KING EIDER MIGRATION AND SEASONAL INTERACTIONS AT THE

INDIVIDUAL LEVEL

By

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KING EIDER MIGRATION AND SEASONAL INTERACTIONS AT THE

INDIVIDUAL LEVEL

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Abstract

Seasonal interactions describe how events during one season of the annual cycle of a migratory bird affect its fitness in subsequent seasons. Understanding the strength and mechanism of seasonal interactions is important to predict how migratory birds will respond to future challenges caused by habitat loss and climate change.

This dissertation explores seasonal interactions between different stages of the annual cycle in an arctic-breeding sea duck, the King Eider (*Somateria spectabilis*). Concerns over recent population declines and potential effects of climate change on marine habitats used by the species highlight the need for a better understanding of its life history. I used satellite telemetry to describe migration routes, timing of migration events, and geographic regions used by King Eiders throughout the year. I found highly variable movement patterns, and wide dispersion of King Eiders to three regions in the Bering Sea during winter. I then developed stable isotope techniques to examine seasonal interactions at the individual level. First, I examined the relative contribution of body reserves to egg production using stable isotope analysis of egg components and blood. I found that most birds use only small proportions of body reserves to produce eggs, but rather rely on nutrients obtained on breeding grounds to form a clutch. Thus, contrary to general expectation, King Eiders use an income strategy to produce eggs, and I hypothesize that they may retain body reserves for incubation. Body reserves may reflect the residual body condition from the previous winter. I further examined whether females wintering in different regions in the Bering Sea had different rates of nest survival. The northern Bering Sea has a higher benthic biomass and is closer to breeding grounds than winter regions farther south. However, nest survival rates of female King Eiders in northern Alaska did not differ between females that had wintered in the northern or southern Bering Sea.

Overall, I found large individual variation in movement and breeding strategies, and little evidence for strong seasonal interactions between winter, spring, and summer. This indicates that King Eiders are a very adaptable species that depend on resources acquired on breeding grounds to a larger extent than previously assumed.

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Introduction

Seasonal interactions describe how events or conditions during one season of the annual cycle of a migratory bird affect its fitness or behavior in subsequent seasons. Seasonal interactions have recently been found to be important in migratory birds, both at the population and individual level (Marra et al. 1998, Gill et al. 2001, Norris and Marra 2007). At the population level, seasonal interactions result from density-dependent effects during different stages of the annual cycle. If changes to a species' habitat during one season result in mortality and a decrease in population size, the reduced population may achieve higher per-capita fitness in a following season due to reduced density (Webster and Marra 2005, Norris and Marra 2007). At the individual level seasonal interactions describe non-lethal residual effects of events during one season on the fitness of individuals in subsequent seasons. These so-called 'carry-over effects' are mediated via the body condition of individuals – if events during one season result in poor body condition, then the fitness of individuals in subsequent seasons can be reduced (Norris et al. 2003, Studds and Marra 2005, Lehikoinen et al. 2006).

For migratory bird species the examination of seasonal interactions requires knowledge of the geographic areas used during the annual cycle. Areas used during and outside the breeding season are connected via the movement of individuals, and the pattern of those connections is described by the term 'migratory connectivity' (Webster et al. 2002, Webster and Marra 2005). If migratory connectivity is strong, all individuals from a single breeding area winter in the same wintering area and vice versa. At the opposite end of the spectrum, weak or diffuse connectivity describes a breeding population that is composed of individuals that winter in several separate wintering areas and vice versa (Webster et al. 2002, Webster and Marra 2005). Determining the degree of migratory connectivity is essential to elucidate the mechanisms by which seasonal interactions may affect populations of migratory birds. In turn, understanding the strength and mechanism of seasonal interactions is important to predict how migratory birds will respond to future challenges caused by habitat loss and climate-driven habitat changes (Webster and Marra 2005, Norris and Taylor 2006).

Carry-over effects at the individual level are important in birds that rely on body reserves during the breeding season. Most arctic-nesting species of waterfowl, including many sea ducks, rely to some extent on stored body reserves for either the formation of eggs or to cover metabolic costs during incubation (Ankney and MacInnes 1978, Parker and Holm 1990, Kellett and Alisauskas 2000). Sea ducks nesting in the Arctic are therefore likely subject to seasonal interactions (Lehikoinen et al. 2006). Many of these species have suffered population declines over the past decades (Kertell 1991, Stehn et al. 1993, Ely et al. 1994, Goudie et al. 1994, Conant and Groves 1995, Dickson et al. 1997, Gratto-Trevor et al. 1998, Mosbech and Boertmann 1999, Suydam et al. 2000). The causes of these declines are poorly understood, but ecosystem changes on wintering areas leading to lower adult survival and physical body condition are suspected to play a role in the declines of several species (Lovvorn et al. 2003, Petersen and Douglas 2004). Changes to sea duck habitats at sea have occurred as a result of warming water temperatures and receding sea ice over the same time period in which sea duck populations declined (Grebmeier et al. 2006, Walsh 2008). Benthic communities, which form the main prey source for sea ducks, have experienced changes in species composition and total biomass (Richman and Lovvorn 2003, Lovvorn et al. 2005, Bluhm and Gradinger 2008). These changes may adversely affect the body condition of sea ducks during winter, and may carry over to the breeding season resulting in poorer reproductive performance (Lovvorn et al. 2003, Lehikoinen et al. 2006). Elucidating the importance of such carry-over effects requires a better understanding to what extent sea ducks rely on body reserves accumulated at sea throughout the annual cycle.

This dissertation addresses several questions regarding the life history of a widespread arctic sea duck – the King Eider (*Somateria spectabilis*). While this species is still common, populations in North America have declined substantially between the 1970s and 1990s (Frimer 1995, Gratto-Trevor et al. 1998, Mosbech and Boertmann 1999, Suydam et al. 2000, Dickson and Gilchrist 2001), and the causes for population declines are unknown. Changes to marine habitats used outside the breeding season have been suspected as potential causes of population declines. In this dissertation, I will examine to

what extent breeding and non-breeding seasons are linked for King Eiders in Alaska. This will improve knowledge of King Eider life history and enable predictions of how King Eiders may respond to projected changes to their habitats.

The dissertation is structured in three parts examining migratory and winter movements (Chapters 1 and 2), the interaction between spring migration and egg formation (Chapters 3–5), and potential carry-over effects between winter and breeding season (Chapters 6 and 7).

In Chapter 1, I describe migration distances, phenology, and winter movements of King Eiders in the Bering Sea. This chapter examines the degree of migratory connectivity between western North American breeding grounds and wintering regions in the Bering Sea. I show that there are three distinct wintering regions in the Bering Sea, and that migratory connectivity is weak. Chapter 1 thus sets the stage for further investigations of seasonal interactions in relation to conditions in those three winter regions.

Chapter 2 examines the winter ecology of King Eiders in more detail by exploring factors that may motivate individual birds to depart from a winter site and fly to another site. I consider effects of sea ice cover, habitat quality, geographical location, and day length, and incorporate individual differences in movement behavior in a new analytical approach using an algorithmic RandomForest model. This chapter provides quantitative evidence of the large individual variability in movement behavior, and thus offers some insight to large individual variation found in the remainder of my dissertation.

Chapters 3-5 revolve around the question to what extent King Eiders use body reserves accumulated during migration for the synthesis of eggs. Eiders are usually considered capital breeders, relying on endogenous reserves for reproduction, and eggs should therefore contain a large proportion of marine-derived nutrients. This assumption has largely been based on studies of Common Eiders (*S. mollissima*). I examine the allocation of nutrients to King Eider eggs using stable isotopes. Existing applications have not accounted for individual variation, so I first developed a technique to account for individual differences in food choice on breeding grounds. This technique is

presented in Chapter 3, which shows that isotopic values of eggshell membranes do not change during incubation. The membranes, which can be collected from hatched and depredated nests, offer a female-specific isotope signal of diet consumed during egg formation. Chapter 3 thus introduces one of the endpoints of the isotope mixing model used in Chapter 5.

Lipids can confound the interpretation of isotope studies. Because egg yolk consists of a large proportion of lipids, they need to be examined separately in isotopic nutrient allocation studies. Separation is achieved through chemical lipid extraction prior to isotope analyses of egg yolk. In Chapter 4 I take a closer look at how this procedure affects stable isotope ratios, and whether there is an alternative in the form of arithmetic correction. I conclude that arithmetic correction is currently not an option for wild migratory birds.

Chapter 5 combines the techniques and findings from the two previous chapters to examine in detail the origin of nutrients in King Eider eggs in northern Alaska. I use two different mixing model approaches, at the individual and population level, to examine the origin of both carbon and nitrogen in egg yolk and albumen. Data for this chapter were collected during three seasons (2005-2007) at two sites, and I contrast the two sites where eggs were collected in the context of their distance from an important spring migration site (Chapter 8) where nutrient reserves could be accumulated. I found individual differences in foraging, and show that there are also individual differences in nutrient allocation strategies. Overall, this chapter refutes the idea that King Eiders are capital breeders, as most of the nutrients in eggs are derived from food obtained on breeding grounds.

Chapters 6 and 7 examine carry-over effects between winter and the breeding season at the individual level. Such carry-over effects have recently been found in migratory songbirds (Marra et al. 1998, Norris 2005, Norris and Marra 2007) and some larger waterbirds (Lehikoinen et al. 2006, Guillemain et al. 2008, Hebert et al. 2008, Yerkes et al. 2008). Given concern about changes to the benthic prey base of King Eiders in the Bering Sea (Bluhm and Gradinger 2008), I examine whether nest survival of King

Eiders in Alaska differs among birds that winter in regions in the Bering Sea that have different amounts of available benthic prey resources. I first develop a technique that assigns nesting females to a winter region in the Bering Sea using stable isotope ratios of feathers (Chapter 6). I then use the data from females captured on nests with known nest fates to explore whether females wintering in different regions achieve equal nest survival (Chapter 7). Despite hypothesized advantages for birds wintering in the northern Bering Sea, nest survival was similar among winter regions.

Chapters 1, 5, and 7 indicate that the eastern Chukchi Sea is an extremely important staging area on spring migration for King Eiders. This region is currently being considered for oil and gas development, thus a description of when and how long birds use the eastern Chukchi Sea is needed for managers to assess the importance of this region. In Chapter 8 I summarize data from 10 years of satellite telemetry to demonstrate the importance of the eastern Chukchi Sea to a large portion of King Eiders breeding in the western Arctic.

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1. Timing and Distance of King Eider Migration and Winter Movements[1]

1.1.   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 103 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.

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

1.2. 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 1995, Mosbech and Boertmann 1999), and during migration have declined substantially (Suydam et al. 2000, Dickson and Gilchrist 2001). The causes for 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.

1.3. Methods

1.3.1. 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, two males (3% of all birds marked) died within three weeks of surgery, and seven more birds (9%) died in spring or summer the year after they were equipped with transmitters. In six 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, one 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.

1.3.2. 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 the trigger for migration (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.

1.3.3. 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 direction (extension or substitution of fall migration) or a northerly direction (precursor of spring migration). 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.

1.3.4. 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.

1.3.5. 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.

1.4.   Results

1.4.1. 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).

1.4.2. 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, 18 October–12 January, $n = 42$; females: ± 26 days, 9 September–10 January, $n = 24$).

1.4.3. 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 between 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, did not differ between sexes

(U = 1033, P = 0.87), among years (χ^2_3 = 0.3, P = 0.96, n = 93), or among the three main wintering regions (χ^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 (χ^2_3 = 2.0, P = 0.58).

1.4.4. 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 (110°E) to Victoria Island, Canada (110°W). 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).

Males and females tagged in northern Alaska started 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 (Spearman $r_S = –0.21$, $P = 0.17$, $n = 42$).

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 nine males migrating to breeding sites in Siberia used this area on spring migration.

1.5.   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 (Oppel and Powell 2009).

We therefore believe that transmitters are unlikely to introduce directional bias in our estimates of migration timing and pattern (Wilson and McMahon 2006).

1.5.1. 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 because reproducing females 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 form 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 more closely 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 migration for several species of birds (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.

1.5.2. 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 high variation and low intrayear site fidelity (Robertson and Cooke 1999) for King Eiders.

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.

1.5.3. 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 (Fig. 1), 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.

1.5.4. Conclusions

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.

## 1.6.	Acknowledgments

1.7.   Literature Cited

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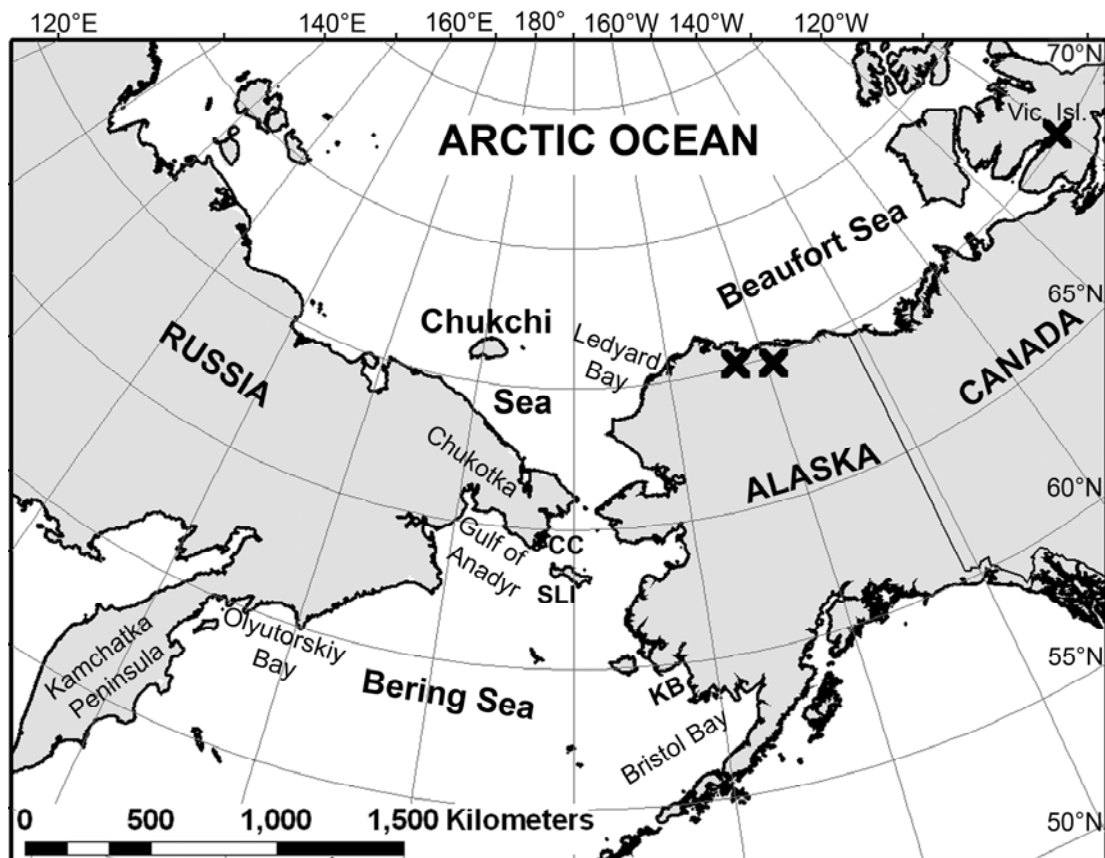
Figure 1.1. Map of northwestern North America and eastern Russia. Locations where King Eiders were captured 2002-2006 are indicated by crosses. Illustrated in a Lamberth Azimuthal map projection centered on 65°N and 170°W. Vic. Isl. = Victoria Island, CC = Cape Chukotskiy, SLI = St. Lawrence Island, KB = Kuskokwim Bay.
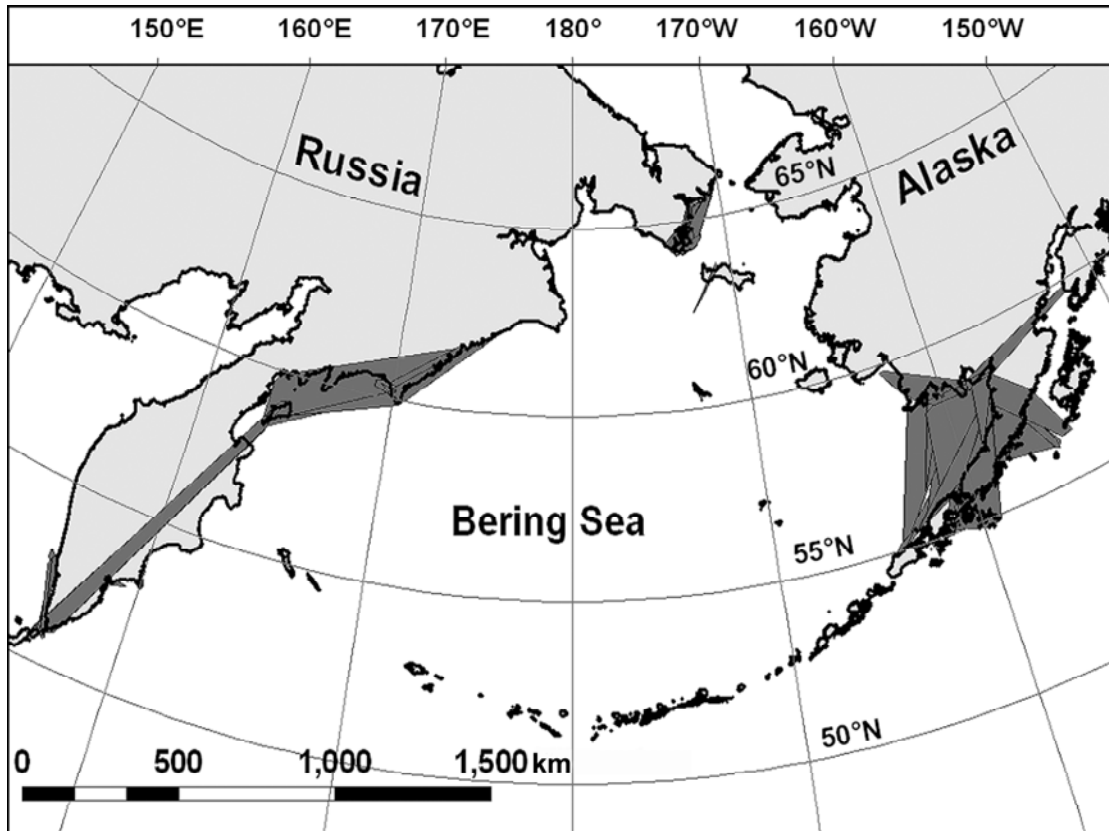
Figure 1.2. Winter ranges of King Eiders in southwestern Alaska and eastern Russia. Calculated as 95% minimum convex polygons from 93 King Eiders tracked with satellite transmitters between 2002 and 2006. Each dark polygon indicates the range of movements of an individual but does not imply its usage of the entire area. Three regions with nonoverlapping ranges can be recognized.
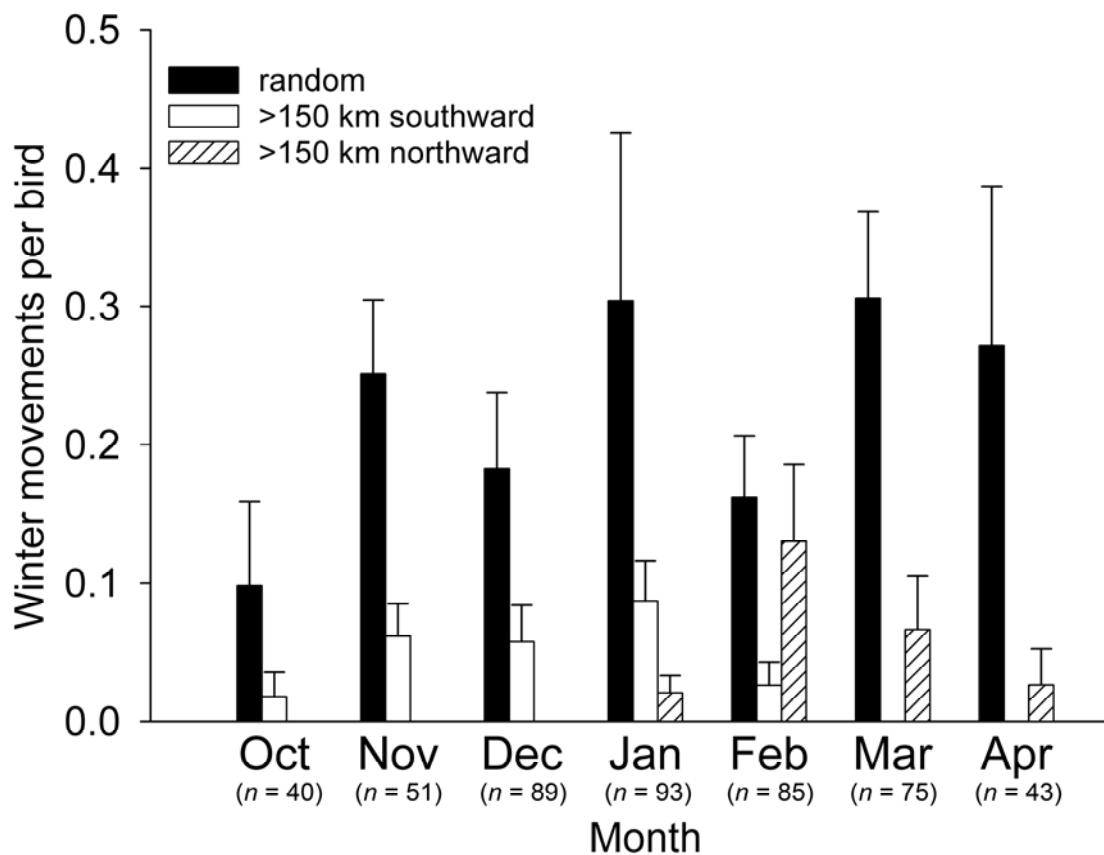
Figure 1.3. Mean number (+ SE) of winter movements per individual King Eider for different months of the nonbreeding period. Calculated from 93 satellite-tracked King Eiders in the Bering Sea between October 2002 and April 2006. White columns show random movements (50–150 km), black columns show movements as extension or substitution of fall migration (>150 km southward), and cross-hatched columns show movements as precursors of spring migration (>150 km northward). Sample sizes indicate the number of wintering birds tracked in each month.

