = 56$). Some individuals remained stationary at a single wintering site, whereas others moved extensively among up to four wintering sites hundreds of km apart. In addition, almost half the birds (41 out of 93) reversed winter movements and returned to wintering sites that they had left previously. The duration of the winter period accounted for little of the variation in winter movements among individuals ($F_{8,79} = 1.7$, $P = 0.10$), but birds without pronounced fall migration had significantly more winter movements than did birds with fall migration ($U = 438$, $P < 0.001$). The number of winter movements however,

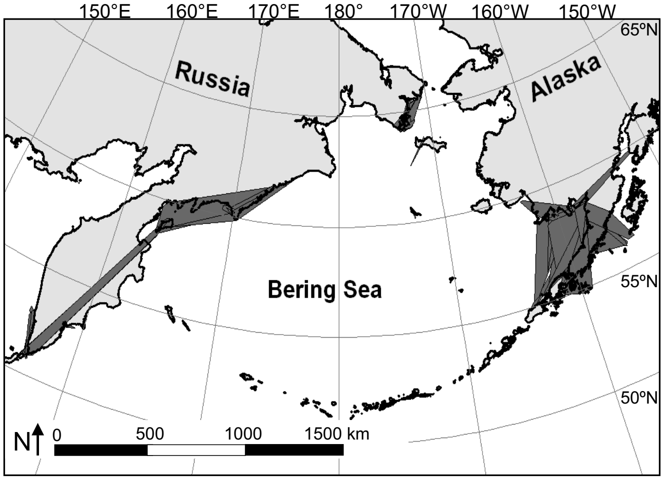

FIGURE 2. Map showing 95% minimum convex polygon winter ranges in southwestern Alaska and eastern Russia of 93 King Eiders tracked with satellite transmitters between 2002 and 2006. Each dark polygon indicates the range of movements of an individual but does not imply its usage of the entire area. Three regions with non-overlapping ranges can be recognized.

did not differ between sexes ($U = 1033$, $P = 0.87$), among years ($\chi^2_3 = 0.3$, $P = 0.96$, $n = 93$), or among the three main wintering regions ($\chi^2_2 = 3.0$, $P = 0.22$, $n = 93$).

We classified 42 (27%) of 156 winter movements as having migratory character. Winter movements representing extension or substitution of fall migration occurred between October and February and were as common (48% of migratory movements, $n = 20$) as precursors of spring migration (52%, $n = 22$). The earliest northbound winter movements with migratory character occurred in early January. The number of random (nondirectional) winter movements per month and individual remained fairly constant from November through April (Fig. 3).

The mean winter range size was 6905 ± 11 523 km^2 (range: 13–66 722 km^2, $n = 92$), even though only 32% of individuals had winter ranges >5000 km^2 (Fig. 2). There were no differences in the size of winter ranges between sexes ($U = 963$, $P = 0.58$, $n = 92$) or among years ($\chi^2_3 = 2.0$, $P = 0.58$).

SPRING MIGRATION

Many satellite transmitters failed in April or May the year after their deployment. This loss limited our sample size of birds that completed a spring migration to 16 females and 26 males. Spring migration was different between sexes, in that all females returned to their original capture locations, but males migrated to breeding grounds ranging from the Taimyr Peninsula, Russia (110ºE) to Victoria Island, Canada (110ºW). Thus, spring migration distances were significantly different between females originally captured at and returning to Alaskan or Canadian breeding grounds ($U = 9$, $n = 24$, $P < 0.001$), but not for males originally captured in Alaska or Canada ($U = 67$, $n = 32$, $P = 0.62$; Table 2).

