Multiple Spring Migration Strategies in a Population of Pacific Common Eiders - Estrategias Múltiples de Migración de Primavera dentro una Población de Somateria mollissima v-nigrum
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MULTIPLE SPRING MIGRATION STRATEGIES IN A POPULATION OF PACIFIC COMMON EIDERS

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Abstract. Spring migration strategies vary within and among species. Examination of this variability extends our understanding of life histories and has implications for conservation. I used satellite transmitters to determine migration strategies and evaluate factors influencing the timing of spring migration of Pacific Common Eiders (*Somateria mollissima v-nigrum*) that nest along the western Beaufort Sea coast. Adult females were marked at nesting colonies in the summers of 2000, 2001, and 2003, and were followed throughout spring migration the following year. Each year approximately equal proportions of eiders used three distinct migration strategies varying in duration, staging locations (waters near the Chukotka Peninsula, Russia, and the Chukchi and Beaufort seas, Alaska), and arrival dates at the nesting areas. It is unlikely that differences in the timing of movements to stopover sites in the Chukchi and Beaufort seas were a result of responses to changes in weather, particularly wind direction. Ice distribution and melt/movement patterns vary substantially among staging areas and thus may affect risk of starvation and reproductive potential. Long-term (decadal) changes in climate may favor birds using one strategy during "warmer" and another during "colder" years.

Key words: climate change, *Common Eider*, *ice*, *migration*, *polynyas*, *stopover*, Somateria mollissima v-nigrum.

Estrategias Múltiples de Migración de Primavera dentro una Población de *Somateria mollissima v-nigrum*

Resumen. Las estrategias migratorias de primavera varían en una misma especie y entre especies diferentes. El estudio de esta variabilidad permite extender nuestro entendimiento sobre historias de vida y tiene implicaciones para la conservación. Utilicé transmisores satelitales para determinar las estrategias migratorias y para evaluar los factores que afectan el momento en que ocurre la migración de los individuos de *Somateria mollissima v-nigrum* que anidan a lo largo de la costa oeste del Mar de Beaufort. Se equiparon hembras adultas con transmisores en las colonias de anidación durante los veranos de 2000, 2001 y 2003, las que fueron seguidas durante la migración de primavera al año siguiente. Cada año, aproximadamente las mismas proporciones de individuos de *S. m. v-nigrum* usaron tres estrategias migratorias diferentes que variaron en duración, en las localidades de parada (aguas cercanas a la Peninsula Chukotka, Rusia, y los mares de Chukchi y Beaufort, Alaska) y en las fechas de llegada a las áreas de anidación. Es poco probable que las diferencias en los momentos en que ocurren los movimientos hacia los puntos de parada en los mares de Chukchi y Beaufort sean el resultado de respuestas a cambios en el clima, particularmente cambios en la dirección del viento. La distribución del hielo y el derretimiento/patrones de movimiento entre las áreas de parada varían substancialmente y por lo tanto pueden tener un efecto sobre el riesgo de inanición y el potencial reproductivo. Cambios climáticos en el largo plazo (décadas) pueden favorecer a las aves que utilizan una estrategia en años más cálidos y otra en años más fríos.

INTRODUCTION

Spring migration is an energetically demanding and hazardous time of a bird's life. During migration birds must meet the energetic demands of flight, avoid predation and environmental hazards, and arrive at the nesting site at the optimal time (Alerstam and Lindström 1990). Migration strategies of many species include the use of stopover locations to regain reserves for continued migration (Lindström and Alerstam 1992, Alerstam and Hedenström 1998, Green et al. 2004, Drent et al. 2003, Prop et al. 2003). In addition, some birds nesting in the Arctic acquire reserves for reproduction before reaching the breeding grounds (see Klaassen 2003, Arzel 2006, Drent et al. 2006).

Studies of individually marked birds show that the duration and timing of spring migration vary from individual to individual within a population (Forstmeier 2002, Green et al. 2002, Bêty et al. 2004, Gunnarsson et al. 2006). In addition, not all marked individuals within a population stage at the same locations during spring migration (Beekman et al. 2002, Petersen and Flint 2002, Bauer et al. 2006, Mosbech et al. 2006). Furthermore, a reduction or change in available

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food resources at spring stopover areas, due to either anthropogenic (disturbance, subsistence and commercial harvest) or natural events (adverse weather, unusual sea-ice conditions), correlates with reduced propensity to breed, breeding failures, and die-offs (Ebbinge 1989, Suter and Van Eerden 1992, Fournier and Hines 1994, Oosterhuis and van Dijk 2002, Drent et al. 2003, Gaston et al. 2005), which in turn can influence population levels (Newton 2004, 2006).

Factors that influence the length of stay and the timing of departure from stopover areas include winds, predation, food resources, and the interactions among these factors. Winds may influence the timing of spring migration and migration paths of many birds that fly to the Arctic (Piersma and van de Sant 1992, Green 2004, Klaassen et al. 2004). Once a bird acquires reserves, the length of its stay at spring stopover areas is often influenced by local wind and weather conditions (Åkesson and Hedenström 2000, Fox et al. 2003) and toward the end of migration is often correlated with date rather than weather (Piersma et al. 1990, Piersma and van de Sant 1992). These conditions can have a substantial effect on the timing of arrival and departure of birds at spring stopover areas as well as the breeding grounds (Beekman et al. 2002, Klaassen et al. 2004). Thus, an understanding of the influence of weather on the timing of movement of individuals to and from stopover areas can provide insight into migration patterns.