Table 1.1 Range and average timing of migration events for adult male and female King Eiders. King Eiders were 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.

Migration Event	Male				Female			
	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 Jan
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 1.2. Minimal travel distance (km) for King Eiders tracked with satellite telemetry. King Eiders were tracked from breeding areas in 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

2. Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck[1]

2.1.   Summary

Many migratory birds are assumed to remain fairly stationary during winter. However, recent research indicates that mid-winter movements are evident in a variety of bird species, and the factors causing individuals to move are poorly understood.

We examined the winter movements of 95 individual king eiders (*Somateria spectabilis,* L.) tracked with satellite transmitters in the Bering Sea between 2002 and 2006 to explore whether environmental factors such as day length, location, sea ice, and habitat quality could explain the occurrence of winter movements longer than 50 km.

We used a novel algorithmic random forest model to assess the importance of variables predicting whether a bird remained or departed from a wintering site.

We found extremely high individual variability in winter movement decisions by king eiders. The most important variable was the individual bird, followed by location, date, and an indicator of body size.

We conclude that individual strategies exist that interact with environmental conditions to form multiple movement patterns.

While a minor proportion of winter movements may be forced by environmental conditions, we propose that many winter movements may be of an exploratory nature where individuals aim to acquire information about alternative wintering sites that

may enhance their survival probability at some point in time when environmental fluctuation renders their preferred wintering site unsuitable.

Key Words: algorithmic model, king eider, random forest, social information, winter movements

2.2.   Introduction

The winter period of migratory birds has received less attention than other parts of the annual life cycle. Many migratory birds are believed to be relatively sedentary at a single wintering site at which they arrived following migration (Robertson and Cooke 1999b, Remsen 2001, Stouffer 2001). Some species, however, retain the physiological ability to conduct long-distance movements in winter. Such patterns have been described for passerine migrants (Lack 1983, Terrill and Ohmart 1984, Pearson and Lack 1992), non-passerines (Ruiz et al. 1989, Berthold et al. 2002), and especially arctic nesting waterfowl wintering at temperate or sub-arctic latitudes (Haila 1980, Fox et al. 1994, Vaitkus 1999). Food availability is recognized as an important factor governing winter movements (Fox et al. 1994, Lindberg et al. 2007), but in many cases it remains poorly understood what factors influence variation in movement decisions among individuals.

Most ducks of the tribe Mergini (sea ducks) spend the winter in marine environments in temperate or sub-arctic latitudes where they forage for invertebrate prey by diving to the sea floor (Madge and Burn 1988). Most sea ducks live in social congregations during the non-breeding period. While some species have been shown to remain within a small discrete area throughout winter (Petersen and Douglas 2004, Iverson and Esler 2006), some sea ducks in the Baltic Sea are known to conduct extensive winter movements (Haila 1980, Vaitkus 1999). These movements are generally believed to be facultative extensions of fall migration, triggered by ice formation that

abruptly renders wintering sites at higher latitudes unsuitable. As sea ducks require open water to forage, sea ice cover that prevents access to open water will force birds to move away from an area (Guillemette et al. 1993, Bump and Lovvorn 2004). Sea ice can build up very rapidly, thus forcing all ducks at a given area to depart simultaneously. The common pattern of winter movements is therefore one of mass movements of ducks from northern to more southern wintering sites once sea ice cover prevents efficient foraging (Haila 1980, Vaitkus 1999).

King eiders (*Somateria spectabilis,* L.) in the Bering Sea winter over a large latitudinal range, from 50°N to 65°N (Suydam 2000, Phillips et al. 2006)(Fig. 2.1), thus covering areas that range along a gradient from ice free to areas that are largely covered by sea ice for several months of the year. Through recent satellite telemetry we have established that king eiders display a very large individual variation in winter movements, with some birds travelling 1500 km in winter between up to four different wintering sites, whereas other birds remain at a single site throughout the entire wintering period (Oppel et al. 2008). In this study we examine a variety of environmental factors that may contribute to an individual's decision to stay at a site or to move to another site during the winter period. In order to account explicitly for individual variation we used a novel multivariate algorithmic modelling approach to examine which factors are most influential in the decision of individuals to depart from a wintering site.

Based on available information from other systems, we hypothesized that the probability of king eiders moving away from a wintering site should increase with (i) increasing sea ice cover (Vaitkus 1999, Bump and Lovvorn 2004), (ii) decreasing food abundance (Guillemette et al. 1996, Lindberg et al. 2007), and (iii) decreasing day length (Systad et al. 2000, Mosbech et al. 2006). We also predicted that most movements would be conducted by several individuals wintering at the same site at the same time.

2.3.   Materials and methods

2.3.1. Satellite telemetry

From 2002 through 2005 we trapped 80 adult pre-breeding king eiders in Alaska, USA
(32 females, 48 males), and 23 (10 females, 13 males) in the Northwest Territories,
Canada, and equipped each bird with an intra-abdominal satellite transmitter (38g PTT
with external whip antenna, Microwave Telemetry Inc., USA). We captured 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). We measured wing chord
length of each bird using a ruler, and culmen and total tarsus length using digital
callipers. The transmitters were implanted following standard surgical methods described
by Korschgen et al. (1996) and Mulcahy and Esler (1999). We released king eiders two
hours after surgery where they were caught. Transmitters were programmed to different
duty cycles throughout the year, with shorter duty cycles (4-6 hrs of transmission every
1-4 days) from June through November, and longer duty cycles (6 hrs every 6-7 days)
from December through March. In this analysis we consider only birds that survived with
an intact transmitter until spring migration (n = 95). Further details on annual migration
timing and distances, as well as mortality of tagged individuals have been presented
elsewhere (Oppel et al. 2008, Chapter 1). We did not find any significant difference in
movement parameters pertaining to the winter period between birds captured in Canada
and Alaska, among years, or among sexes (Oppel et al. 2008, Chapter 1), and therefore
pooled the data for the present study. Migration of satellite-tracked birds conformed with
ground observations of unmarked king eiders near Barrow, Alaska (Suydam et al. 2000,
Day et al. 2004) and in the Beaufort Sea (Dickson and Gilchrist 2001), and we do not
have any evidence that suggests that birds implanted with a transmitter exhibited
abnormal movements. We received location data from Service ARGOS and filtered them
for unreasonable locations using the Douglas ARGOS Filter algorithm (Douglas 2006).

This algorithm selected the best location per duty cycle based on the ARGOS location class and the distance, angle and rate to the previous and subsequent locations (Kenow et al. 2002). The filter program also provided the distance between subsequent locations calculated as great circle routes, the shortest possible distance between two points on the surface of the earth accounting for the curvature of the surface (Imboden and Imboden 1972). We imported all locations into ArcGIS 9.1 on a Lambert Azimuthal projection centered on 65° N and 165° W, and overlaid all locations with layers containing environmental information (see below).

2.3.2. Definition of winter and winter movements

Due to large differences in the extent and timing of migration, the wintering period needs to be defined carefully based on migratory strategies (Remsen 2001, Stouffer 2001). We defined the wintering period for each individual separately as the time between the end of outward migration and the onset of spring migration, as indicated by the information from individuals' satellite telemetry data. The outward migration of a king eider can consist of two components, the obligate molt migration (June – September) and a facultative fall migration (September – December) not undertaken by all individuals. Due to these differences in migration strategy, individuals could arrive on their wintering grounds either after molt migration or after fall migration. The length of the wintering period ranged from 39 to 287 days among individuals, and spanned the period between late July and late May the following year (Oppel et al. 2008, Chapter 1).

During this time period we considered any movement of more than 50 km as a discrete winter movement, corresponding to ca. 10% of all displacements recorded by satellite telemetry during the winter period. If an individual conducted two movements in sequence, indicated by three or more successive locations being > 50 km from the previous location, we counted this as one movement if the absolute turning angle at the intermediate location was < 90° and as two separate movements if the absolute turning

angle was > 90°. We used 50 km as a cut-off as this distance exceeds common foraging movements of wintering sea-ducks (Iverson and Esler 2006, Merkel et al. 2006).

2.3.3.   Correlates of winter movements

To assess whether king eider winter movements represent winter escape movements in response to environmental conditions, we first calculated the proportion of winter movements that occurred simultaneously among individuals at a given site, and then calculated the change in sea ice cover at the departure site for the time interval of the respective movement.

To calculate the proportion of movements that were initiated simultaneously by more than one individual, we defined simultaneous movements as those initiated by two or more individuals within seven days and originating from within 25 km of each other. Depending on the number of birds from which satellite-transmitted locations were available at a given site and time, we divided the results into three categories: (1) no other bird moved simultaneously, (2) all other birds moved simultaneously, or (3) some birds did move simultaneously but some birds did not. Winter movements of individuals that originated from sites with no other satellite-tracked bird present at the same time within 25 km were excluded from this analysis (50 of 177 movements, 28%).

We then obtained sea ice coverage files from the US National Ice Center (National Ice Center 2006), which are freely available for the entire Bering Sea at a temporal resolution of 3-4 days. Sea ice coverage maps delineate areas of homogenous sea ice concentration, which are reported for each area in categories corresponding to sea ice cover (in 10%) of that area. We overlaid all king eider positions relating to winter movements with the sea ice coverage file for the specific date of the recorded location using ArcGIS. These were the location from which a movement originated (departure location), and the location at which a movement terminated (arrival location). To track the change in sea ice cover at the departure location over the time frame during which a

movement occurred, we also overlaid the departure location with the sea ice file corresponding to the arrival date of the respective movement. If sea ice coverage files were not available for the exact date of a recorded bird location, we used the closest available on the 'safe' side of the location, i.e. 1-2 days prior to the date of departure locations or 1-2 days after the date of arrival locations. We then examined at the population level whether sea ice concentration differed between departure and arrival locations, as well as before and after a movement by calculating a departure index of the respective frequency distributions (Menning et al. 2007). This index quantifies the direction and magnitude of a difference between two frequency distributions. We constructed 95% confidence intervals around the reference distribution (sea ice concentration at departure location prior to movement) by taking 1000 bootstrap samples with replacement from the reference data, and considered the departure index statistically significant if it fell outside the 95% confidence intervals (Menning et al. 2007).

2.3.4. Multivariate modelling of departure decisions

To determine what factor is most important for a king eider's decision to stay at or depart from a wintering site we constructed a multivariate model of departure decisions including 13 environmental and 5 bird-specific predictor variables (Table 2.1). Using sequential observations of individuals in ecological studies is frequently addressed by using mixed effects models, in which the individual is included as a random effect to overcome potential effects of pseudo replication (Austin et al. 2006, Gillies et al. 2006). In applications with a binary dependent variable, where the goal is to rank competing models to infer the importance of variables, the application of mixed effects models becomes problematic as the calculation of Akaike's information criterion is not straightforward (Vaida and Blanchard 2005). Selection of mixed effects models with a binary dependent therefore currently requires a stepwise approach, which may introduce bias (Whittingham et al. 2006). We used a novel approach with an algorithmic random

forest model (Breiman 2001a) to determine the importance of predictor variables. A random forest is a machine learning algorithm based on classification and regression tree analysis (Breiman et al. 1984, De'ath and Fabricius 2000) that combines a large number of single trees for prediction. This technique is known to be robust against over-fitting, can accommodate a large number of predictor variables, and yields highly accurate predictions (Breiman 2001b, Prasad et al. 2006, Cutler et al. 2007). We explored which factors affect an individuals' decision to depart from a site by classifying locations as stationary (<25 km distance to the next accepted location of that individual) or departing from a winter site (>50 km to next location). To our knowledge, this is the first time that a machine learning algorithm has been applied to elucidate behavioural patterns of wild animals.

We used a random forest procedure with unbiased classification trees based on a conditional inference framework (Hothorn et al. 2006b) to overcome bias in variable importance measures among categorical variables with different numbers of levels (van der Laan 2006, Strobl et al. 2007). We constructed 1500 regression trees and used a random subset of 64% of the data without replacement to build single trees. We validated our model by applying model output to the remaining data to estimate accuracy of predictions. Model performance was assessed by the area under a relative operating characteristics (ROC) curve (Mason and Graham 2002). The importance of a variable was calculated with a permutation procedure, where the values for a given variable are randomly permuted over the test data set and the resulting reduction in model accuracy is assessed. Variable importance is inversely related to the reduction in model accuracy after permutation (Strobl et al. 2007). For easier interpretation, the variable importance was standardized, with the most important variable being assigned a relative variable importance of 100%. We conducted our analyses in R 2.5.0 (http://www.r-project.org/index.html) with the add-on package "party" (Hothorn et al. 2006a).

We used the following predictor variables (Table 2.1): individual identity, sex, indicators of the structural body size of each bird (wing length, tarsus length, and culmen length), the bird's location (latitude and longitude), the broad geographic region (northern

Bering Sea, eastern Bering Sea around Bristol Bay, Alaska, and western Bering Sea along the coast of Kamchatka, Russia, Fig. 2.1), date, day length calculated for every location as a function of date and latitude, sea ice cover at each location prior to departure and a week after departure, and benthic biomass as an indicator of food abundance.

King eiders forage mainly on benthic invertebrate prey at sea (Suydam 2000, Merkel et al. 2007). Quantification of prey availability is difficult due to logistical constraints in accessing all areas where king eiders winter and by the lack of knowledge of feeding preferences and prey items consumed. We therefore used model-predicted information on the abundance of benthic biomass in the Bering Sea. This benthic biomass model was built using a similar random forest procedure as described above (Huettmann and Oppel 2007). Briefly, we used publicly available benthic biomass data from 624 sampling stations in the Bering Sea to relate biomass (wet weight in g m^{-2}) to sea surface temperature, bathymetry, long-term average sea ice cover, chlorophyll-a concentration, sea bottom salinity, sea bottom temperature, and distance to coastline (all data publicly available online). We created a spatial grid with a resolution (grid cell size) of 10×10 km and used the environmental data from each grid cell in which a sampling station was located to train the random forest algorithm. We then used the environmental variables of all grid cells across the Bering Sea to predict benthic biomass in each grid cell based on the random forest algorithm (Huettmann and Oppel 2007). The model was able to accurately predict benthic biomass at 74% of sampling stations and agreed qualitatively with alternative data not used for model training in areas of the Bering Sea where such data were available (Grebmeier et al. 2006). By using the modeled information we implicitly assume that for any given site in the study area the abundance of benthic biomass is positively correlated to food abundance for king eiders.

Weather conditions are known to influence bird movements (Elkins 1983). Weather systems in the Bering Sea are highly dynamic (Rodionov et al. 2005), and a wide variety of conditions generally existed for each time window over which a movement of a satellite-tracked bird occurred. After considering weather factors (pressure systems, wind speed and direction, temperature) as potential variables

influencing king eider movements in the Bering Sea, we concluded that the temporal resolution of our satellite telemetry locations was insufficient to reveal meaningful patterns of movement due to current weather conditions at a given site. We therefore did not include weather variables in our model.

2.4.   Results

For 126 of 177 distinct winter movements of > 50 km we had information from more than one bird present at the departure location. In 49% ($n = 61$) of these movements none of the other birds present in the vicinity moved simultaneously, and in another 33% ($n = 42$) of movements at least some birds remained at the departure location. Thus only in 18% ($n = 23$) of all the winter movements for which we had information from >1 bird at the departure site did all tracked king eiders move away from a given site simultaneously. In only 26% of those 23 movements did the sea ice concentration at the departure site increase to more than 90% after the birds had departed.

The mean sea ice concentration at sites from which king eiders departed on a winter movement was 35% ($\pm 42\%$), and the mean ice concentration at arrival locations was 36% ($\pm 41\%$). Thus, there was on average no difference in the sea ice concentration between departure and arrival locations (departure index $M = 0.02$, range: -0.65 to 1.35, 95% CI: -0.03 to 0.05; Fig. 2.2). Of 177 discrete movements 52% led to an area with identical sea ice concentration as at the departure site. Equal proportions of movements (24%) led to sites with a lower or higher sea ice concentration, respectively.