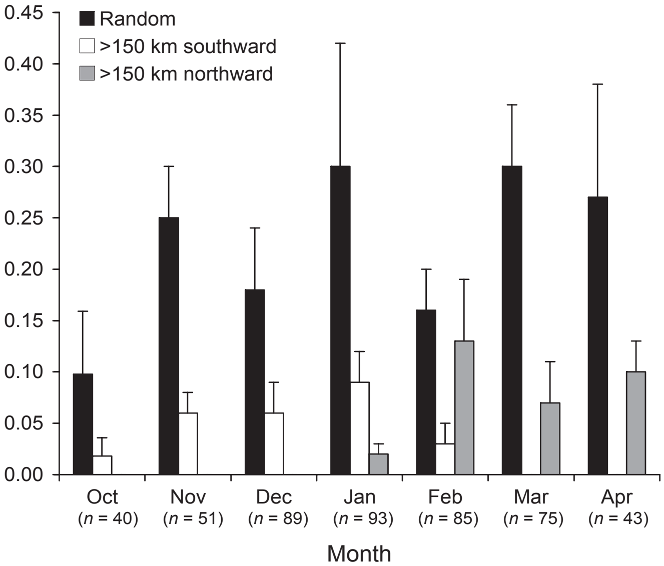

FIGURE 3. Mean number (± SE) of winter movements per individual King Eider for different months of the nonbreeding period, as calculated from 93 satellite-tracked King Eiders in the Bering Sea between October 2002 and April 2006. Black columns show random movements (50–150 km), white columns show movements as extension or substitution of fall migration (>150 km southward), and gray columns show movements as precursors of spring migration (>150 km northward). Sample sizes indicate the number of wintering birds tracked in each month.

Males and females tagged in northern Alaska began and completed spring migration at the same time (Table 1), despite migrating to different destinations (Table 2). There was a strong tendency for birds wintering at lower latitudes to initiate spring migration earlier than did birds wintering farther north ($r_S = 0.40$, $P < 0.001$, $n = 86$), but spring arrival time on breeding grounds was not correlated with wintering latitude ($r_S = -0.21$, $P = 0.17$, $n = 42$).

Alaskan King Eiders spent on average 62 ± 24 days (9–110, $n = 42$) in spring migration. Because of the longer spring travel distance of males in our study, the speed of spring migration was significantly higher for males (61 ± 18 km day^{-1}, $n = 26$) than females (46 ± 27 km day^{-1}, $n = 16$; $U = 92$, $P = 0.003$).

Ledyard Bay, in the eastern Chukchi Sea (Fig. 1), was the most important staging area during spring migration. All 33 males and females migrating to North American breeding sites and 67% of the 9 males migrating to breeding sites in Siberia used this area on spring migration.

DISCUSSION

The timing and duration of migratory seasons in North American King Eiders is highly variable among individuals, and a clear distinction between fall migration and winter is lacking among many birds. The least-variable migration events were the onset and duration of molt migration and arrival time at breeding grounds, suggesting that substantial selection pressure exists for the timing of these events. In contrast, fall migration and winter period were highly variable in both timing and distance traveled, suggesting that multiple strategies are viable in a highly variable marine environment like the Bering Sea.

Our estimates of migration timing assessed via satellite telemetry conform with ground-based observations of migrating King Eiders near Barrow, Alaska (Suydam et al. 2000, Day et al. 2004) and in the Beaufort Sea (Dickson and Gilchrist 2001). We found that the proportion of birds wintering in different regions of the Bering Sea were similar to estimates inferred from stable isotope analyses of feathers (SO and ANP, unpubl. data). We therefore believe that transmitters are unlikely to introduce directional bias in our estimates of migration timing and pattern (Wilson and McMahon 2006).

MOLT AND FALL MIGRATION

Postbreeding flight-feather molt in sea ducks is an energy-expensive process, during which most species are flightless (Guillemette et al. 2007). Migrating to areas that offer safety from predators and an abundant food supply is therefore an adaptive strategy. Since the departure time of females is constrained by their involvement in nesting, they must complete migration to molting sites and wing molt in a shorter time span than males to regain mass and flight ability prior to the onset of winter. This might explain the higher migration speed we found for females compared to males. Our sample to date did not include females that raised offspring in the year of tracking. The molt migration schedule for females that are raising offspring is slightly different from females in our study in that they depart later than unsuccessful females and likely migrate faster to molting areas (SO and ANP, unpubl. data).