Recognition of variation among individuals can increase understanding of evolutionary processes influencing a population and improve conservation and management of populations (Bolnick et al. 2003). The timing of movements in spring to staging sites, the duration that birds remain at an area, and individual variation within a population are poorly understood in arctic-nesting Anatidae (Arzel et al. 2006). Spring migration of the Common Eider (*Somateria mollissima*) has been described in the literature on the basis of observations of flocks migrating past a point, radar data, and arrival and departure dates from wintering, staging, and nesting areas (Alerstam et al. 1974, Gauthier et al. 1976). These data provide a general description of migration patterns, correlations with weather and time of migration, the timing of passage, and information on movements. Greater understanding of this portion of the eiders' life history requires more complete knowledge of birds throughout their migration period. Alerstam et al. (2003), Drent et al. (2003, 2006), Newton (2006), and others have underscored the need to study spring migration to better understand and evaluate evolutionary processes of migration and the effects on populations. This knowledge can be obtained, in part, by following individuals throughout the spring and evaluating how their migration strategies differ and how they fit into the population as a whole.

My goal was to describe the spring migration strategies of an arctic-nesting sea duck, the Pacific Common Eider (*S. m. v-nigrum*), and to evaluate factors that may influence variation within this population. I used location data from breeding eiders marked with satellite transmitters to describe spring migration from their wintering to nesting areas. To determine if an eider's timing of migration and length of stay at a stopover or staging area varied with weather, I evaluated meteorological variables from before the earliest migrant was reported until after the latest migrant had passed. I then examined these variables in relation to timing of movements and arrival at nesting areas. From these data, I describe annual and individual variation in migration timing and strategies, discuss how persistence of this variation might affect population stability, and predict changes in response to long-term climate change.

METHODS

POPULATION AND STUDY AREA

The study area includes coastal and nearshore waters of the northern Bering, eastern Chukchi, and western Beaufort seas (Fig. 1). From mid- to late winter, and in some years well into spring, this large area is generally ice-covered but has ephemeral flaw leads (offshore of land-fast ice) and polynyas. The eiders winter in openings in broken ice; ice is broken or gone in April (Brower et al. 1988a). The flaw leads and coastal polynyas of the eastern Chukchi Sea and western Beaufort Sea open and close repeatedly through the winter (Mahoney et al. 2007a). Through the mid-1980's ice-free areas appeared in the eastern Chukchi Sea in early May, and ice was gone by early August (Brower et al. 1988b). From 1996 to 2004 the region was free of fast ice two weeks earlier than in the 1970's (Mahoney et al. 2007a). Shore-fast ice around Peard Bay breaks up in early June, and the bay is ice-free later in June (Eicken et al. 2006). Along the Beaufort Sea coast open waters are found at the mouths of rivers and offshore leads. A lead from Mackenzie Bay, Canada, west to Point Barrow opens and closes through the winter, and waters at MacKenzie Bay are usually open by mid-May (Smith and Rigby 1981). In the western Beaufort Sea, open water is found between the coast and the shore-fast ice in May; ice becomes broken in early June and is gone by late June (Mahoney et al. 2007a). Seasonal shore-fast ice is variable along the eastern Chukchi Sea coast and more so off the western Beaufort Sea coast (Brower et al. 1988b).

Stringer et al. (1980) described the climate along the western Beaufort Sea coast as uniform. Winds along the western Beaufort Sea coast are predominantly from the northeast, east, and south in spring (May–June); weather at Pt. Barrow (71° 26′ N, 156° 27′ W) is cold and windy with very few calm days (Brower et al. 1988b). These prevailing winds play an important part in the occurrence of flaw leads and polynyas and can explain the general lack of open water in the western Beaufort Sea (Eicken et al. 2006). Along the eastern Chukchi Sea coast the weather is warmer, wetter, and more variable than that in the western Beaufort Sea (Stringer et al. 1980). Winds along the eastern Chukchi Sea coast are predominantly from the east and northeast in May and June; along the southeast