The sea ice concentration at the departure site did not change during the time interval in which the movement occurred for 55% of movements ($n = 177$). An increase in sea ice concentration was recorded for 28% of movements, while a decrease occurred only for 17% of movements. On average, the mean ice concentration at departure locations at the time individuals were recorded at the arrival location was 43% ($\pm 43\%$).

This resulted in a small but significant shift towards higher sea ice concentrations at departure locations after birds had left (departure index $M = 0.17$, range: -0.65 to 1.35, 95% CI: -0.03 to 0.05; Fig. 2.2).

The random forest model predicting under what conditions king eiders departed from wintering sites had very good accuracy for both the training (area under ROC curve = 0.95) and the independent test data (area under ROC curve = 0.80). The individual bird was the most important variable in explaining movement decisions (Fig. 2.3). Almost equally important were a group of five variables including latitude and region of the location, sea ice concentration after departure, date, and structural body size. Movements were most common in Bristol Bay and least common on the northern wintering sites in the Kamchatka region. The relationship of latitude with predicted movement rate showed considerably lower movement rates between 60º-64º N (Fig. 2.4a). Date predicted that movements were unlikely before the end of October, and fairly uncommon through January (Fig. 2.4b). Structural body size, indicated by tarsus length showed that highest movement rates were predicted for largest and for fairly small birds, with intermediate birds having a lower tendency to move (Fig. 2.4c). This was also reflected by culmen length, which was a slightly less important variable (Fig. 2.3), but showed a similar pattern as tarsus length. The highest movement rates were predicted from February through late May. Movements were also more common if the sea ice concentration after departure increased (Fig. 2.4d). All other variables were relatively unimportant (~ 20% of individual bird, Fig. 2.3).

2.5.   Discussion

The decision whether to stay at or depart from a winter site differed widely among individual king eiders, and movements occurred under a wide variety of conditions. Individual specialization (Bolnick et al. 2003) or personality differences (Dall et al. 2004)

have recently been recognized to be widespread across many taxa and behaviours, including movement decisions (Sheppard et al. 2006, Roshier et al. 2008b). Individual differences in behaviour have therefore been successfully incorporated in a variety of ecological models (DeAngelis and Mooij 2005). In our study most of the variation in movement decisions was associated with individuals, suggesting that individuals may have different wintering strategies with higher or lower degree of site fidelity. We believe that the importance of individual differences in movement behaviour of migratory birds has not received sufficient attention in the past. We suggest that individual differences in behaviour may be prevalent in many aspects of annual routines that are considered for management and conservation (Festa-Bianchet and Apollonio 2003, Roshier et al. 2008b).

The variation we found among individuals could result from a variety of individual traits that we were not able to measure in this study. These individual traits include physiological body condition, age, or social status. Body condition is known to be a major factor influencing whether birds move between areas (Senar et al. 1992, Wingfield 2003). However, as movements are costly, poor body condition may also restrict birds to stay in a small area if their physiological state does not allow for long-distance travel (McIntyre and Wiens 1999, Brodersen et al. 2008). There is currently no feasible way to monitor a bird's body condition via satellite transmitters, but future technological developments may enable such analyses. We could also not determine precise ages of tracked birds, as all birds we tracked were presumably >2 years old when caught in spring on breeding grounds. Recent studies have shown that age-related changes of phenotype exist in seabirds (Ezard et al. 2007), thus the wintering strategy may change during the lifetime of long-lived species like king eiders. Sea ducks presumably pair on wintering grounds (Rohwer and Anderson 1988, Robertson and Cooke 1999a), and it is possible that the search for a mate will especially motivate males to travel large distances. Future investigations need to focus on these individual traits as potentially motivating factors for movements of birds during winter.

Despite the large individual variation our multivariate algorithmic model identified five other variables as important for movement decisions of wintering king eiders. We found that movements were more likely when sea ice concentration increased, and during late winter when sea ice generally reaches its maximum extent in the Bering Sea (Stabeno et al. 2001). However, movements were common through May when sea ice is receding and escape-type movements are less likely. Further, movements were equally common at both the northernmost locations and at southern latitudes where sea ice may not be present at all in some years (Stabeno et al. 2001). We also found that both very large and small birds were more likely to move away from a winter site, a pattern that is at odds with classical predictions about winter distribution in waterfowl. The classic body size hypothesis (Calder 1974) predicts that larger animals are able to fast longer in colder environments and would therefore be less likely to move in response to food shortage in winter (Myers 1981, Cristol et al. 1999). The non-linear relationships of latitude, body size, and date with movement rate indicate that not a single, but several distinct patterns may explain why some king eiders move long distances in winter (Roshier et al. 2008a).

Our analysis of simultaneous winter movements corroborates the notion that movements may fall into various patterns. In most cases for which we had data from several birds at a site, some king eiders remained at the site from which others departed. Even in cases in which all birds departed simultaneously, sea ice increased to harsh levels at the departure location only in a few instances. Results from satellite telemetry in West Greenland also suggest that most king eider winter movements were not correlated with sea ice changes (Mosbech et al. 2006). However, severe ice conditions coincided with a distribution shift of wintering birds towards more open areas (Mosbech et al. 2006). A similar movement pattern is known from spectacled eiders (*S. fischeri*) wintering in the northern Bering Sea, which rarely leave sites even when ice cover is extreme (Petersen and Douglas 2004). As has been predicted for spectacled eiders at a smaller scale (Bump and Lovvorn 2004), king eiders in our study did not move long distances towards areas with a lower sea ice concentration, but rather to areas with very similar sea ice

concentration. Intermediate concentrations of sea ice may be beneficial for sea ducks as the ice dampens wave action and provides haul-out opportunities which reduce thermoregulatory costs (de Vries and van Eerden 1995, Petersen and Douglas 2004, Mosbech et al. 2006). We conclude that a small proportion of king eider winter movements in the Bering Sea may be caused by extreme or rapidly changing sea ice conditions, but that the majority of the movements we analysed are unlikely to be caused by sea ice conditions.

Food abundance as measured in our model by predicted benthic biomass did not appear to be a major motivating factor for king eider movements. However, we could not include potential depletion of food resources during the course of the winter in our model. Common eiders (*S. mollissima,* L.) have been shown to deplete mussel beds (Guillemette et al. 1996), and prey depletion in mussel farms induced foraging surf scoters (*Melanitta perspicillata,* L.) to move to different habitats in late winter (Kirk et al. 2007). King eiders generally forage in deeper water than surf scoters and common eiders (Bustnes and Erikstad 1988) where prey depletion may be less likely (Larsen and Guillemette 2000). There is currently no information on how the prey base of king eiders is affected by large flocks foraging for several months in a given area. We are therefore not able to determine to what extent prey depletion may have caused movements, but we acknowledge the possibility that higher movement rates after February may have resulted from depletion of food patches.

The environmental factors we included in our model appeared to have only limited influence on the decision of individual king eiders to move away from a wintering site. Several other bird species have been shown to exhibit variable wintering strategies, with more sedentary and more vagrant individuals (Rappole et al. 1989, Ruiz et al. 1989, Winker et al. 1990). Individuals that wander are inferior when territories are held by forest songbirds (Rappole et al. 1989, Winker et al. 1990). Conversely, wintering shorebirds benefited from movements by being able to exploit various resource patches (Ruiz et al. 1989). Since wintering king eiders occur in large congregations of up to 20,000 individuals (Larned 2007), and are presumably not territorial, movements to

explore alternate resource patches may confer an advantage. We therefore propose that some movements of king eiders may be exploratory movements to obtain information of alternative wintering sites that may enhance an individuals' survival probability either instantaneously or at some time in the future when a particular wintering site would become unsuitable due to environmental fluctuation.

Exploratory movements are known in other bird species wintering in fluctuating environments (Bennetts and Kitchens 2000, Gordon 2000, Roshier et al. 2008a). Knowledge obtained through such movements yields an adaptive advantage when survival probability is considerably lower for individuals without knowledge of alternative sites at times when environmental conditions deteriorate (Valone and Templeton 2002, Dall et al. 2005). Environmental fluctuations that cause polynyas to freeze during spring migration have resulted in mass-mortality events in king eiders (Barry 1968, Fournier and Hines 1994). This demonstrates the potential risk associated with site fidelity in variable environments such as arctic and sub-arctic waters. Exploratory behaviour has been shown to be heritable (Dingemanse et al. 2002), and may be under negative frequency dependent selection in a gregarious species where individuals rely on social information when assessing the quality of certain sites (Dall et al. 2004). King eiders are gregarious in winter and can use social information such as foraging success of con-specifics to assess the quality of a foraging site. Negative frequency dependent selection of exploratory behaviour as suggested by Dall *et al*. (2004) would lead to a co-existence of individuals with different strategies, which agrees with our finding of large differences in movement behaviour among individual king eiders.

The exploration hypothesis could also explain high movement rates in late winter when days become longer. During this time of the year, when daylight is no longer a limiting factor and sea ice already recedes in some areas, it may be less risky to leave a suitable wintering site to find an alternative site. Furthermore, the presence of con-specifics as an indicator of the quality of a site (Beauchamp et al. 1997, Cote and Clobert 2007) might render late-winter exploratory movements more effective than in summer or

fall when many birds are on migration or breeding grounds and not all suitable wintering sites may be occupied. Exploratory movements could be more common in Bristol Bay than along Kamchatka, as the entire eastern Bering Sea is fairly shallow, and chances to encounter an area where foraging is possible in any direction are higher than along the coast of Kamchatka (Roshier et al. 2008b). The continental shelf break along Kamchatka lies only 15 km off shore, and any movement that is not parallel to the coast would inevitably lead to very deep waters that are unsuitable for foraging king eiders.

In conclusion, we found very high inter-individual variation in the movement decisions of wintering king eiders, and could not determine a single major motivation for most movements. Some movements may be motivated by deteriorating environmental conditions, however, as many or more movements may be of an exploratory nature. Development of longer-lasting satellite transmitters may present the opportunity in the future to explore the repeatability of individual movement behaviours in subsequent winters, as well as potential fitness consequences of wintering strategies.

2.6.   Acknowledgements

2.7.   References

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Table 2.1. List of factors included in the multivariate random forest model to explain the movement decisions of King Eiders at wintering sites in the Bering Sea.

Code	Description of factor
LAT	latitude of location [°N]
LONG	longitude of location [°W]
IC_now	sea ice concentration at transmission location at time of transmission from bird [%]
IC_prev	sea ice concentration at transmission location 1 week before transmission [%]
IC_post	sea ice concentration at transmission location 1 week after transmission [%]
TURN	absolute turn angle between trajectories from previous and to next location [0-180°]
BEAR_nex	direction to next location [0-360°]
WINREG	wintering region [Alaska, North Bering Sea, Kamchatka]
DAY	date scaled to wintering period starting July 20th [1-312]
SEX	sex of the individual, male or female
YEAR	year of capture, 2002 – 2005
BIOM	model-predicted benthic biomass [g wet weight/m^2]
DAY_HRS	day length [hrs]
CULMEN	length of culmen [mm]
WING	length of wingchord [mm]
TARSUS	length of full tarsus [mm]
BIRD	individual
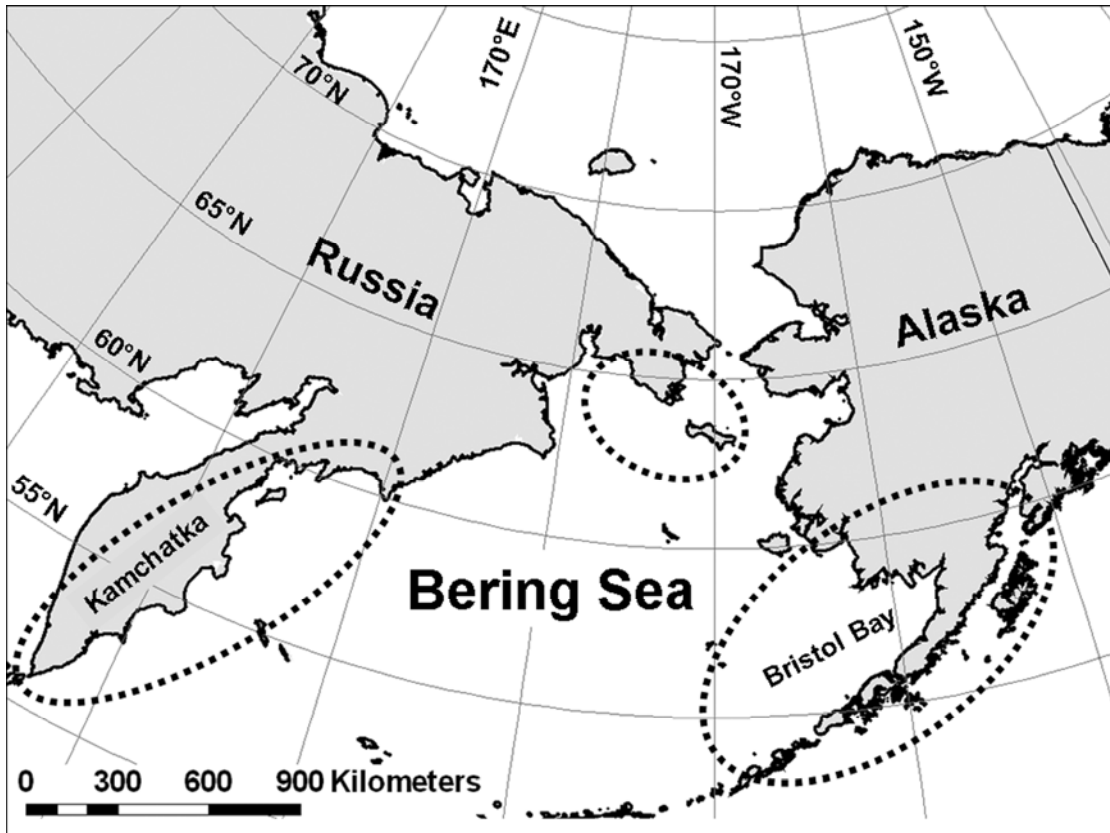
Figure 2.1. Main wintering regions (North Bering Sea, SW Alaska, Kamchatka) of king eiders tracked from breeding areas in western North America to the Bering Sea.
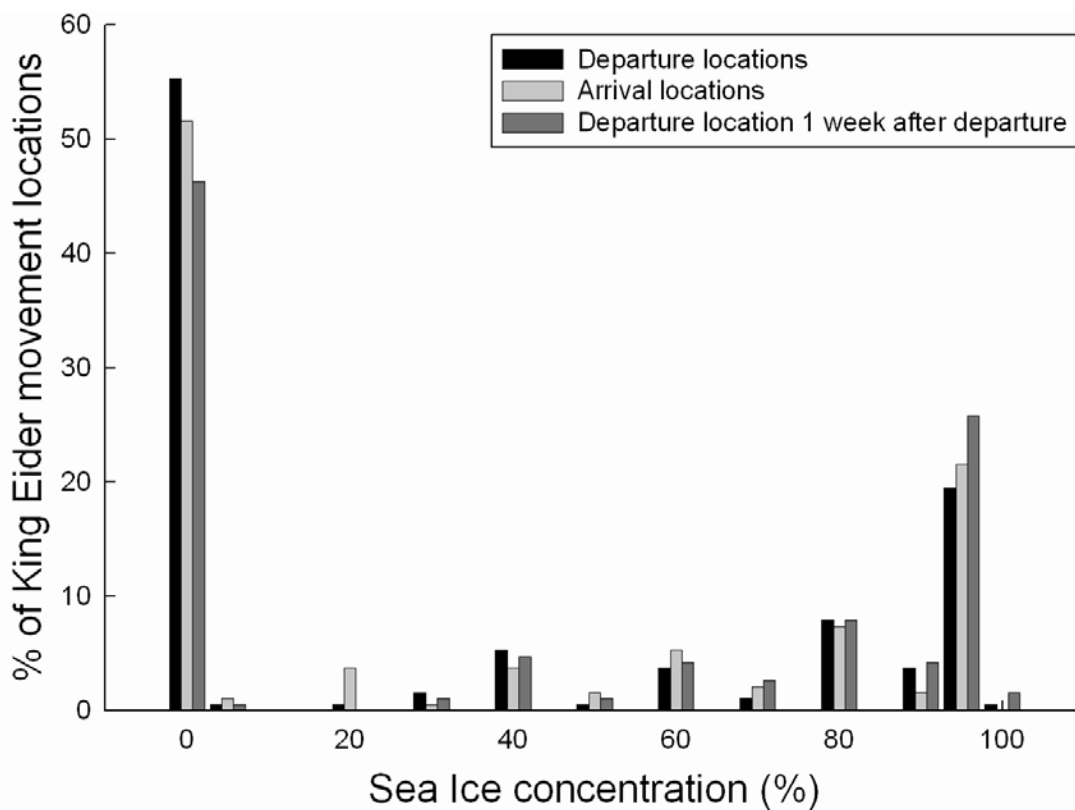
Figure 2.2. Relative frequency of locations associated with king eider winter movements in relation to sea ice concentration in the Bering Sea from 2002 – 2006; black columns represent departure locations prior to departure, white columns represent arrival locations, and gray columns represent departure locations at the time when king eiders were recorded at the arrival location.
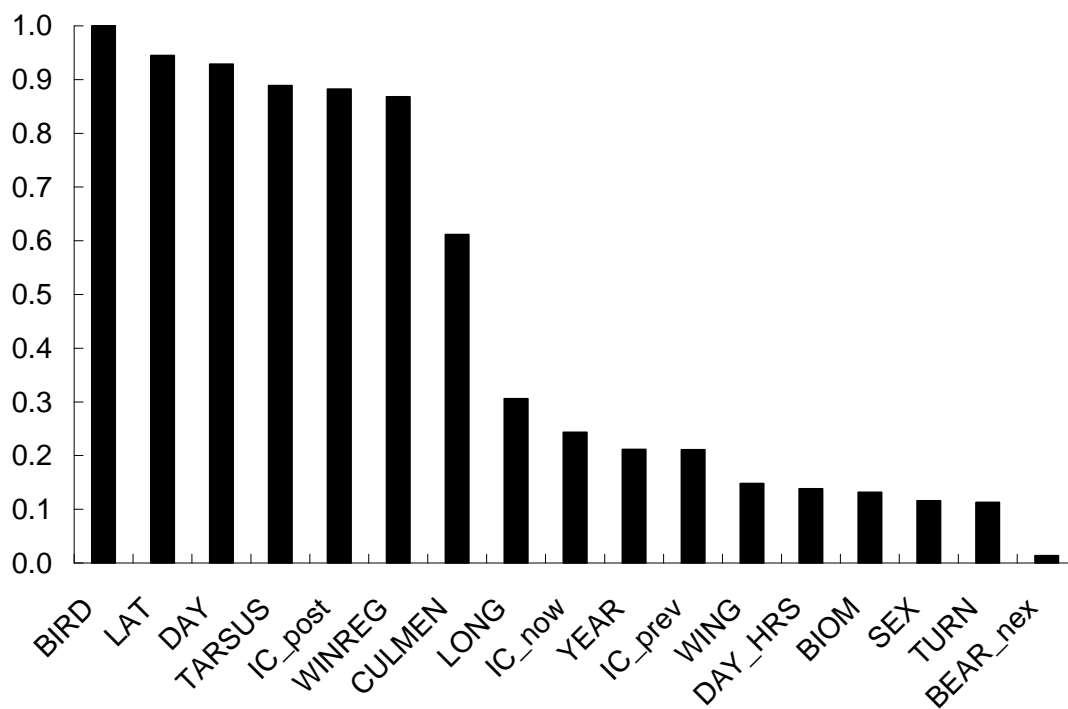
Figure 2.3. Importance of environmental and bird-related predictor variables in order of their relevance to increase accuracy of a random forest model predicting under what conditions individual king eiders depart from a wintering site in the Bering Sea. The importance is scaled to 1 for the most important variable. See Table 2.1 for explanation of variables.
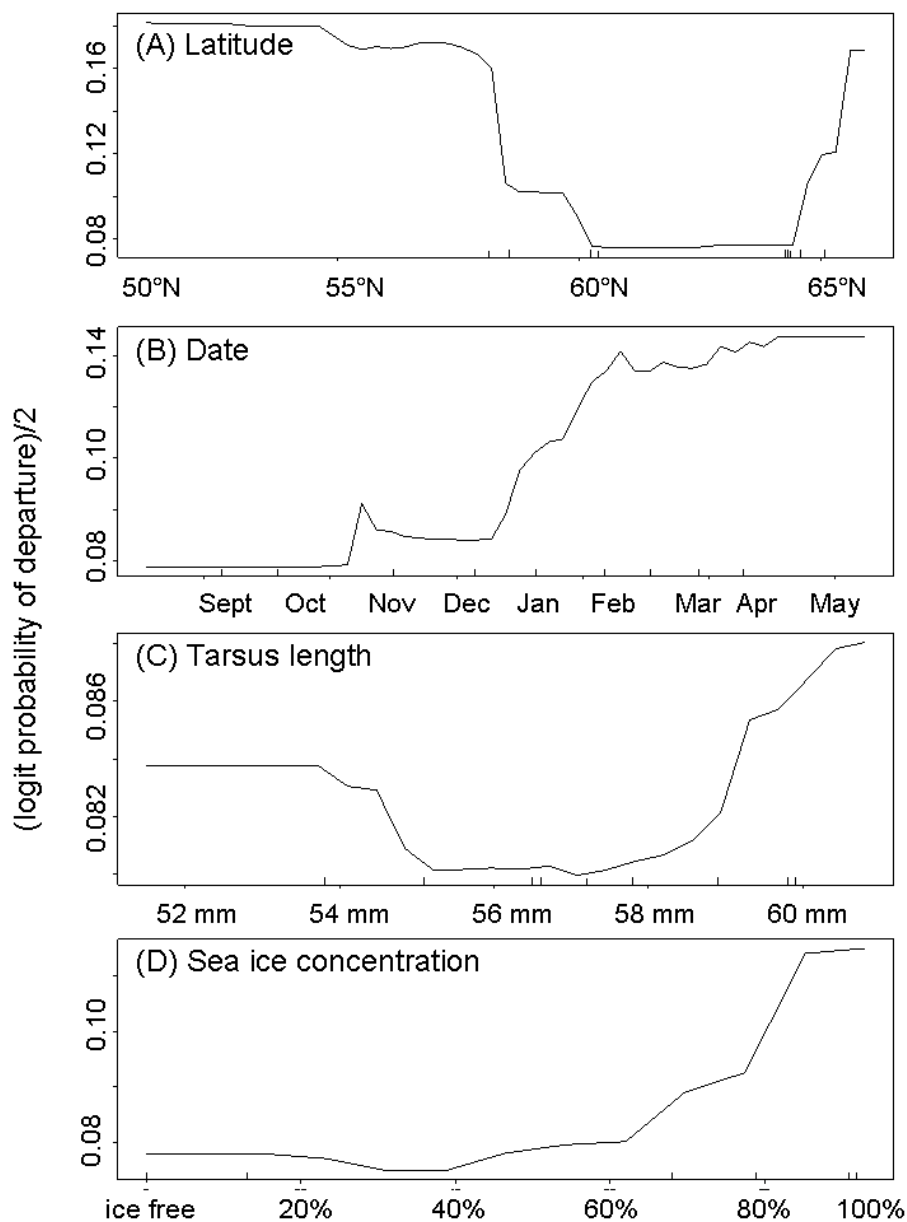
Figure 2.4. Partial dependence plots for four important variables predicting movement rates of king eiders in the Bering Sea. (a) Latitude, (b) date, (c) tarsus length, and (d) sea ice concentration at a location one week after the bird was recorded there. The y-axis is half the logit of the predicted probability of departure from a wintering site, for more information see Cutler et al. (2007).