Several birds did not move away from wing molt areas in winter, and some birds moved only short distances that were characterized as winter movements in our analysis. Fall migration apparently is very short for some individuals and is therefore difficult to distinguish from winter movements, thus obscuring the distinction between fall migration and winter as different seasons. Fall migration may be stimulated mostly by exogenous factors such as environmental conditions and access to food (Terrill and Ohmart 1984, Haila et al. 1986), whereas molt migration occurs in the absence of such external stimuli (Berthold 1996).

Formation of shore-fast and sea ice in fall and early winter on many staging or molting sites may lead to King Eider movements in the forms of delayed and facultative fall migration (Haila et al. 1986, Vaitkus 2001). Facultative fall migration has been hypothesized to be an adaptive strategy for birds that benefit from wintering closer to breeding areas (Terrill and Ohmart 1984). This hypothesis generally is based on the arrival-time hypothesis, which implies that birds wintering closer to breeding grounds have a fitness advantage due to earlier arrival on breeding grounds (Kokko 1999). The spring arrival time of King Eiders found in this study did not differ among birds wintering at different latitudes, rendering a fitness advantage of wintering closer to the breeding location unlikely. A shorter migration distance in both fall and spring may however result in less use of body reserves for migration and better physical condition on arrival at the breeding grounds. Future research needs to determine whether the reproductive performance of King Eiders differs among birds wintering at different distances from the breeding grounds.

Recent climatic changes have altered the timing and extent of several bird species' migration (Cotton 2003), leading to shortened migratory routes or the loss of migratory behavior in some species (Berthold et al. 1998). Because of the lack of historical information on King Eider wintering distributions, we cannot assess whether the omission of fall migration is a recent development. If climatic warming trends continue at the current rate and winter sea ice recedes farther north, future studies need to examine whether the proportion of King Eiders wintering in the Northern Bering Sea increases over time.

WINTER PERIOD AND WINTER MOVEMENTS

Because of their omission of fall migration, some individuals arrived on their wintering areas as early as late July. Others that did migrate arrived as late as January, and southbound movements that represented extensions of fall migration occurred until February among some birds. During the winter period, more than half of the birds we tracked moved among different sites. Given the variability of fall migration and the movements of birds in wintering areas, it is questionable whether a distinct differentiation between fall migration and winter seasons can be applied to King Eiders. Instead, these birds may go through a period of nomadic behavior (Mueller and Fagan 2008) between the termination of wing molt and the onset of spring migration, during which major movements may or may not occur, and a latent condition is maintained that would enable movement without preparatory fattening (Terrill and Ohmart 1984). Such movements during winter are known for bird species wintering in the tropics (Stouffer 2001, Berthold et al. 2002). Remsen (2001) defined winter as the period during which birds are relatively sedentary and no records exist for birds moving to or from a wintering site. Such a period does not exist for King Eiders in the Bering Sea between September and May; in fact, there is a period in January and February when some birds are still moving south, and other birds already are moving north.

The winter movements we described for King Eiders led to range estimates that are two to three orders of magnitude larger than "winter home range" estimates reported for other sea ducks (Petersen and Douglas 2004, Merkel et al. 2006, Reed and Flint 2007). These differences are caused partly by different definitions of winter period, different temporal resolution of locations, and different algorithms (kernel vs. minimum convex polygon) and, hence, are not quantitatively comparable to our estimates. Nonetheless, both the magnitude of the differences and the fact that a third of the King Eiders we tracked had very large individual ranges during winter suggest a highly variable level of intrayear site fidelity (Robertson and Cooke 1999) in King Eiders.

Although they are poorly understood, King Eider winter movements have important implications for conservation and management of marine areas. Bristol Bay and the southwestern coast of Kamchatka are currently being considered for offshore oil exploration. Assessment of the importance of certain areas generally is based on aerial surveys and censuses. Because of the widespread movements and resulting turnover of individual King Eiders at a single area, one-time censuses will likely underestimate the number of ducks actually using an area over the course of a winter. This potential bias needs to be addressed explicitly when assessing the potential effects of man-made structures (West and Caldow 2006) and of other human impacts at sea.