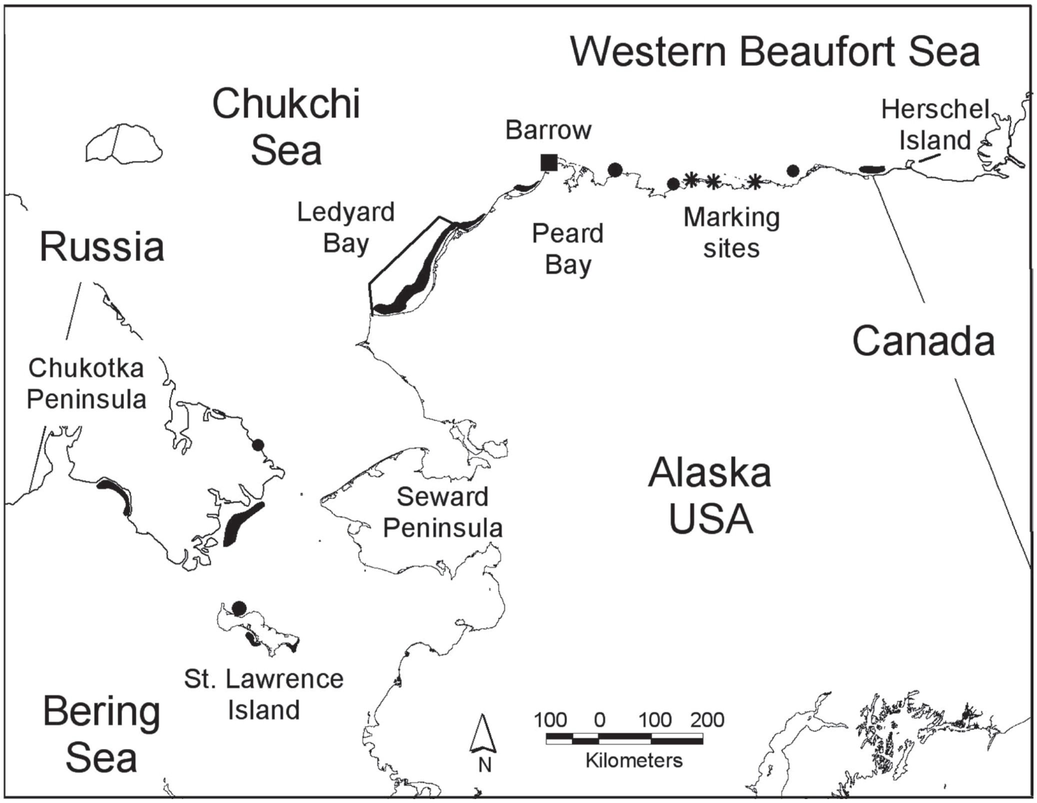

FIGURE 1. Areas of the Chukotka Peninsula and eastern Chukchi and western Beaufort seas used by Pacific Common Eiders marked with satellite transmitters. Staging areas (filled circles and polygons) outlined are based on high-quality (SD ≤ 1 km; Argos 2007) location data.

coast of the Chukotka Peninsula winds are variable but predominantly calm or from the north or south (Brower et al. 1988a, 1988b). During May and June along the coasts of the Beaufort and Chukchi (Ledyard Bay to Barrow, Alaska) seas, warmer temperatures are associated with winds from the south and southwest (Brower et al. 1988b).

In the western Beaufort Sea study area, Pacific Common Eiders nest on islands in loose colonies (Johnson and Herter 1989). Nests are initiated from mid-June through mid-July (Schamel 1977, Johnson et al. 1987, Flint et al. 2003). During my study, median nest-initiation dates were 24 June in 2001 and 1 July in 2002 (Flint et al. 2003). Birds nesting along the western Beaufort Sea coast winter 1300–2100 km distant in the Bering Sea (Petersen and Flint 2002). During spring, birds stage in coastal areas of the Chukotka Peninsula, northwestern Alaska, and Beaufort Sea (Fig. 1) (Petersen and Flint 2002), generally in waters within 50 km of shore and ≤30 m in depth (Petersen unpubl. data).

The general timing and characteristics of eider migration along the Beaufort Sea were first described by Murdock (1885). Subsequently birds migrating past Pt. Barrow have been monitored from land in spring and fall (Woodby and Divoky 1962, Thompson and Person 1963, Johnson 1971, Timson 1976, Suydam 1997, 2000b) and have been studied by radar there and elsewhere along the western Beaufort Sea coast (Flock 1973, Richardson and Johnson 1981, Day et al. 2004).

MARKING AND DATA COLLECTION

I located individuals by satellite telemetry to determine timing and routes of migration and to identify staging areas (Petersen et al. 1995, 1999, Beekman et al. 1996, Fox et al. 2003, Miller et al. 2005, Alerstam et al. 2006). I assumed a transmitter with a percutaneous antenna had only a small effect on the movement patterns of each individual. Using this type of transmitter in Canada Geese (*Branta canadensis*), Hupp et al. (2006) found a delay of 1 or 2 days in arrival date during a spring with less favorable migration conditions; they found no effect on nest-initiation dates, clutch size, mean egg volume, and propensity to nest. There was no measurable effect on annual survival of Common Eiders marked in 2000 (Petersen and Flint 2002); other effects were unknown.

In 2000, 2001, and 2003, Common Eiders were captured on their nests within a week of their eggs hatching and implanted with satellite transmitters (PTT-100s, 38–42 g, purchased from Microwave Telemetry, Inc.), according to surgical procedures described by Korschgen et al. (1996) with modifications by Mulcahy and Esler (1999), Mulcahy et al. (2003), and Iverson et al. (2006). In 2000, 10 birds were anesthetized with isoflurane and 10 with propofol (Mulcahy et al. 2003); in 2001 and 2003 all eiders were anesthetized with propofol. All birds were returned to their nests and released no sooner than 1 hour following surgery. Transmitters from females marked in 2000, 2001, and 2003, provided data in spring 2001, 2002, and 2004, respectively.

Transmitters deployed in 2000 were programmed to provide location data for 6 hours every 72 hours (3.25-day cycle) with enough battery power to last from deployment (July) through the following spring migration. In 2001 and 2003, transmitters were programmed to provide data for 6 hours every 19 hours (1.04-day cycle) from 15 April the following spring (2002 and 2004, respectively) until late June, when the batteries were expected to fail. Transmitters were equipped with sensors to monitor the bird's body temperature and battery's voltage, thereby providing data on the status of the bird (dead or alive) and the battery.

I used the ARGOS® Data Collection and Location System in Landover, Maryland (Argos 2007), to analyze transmitter signals. I used both standard and auxiliary locations. I used the filtering algorithm developed by Douglas (2006) to select the single best location within each 6-hr transmission period. I used the highest-quality standard location or, if two or more locations were of the highest quality, the location with the most signals. When only auxiliary locations (lower quality) were available, I selected the best of two or more locations on the basis of redundancy (minimum distance, rate, and angle) within that transmission period. I also retained sequential locations that indicated continuous directional movements (flight) within a 6-hr transmission period and retained only those locations that met angle and rate specifications.

I defined total migration period as the time it took an individual to travel from the wintering areas to the breeding area. I defined a migrating bird as an individual moving >50 km from its location the previous day and continuing to move in the same general direction on subsequent days (Petersen and Flint 2002, Petersen et al. 2006).