3. Using eggshell membranes as a non-invasive tool to investigate the source of nutrients in avian eggs[1]

3.1.   Abstract

Development of minimally invasive techniques to collect nutritional information from free-living birds is desirable for both ethical and conservation reasons. Here we explore the utility of waterfowl eggshell membranes to determine the nutrient source of egg formation by using stable isotope ratios. We compared δ^{13}C and δ^{15}N of membranes from complete king eider (*Somateria spectabilis*) eggs to membranes of hatched or depredated eggs of the same clutch remaining after incubation. Despite large variation among membranes (δ^{13}C: -26 to -14‰) we found a highly predictable relationship between δ^{13}C of complete egg membranes and remaining (hatched or depredated) membranes from the same clutch. We did not find a consistent change in either δ^{13}C or δ^{15}N of eggshell membranes during incubation. We suggest that isotope ratios of membranes can be used to determine the source of exogenous nutrients for egg production in income breeders, and that membranes may offer a clutch-specific reference point for dietary nutrients ('income endpoint') in isotopic mixing models quantifying nutrient allocation in capital or mixed-strategy breeders.

Keywords Eggshell membrane – King eider – Nutrient allocation – *Somateria spectabilis* – Stable isotopes – Waterfowl

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3.2.   Introduction

Stable isotope ratios of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulfur ($^{34}S/^{32}S$) are increasingly used in ecological studies to reconstruct diets and explore the source of nutrients in animal tissues (Gannes et al. 1998, Fry 2006). If animals rely on a combination of isotopically distinct diets for nutrition, the proportional contribution of each source can be estimated by analyzing the stable isotope ratios of animal tissues and nutrient sources (Phillips 2001, Phillips et al. 2005). The application of stable isotope techniques has advanced several aspects of avian ecology, including quantitative analyses of the origin of nutrients that are incorporated into eggs (Hobson et al. 1997, Gauthier et al. 2003). The general approach in these investigations was to collect whole eggs to analyze their components for ^{13}C, ^{15}N, and/or ^{34}S. Removal of complete eggs may, however, conflict with conservation interests and ethical considerations especially for endangered species (Vucetich and Nelson 2007). Egg removal may also not be feasible if simultaneous studies assessing egg survival rates mandate that clutches are left intact. A potential solution to this problem is to use blood or natal down of hatchlings (Klaassen et al. 2001, Lecomte et al. 2006), or use a syringe to obtain samples of yolk and albumen from eggs left otherwise intact in the nest (Schwabl 1993, Morrison and Hobson 2004). The former approach requires precise timing of a nest visit to capture precocial young. The second approach requires a fairly delicate operation and may result in contaminated samples and/or affect development of embryos (Finkler et al. 1998, Klaassen et al. 2004). A more robust and less intrusive alternative to sample egg tissues for stable isotope analysis is therefore needed.

Most waterfowl and some shorebirds leave eggshell membranes in the nest bowl after hatching (Milne 1965, Sotherland and Rahn 1987, Mabee 1997). These membranes can be collected for analysis without any detrimental effects on the clutch. Shell membranes are synthesized in the isthmus region of the oviduct at the end of the egg formation process, approximately 20 hours before the egg is laid (Taylor 1970, Burley and Vadehra 1989, Alisauskas and Ankney 1992). Nutrients for eggshell and membrane

formation are most likely derived from the birds' current diet, which potentially renders membranes a useful tool to determine the diet during egg production (Schaffner and Swart 1991).

The shell membranes facilitate gas exchange during embryonic development. They do not provide nutrients for the developing embryo, but may undergo modification due to incorporation of collagen. This may lead to a difference in the isotopic composition of membranes from hatched or partially incubated eggs (Schaffner and Swart 1991, Hobson 1995). Currently, no information is available on the isotopic change of membranes during incubation.

In this study we investigate the carbon and nitrogen isotope ratios of king eider (*Somateria spectabilis*) eggshell membranes to examine whether the isotopic composition of membranes changes during incubation. By collecting one complete egg of known incubation stage plus membranes from hatched or depredated eggs of the same clutch, we provide an estimate of changes in isotope ratios in membranes during incubation. Our goal was to evaluate whether membranes can be used as a non-invasive tool to explore the source of nutrients used for egg production.

3.3. Materials and methods

3.3.1. Study area

We monitored nests and collected eggs and eggshell membranes (hereafter: membranes) of king eiders on the Arctic coastal plain of Alaska in June and July 2006 and 2007 at two study locations: near Teshekpuk Lake (70°26' N, 153°08' W), and in the Kuparuk oilfield (70°20' N, 149°45' W). Both areas consist of lowland arctic tundra and support intermediate densities (1-2 nests/km^2) of nesting king eiders.

3.3.2. Study species

King eiders nest in arctic tundra ecosystems around the world and spend about 10 months per year at sea. During the non-breeding season the birds forage on marine benthic invertebrates by diving to the sea floor (Suydam et al. 2000). On the breeding grounds females forage for aquatic insects and larva, but also ingest vegetation (Lamothe 1973, Holcroft-Weerstra and Dickson 1997). Female king eiders arrive on their breeding grounds in early June (Phillips et al. 2007) and spend about two weeks in a terrestrial/freshwater environment prior to laying a clutch consisting of 4-7 eggs. Eggs are laid at a rate of approximately one per day, incubation starts with the last egg laid, and the female incubates the clutch for 23-26 days before chicks hatch (Kellett and Alisauskas 1997, Suydam 2000).

3.3.3. Field collection

We located nests by systematically searching study areas in June, and collected one complete egg from each nest the first day it was found. Incubation stage of the egg was estimated by egg candling (Weller 1956), and ranged from 0-15 days of incubation. At the completion of incubation, we collected all remaining membranes and stored membranes belonging to different eggs from the same clutch separately. If nests were depredated or abandoned we collected remaining eggs and eggshells with membranes and determined their incubation stage at death by calculating the time difference to the day when the nest was found. For preservation of samples, we boiled complete eggs in the field for 15 minutes and then kept them frozen until analysis (Gloutney and Hobson 1998). Membranes were air dried at ambient temperature, stored in sealed paper envelopes, and kept in a dry box until analysis.

3.3.4. Laboratory analyses

We separated whole eggs into yolk, albumen, membrane, and shell. We cleaned all membranes with a small brush in de-ionized water (Hobson 1995); oven dried them at 60°C for 24 hours, and then broke them into tiny pieces using a mortar and pestle. From each egg, we placed several membrane pieces weighing 0.2–0.4 mg in total into tin cups and analysed them for carbon and nitrogen isotope ratios at the Alaska Stable Isotope Facility using a continuous flow stable isotope-ratio mass spectrometer (ThermoElectron Delta V Plus). We report results of isotopic analyses as ratios in delta notation relative to international standards (PeeDee Belemnite for C, atmospheric air for N) according to the following equation: $\delta X = ([R_{sample}/R_{standard}]-1) \times 1000$, with X denoting either ^{13}C or ^{15}N, and R representing the ratio of $^{13}C /^{12}C$ or $^{15}N /^{14}N$, respectively. The precision of measurements was ±0.1‰ and ±0.1‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, in peptone standards that were run concurrently with samples.

3.3.5. Statistical analysis

We first examined whether isotope ratios of membranes differed between our two study years using a non-parametric Mann-Whitney U-test. We used a reduced major axis regression to examine the relationship between isotope ratios of membranes from complete eggs and from remaining membranes of the same clutch as the isotope ratios on both axes were measured with the same error (Sokal and Rohlf 1995, Bohonak and van der Linde 2004). We tested whether this relationship deviated from a slope of 1.0, and report statistical significance for this hypothesis. We used an ANOVA to test whether within-clutch variation in membrane isotope ratios of all membranes was higher than variation among clutches. To assess temporal change in $\delta^{13}C$ and $\delta^{15}N$ we calculated the difference in $\delta^{13}C$ and $\delta^{15}N$ between the membrane of the complete egg and the remaining membranes of a clutch and the time difference (in days) between collections.

We averaged differences in isotope ratios for each clutch from which we had more than one remaining membrane. We then used a linear regression of the average change in $\delta^{13}C$ or $\delta^{15}N$ over the time difference between collections. We hereby assume that a slope different from zero would indicate a systematic change in $\delta^{13}C$ or $\delta^{15}N$ due to incubation of the eggs from which we collected remaining membranes. We present isotope ratios as mean ± standard deviation, and regression coefficients as estimate ± standard error. All tests were two-tailed and used $\alpha = 0.05$.

3.4.   Results

We collected one complete egg from 28 clutches and 73 membranes of hatched or depredated eggs from those same clutches (range 1-5 remaining membranes per clutch) in 2006, and one complete egg from 18 clutches and 56 remaining membranes (1–5 per clutch) in 2007. Isotope ratios did not differ between years ($\delta^{13}C$: $P = 0.34$, $\delta^{15}N$: $P = 0.35$), and we pooled data from both years in all analyses.

Membrane $\delta^{13}C$ ranged from -26.1‰ to -14.6‰, and membrane $\delta^{15}N$ ranged from 5.5‰ to 11.9‰. The mean standard deviation for membranes of different eggs from the same clutch was 0.6‰ (range 0.5–1.7‰, $n = 46$) for $\delta^{13}C$, and 0.7‰ (range 0.5–1.7‰, $n = 46$) for $\delta^{15}N$. The variation among membranes from different clutches was higher than among membranes of the same clutch ($\delta^{13}C$: ± 2.1‰, $F_{45,127} = 30.44$, $P < 0.001$; $\delta^{15}N$: ± 1.0‰, $F_{45,129} = 5.40$, $P < 0.001$).

We found a highly predictable relationship between $\delta^{13}C$ of complete egg membranes and remaining membranes ($b = 1.024 \pm 0.046$, $r^2 = 0.75$, $P = 0.60$, $n = 127$, Fig. 3.1a). The relationship for $\delta^{15}N$ was less predictable, but the slope of the relationship did not indicate a deviation from 1.0 ($b = 0.995 \pm 0.077$, $r^2 = 0.17$, $P = 0.95$, $n = 129$, Fig. 3.1b).

We found no evidence for systematic isotopic change in membranes during incubation. The difference in both $\delta^{13}C$ and $\delta^{15}N$ between complete egg and remaining membranes did not deviate from zero (paired *t*-test, $\delta^{13}C$: $t_{126} = 0.69$, $P = 0.49$; $\delta^{15}N$: $t_{128} = 0.51$, $P = 0.61$). There was no change in either $\delta^{13}C$ or $\delta^{15}N$ over the time interval between collections of membranes from the same clutch ($\delta^{13}C$: $b = -0.02$, $P = 0.26$, $\delta^{15}N$: $b = -0.03$, $P = 0.17$, Fig. 3.2).

3.5.   Discussion

Our study found large variation in both $\delta^{13}C$ and $\delta^{15}N$ among eggshell membranes, and showed that $\delta^{13}C$ of fresh membranes could be predicted from remaining membranes. Fresh membrane $\delta^{15}N$ was less predictable from remaining membrane $\delta^{15}N$. Further, $\delta^{13}C$ in membranes did not change systematically during incubation. This enables the use of membranes collected from hatched or depredated eggs for estimation of dietary $\delta^{13}C$ used for egg synthesis.

The weaker relationship between fresh and remaining membrane $\delta^{15}N$ may be due to intra-clutch variability of $\delta^{15}N$ resulting from dietary differences, but could be due to unknown effects of $\delta^{15}N$-depleted uric acid accumulation during the growth of an embryo inside an egg (Fiske and Boyden 1926, Packard and Packard 1986). Even though we did not detect a significant decrease of $\delta^{15}N$ in remaining membranes, we caution researchers to critically evaluate the utility of $\delta^{15}N$ for their study species.

The large variation in both $\delta^{13}C$ and $\delta^{15}N$ among clutches in our study is consistent with large variation found in pre-breeding blood plasma samples of adult females from the same population (Chapter 5). We interpret this variation as the result of different foraging preferences of individual females (Bolnick et al. 2003), as potential prey items available in the study area also show large isotopic variation (Chapter 5). This variation is most likely a result of different carbon fixation pathways of algal and

terrestrial primary producers (Peterson and Fry 1987, Hershey et al. 2006). Within-clutch variation may result from females foraging on different prey items in different water bodies during egg formation, or from isotopic variation within major prey species (Grey et al. 2004).

Membranes comprise only a small fraction (~1%) of the total amount of nutrients in an egg (Sotherland and Rahn 1987, Burley and Vadehra 1989), and the allocation of nutrients to yolk, albumen, and membranes may differ depending on the breeding strategy of a species (Jönsson 1997, Meijer and Drent 1999, Klaassen et al. 2006). For birds relying mostly on exogenous, recently ingested nutrients for egg formation (income breeders), hatch membranes offer a non-intrusive alternative to the collection of whole eggs to determine important diet components for egg formation. Recent evidence suggests that income breeding may be fairly widespread even at high latitudes (Klaassen et al. 2001, Klaassen et al. 2006, Bond et al. 2007), offering great potential for the application of the method suggested here.

In birds relying partially on endogenous reserves for egg formation (capital and mixed-strategy breeders), these reserves will most likely be used in yolk and, to a lesser extent, in albumen. However, nutrients for membrane formation are most likely derived from the birds' current diet, as the membrane does not require large amounts of nutrients and is synthesized at the end of the egg formation process immediately before the calcified shell is laid down (Taylor 1970, Burley and Vadehra 1989, Schaffner and Swart 1991). Due to this potential for differential allocation of body reserve and dietary nutrients to egg components, the isotopic signature of membranes may not reflect the isotopic signature of other egg components in capital or mixed-strategy breeders. We found this pattern for king eiders, where variation in eggshell membrane $\delta^{13}C$ accounted for approximately 70% of the variation in $\delta^{13}C$ in lipid-free yolk, indicating that some yolk nutrients were not derived from dietary nutrients (Chapter 5). Researchers therefore need to consider carefully how representative eggshell membrane isotope ratios are for the species under investigation, and we recommend initial validation of the relationship between membrane and other egg components for each study species.