The northernmost wintering sites of King Eiders are in the Sireniki polynya, an area of ~2000–5000 km^2 of open water within the seasonal pack ice along the southern coast of Chukotka (Stringer and Groves 1991). Given the ability of King Eiders to cover long distances in midwinter and the presumed low tolerance for high sea-ice cover (Phillips et al. 2006), it is surprising that no movement occurred from the northernmost wintering sites to more southerly areas off Kamchatka or Alaska after December: the sea ice in the Bering Sea reaches its maximal extent in March (Parkinson and Cavalieri 2002), and the Sireniki polynya is smallest in February (Stringer and Groves 1991). Ice formation can occur in polynyas, forcing sea ducks to move to different areas (Bump and Lovvorn 2004), and sea ice formation often results in southward migration of sea ducks in the Baltic Sea (Haila et al. 1986, Vaitkus 1999). It would appear plausible for King Eiders to depart from the Northern Bering Sea in late winter when sea ice cover approaches its maximal extent and polynyas decrease in size. We did not observe this pattern in our study and conclude that the Sireniki polynya currently offers King Eiders sufficient open water even at times of maximal sea ice cover.

SPRING MIGRATION

King Eiders are believed to form pair bonds on wintering areas and migrate as pairs in spring (Suydam et al. 2000). Assuming that the onset of spring migration is determined primarily by the females' migratory restlessness, male departure dates in our study represent the departure dates of their accompanying females migrating to more distant breeding sites (Phillips and Powell 2006). Based on our definition, the onset of spring migration was almost identical for males and females, with birds that wintered farther south departing earlier. This latitudinal difference in departure dates indicates that the distance from wintering areas to staging areas in the Chukchi Sea is likely to affect departure date more than does the distance from the Chukchi Sea to breeding grounds. The eiders' progress into the Arctic Ocean may be limited by the availability of annually recurring open leads in the sea ice (Fournier and Hines 1994, Dickson et al. 1997, Suydam 2000); hence, earlier departure may carry undue risks (Barry 1968, Fournier and Hines 1994). Therefore, the birds cannot depart earlier from staging areas in the Chukchi Sea, even if they have to migrate a longer distance to breeding locations. Thus, the total distance to breeding locations may have little influence on the departure time from wintering areas.

The different distances to breeding grounds are most likely covered by higher migration speeds in spring. Males in our study compensated for longer spring migration distances with faster migration rates than females in our study. Because of the longer distance and a higher migration speed, birds breeding farther away from staging areas in the Chukchi Sea therefore may require more energy to complete their spring migration than birds breeding closer to these areas (Arzel et al. 2006).

The most important spring staging area in the Chukchi Sea is Ledyard Bay, which was used by 93% of all King Eiders tracked in this study, including male birds that later crossed the Chukchi Sea to migrate to Siberian breeding areas. This usage pattern suggests that Ledyard Bay is a critical area to King Eiders breeding not only in Alaska, but also in Siberia and in northwestern Canada.

In conclusion, the broad winter distribution pattern of King Eiders coming from a small number of breeding locations, the tendency to move among different wintering sites, and the apparent presence of birds from a wide range of breeding areas at given wintering sites suggest that migratory connectivity is very diffuse in King Eiders. This diffuse connectivity is in contrast to the pattern found in both Pacific Common Eiders (*S. mollissima v-nigrum*), and Spectacled Eiders breeding in Alaska: in those species, birds from certain breeding areas winter in specific areas each year (Petersen et al. 1999, Petersen and Flint 2002). Strong connectivity can lead to local adaptation and can impede responses to climatic changes such as those resulting from global warming (Webster and Marra 2005). The diffuse connectivity found in King Eiders may explain the lack of spatial genetic population structure (Pearce et al. 2004) and may in part be a result of the high phenotypic plasticity in the timing and extent of migration.

Long-distance migrants with high degrees of migratory connectivity have been shown to suffer from environmental changes that can lead to a mismatch between their migration phenology and environmental conditions (Visser and Both 2005). Our study has shown a wide range of phenotypic plasticity in the extent and timing of migration in King Eiders, and it therefore is possible that King Eiders have the ability to respond to environmental changes and anthropogenic modifications of marine habitats to a larger degree than related sea duck species with narrower ranges of migratory flexibility.

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