I evaluated locations of birds flying during the 6-hr transmission period (>100 km total distance) to determine their migration path. These eiders were assumed to continue in the same general location beyond the 6-hr flight period. Exceptions were when birds turned east near Pt. Barrow and when birds turned south onto the nesting area. For transmitters on a 25-hr cycle, if a bird was not recorded flying east past Pt. Barrow, I assumed the date the bird migrated was the first day it was observed past that point. Similarly, when an eider was not recorded in flight, I assigned the first date it was recorded at the nesting area as its arrival date. Arrival and departure dates of birds marked in 2000 (3.25-day cycle) and not recorded in flight were defined as the midpoint between dates; these data were not used in the analysis of the relationship between weather and migration. If winds on the estimated date of migration, however, were the same throughout the 3.25-day period the transmitter was off, I used the direction data from that estimated date.

An accurate and precise direction of flight based on sequential locations within a 6-hr transmission period cannot be determined from the location data. The quality of the locations that make up each track can vary from high (L1, L2, L3; SD ≤ 1 km; Argos 2007) to low (animal tracking) (L0 and LA, mean SD ≤ 7.5 km; LB, mean SD = 35.4 km; Britten et al. 1999). Although an animal may be migrating primarily in a single direction, the track line within the 6-hr period may change because of bird movement or appear to do so as a result of location error (Richardson and Johnson 1981, Pennycuick et al. 1996, Desholm 2003). I thus estimated track lines by eye to the nearest 10° block.

DATA ANALYSES

I used data from established stations to evaluate the effects of weather on the timing of migration as it may influence migration strategies. Weather data along the eiders' migration routes in Alaska are sparse and discontinuous. Complete data sets for spring 2001, 2002, and 2004 were available only from Barrow, 300–400 km from the western Beaufort Sea nesting areas and the demarcation point between the Chukchi and Beaufort seas. I purchased meteorological data for Barrow from the National Climatic Data Center (NCDC 2007). To evaluate how representative the years of the study were, I examined data on wind speed and direction during 2001, 2003, and 2004 relative to the long-term annual variability. I examined correlations of migration dates to local weather including minimum and maximum temperatures, temperature departures from normal, and resultant, average, and maximum 5-sec and 2-min wind speeds. I used resultant wind direction that had been categorized in 22.5° blocks (compass direction) to evaluate winds in relationship to migration movements.

I calculated the total migration time from the date the bird left the wintering area until its arrival at the nesting area and determined the amount of time an individual spent in the Chukchi Sea from the date it entered Ledyard Bay until it passed Pt. Barrow. Similarly, I calculated the amount of time an individual was in the Beaufort Sea by subtracting the date it passed Pt. Barrow from its arrival date at the nesting area.

On the basis of previous studies of migrating eiders in the region (Murdoch 1885, Johnson 1971, Woodby and Divoky 1982, Suydam et al. 1997, 2000b), I expected that the dates Common Eiders arrived at the breeding area were correlated with indices of wind, temperature, and general conditions as exemplified by the difference in mean temperature from that in April, May, and June of the previous 10 years. The date an individual migrated past a point was expected to be correlated with weather on that day. Weather data included here are from the 42 days from 10 May to 20 June, the 5 days before and after the first and last migrant, respectively. Because diurnal values of wind speed varied during May and June (Brower et al. 1988b) and the precise time many birds (67% of 37) passed Barrow was unknown, the local weather during flight could not be determined precisely. However, wind direction along the western Beaufort Sea coast varies little throughout the region (Brower et al. 1988b). Thus I assumed that weather on the date birds migrated past Barrow correlated with the daily averages provided by NCDC and that conditions at Barrow generally represented conditions up to 250 km from that weather station. I evaluated migration tracks after the birds moved east past Pt. Barrow toward the nesting area in relation to wind speed and direction at Pt. Barrow.

I used nonparametric tests to examine annual variation in migration dates and dates of arrival at breeding areas and Pearson's partial correlation coefficient (*r*) to examine correlations of arrival dates at nesting areas with weather variables. Following Zar (1996), I used the program Oriana V2 (Kovach 2003) to analyze velocity vectors. I used SPSS v.14 (SPSS, Inc. 2005) for other noncircular statistical tests. Migration dates are presented as median and quartiles (25% quartile Q_1, 75% quartile Q_3), linear data as mean ± SE. Angular data are presented as circular mean ± circular SD and *r* (length of mean vector). All tests were two-tailed, and samples were considered independent. Locations were mapped in stereographic projections centered at 65° N, 165° W.

RESULTS

Satellite transmitters implanted in 37 adult female Common Eiders (2001 = 12, 2002 = 7, 2004 = 18) provided information during spring migration. Sample sizes varied through the study; one bird was shot and two transmitters failed before birds arrived at the nesting area. Most (71%; $n = 1542$) of the daily locations between 15 April and 25 June were high quality (L1–L3), and redundancy of lower-quality locations was used to identify the remainder.

ANNUAL VARIATION

I detected no significant differences among years in the dates birds arrived in the Beaufort Sea (3 June, 28 May–5 June; $n = 37$, Kruskal–Wallis, $\chi^2_2 = 0.4$, $P = 0.81$) or at the breeding area (7 June, 5–13 June; $n = 34$, Kruskal–Wallis, $\chi^2_2 = 0.8$, $P = 0.67$). Therefore I pooled all years' data on arrival dates. Similarly, I detected no significant correlations of arrival dates at the nesting area with minimum or maximum temperature, temperature deviation from normal, wind speed, or annual deviations each year from the 10-year average for April, May, and June ($P > 0.2$).