Membranes may nonetheless offer a valuable tool for the exploration of nutrient allocation to eggs in capital and mixed-strategy breeders. For studies attempting to quantify the proportion of egg nutrients derived from diet assimilated on the breeding grounds, an isotopic endpoint reflecting those nutrients is required (Hobson 2006). Birds may exhibit individual dietary preferences (Durell 2000, Bolnick et al. 2003), resulting in variation in isotopic signatures within a population (Klaassen et al. 2004, Bearhop et al. 2006). Due to this individual variability, population-wide averages of diet isotope ratios may not be appropriate endpoints for assessing breeding strategy. An alternative is to obtain isotopic information of current diet from each individual during the egg-laying phase or shortly after the onset of incubation (Gauthier et al. 2003, Schmutz et al. 2007). This approach can, however, be logistically challenging, and will in many cases lead to nest abandonment (Criscuolo 2001, Bourgeon et al. 2006). Membranes provide an isotope signature of recent diet that can be collected non-intrusively. By averaging isotope signatures from several membranes of a clutch, one can derive a reliable estimate of the laying female's average diet during egg formation. Since only a few milligrams of membrane are required for stable isotope analyses, even small fragments remaining in hatched or depredated nests are sufficient for analysis. Membranes therefore provide a non-intrusive alternative for estimating income endpoints for mixed-strategy breeders, especially in populations exhibiting individual diet specialization (Durell 2000, Bolnick et al. 2003). Our results showed that intra-clutch variation of membrane signatures in king eiders was relatively small compared to the variation among clutches, and thus among individual females. Therefore, membrane averages for each clutch provide a more accurate endpoint to quantify the origin of nutrients than a population-wide average of diet isotope ratios.

Eggshell membranes are mostly composed of proteins and contain only small amounts (<5%) of carbohydrates and lipids (Burley and Vadehra 1989). They are isotopically enriched over bulk diet by about 3.2‰ in δ^{13}C and 4‰ in δ^{15}N (Hobson 1995). There is currently very little knowledge about the variability in composition and isotopic differences between macronutrients in membranes, and further experimental

studies are required to determine potential sources of variation in isotope ratios of eggshell membranes both among eggs and within individual eggs.

In summary, we suggest that eggshell membranes collected at any stage during or after incubation can be used to determine the $\delta^{13}C$ of eggs for the estimation of food sources used during egg formation in income breeders. Care needs to be taken when interpreting $\delta^{15}N$ of hatch membranes, as this ratio was not strongly related to that from complete eggs in our study. Another useful application for hatch membranes is their indication of diet signature for individual females: they can provide an estimator of the income endpoint in nutrient allocation studies of capital or mixed-strategy breeders. This technique therefore offers great potential for a wide variety of studies exploring the origin of egg nutrients, especially for vulnerable populations where destructive sampling is not feasible.

3.6.   Acknowledgements

3.7.   References

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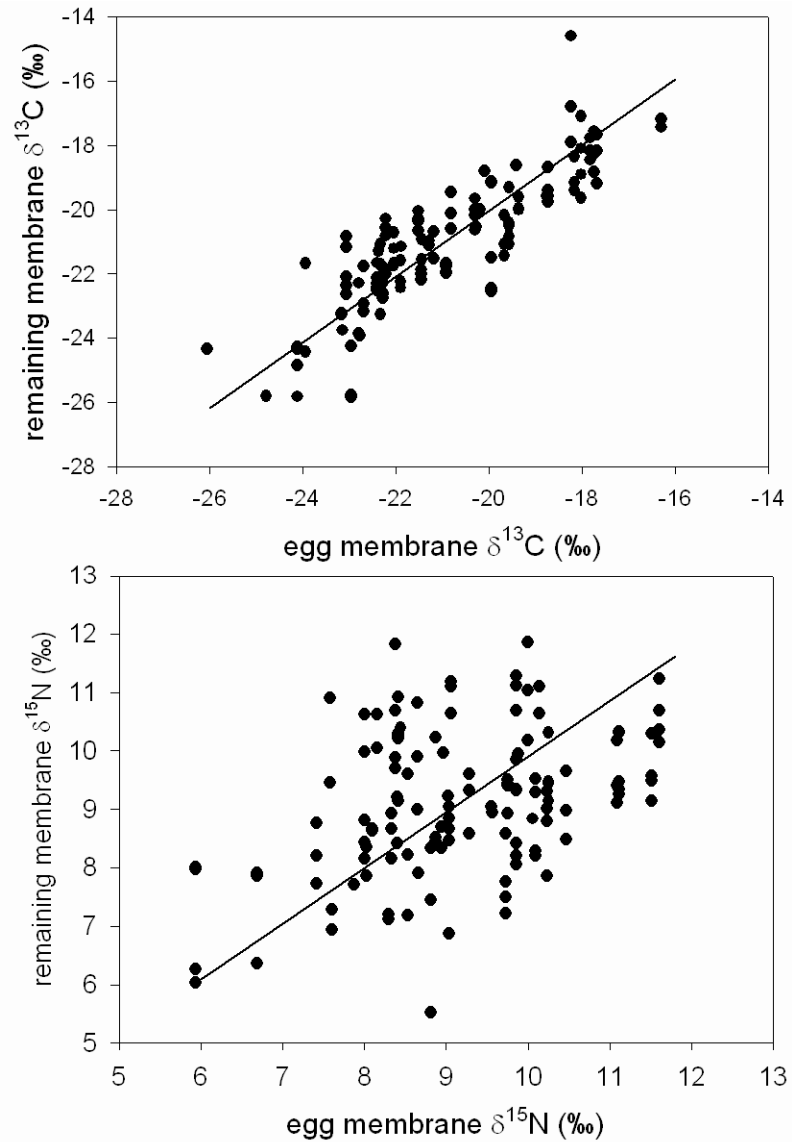
Figure 3.1. Relationship of δ^{13}C (a) and δ^{15}N (b) of king eider eggshell membranes between complete eggs and remaining membranes of the same clutch collected in summer 2006 and 2007 on breeding grounds in North Alaska. Solid line represents reduced major axis regression (Bohonak and van der Linde 2004). δ^{13}C: $r^2 = 0.75$, $n = 127$; δ^{15}N: $r^2 = 0.17$, $n = 129$.
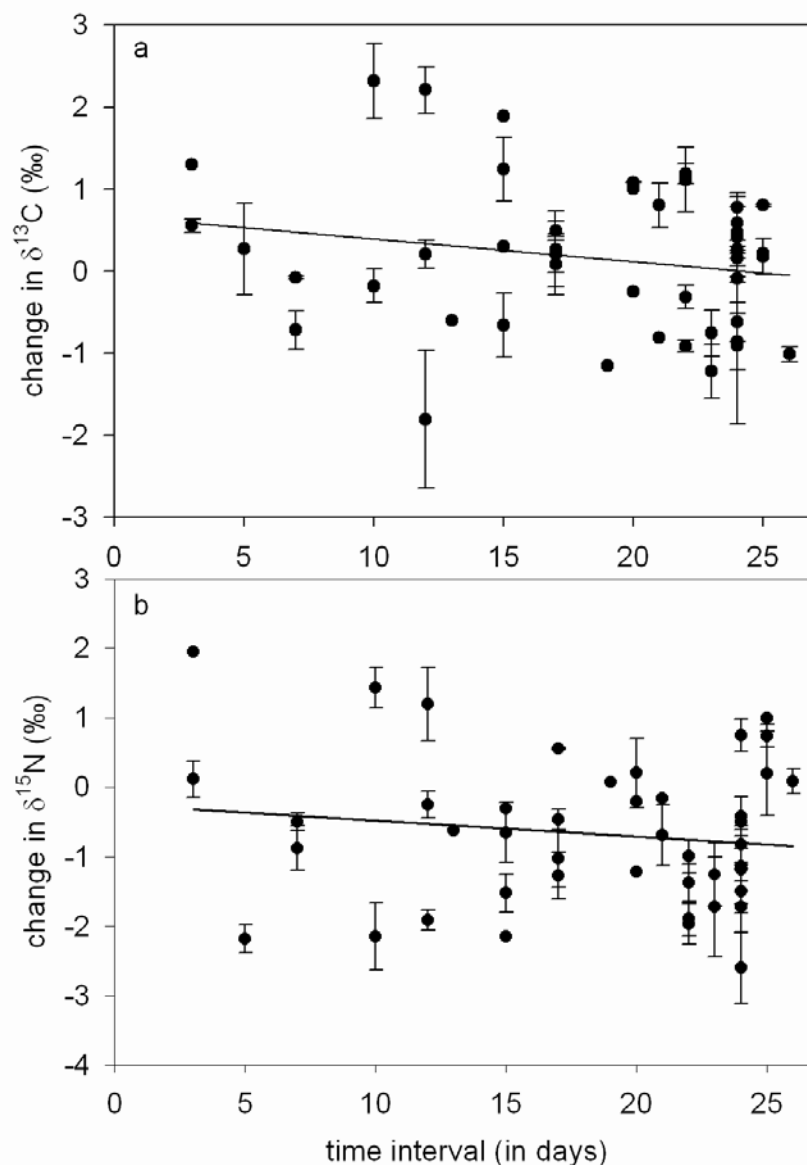
Figure 3.2. Change in $\delta^{13}C$ (a) and $\delta^{15}N$ (b) over time in king eider eggshell membranes calculated from the difference between complete eggs and remaining membranes of the same clutch. Time interval indicates the number of days between collection of the complete egg and remaining membranes. Error bars indicate 1 SD for clutches with more than one remaining membrane. Solid line represents linear regression, $\delta^{13}C$: $r^2 = 0.04$, $n = 46$; $\delta^{15}N$: $r^2 = 0.02$, $n = 46$.

4. Effects of Lipid Extraction on Stable Isotope Ratios in Avian Egg Yolk – is Arithmetic Correction a Reliable Alternative?[1]

4.1. Abstract

Many studies investigating nutrient allocation to egg production in birds use stable isotope ratios of egg yolk to identify the origin of nutrients. Dry egg yolk contains > 50% lipids, which are known to be depleted in ^{13}C. Currently, researchers remove lipids from egg yolk using a chemical lipid extraction procedure before analyzing the isotopic composition of protein in egg yolk. We examined the effects of chemical lipid extraction on δ^{13}C, δ^{15}N, and δ^{34}S of avian egg yolk, and explored the utility of an arithmetic lipid correction model to control for lipid content in whole yolk samples. We analyzed the dried yolk of 15 captive Spectacled Eider and 20 wild King Eider eggs both in the original form and following lipid extraction with a 2:1 chloroform:methanol solution. We found that chemical lipid extraction leads to an increase of (mean ± SD) 3.3 ± 1.1‰ in δ^{13}C, 1.1 ± 0.5‰ in δ^{15}N, and 2.3 ± 1.1‰ in δ^{34}S. The arithmetic lipid correction provided accurate values of δ^{13}C for captive Spectacled Eiders fed on a homogenous high-quality diet. However, arithmetic lipid correction was unreliable for wild migratory birds. We do not recommend to lipid-correct whole yolk δ^{13}C of wild birds which may accumulate macronutrients during migration and transfer macronutrients between isotopically distinct environments.

Key words: ^{13}C, egg yolk, eiders, lipid correction, ^{15}N, ^{34}S, stable isotopes

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4.2.   Introduction

Tracing the origin of nutrients used for reproduction is one of the key goals of many ecological studies, and stable isotopes are increasingly used to determine the sources of nutrients acquired and utilized by animals (Hobson 1995, Gannes et al. 1998, Fry 2006). In many avian studies, stable isotope ratios of egg components have revealed valuable information about the proportional contribution of exogenous and endogenous nutrient sources for egg synthesis (Hobson et al. 1997, Gauthier et al. 2003, Hobson et al. 2004, Morrison and Hobson 2004, Hobson et al. 2005).

Most of the energy in an egg is stored in the yolk (Sotherland and Rahn 1987), hence studies examining nutrient allocation to reproduction in birds generally focus on egg yolk. Dry avian egg yolk is composed of $\geq$ 50% lipids in most bird species (Carey et al. 1980, Sotherland and Rahn 1987, Burley and Vadehra 1989), and lipids are depleted in ^{13}C compared to proteins and carbohydrates (DeNiro and Epstein 1977). Thus, differences in lipid content of samples can confound the interpretation of carbon isotope ratios (Post et al. 2007), and many ecological studies either chemically remove lipids from target tissues or apply an arithmetic correction to account for the higher abundance of lighter carbon isotopes in lipids (Kiljunen et al. 2006, Sweeting et al. 2006, Post et al. 2007). Arithmetic lipid correction has been applied to fish and invertebrate tissues (Kiljunen et al. 2006, Sweeting et al. 2006, Smyntek et al. 2007). However, avian egg yolk typically has a much higher lipid content than fish and invertebrate tissues (5-45%), which may render arithmetic lipid correction for egg yolk unreliable (Post et al. 2007, Logan et al. 2008, Mintenbeck et al. 2008). The current lack of a reliable arithmetic correction makes chemical lipid extraction necessary for avian egg yolk C isotope analysis. Lipid extraction is assumed to normalize C isotope ratios, but has also been shown to affect N isotope ratios in fish and invertebrate tissues (Søreide et al. 2006, Sweeting et al. 2006, Logan and Lutcavage 2008). We are aware of only one study examining isotopic effects of lipid extraction in avian eggs, but that study (Ricca et al.

2007) did not separate yolk and albumen components of eggs. Thus, it is unknown how chemical lipid extraction affects the C, N, and S isotope ratios in avian egg yolk.

In this study we used data from two sea duck species, captive Spectacled Eiders (*Somateria fischeri*) and wild King Eiders (*S. spectabilis*), to examine differences in C, N, and S isotope ratios between whole egg yolk and chemically lipid-extracted yolk. We then evaluated whether an arithmetic lipid correction model, adapted from published equations and adjusted for avian yolk, could be used to reliably estimate C isotope ratios for lipid-free yolk. To our knowledge this is the first study describing lipid-extraction effects on C, N and S isotope measurements of egg yolk.

4.3.   Methods

4.3.1. Study species

King and Spectacled Eiders are sea ducks that nest during a short season in the Arctic and spend the rest of the annual cycle in coastal marine areas at high northern latitudes. During the breeding season, these species lay 4-7 eggs per clutch and eggs average about 67g for King (Suydam 2000) and 71g for Spectacled Eiders (Petersen et al. 2000).

4.3.2. Egg collection

We collected 40 King Eider eggs on the Arctic coastal plain of Alaska in June 2006 and 2007. The study area was located 30 km south of the Beaufort Sea near Teshekpuk Lake (70° 26' N, 153° 08' W). We searched the study area on foot for nests and collected one fresh egg from 20 nests each year. Eggs were boiled in the field and subsequently kept frozen until separation and analysis (Gloutney and Hobson 1998).

Fifteen eggs laid by captive Spectacled Eiders housed at the Alaska Sealife Center (Seward, Alaska) were collected in May and June 2006. These birds were raised and maintained in captivity and fed a homogenous diet consisting of mostly ground corn, wheat, and fishmeal (Mazuri® Sea Duck Diet, Purina Mills, St. Louis, MO) throughout their life. Fresh yolk was separated from the albumen and kept frozen until analysis. Isotope ratios in egg yolk are not affected by boiling and then freezing compared to freezing fresh yolk (Gloutney and Hobson 1998).

4.3.3. Laboratory techniques

Following common practice used in most isotopic studies of avian eggs we lyophilized and then homogenized yolk samples from each egg ($n = 40$ King Eider, $n = 15$ Spectacled Eider) by grinding with a mortar and pestle. We then removed lipids by rinsing samples with a 2:1 chloroform:methanol solution (Bligh and Dyer 1959). We used ~5 mg of dry yolk sample and soaked samples multiple times for 24 h each until the solvent wash was completely clear. We extracted dissolved lipids manually with a pipette and kept them uncovered under a fume-hood at room temperature until all solvent had evaporated. Lipid samples were then kept frozen until analysis. For each component (whole yolk, lipid-free yolk, yolk lipids), we placed 0.2-0.4 mg in small tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. We used 0.9-1.2 mg of whole and lipid-free yolk for $\delta^{34}S$ analysis.

We measured stable isotope compositions by continuous flow isotope ratio mass spectrometry (CF-IRMS) at the Alaska Stable Isotope Facility (University of Alaska Fairbanks, $\delta^{13}C$ and $\delta^{15}N$) using a Finnigan Delta^{plus}XP CF-IRMS, and at the Stable Isotope Ratio Facility for Environmental Research (University of Utah, $\delta^{34}S$) using a Finnigan MAT Delta S CF-IRMS. We report results in delta (δ) notation relative to the internationally recognized standards (Vienna-PeeDee Belemnite for C, atmospheric air for N, Vienna-Canyon Diabolo Troilite for S) according to the following equation: δX

(‰)= ([Rsample/Rstandard]-1) × 1000, with X denoting either ^{13}C, ^{15}N, or ^{34}S, and R representing the ratio of ^{13}C /^{12}C, ^{15}N /^{14}N, or ^{34}S/^{32}S, relative to the respective standards. Standard deviation of known laboratory standards (peptone δ^{13}C = -15.8‰ and δ^{15}N = 7.0‰; bovine liver δ^{34}S = 8.0‰) run concurrently with samples was estimated to be 0.1‰, 0.2‰, and 0.3‰ for C, N, and S isotope measurements, respectively.

4.3.4. Arithmetic correction for lipids in yolk

The difference in δ^{13}C between whole and lipid-extracted tissues depends on the lipid content of the tissue (Post et al. 2007). We estimated the lipid content of egg yolk as a function of the molar C:N ratio according to the following equation (McConnaughey and McRoy 1979):

$$L = \frac{96}{1 + (0.246 \times (C:N) - 0.775)^{-1}} \qquad (1)$$

where L is the estimated proportion of lipid in the yolk sample, and $C:N$ is the molar ratio of carbon and nitrogen content (hereafter C:N ratio). This equation was originally developed for a wide variety of marine organisms (McConnaughey and McRoy 1979), and has recently been applied successfully to tissues of freshwater fishes and invertebrates (Kiljunen et al. 2006, Smyntek et al. 2007, Logan et al. 2008). It rests on three assumptions, namely that (1) biomass contains three organic fractions (protein, lipid, and carbohydrate), (2) biomass contains one nitrogenous fraction (protein), and (3) carbohydrate content is constant among samples (McConnaughey 1978). We adjusted the original equation (which used a numerator of 93 as the cumulative percentage of protein and lipid, McConnaughey 1978, p. 17) to the percentage of protein and lipid in dried avian egg yolk (96%, Burley and Vadehra 1989, p. 176).

To evaluate whether an arithmetic correction based on estimated lipid content could accurately predict δ^{13}C of lipid-free egg yolk, we followed the approach used by

Kiljunen et al. (2006) to build a correction model. We explored two alternative correction models (Post et al. 2007, Logan et al. 2008), but these models did not provide more accurate results and we briefly refer to them in the discussion. We used the following equation to calculate lipid-corrected $\delta^{13}C_{corrected}$:

$$\delta^{13}C_{corrected} = \delta^{13}C + D \times (I + \frac{3.90}{1 + 287/L}) \tag{2}$$

where $\delta^{13}C_{corrected}$ is the lipid-corrected value of the yolk sample, $\delta^{13}C$ is the measured value of the whole yolk sample, D is the isotopic difference in $\delta^{13}C$ between lipid-free yolk and yolk lipids, L is the estimated lipid content calculated according to equation 1, and I is a constant assigned a value of 0.048 (Kiljunen et al. 2006). We compiled published data on D from a variety of bird species and used an average D for carnivorous ducks for our model ($D = 5$‰, Table 4.1). We present all published values of D found in our review to facilitate easy application of this model to other bird species.

To test the accuracy of this arithmetic correction, we compared the $\delta^{13}C_{corrected}$ estimates to actual $\delta^{13}C_{extracted}$ values of chemically extracted yolk samples using a paired samples two-tailed t-test with $\alpha = 0.05$. We report prediction error ($\delta^{13}C_{corrected}$ - $\delta^{13}C_{extracted}$ in ‰) separately for Spectacled and King Eiders.

We then assessed the validity of model assumptions for our study species. Specifically, we calculated the difference, D, in $\delta^{13}C$ between lipid-free yolk and yolk lipids for our samples to examine whether the model assumption of D being constant was met in our samples. We further explored whether measurements of D for individual King Eider eggs were related to the prediction error for those eggs in our model. We report all results as mean ± SD.

4.4.   Results

Extraction of lipids from eider egg yolk led to a significant increase in sulfur, nitrogen, and carbon isotope ratios of yolk samples (Table 4.2). The C:N ratio of whole

yolk samples ranged from 13.2-17.1 (Table 4.3). There was no relationship between C:N ratio of whole yolk and the difference ($\Delta\delta^{13}C$) between whole yolk $\delta^{13}C$ and lipid-extracted yolk $\delta^{13}C$ in either King (linear regression, $P = 0.60$) or Spectacled Eider eggs ($P = 0.24$; Fig. 4.1).

Estimated lipid content was on average 71% ± 1.5% and very similar for both species (Table 4.3). We used estimated lipid content, $\delta^{13}C$ of whole yolk samples, and $D = 5.0‰$ for carnivorous ducks in equation 2 to estimate the lipid-corrected $\delta^{13}C_{corrected}$. This model predicted $\delta^{13}C$ extremely well in 15 Spectacled Eider eggs: there was no difference between predicted $\delta^{13}C_{corrected}$ and the $\delta^{13}C_{extracted}$ measurement (prediction error = 0.1‰ ± 0.2‰, paired t-test $t_{14} = -0.73$, $P = 0.47$). But when we tested the performance of the arithmetic lipid correction using wild King Eider eggs, $\delta^{13}C_{corrected}$ was on average 1.3‰ ± 1.2‰ higher than $\delta^{13}C_{extracted}$ ($t_{19} = -4.94$, $P < 0.001$, Fig. 4.2).

We then assessed a key assumption of the lipid correction model, namely that the mean difference D in $\delta^{13}C$ between yolk lipids and lipid-free yolk is constant. D was much more variable in King than in Spectacled Eider yolk (Table 4.3). The prediction error of the lipid correction model was small when measured D was similar to the constant used in the model, but increased significantly the more D deviated from the constant (Fig. 4.3). Thus, non-constant values of D in a wild migratory bird resulted in poor performance of the lipid correction model.

4.5.   Discussion

We found that the current practice of using chemical lipid extraction to prepare avian yolk samples for isotope analysis affects the $\delta^{15}N$ and $\delta^{34}S$ values of treated samples. The increase in both $\delta^{15}N$ and $\delta^{34}S$ may alter the conclusions of nutrient allocation studies. Therefore, we recommend using whole yolk samples instead of lipid-extracted yolk samples for the analysis of $\delta^{15}N$ and $\delta^{34}S$.

The effect of lipid extraction on $\delta^{15}N$ in this study is similar to the increase of 0.3-2.8‰ found in invertebrate and fish tissues (Sotiropoulos et al. 2004, Søreide et al. 2006, Sweeting et al. 2006). This is most likely due to the accidental leaching of proteins from yolk, as the polar solvent used (methanol) is not lipid-specific and will also dissolve hydrophobic proteins in membranes. Some polar structural lipids are associated with proteins, and, by removing polar lipids, the loss of associated proteins could lead to the increase in $\delta^{15}N$ (Sotiropoulos et al. 2004, Sweeting et al. 2006). A different solvent (e.g., diethyl ether) that does not remove polar lipids did not alter $\delta^{15}N$ in whole eggs (Ricca et al. 2007), but may be less effective in removing all lipids (Manirakiza et al. 2001, Schlechtriem et al. 2003).

We also found a previously undocumented increase in $\delta^{34}S$ in lipid-extracted King Eider yolk samples. The increase averaged 2.3‰ and thus was higher than for $\delta^{15}N$. Sulfur is mainly associated with sulfur-bearing amino acids in proteins, and incidental loss of proteins associated with polar structural lipids could also cause a loss of isotopically depleted sulfur. A further potential cause for the increase in $\delta^{34}S$ is the loss of sulfolipids through the extraction process (C. Stricker, pers. comm.). Sulfolipids are vital components of all photosynthetic membranes and are the most abundant biological sulfur compound after amino-acids (Benson 1963, Harwood and Nicholls 1979). They are soluble in chloroform and removal by lipid extraction may therefore alter the $\delta^{34}S$ signature of yolk samples (Joyard et al. 1988).

Given that chemical lipid extraction changes both nitrogen and sulfur isotope ratios, it would be desirable to use an arithmetic lipid correction for $\delta^{13}C$ of whole yolk samples. Lipid correction has been shown to be feasible in a wide variety of terrestrial and aquatic animals (Kiljunen et al. 2006, Post et al. 2007, Smyntek et al. 2007, Logan et al. 2008). We found that our arithmetic lipid correction model provided highly accurate results for captive Spectacled Eiders fed a homogenous high-quality diet, indicating that arithmetic lipid correction is a feasible alternative for egg yolk.

However, our model performed poorly for wild King Eider eggs in that model-predicted $\delta^{13}C_{corrected}$ was on average 1.3‰ higher than measured $\delta^{13}C_{extracted}$. This

difference can significantly affect the outcome of mixing models and thus alter the conclusions of isotopic studies (Phillips 2001).

We tested two alternative models, but neither provided more reliable predictions than the model we introduced in this paper. The Logan et al. (2008) model also requires an estimate for D as well as an estimate for lipid-free C:N ratio, and is therefore subject to the same limitations as our model. The Post et al. (2007) model depends on a relationship between C:N ratio and $\Delta\delta^{13}C$ (Fig. 4.1), which did not exist in our samples. The original parameters (Post et al. 2007) did not work for avian egg yolk (prediction error > 8‰), and we advise against using the Post et al. (2007) model to lipid-correct egg yolk.

Why did the lipid correction model perform accurately for captive, but not for wild eiders? We hypothesize that the most likely source of prediction error in wild migratory birds results from the variable origin of macronutrients in egg yolk. If protein and lipid in egg yolk are derived from isotopically different sources, the isotopic difference between protein and lipid (parameter D) is confounded by the isotopic difference between the sources. This results in variation in D (Table 4.3), which violates the assumption of lipid correction models that D is constant. We showed that variability in D explained most of the prediction error in wild King Eider eggs (Fig. 4.3). Migratory birds can obtain macronutrients for egg production at different stages of the annual life cycle (Hobson et al. 2000), and we believe that this is the most likely cause for variation in D and thus the poor performance of the lipid correction model for wild King Eider eggs.

King Eiders breed in arctic freshwater environments, but may incorporate macronutrients into eggs that were synthesized during spring migration in a marine environment. Body reserves accumulated in a marine environment are enriched in ^{13}C compared to freshwater nutrients (Hobson 2006). The isotopic difference between protein and lipids in egg yolk can therefore deviate from the assumed constant value of 5.0‰ used in our model, depending on which macronutrient is routed from a freshwater diet into yolk. This results in a more variable isotopic difference between protein and lipids

than if lipids were derived from the same ecosystem as proteins (Fig. 4.4). A further complicating factor for the use of our lipid-correction model is variability in D resulting from metabolic routing. Lipids can be synthesized from dietary carbohydrates or lipids, potentially introducing variance in isotopic composition (Podlesak and McWilliams 2007). Additional factors such as individual and within-clutch variation in nutrient allocation patterns (Klaassen et al. 2004, Hobson et al. 2005), as well as diet quality (Robbins et al. 2005) may cause variation in discrimination and thus influence the value of D. We recommend careful consideration of the potential origins of lipids and protein in yolk. The arithmetic correction developed in this paper is unreliable if proteins and lipids in egg yolk originate to varying degrees from isotopically distinct sources and are thus poorly represented by a constant parameter D.

4.5.1. Recommendations for future studies

In summary, we caution against the interpretation of $\delta^{34}S$ and $\delta^{15}N$ values from chemically-treated yolk samples. We do not recommend an arithmetic lipid-correction of egg yolk $\delta^{13}C$ for wild birds that are likely to differentially allocate lipids and protein from different diet sources or environments. Yolk samples from those species should be analyzed in both the lipid-extracted (for $\delta^{13}C$) and bulk form (for $\delta^{34}S$ and $\delta^{15}N$).

The arithmetic lipid-correction model presented in this paper will, however, yield reliable results for birds that derive lipids and proteins from isotopically homogenous sources. We recommend to initially lipid extract 10 yolk samples and to calculate D for each study species. If measured values of D show a small range (<1‰) and small variation (SD < 0.4‰), then the measured values of D can be used as a constant in equation 2 to calculate lipid corrected $\delta^{13}C$ values for remaining eggs of that species. We encourage researchers to validate the conclusions drawn in our study of captive Spectacled Eiders for species in the wild.

4.6.   Acknowledgements

4.7.   Literature Cited

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Table 4.1. Published data on the mean difference in δ^{13}C between chemically lipid-extracted yolk and yolk lipids (parameter *D*) from a variety of bird species. *D* is used as a constant in arithmetic lipid correction models. Multiple rows for a single species represent different study years or study sites. Data for *D* from species in boldface (carnivorous ducks) were used in our model for sea ducks.

Species		*n*	δ^{13}C Lipid-free Yolk	δ^{13}C Yolk Lipids	*D*	Source
Double-crested Cormorant	*Phalacrocorax auritus*	10	-22.8	-25.3	2.5	Hobson et al. 1997
Double-crested Cormorant	*Phalacrocorax auritus*	6	-23.9	-25.7	1.8	Hobson et al. 1997
Greater Snow Goose	*Chen caerulescens atlantica*	20	-25.3	-29.2	3.9	Gauthier et al. 2003
Greater Snow Goose	*C. caerulescens atlantica*	20	-25.0	-28.6	3.6	Gauthier et al. 2003
Greater Snow Goose	*C. caerulescens atlantica*	25	-24.5	-27.3	2.9	Gauthier et al. 2003
Greater Snow Goose	*C. caerulescens atlantica*	18	-25.0	-27.1	2.1	Hobson et al. 2000
Ross's Goose	*A. rossii*	18	-25.8	-28.0	2.2	Hobson et al. 2000
Mallard	*Anas platyrhynchos*	16			2.7	Hobson 1995
Redhead	*Aythya americana*	32	-29.2	-32.9	3.7	Hobson et al. 2004
King Eider	*S. spectabilis*	44	-23.8	(-26.4)		Lawson 2006
Long-tailed Duck	*Clangula hyemalis*	29	-23.6	(-25.9)		Lawson 2006
Barrow's Goldeneye	*Bucephala islandica*	24	-24.7	-31.0	6.3	Hobson et al. 2005
Parasitic Jaeger	*Stercorarius parasiticus*	10	-24.4	-27.5	3.1	Hobson et al. 2000

Table 4.1 continued

Bonaparte's Gull	*Larus philadelphia*	8	-24.8	-29.0	4.2	Hobson et al. 2000
Ring-billed Gull	*L. delawarensis*	10	-23.6	-26.8	3.2	Hobson et al. 2000
Mew Gull	*L. canus*	23	-25.0	-27.9	2.9	Hobson et al. 2000
Herring Gull	*L. argentatus*	12	-24.0	-26.2	2.2	Hobson et al. 1997
Herring Gull	*L. argentatus*	5	-21.8	-23.2	1.4	Hobson et al. 1997
Herring Gull	*L. argentatus*	12	-21.7	-25.6	3.9	Hobson et al. 1997
Herring Gull	*L. argentatus*	24	-24.9	-30.7	5.8	Hobson et al. 2000
California Gull	*L. californicus*	10	-26.2	-30.4	4.2	Hobson et al. 2000
Common Tern	*Sterna hirundo*	10	-22.3	-22.8	0.5	Hobson et al. 2000
Arctic Tern	*S. paradisaea*	25	-24.8	-26.7	1.9	Hobson et al. 2000
Black Tern	*Chlidonias niger*	10	-26.9	-27.4	0.5	Hobson et al. 2000
Caspian Tern	*S. caspia*	16	-25.0	-27.0	2.0	Hobson et al. 1997
Caspian Tern	*S. caspia*	10	-18.6	-21.2	2.6	Hobson et al. 1997
Caspian Tern	*S. caspia*	9	-22.8	-27.7	4.9	Hobson et al. 2000
Ruddy Turnstone	*Arenaria interpres*	24	-25.3	-30.4	5.1	Morrison and Hobson 2004
Prairie Falcon	*Falco mexicanus*	2			3.7	Hobson 1995
Peregrine Falcon	*F. peregrinus*	6			3.5	Hobson 1995
Gyrfalcon	*F. rusticolus*	4			3.3	Hobson 1995
Japanese Quail	*Coturnix japonica*	9			2.7	Hobson 1995

Table 4.2. Comparison of whole yolk and chemically lipid-extracted yolk isotope values (mean ± SD) of captive Spectacled Eider (SPEI) and wild King Eider (KIEI) eggs. All differences are statistically significant with $P < 0.001$.

Species	Isotope (δ)	n	Whole Yolk (‰)	Lipid-free Yolk (‰)	Difference (‰)
SPEI	^{13}C	15	-23.3 ± 0.3	-19.2 ± 0.2	4.1 ± 0.4
KIEI	^{13}C	20	-24.0 ± 2.4	-21.2 ± 2.3	2.8 ± 1.2
SPEI	^{15}N	15	9.4 ± 0.6	10.6 ± 0.4	1.2 ± 0.7
KIEI	^{15}N	20	9.2 ± 1.4	10.2 ± 1.4	1.0 ± 0.3
KIEI	^{34}S	30	9.8 ± 2.3	12.1 ± 2.4	2.3 ± 1.1

Table 4.3. Estimated lipid content (%), difference in $\delta^{13}C$ between chemically lipid-extracted yolk and yolk lipids (parameter *D*), and C:N ratio of whole yolk from 20 wild King Eider and 15 captive Spectacled Eider eggs.