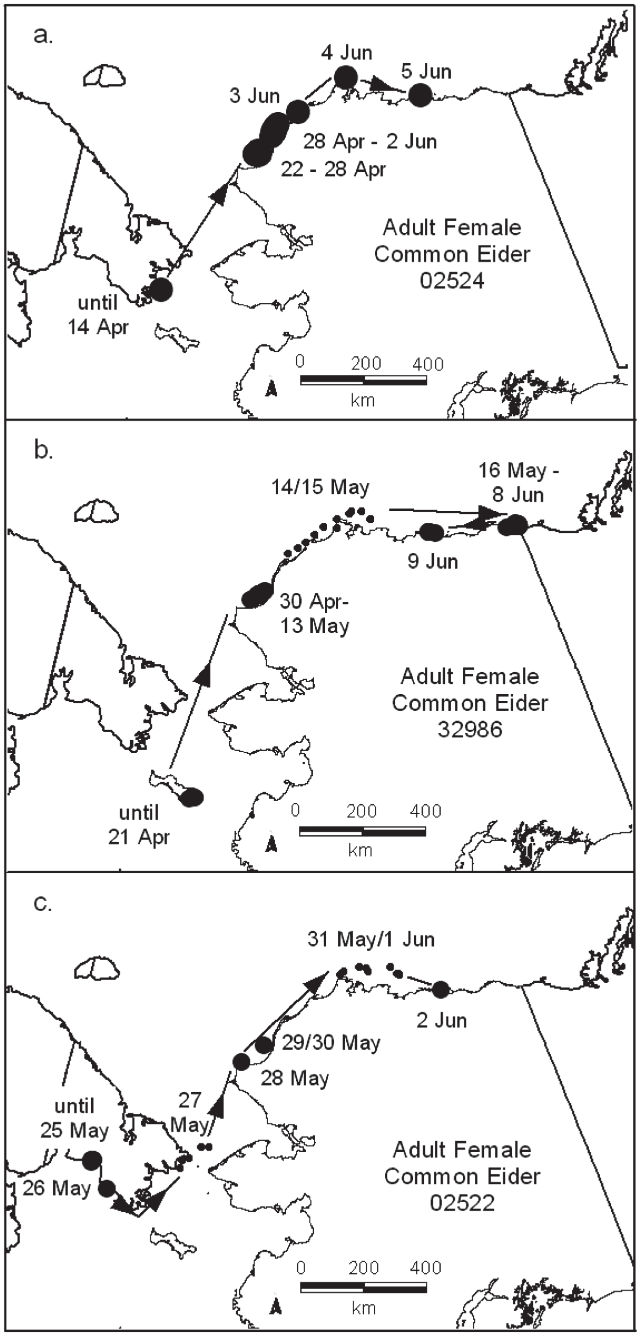

FIGURE 2. Examples of spring migration strategies of individual Common Eiders. Each map depicts a strategy: a, Chukchi Strategy; b, Beaufort Strategy; c, Winter Strategy. The first location is the wintering area, the last the subsequent year's probable nesting area. Arrows depict migration direction and link sequential locations; they do not describe an individual's migration route. Small filled circles identify sequential locations within a 6 hr transmission period. Larger filled circles represent daily locations.

MIGRATION STRATEGIES

Marked eiders used three distinct strategies when migrating from wintering to nesting areas. Fifteen individuals (41% of 37) staged in spring primarily in the Chukchi polynya then flew directly to the breeding area (Chukchi Strategy; Fig. 2a). Thirteen (35%) remained briefly at the Chukchi polynya then moved to staging areas in the Beaufort Sea (Beaufort Strategy; Fig. 2b),

TABLE 1. Length of stay within each staging area and total migration time of birds using each migration strategy.

Migration strategy	Days in Chukchi Sea (*n*)	Days in Beaufort Sea (*n*)	Migration time (days)
Chukchi	29 ± 2 (15)	1 ± 1 (14)	34 ± 3
Beaufort	16 ± 3 (13)	19 ± 1 (12)	34 ± 4
Winter	5 ± 1 (9)	1 ± 1 (8)	9 ± 2

where they either used open waters near the nesting area, moved east parallel to the coast to a recurring lead, or went west to the Peard Bay polynya. Nine (24%) eiders remained on the wintering area along the Chukotka Peninsula and St. Lawrence Island throughout the spring then migrated directly to the breeding area without staging elsewhere (Wintering Strategy; Fig. 2c). The proportion of individuals using each migration strategy did not differ ($\chi^2_4 = 1.70$, $P = 0.38$) by year.

The total migration time of birds using the various migration strategies differed, as did their length of stay at each staging area (Table 1). Eiders staging only in the Chukchi Sea remained there the longest; their total migration time, however, was similar to that of eiders staging both in the Chukchi and Beaufort seas. Birds staging in the Chukchi polynya left the wintering area the earliest (Table 2). Eiders staging in the Beaufort Sea arrived there before other birds, yet their final arrival at the previous year's nesting area was later (Table 2).

TABLE 2. Migration dates of individual Common Eiders staging in the Chukchi and Beaufort seas and the wintering area. Median and quartiles ($Q_1 = 25\%$, $Q_3 = 75\%$). Chukchi Sea, eastern Chukchi Sea primarily in waters off shore-fast ice of Ledyard Bay; Beaufort Sea, western Beaufort Sea in waters off shore-fast ice and near shore; wintering area, adjacent to the shore-fast ice of the eastern and southeastern Chukotka Peninsula coast and St. Lawrence Island.