	King Eider				Spectacled Eider			
	mean	SD	min	max	mean	SD	min	max
lipid content (%)	70.5	1.2	68.3	72.0	71.8	1.6	68.6	74.4
D (‰)	4.3	1.7	0.5	6.3	5.5	0.3	4.7	5.9
C:N $_{whole\ yolk}$	14.4	0.7	13.2	15.3	15.3	1.1	13.3	17.1
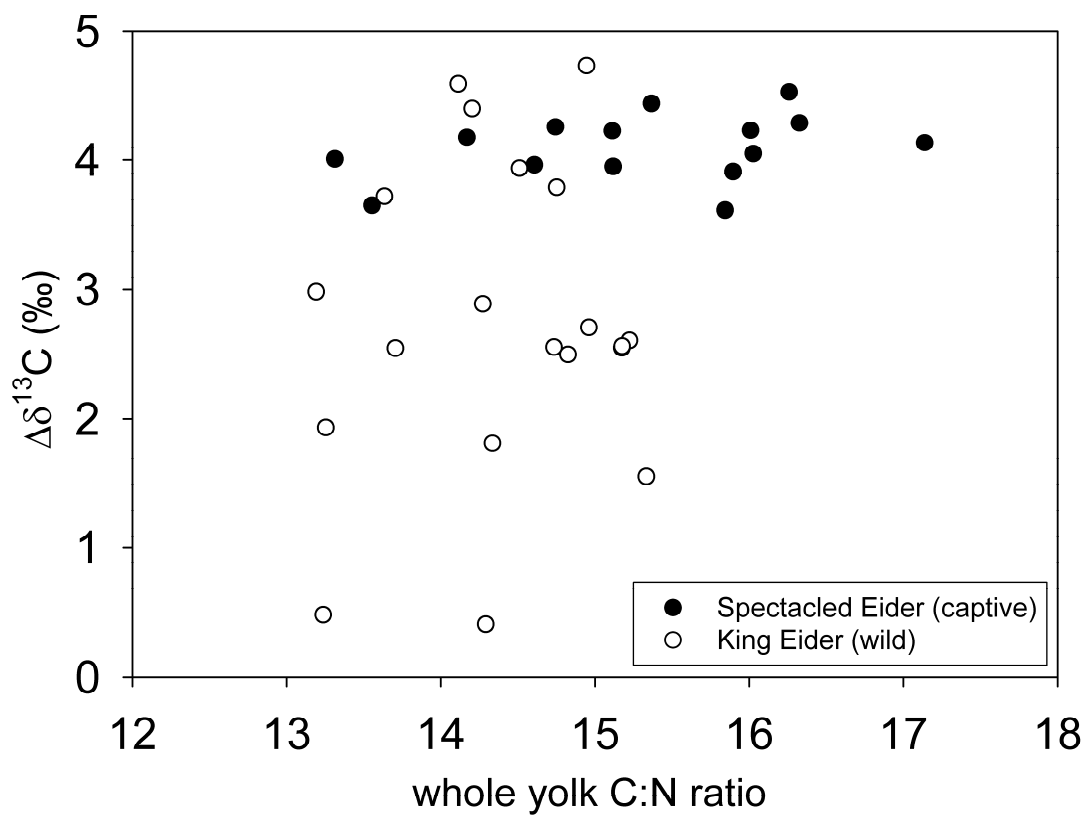
Fig. 4.1. Relationship between the C:N ratio of whole yolk and the difference ($\Delta\delta^{13}C$) between whole yolk $\delta^{13}C$ and chemically lipid-extracted yolk $\delta^{13}C$ of wild King Eider (white circles) and captive Spectacled Eider (black circles) eggs.
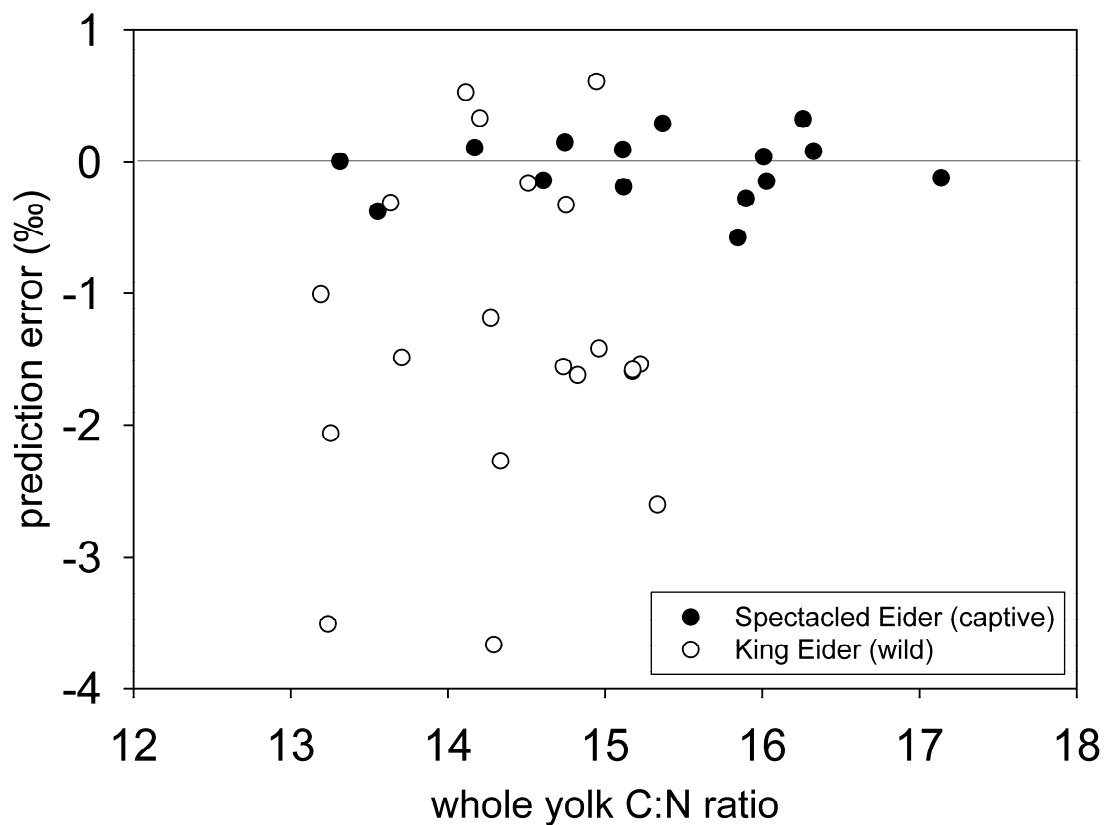
Fig. 4.2. Prediction error ($\delta^{13}C_{corrected}$ - $\delta^{13}C_{extracted}$ in ‰) of the arithmetic lipid correction model (Eq 2) in egg yolk of wild King Eiders (white circles) and captive Spectacled Eiders (black circles) was independent of whole yolk C:N ratio. Solid reference line indicates a perfect match between model prediction and lipid-extracted samples.
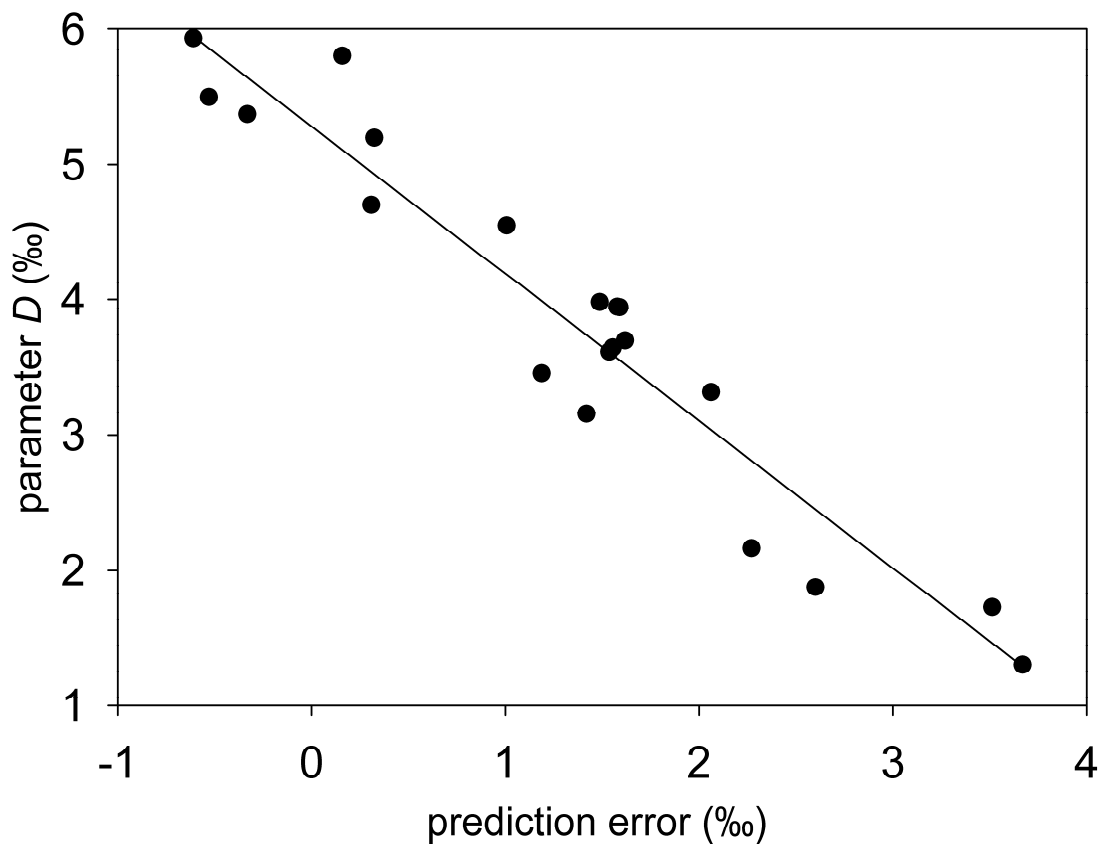
Fig. 4.3. Relationship describing the isotopic difference between protein and lipid fraction in egg yolk (parameter *D*) as a function of the prediction error ($\delta^{13}C_{corrected}$ - $\delta^{13}C_{extracted}$ in ‰) of lipid-corrected yolk samples from 20 wild King Eider eggs (linear regression, *b* = -1.1, r^2 = 0.92).
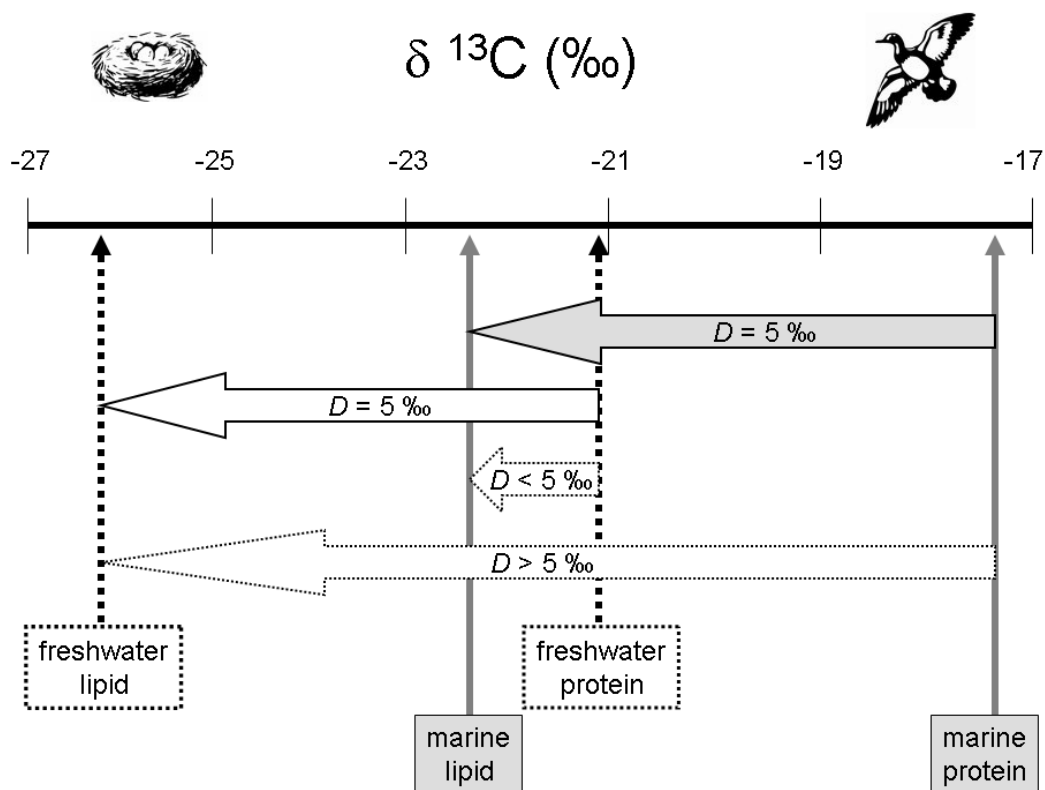
Fig. 4.4. Schematic presentation of how parameter *D* (the isotopic difference between protein and lipid fractions in egg yolk) can vary in bird species that obtain macronutrients from different ecosystems. The concept is demonstrated for birds that breed in a freshwater environment with food depleted in $\delta^{13}C$, but migrate and/or winter in a marine environment with food enriched in $\delta^{13}C$. *D* can assume values greater or smaller than the hypothetical constant *D* = 5‰ depending on which macronutrient is transferred between ecosystems.

5. Nutrient Allocation in an Arctic Sea Duck – King Eiders use an income strategy to produce eggs[1]

5.1. Abstract

Many arctic bird species produce eggs at a time when food abundance may be low. This challenge can be overcome by using body reserves for egg production, a strategy termed capital breeding and previously believed to be widespread in arctic-nesting birds. We investigated nutrient allocation to egg production in a large-bodied, arctic-nesting sea duck, the King Eider (*Somateria spectabilis*), at two sites in northern Alaska approximately 350 and 500 km from an important spring staging area. We predicted that King Eiders would rely primarily on body reserves accumulated on marine staging areas to provision eggs. We used two independent isotopic mixing models to quantify the amount of endogenous carbon and nitrogen invested into eggs based on ^{13}C and ^{15}N isotope ratios of the laying female's diet and body reserves. We found very large isotopic variation among prey items on the nesting grounds, and this variability was reflected in the plasma of nesting females, indicating that individuals differed in prey choice on breeding grounds. Thus, we used a novel approach to define the isotopic signature of current diet individually for every nesting female based on isotope ratios of eggshell membranes. At the population level, King Eiders used an income strategy for egg production with the majority of carbon and nitrogen in albumen (C: 86 ± 18%, N: 99 ± 1%) and yolk protein (C: 54 ± 24%, N: 90 ± 15 %) being derived from food consumed on breeding grounds. Yolk lipids were highly variable but also appeared to be derived from exogenous sources in most eggs. At the individual level, nutrient allocation was variable among females, and we recommend that future investigations examine the sources of this variation.

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5.2.   Introduction

Birds breeding at arctic latitudes produce and raise offspring during a short summer, and this may require egg formation at a time when food on breeding grounds may be scarce or absent (Perrins 1996). One way to overcome this challenge is to carry nutrients from an earlier stage of the annual cycle to provision the reproductive effort, a strategy referred to as capital breeding (Jönsson 1997, Meijer and Drent 1999). Traditionally, arctic-nesting birds have been viewed as capital breeders that produce eggs mainly from stored body reserves (Ankney and MacInnes 1978). However, the capital breeding paradigm has recently been challenged because several arctic-nesting species are at least partial income breedersthat produce eggs from nutrients obtained on breeding grounds (Klaassen et al. 2001, Gauthier et al. 2003, Morrison and Hobson 2004).

Capital and income breeding are the two extremes of a continuum of breeding strategies. The position of a species on that continuum depends not only on resource availability at breeding areas, but also on the distance to the nearest area where reserves can be accumulated (Klaassen et al. 2006), the quality of this area in relation to the breeding area (Drent et al. 2007), and costs associated with accumulating and transporting reserves from a distant staging area (Alerstam 2006). Klaassen et al. (2001) hypothesized that it might be energetically too costly for small birds to carry sufficient body reserves through spring migration to breeding grounds to form complete clutches of eggs. Consequently, capital breeding should be more prevalent in large-bodied species (Klaassen et al. 2006, Nager 2006, Nolet 2006).

Eiders (*Somateria* spp.) are the largest carnivorous waterfowl breeding in the Arctic. Common Eiders (*S. mollissima*) have been described as true capital breeders (Parker and Holm 1990). Common Eiders accumulate body reserves very close (<100

km) to breeding areas (Oosterhuis and van Dijk 2002, Guillemette and Ouellet 2005). In contrast, slightly smaller King Eiders (*S. spectabilis*) migrate several hundred kilometers between spring staging areas and breeding areas (Phillips et al. 2007, Oppel et al. 2008). King Eiders rely on body reserves to fuel their metabolism during incubation (Kellett and Alisauskas 2000, Bentzen et al. 2008), and should be able to carry sufficient reserves to pursue a capital strategy for egg formation based on allometric equations of energy expenditure during migration and clutch formation (Nolet 2006). However, the source of nutrients for egg synthesis in King Eiders is not known.

In this study we examined nutrient allocation to egg production of King Eiders using stable isotopes of carbon and nitrogen to quantify the proportion of egg nutrients derived from body reserves (Hobson 2006). We studied a breeding population in northern Alaska approximately 350-500 km from the main spring staging area, a relatively short distance for this species (Oppel et al. 2008). We utilized the well-described isotopic differences between marine and freshwater environments to distinguish egg nutrients accumulated in marine staging areas from nutrients derived from a diet available on tundra breeding areas. We introduce a novel extension of this technique to account for individual variation in diet choice on breeding grounds, by using the isotope ratios of eggshell membranes as a clutch-specific isotope signal of the maternal diet (Oppel et al. 2009, Chapter 3). Thus, we assess nutrient allocation in two ways: at the level of individual females, using two-source isotopic mixing models (Phillips 2001), and at the population level using a Bayesian mixing model to account for variability in endpoints and fractionation (Jackson et al. 2008, Moore and Semmens 2008). We assess nutrient allocation to egg yolk and albumen separately and independently using both carbon and nitrogen isotopes.

5.3.   Material and Methods

5.3.1. Study area

We studied King Eiders in June and July 2005–2007 at two sites located on the Arctic coastal plain of Alaska. 'Olak' was near Teshekpuk Lake, approximately 30 km south of the coast of the Beaufort Sea (70° 26' N, 153° 08' W), and 'Kuparuk' was ~150 km to the east within an active oilfield 10 km south of the coast (70°20' N, 149°45' W). Both sites consisted mainly of low lying tundra with numerous ponds, lakes and wetland complexes. Satellite telemetry has shown that King Eiders arrive in the study areas in the first week of June, and do not commute between breeding grounds and marine foraging sites after arriving on the tundra (Phillips et al. 2007). Thus, nutrients obtained during foraging on breeding grounds can be assumed to be entirely terrestrial and/or freshwater, and thus should exhibit a different isotopic signature than nutrients derived from the marine diet during migration (Peterson and Fry 1987). King Eiders nesting in both study areas winter in the Bering Sea and use the Eastern Chukchi Sea for approximately 3 weeks during spring migration (Chapter 8). Some birds spend another 10-15 days in the Beaufort Sea off the Alaskan coast, where body reserves could be replenished. However, the Beaufort Sea has a markedly lower density of benthic biomass than the Eastern Chukchi Sea (Dunton et al. 2005), and it is likely that reserve accumulation is mostly accomplished in the Chukchi Sea. This staging area is approximately 350 km (flying route) from Olak and 500 km from Kuparuk.

5.3.2. Field measurements

We located King Eider nests by randomly searching each study site between mid-June and mid-July, and estimated incubation stage of nests by candling eggs on the day a nest was found (Weller 1956). We calculated the day of nest initiation as the day the nest was

found minus the incubation stage (in days) of the oldest egg in the nest minus 2 days to adjust for the initial laying stage during which eggs are not incubated (Suydam 2000).

5.3.3. Tissue and food source collection

We collected one fresh egg from each clutch in 2006 and 2007, as well as all infertile eggs and eggs from abandoned or partly depredated nests in 2005 – 2007. We also collected all remaining eggshell membranes (hereafter: membranes) from depredated and hatched nests. Eggshell fragments were sorted to ensure that each membrane sample represented an individual egg. Membranes were stored individually in paper envelopes and kept dry. Whole eggs were boiled in the field and subsequently kept frozen until analysis (Gloutney and Hobson 1998).

All King Eiders at our study sites migrate past Point Barrow, Alaska, in spring (Phillips et al. 2007), approximately 150 and 300 km west of Olak and Kuparuk, respectively. In 2003, 8 female King Eiders shot by subsistence hunters during the spring migration hunt in Barrow were collected for another study; we excised sections of breast muscle and abdominal fat depots from those birds to analyze the isotope ratios of King Eider protein and lipid stores (Gauthier et al. 2003).

In 2006 and 2007 we captured 21 female King Eiders on the breeding grounds during the pre-nesting period (8-20 June) using mistnet arrays and decoys. Most of these birds were not associated with the nests sampled in our study. We collected 1 ml of blood from each bird by jugular venipuncture. Blood samples were separated into blood plasma and red blood cells (RBC) using a portable centrifuge and a precision syringe. We stored plasma and RBC samples frozen in liquid nitrogen until analysis.

We collected potential food items by manually sieving through mud in ponds and lakes of the study areas in July 2005, and by netting pelagic invertebrates in June 2006 and August 2007 from ponds where female King Eiders were observed foraging. We kept all invertebrate samples frozen until analysis. In 2006 we also collected aquatic plant

leaves (mostly *Carex* spp., Cyperaceae) from the same ponds. We air-dried plant samples and kept them dry until analysis.

5.3.4. Stable isotope analysis of tissues

We separated whole eggs manually into yolk, albumen, membrane, and shell. Membranes were cleaned with a small brush in de-ionized water to remove surface contaminants, oven-dried at 60°C for 24 hours, and then crumbled in a plastic bag. Albumen and yolk were freeze dried to constant mass for 48 hours, and then ground into powder using mortar and pestle. We extracted yolk lipids by using several rinses with a 2:1 chloroform:methanol solution (Bligh and Dyer 1959, Hobson 1995), and evaporated all remaining solvent from both the extracted lipids and the remaining protein fraction under a fume hood. We cleaned breast muscles and abdominal fat in de-ionized water, freeze-dried and ground them into powder, and extracted lipids from breast muscle using a 2:1 chloroform:methanol solution (Gauthier et al. 2003). We also freeze-dried plasma and RBC samples and homogenized them using mortar and pestle. We did not remove lipids from blood or membrane samples, as these tissues contain very little lipid (Burley and Vadehra 1989, Cherel et al. 2005).

We removed calcified shells from freshwater invertebrates, rinsed soft parts in de-ionized water, oven dried them at 60°C for 24 hours, and then ground them into powder using mortar and pestle. We used an arithmetic correction for lipid content in invertebrate samples based on mass balance and the C/N ratio of samples (Smyntek et al. 2007). Tadpole shrimps and fairy shrimps (Crustacea: Branchiopoda) collected in August 2007 were lipid extracted with a 2:1 chloroform:methanol solution, and we analyzed extracted lipids and lipid-free body tissues separately.

All dried and homogenized materials were analyzed for carbon and nitrogen isotope ratios at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using a continuous flow stable isotope-ratio mass spectrometer. We analyzed RBC, plasma, yolk, and albumen for sulfur isotope ratios, but sulfur did not contribute to a better

understanding of nutrient allocation and those results are listed in Appendix 5.1. We report results of carbon and nitrogen isotope analyses in delta (δ) notation relative to international standards (Vienna PeeDee Belemnite for C, atmospheric nitrogen for N) according to the following equation: $\delta X = ([R_{sample}/R_{standard}]-1) \times 1000$, with X denoting either ^{13}C or ^{15}N, and R representing the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. The analytical error was estimated to be less than ±0.2‰ for carbon and ±0.2‰ for nitrogen in peptone standards run concurrently with samples.