Staging area	*n*	Median	Q_1	Q_3	Mean rank
Date left winter area[a]					
Chukchi Sea	15	8 May	29 Apr	12 May	14.1
Beaufort Sea	13	7 May	25 Apr	18 May	15.7
Wintering area	9	27 May	24 May	31 May	31.9
Arrived in Beaufort Sea[b]					
Chukchi Sea	15	5 Jun	4 Jun	10 Jun	27.2
Beaufort Sea	13	28 May	22 May	28 May	7.1
Wintering area	9	3 Jun	1 Jun	5 Jun	22.3
Arrived at nesting area[c]					
Chukchi Sea	14	6 Jun	5 Jun	11 Jun	14.9
Beaufort Sea	12	13 Jun	9 Jun	16 Jun	25.5
Wintering area	8	5 Jun	3 Jun	8 Jun	10.2

[a] Departure dates from the wintering area among birds using different staging areas (Kruskal–Wallis, $\chi^2_2 = 17.0$, $P < 0.001$).
[b] Arrival dates in the Beaufort Sea among birds using different staging areas (Kruskal–Wallis, $\chi^2_2 = 25.9$, $P < 0.001$).
[c] Arrival dates at the nesting area among birds using different staging areas (Kruskal–Wallis, $\chi^2_2 = 13.1$, $P < 0.001$).

Birds using the Beaufort Strategy flew 2075 ± 74 km before returning to the nesting area; birds using the Chukchi (1349 ± 45 km) and Winter (1471 ± 66 km) strategies migrated shorter distances (Kruskal–Wallis, $\chi^2_2 = 22.5$, $P < 0.001$). Eiders using the Beaufort Strategy either (1) first migrated to the breeding area then returned to the Barrow/Peard Bay region to stage before again migrating to the nesting area, or (2) continued migrating east to open waters near Herschel Island, Canada, substantially increasing their migration distance. Migration rates of birds using the Chukchi (46 ± 6 km day^{-1}), Beaufort (69 ± 9 km day^{-1}), and Winter (230 ± 49 km day^{-1}) strategies were significantly different (Kruskal–Wallis, $\chi^2_2 = 18.4$, $P < 0.001$).

WIND SPEED AND DIRECTION

From 1984 to 2005 wind speed and direction during the 42 days from 10 May to 20 June varied annually. In some years wind directions did not differ from a uniform (random) distribution (e.g., Fig. 3a). In other years winds were predominantly headwinds, but with higher ($r > 0.5$, $P < 0.01$) or lower ($r > 0.7$, $P < 0.001$) variability. In 2002 and 2004 winds were predominantly from the east (Fig. 3b, c). Over the 22-year period, wind speed and direction were not correlated in 18% ($n = 4$; $r < 0.25$, $P > 0.05$) of the years, highly correlated in 50% ($n = 11$; $r < 0.40$, $P < 0.001$), and very highly correlated in 32% ($n = 7$, $r > 0.40$, $P < 0.0001$).

In the three years of the study the proportion of days with headwinds (NNE–SSE) during the 42-day migration period did not vary (76%; $n = 126$, Kruskal–Wallis, $\chi^2_2 = 5.1$, $P = 0.08$). The migration strategies did not differ significantly in proportion of days with headwinds (Kruskal–Wallis, $\chi^2_2 = 5.8$, $P = 0.06$; Chukchi Strategy, 73%, Beaufort Strategy, 100%, Winter Strategy, 54%). Wind direction on days no birds migrated differed significantly from wind directions on the days they did migrate (Kruskal–Wallis, $\chi^2_2 = 35.9$, $P = 0.002$). I found a significant difference in the direction of headwinds between days when birds migrated (southeast; 139° ± 57°, $r = 0.61$) and those without migration (east; 90° ± 69°, $r = 0.49$) ($\chi^2_{15} = 35.5$, $P = 0.002$). Marked eiders migrated into headwinds, less often into headwinds from the east. I detected no significant difference ($n = 126$, $\chi^2_1 = 2.5$, $P = 0.12$) in the proportion of days with tailwinds on which marked eiders migrated (38%) or did not migrate (22%). Wind speed and direction were correlated in both instances (no migration, $r = 0.21$, $P = 0.01$; migration, $r = 0.53$, $P = 0.005$), although there is little evidence to suggest that birds tended to migrate during lower wind speeds (Mann–Whitney *U*-test, $n = 126$, $U = 1771$, $P = 0.77$).

The migration tracks of 12 of the 37 individuals were recorded between Barrow and the nesting area. These birds flew to the ESE (110° ± 17°, $r = 0.96$) into headwinds from the ESE (103° ± 48°, $r = 0.71$). On only one day were there tail-winds (from the WSW) when an individual was tracked migrating to the east.

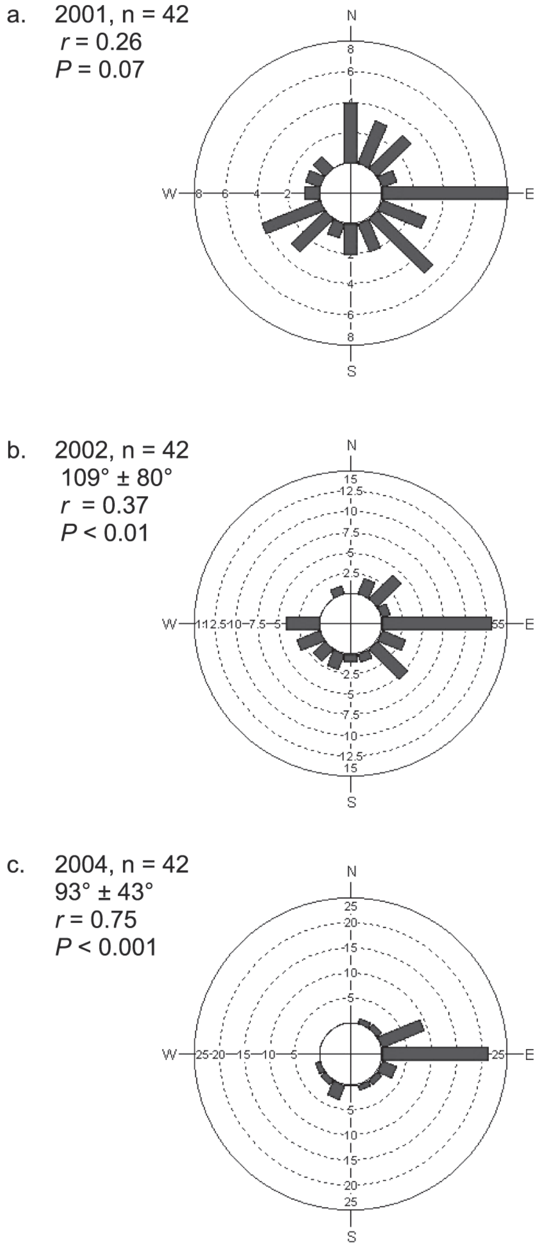

FIGURE 3. Wind directions at Barrow, Alaska, by year from 10 May to 20 June, presented in 22.5° blocks (compass direction). Data are presented as circular mean ± circular SD with χ^2 probability.

Wind speeds varied by year (Kruskal–Wallis, $\chi^2_2 = 7.6$, $P = 0.02$), with winds lighter in 2001 (4.1 ± 0.2 m sec^{-1}) than in 2002 and 2004 (5.1 ± 0.3 m sec^{-1} and 5.8 ± 0.4 m sec^{-1}, respectively). During migration of marked birds wind speed averaged 4.9 ± 0.4 m sec^{-1}.

DISCUSSION

I have shown that within a single breeding population of the Common Eider individuals used different spring migration strategies. These strategies were defined by the selection of and time spent at stopover locations during migration. There was no evidence to suggest that weather conditions (wind and temperature) during migration influence differences among migration strategies in the timing of migration observed. Each strategy may have different costs and benefits, which vary with the presence or absence of ice. These strategies are likely maintained by the high annual variability in ice patterns in the Chukchi and Beaufort seas and will likely benefit birds following one strategy over the others as the Arctic warms.

MIGRATION STRATEGIES

Spring migration strategies vary greatly among species as well as within species. Fidelity to stopover locations varies and is likely a result of availability of suitable habitat (see Newton 2008). For species with high fidelity to stopover sites, variation in use of these areas from year to year is frequently attributed to variability of weather, habitat, and physiological condition (Farmer and Wiens 1998, Beekman et al. 2002, Prop et al. 2003, Bauer et al. 2006) and, within a year, to differences of age and sex (Evans and Davidson 1990, Ueta and Higuchi 2002). It is likely that there are many populations that have a single wintering area and a single breeding area but comprise subgroups that have discrete, consistent migration strategies. The documentation of this, however, requires following individuals throughout their migration and has recently become possible with the use of satellite transmitters.

I show that Common Eiders from the western Beaufort Sea breeding population use three spring migration strategies that vary in duration of migration and stopover locations. Individuals using the Beaufort Strategy migrate to the nesting area early; birds using the Chukchi and Wintering strategies arrive at the same time but later than eiders using the Beaufort Strategy. Because they share common nesting and wintering areas, the distances they must travel are similar; however, individuals using the Beaufort Strategy migrate a greater total distance. Birds using the Wintering Strategy remain on the wintering area later in spring and migrate much more quickly than individuals using the other strategies.

In contrast to the variability I observed, Mosbech et al. (2006) found little difference in the duration of spring migration among various breeding populations of the Northern Common Eider (*Somateria mollissima borealis*) in Greenland and arctic Canada migrating by different routes. Although average migration speeds of Common Eiders migrating from Greenland were similar (Mosbech et al. 2006), those of the western Beaufort Sea were not. Mosbech et al. (2006) suggested that the similarity in the strategies they observed is maintained by the need to feed during migration or sea-ice conditions or both.

Common Eiders using the Beaufort Strategy migrated farther than birds using the other strategies. Although their strategy is energetically more costly, these individuals may benefit by remaining near the nesting area and moving early to nesting islands. Thus, they may still have an advantage over individuals that use other migration strategies (Alerstam and Lindström 1990).

The annual variability in migration strategies is consistent despite differences in weather conditions from year to year. There is high annual variability in ice conditions within regions used as stop-over locations (Smith and Rigby 1981, Brower et al. 1988a, 1988b, Eicken et al. 2006, Mahoney et al. 2007a). This variability may play some role in the maintenance of these migration strategies.

WEATHER EFFECTS

Migration of large numbers of waterfowl and shorebirds is often correlated with meteorological variables including temperature, change in temperature, and wind speed and direction, although the results of various studies are contradictory (reviews in Richardson 1978, 1990a, 1990b, 1991). Although confounded by small sample sizes, I could detect no correlation with local temperatures, wind speeds, and differences from 10-year mean temperatures (cold vs. warm springs) and dates of migration and arrival at the nesting area. In only one year, 2001, however, was there any substantial variability in weather as described by wind speed and direction.

Some waterfowl and shorebirds migrate in spring with tailwinds and avoid days with headwinds (Beekman et al. 1996, Pennycuick et al. 1996, Green et al. 2002, Fox et al. 2003). In the western Beaufort Sea, headwinds (northeast, east, and southeast) during the migration period predominated in May and June (Brower 1988b) with little annual variability. Common Eiders from the Beaufort Sea migrated during days with headwinds regardless of the variability in wind direction; even when winds were highly variable, there was no evidence to suggest that birds preferentially migrated on days with tailwinds (Byers and Dickson 2001, this study). This finding is consistent with the prediction of Weber et al. (1998) that if the probability of tailwinds is low, birds will migrate into less favorable headwinds. It is thus unlikely that during the years of my study wind direction influenced differences in the timing of migration observed among migration strategies. More likely, the dates of migration of individuals to their arctic breeding area reflected other factors affecting their survival and reproduction (Alerstam 2006) and were not significantly influenced by headwinds or weather, unless severe (Byers and Dickson 2001).

Winds influence ice distribution in arctic waters (Dunbar 1981, Smith and Rigby 1981, Stringer and Groves 1991, but see Mahoney et al. 2007b), and polynyas and flaw leads in the Beaufort and Chukchi seas are subject to rapid opening and closing (Stringer and Groves 1991). In combination with other factors, offshore winds may push free-floating ice away from the coast. Along the coast of the western Beaufort Sea, such winds are primarily southerly. A significant proportion of the western Beaufort Sea population of the Common Eider migrated into southeast headwinds, so they were more likely to encounter open waters near the nesting colonies.

POTENTIAL ICE EFFECTS

Late break-up of sea ice in spring has been correlated with delayed nest initiation in the Common Eider (Parker and Mehlum 1991, but see Lehikoinen et al. 2006) and delayed nest initiation and reduced clutch sizes in the Thick-billed Murre (*Uria lomvia*), Black-legged Kittiwake (*Rissa tricactyla*), and Glaucous Gull (*Larus hyperboreus*) (Gaston et al. 2005). Unusually severe ice conditions have resulted in mass mortality of sea ducks and may have a major impact on populations (Barry 1967, Fournier and Hines 1994, Robertson and Gilchrist 1998, Newton 2007). Unusual mortality and poor condition of Common and King (*Somateria spectabilis*) eiders have been reported from coastal areas of the northern Chukchi and western Beaufort seas (summarized by Myers 1958), in association with little open water at stopover areas, high winds, and ice-fog. Sea ice that remains well into spring near nesting areas may prevent access and nesting by sea ducks (McLaren and Alliston 1985). Similarly, ice persisting around islands may delay nest initiation or movement to different areas (Schamel 1977, Parker and Mehlum 1991, Flint et al. 2003).

Each of the three migration strategies used by Common Eiders in arctic Alaska has a different potential risk of mortality associated with ice movement. The high annual variability in ice conditions, however, likely assures that different groups of individuals benefit each year, depending on their migration strategies. Common Eiders that migrate early to the Beaufort Sea may encounter stopover areas closed in by ice or delayed break-up as a consequence of persistent easterly winds or become ice-covered in cold, calm weather but may nest quickly in years the ice retreats early. In the eastern Chukchi Sea waters open earlier than near the shore of the Beaufort Sea (Stringer et al. 1980, Brower et al. 1988b). Although unusual ice events in spring may close nearshore waters on the Chukchi Sea (Mahoney et al. 2004), waters generally remain open in May and June (Brower et al. 1988b), and birds have a more predictable access to forage. Ice is usually gone from the wintering areas in April or May (Brower 1988a, Stringer and Groves 1991), and eiders that remain here may benefit in years when ice persists late and delayed ice retreat opens foraging areas after other birds have migrated.

The different migration strategies may be maintained by the variability in survival and reproduction associated with constantly changing sea ice. Change of the Arctic Oscillation Index ultimately results in changes of water temperature and circulation and contributes to variability in ice conditions in the Beaufort Sea (Eicken et al. 2006). Also, other factors occurring at irregular intervals may result in abnormal ice patterns along the Beaufort Sea coast (Eicken et al. 2006). Analyses of the extent of sea ice in the southern Beaufort and Chukchi seas suggest an annual decline of 3.3% per year from 1988 to 2001 (Belchansky et al. 2004a). However, the length of time sea ice takes to melt in the northern Chukchi Sea varies substantially from year to year (Belchansky et al. 2004b). From 1996 to 2004 break-up of coastal ice in the western Beaufort Sea was three weeks earlier than from 1973 to 1977 (Mahoney et al. 2007a). On average this trend would favor individuals migrating early to the Beaufort Sea. Annual variation in sea ice, however, would favor individuals using other strategies in years of extremely extensive sea ice and late break-up.

INDIVIDUAL VARIATION

Individual variation in staging strategies may result in differing reproductive success and survival; however, it is unlikely these annual differences affect population trends and numbers (Newton 2006, 2008). On the basis of studies on Anatidae, Arzel et al. (2006) also concluded that these types of environmental conditions are proximate factors influencing reproductive success. In the infrequent years of extreme ice when key wintering or staging areas become iced in or severely restricts access, a large proportion of birds may die (Barry 1967, Fournier and Hines 1994). If the Pacific Common Eider population of the Beaufort Sea continues to decline as it did from 1976 to 1996 (Suydam et al. 2000a), such mortality could have a major effect on the population. As the pack ice continues to recede in the Arctic, major ice events become more likely (Mahoney et al. 2004). Also, concurrent changes in the distribution and abundance of forage species may have corresponding detrimental effects on sea-duck populations (Dickson and Gilchrist 2002). The individual variability in migration strategies may lessen the effect on the population of a catastrophe at any single staging area.

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