5.3.5. Calculation of source contribution

We used a simple linear mixing model to quantify the contribution of two sources (marine-derived body reserves vs. freshwater diet) to a mixture (egg components) using a single isotopic dimension (Phillips 2001). We performed these calculations using both carbon and nitrogen, to independently verify our results and assess whether allocation patterns differed between these elements. We estimated the contribution of body reserves and freshwater dietary nutrients separately for lipid-free yolk and albumen. We applied corrections for isotopic discrimination between diet, body reserves, and egg components following the approach of Gauthier et al. (2003), and assumed that discrimination between body reserves and egg components is equivalent to discrimination exhibited by carnivorous income breeders (Gauthier et al. 2003). For albumen, we corrected for discrimination by adding +0.9‰ to the $\delta^{13}C$ values of endpoints, and +3.2‰ to $\delta^{15}N$ values. For lipid-free yolk, we added +3.4‰ to $\delta^{15}N$ of endpoints, and assumed no discrimination in $\delta^{13}C$ (Hobson 1995).

Red blood cells and muscle exhibit similarly slow rates of isotopic turnover (Hobson and Clark 1993, Bearhop et al. 2002); therefore, we used mean $\delta^{13}C$ and $\delta^{15}N$ of RBC from pre-nesting King Eiders to reflect body reserves (capital endpoint). Breast muscle $\delta^{13}C$ and $\delta^{15}N$ of females collected during spring migration were only slightly enriched over RBC (Table 5.1), confirming that RBC accurately reflected the

assimilating body protein pool after arrival on breeding grounds (Morrison and Hobson 2004, Schmutz et al. 2006).

The diet of King Eiders on breeding grounds is poorly known, and we found very large isotopic variation among potential prey items in our study area (Table 5.1). We also found a wide range of isotopic values in blood plasma of females during egg formation, which indicated that individual females specialized on prey items with different isotope ratios (Bolnick et al. 2002, Matthews and Mazumder 2004). Due to this variation both in diet items and in foraging behavior, a mean isotope signature reflecting exogenous nutrients (income endpoint) was inappropriate for all individuals. Instead, we used a novel approach of assigning eggshell membrane isotope ratios as a clutch-specific income endpoint.

As eggshell membranes are thought to be synthesized from current diet (Schaffner and Swart 1991, Hobson 1995), and their isotope ratios do not change during incubation (Oppel et al. 2009), we propose that they can be used to indicate diet on breeding grounds for each individual nesting female. Two lines of evidence suggest that there is no endogenous nutrient contribution to membrane formation. First, we captured two females during egg formation and later identified them on a nest, allowing us to compare plasma and membrane $\delta^{13}C$ and $\delta^{15}N$ of individual females. In both birds plasma was enriched in both $\delta^{13}C$ and $\delta^{15}N$ compared to all eggshell membranes after correcting for discrimination. Thus, membranes may reflect current diet better than plasma, as incomplete turnover of plasma may have led to slightly elevated isotopic signatures. Secondly, calculations using the average female plasma isotope ratio as a population-wide income endpoint yielded consistently higher exogenous source contributions for both C and N in both yolk and albumen. This is opposite of what would be expected if membranes would contain endogenous nutrients. We are thus confident that membranes reflect local diet (Hobson 1995).

We used the average $\delta^{13}C$ and $\delta^{15}N$ of all membranes collected from a clutch to describe the isotope signature of each laying female's diet, enabling us to estimate endogenous and exogenous source contributions to egg formation. If the difference

between the membrane (income) endpoint and the RBC (capital) endpoint was <2‰ in δ^{13}C or δ^{15}N, we excluded these eggs (12 of 140 for yolk and 10 of 116 for albumen) from source contribution calculations, as the error in calculations increases exponentially as the isotopic difference between endpoints decreases (Phillips and Gregg 2001). We calculated source contribution at the individual level, and present results for each isotope and egg component as mean ± standard deviation (SD) and range for the population.

To explicitly take uncertainty in endpoints and discrimination factors into account, we validated our results by using a Bayesian mixing model at the population level. This model incorporates variability in endpoints and discrimination factors to calculate a posterior probability distribution of source contributions (Jackson et al. 2008, Moore and Semmens 2008). We used the mean and SD of King Eider RBC and eggshell membranes (Table 5.1) as endogenous and exogenous endpoints, respectively, after accounting for discrimination. For discrimination, we used the mean and SD of published (Hobson 1995) and unpublished (R. Federer, Alaska Sea Life Center, personal communication, preliminary unpublished data from 17 captive Spectacled Eiders, *S. fischeri*) discrimination factors, resulting in the following discrimination factors used in the model: membrane–albumen: -1.4 ± 1.2‰ for δ^{13}C and -0.9 ± 1.1‰ for δ^{15}N; RBC–albumen: +2.2 ± 0.9‰ and +3.3 ± 0.6‰, membrane–lipid-free yolk: -2.0 ± 1.1‰ and -0.6 ± 1.2‰; RBC–lipid-free yolk: +1.5 ± 0.7‰ and +3.6 ± 0.8‰. We used SIAR v 2.07 in R 2.7.2 (Parnell 2008) to create posterior probability distributions for endogenous and exogenous contributions.

5.3.6. Statistical analysis

We report all results as mean ± SD. We used non-parametric Mann-Whitney *U*-Tests or Kruskal-Wallis tests to test for significant differences among groups at $\alpha = 0.05$. In multiple comparisons we used a Bonferroni correction to adjust the error rate to the number of comparisons. We used an ANOVA to examine whether within-clutch variation

in nutrient allocation was larger than variation among clutches, and we restricted this analysis to clutches from which we estimated nutrient allocation of more than two eggs. All analyses were carried out using SPSS 11.0.

5.4. Results

5.4.1. Isotopic signatures of body tissues

Plasma and RBC of birds captured prior to nesting on breeding grounds did not differ between years (all $P > 0.1$), so we pooled samples from 2006 and 2007. Muscle δ^{13}C of female King Eiders collected on spring migration was enriched by 1.7‰ over RBC δ^{13}C collected from birds on breeding grounds during the pre-nesting period, but muscle and RBC did not differ in δ^{15}N (Table 5.1). δ^{13}C in abdominal lipid of collected females was depleted by 6.2‰ compared to muscle (Table 5.1). Isotope ratios of RBC of King Eiders captured during the pre-nesting period did not differ between sites (δ^{13}C: $P = 0.12$, δ^{15}N: $P = 0.64$, $n = 21$). We therefore used the pooled sample of RBC δ^{13}C and δ^{15}N from both sites as our capital endpoint (δ^{13}C: -19.5 ± 0.8‰, δ^{15}N: 14.6 ± 0.6‰).

5.4.2. Isotopic signatures of diet on breeding grounds

We found extremely high variation in freshwater invertebrates collected on breeding grounds, ranging from -33.0‰ to -20.3‰ in δ^{13}C and from 0.0‰ to 9.9‰ in δ^{15}N (Table 5.1). The C/N ratio of whole invertebrates ranged from 4.1 to 8.6 (mean 5.6 ± 1.1), resulting in an estimated average lipid content of 33 ± 9% (McConnaughey and McRoy 1979). Lipids extracted from tadpole shrimp (*Triops* spp.) and fairy shrimp (Anostraca: Artemiidae) were 4.2 ± 0.9‰ depleted in δ^{13}C compared to lipid-free body tissues of

these animals, but were only 1.4‰ depleted compared to the overall lipid-corrected invertebrate average δ^{13}C (Table 5.1). Aquatic plants were on average about 4‰ depleted in δ^{13}C compared to all invertebrates, but fell completely within the range of δ^{13}C variation of invertebrates (Table 5.1).

5.4.3. Evidence for individual differences in diet

Isotopic variation in eggshell membranes was as large as in diet items (Table 5.1). We found evidence for individual diet specialization among nesting King Eiders by calculating the within-individual component of the isotopic variance in membranes (Bolnick et al. 2002). We found that within-clutch membrane isotopic variance was small compared to the total variance in the population (δ^{13}C WIC/TNW = 0.24, δ^{15}N WIC/TNW = 0.30, based on 57 clutches with >1 membrane), and concluded that individual female King Eiders forage on isotopically different sources during egg formation.

5.4.4. Isotopic signatures of egg components

We found large variation in both δ^{13}C and δ^{15}N in King Eider egg components (Table 5.1). There were no differences in egg isotope signatures among years (all Bonferroni-corrected $P > 0.05$), and we pooled all years for analysis. We found statistically significant differences between Olak and Kuparuk in δ^{13}C of lipid-free yolk and albumen, as well as δ^{15}N of membranes (all $P < 0.005$). However, the magnitude of the difference was <1.3‰ in all cases, and thus smaller than the standard deviation within either site.

5.4.5. Proportional contribution of exogenous nutrients to albumen

We did not find differences in exogenous nutrient allocation to albumen or yolk for either C or N across the three years of our study (all $P > 0.1$), and thus pooled all three years for further analysis.

Albumen was predominantly synthesized from nutrients consumed on breeding grounds. We estimated that exogenous C made up $86 \pm 18\%$ (range 26-149%, $n = 106$) of albumen C, with most eggs (65%) having exogenous C contributions of >80% (Fig. 5.1). Exogenous N contributed 87%-142% to albumen N ($109 \pm 10\%$, $n = 116$). Values exceeding 100% reflect error propagation through mixing model calculations; however, the mean contribution of exogenous N to albumen was indistinguishable from 100%. If we adjusted N contributions to egg albumen to a maximum value of 100% (in $n = 96$ eggs), the average contribution of exogenous N was $99 \pm 1\%$ ($n = 116$).

5.4.6. Proportional contribution of exogenous nutrients to yolk

Exogenous C contributions to yolk protein were significantly lower than to albumen, with an average of $54 \pm 24\%$ (range: 0-148%, $n = 128$) of lipid-free yolk C derived from tundra food sources. We found large variation in C allocation to lipid-free yolk among eggs, with similar proportions of eggs having almost none (0-20%) and almost all (80-100%) C derived from exogenous sources (Fig. 5.1). C and N allocation to yolk protein were positively correlated ($b = 1.16 \pm 0.13$, $P < 0.001$, $R^2 = 0.38$), but the proportion of exogenous N allocations to yolk protein was on average 30% larger than exogenous C allocation (paired samples t-test, $t_{127} = 20.59$, $P < 0.001$). Based on $\delta^{15}N$ of lipid-free yolk we estimated that $90 \pm 15\%$ of yolk N was derived from exogenous sources. Only 4% of eggs had exogenous N contributions of <60%, and most eggs (82%) had very little (0-20%) endogenous N invested in yolk protein ($n = 137$, Fig. 5.1).

We could not apply a mixing model to the data for yolk lipids because yolk lipids were depleted in δ^{13}C by 2.4‰ compared to body fat from eiders, and by 0.5‰ compared to invertebrate lipids ($n = 30$, Table 5.1). In only 2 eggs (7%) were the lipids clearly of endogenous origin (δ^{13}C > -20‰), whereas in 16 eggs (55%) the lipids were of exogenous origin (δ^{13}C < -27‰, Fig. 5.2).

5.4.7. Variation in nutrient allocation

The large variation in C allocation we found among eggs could be either due to variation in nutrient allocation within a clutch, or due to variation in nutrient allocation among females. Within-clutch variation could be caused by laying order, whereas variation among females could be a result of individual nutrient allocation strategies. We were not able to determine laying order of King Eider eggs within a clutch, but examined whether C allocation was related to nest initiation date among clutches from which we collected more than one egg. Neither the minimum, maximum, nor average amount of exogenous nutrients allocated to lipid-free yolk in these clutches was correlated with nest initiation date (all $P > 0.15$, $n = 16$ nests, Fig. 5.3).

We then examined whether the variation in C allocation was a result of differences among individual females. For seven clutches from which we had >2 eggs, exogenous C contributions to yolk protein were less variable within clutches than among clutches (ANOVA, $F_{6,21} = 3.79$, $P = 0.01$). Similarly, exogenous C contributions to albumen were less variable within than among clutches ($F_{5,18} = 14.94$, $P < 0.001$, Fig. 5.3).

King Eiders nesting at Olak incorporated on average more endogenous nutrients into yolk (δ^{13}C: Olak $50 \pm 26\%$, Kuparuk $35 \pm 15\%$, $P = 0.003$; δ^{15}N: Olak $13 \pm 14\%$, Kuparuk $7 \pm 9\%$, $P = 0.002$, $n = 128$) and albumen (δ^{13}C: Olak $18 \pm 16\%$, Kuparuk $8 \pm 8\%$, $P = 0.002$, $n = 106$; δ^{15}N: Olak $1 \pm 2\%$, Kuparuk $0 \pm 1\%$, $P = 0.018$, $n = 116$) than birds nesting at Kuparuk (Fig. 5.4).

5.4.8. Bayesian analyses of population level nutrient allocation

Results from the Bayesian mixing model estimating nutrient allocation at the population level indicated that for albumen, both C and N were mostly (>90%) derived from exogenous sources (Fig. 4). This result agrees closely with the result based on individual-level mixing models. For lipid-free yolk, the Bayesian approach indicated that most (>80%) of N in lipid-free yolk was derived from exogenous sources (Fig. 4). For C, the posterior probability distribution indicated exogenous contributions between 70-90%, which was higher than the mean contribution calculated from averaging individual mixing models (Fig. 5.5). The discrepancy between calculations was a direct result of accounting for uncertainty in discrimination; if we used only published discrimination values (Hobson 1995) the Bayesian mixing model yielded a posterior probability distribution encompassing our average population estimate from individual mixing models.

5.5. Discussion

In contrast to our expectation, we found that King Eiders in northern Alaska largely use an income strategy to produce eggs. This result is surprising given their large body size, allometric considerations of transport costs, and the relatively short distance to the main spring staging site in the Chukchi Sea (Nolet 2006). It suggests that changes of freshwater foraging habitats on breeding grounds could have significant consequences for the ability of King Eiders to produce a normal clutch of 4-7 eggs.

Endogenous nutrients are still likely to be important to successful reproduction, in that female King Eiders lose about 35% of their arrival body mass during the breeding season (Kellett and Alisauskas 2000, Bentzen et al. 2008). Because only very little of these body reserves are invested in eggs, we suggest that they may support metabolic costs during the incubation period when eiders rarely leave the nest to forage (Kellett and

Alisauskas 2000). A bird of similar mass, the dark-bellied Brent Goose (*Branta bernicla*), arriving with a mass of 1500g on breeding grounds in the Siberian Arctic, invested half of the available body reserves into eggs (Spaans et al. 2007). However, these geese laid the entire clutch within a week of arrival. In contrast, mean arrival and nest initiation dates are two weeks apart for King Eiders in our study area, and none of the females collected on spring migration in Barrow showed enlarged follicles. Thus, rapid follicle growth is likely initiated after arrival on breeding grounds in most individuals, which explains the large proportions of exogenous nutrients even in yolk.

During incubation, King Eiders forage for less than 30 minutes per day (Bentzen et al. 2008), as opposed to Brent Geese that forage for an average of 3 hrs per day (Spaans et al. 2007). Thus, while Brent Geese invest their body reserves in eggs and therefore have to forage extensively during incubation, King Eiders may use exogenous resources for egg formation in order to retain body reserves for incubation (Bond et al. 2007, Gorman et al. 2008). As a consequence, there is potential for both endogenous and exogenous nutrient sources to be limiting to King Eider reproduction.

In contrast, Common Eiders rely heavily on body reserves both during laying (Parker and Holm 1990) and incubation (Bolduc and Guillemette 2003). They generally nest close to areas where they can accumulate large amounts of body reserves. King Eiders may use more exogenous nutrients for egg production because they nest farther away from staging areas (Klaassen et al. 2006). We found that King Eiders at Olak invested on average more body reserves in egg components than at Kuparuk. Birds nesting at Kuparuk have to fly approximately 150 km farther to their nesting grounds, and the difference we found is therefore consistent with the hypothesis that a capital strategy would be more pronounced for birds nesting closer to staging areas (Alerstam 2006, Klaassen et al. 2006, Nolet 2006). We can not, however, exclude the possibility that other factors like food quality, disturbance levels, or local microclimate may have caused the observed difference.

5.5.1. Variation in isotopic signatures and nutrient allocation

We found very large isotopic variation in egg components of King Eiders, which reflected mostly isotopic variation in diets consumed by laying females. King Eiders are known to forage opportunistically on a wide range of prey species at sea (Frimer 1997, Merkel et al. 2007), and our study suggests that foraging differences among individuals also occur in freshwater breeding areas. We recommend examining whether a population consists of individual specialists (Bearhop et al. 2004, Matthews and Mazumder 2004, Woo et al. 2008) before using population-wide average estimates of diet isotope ratios in nutrient allocation studies. A Bayesian mixing model yielded very similar results as an average derived from multiple clutch-specific linear mixing models, but did not indicate the large variation in nutrient allocation strategies among individuals (Fig. 5.5). This variation would be obscured by all approaches using a population-wide average endpoint for exogenous sources.

The novel approach of using membrane isotope ratios as a clutch-specific income endpoint enabled us to detect large variation in nutrient allocation among eggs, and much of the variation in C allocation was attributable to differences among females. Reviews of the capital-income dichotomy have emphasized that the breeding strategy of most species likely falls along the continuum between the two extremes of pure capital and income breeding (Jönsson 1997, Meijer and Drent 1999, Klaassen et al. 2006). Our study shows that with respect to egg formation nutrient allocation strategies can vary even within a species. This variation may be attributable to the timing of nest initiation. Although we did not find a relationship between nest initiation date and nutrient allocation strategy (Fig. 5.3), migratory schedules differ among individuals in our study area (Oppel et al. 2008, Chapter 1), and the time between arrival and laying may have a larger influence on nutrient allocation than the laying date *per se*. Future studies should investigate migratory schedules of individuals as causes of individual differences in nutrient allocation (Bêty et al. 2004, Ely et al. 2007).

In addition to the variation in endogenous nutrient contribution among eggs, we found differing contributions of endogenous C and N within eggs. Generally, we found a lower endogenous contribution of N than C in lipid free yolk. This is important because many diet mixing models assume that C and N are similarly allocated into tissues and eggs. The higher endogenous carbon contribution may result from catabolism of body reserves, particularly fat, and incorporation of some of this endogenous carbon into eggs (Podlesak and McWilliams 2006). Alternatively, the difference in the mixing models based on ^{13}C and ^{15}N could be due to uncertainty in discrimination factors. For example, if we applied a different diet–lipid-free yolk discrimination factor of +2.0‰ for δ^{13}C (R. Federer, unpubl. data), we estimated endogenous contributions to lipid-free yolk at 17 ± 18%, and thus identical to estimates from our δ^{15}N mixing model. This highlights the need for a better understanding of discrimination factors across a wider range of species (Gannes et al. 1997).

5.5.2. Conclusion

King Eiders primarily use an income strategy for egg production, suggesting that changes of freshwater foraging habitats on breeding grounds could have significant consequences for reproductive success. However, individual females varied in their reliance on endogenous nutrients for egg production, with a few producing eggs mostly from body reserves. Therefore, we caution against assigning a single nutrient allocation strategy to this species, and recommend that further investigations focus on causes and consequences of individual variation. Different nutrient allocation strategies may be a consequence of individual quality, age and nesting experience, or migratory strategies and schedules. Future research needs to determine whether extrinsic or intrinsic factors explain nutrient allocation strategies of individual females.

5.6.   Acknowledgments

5.7.   Literature Cited

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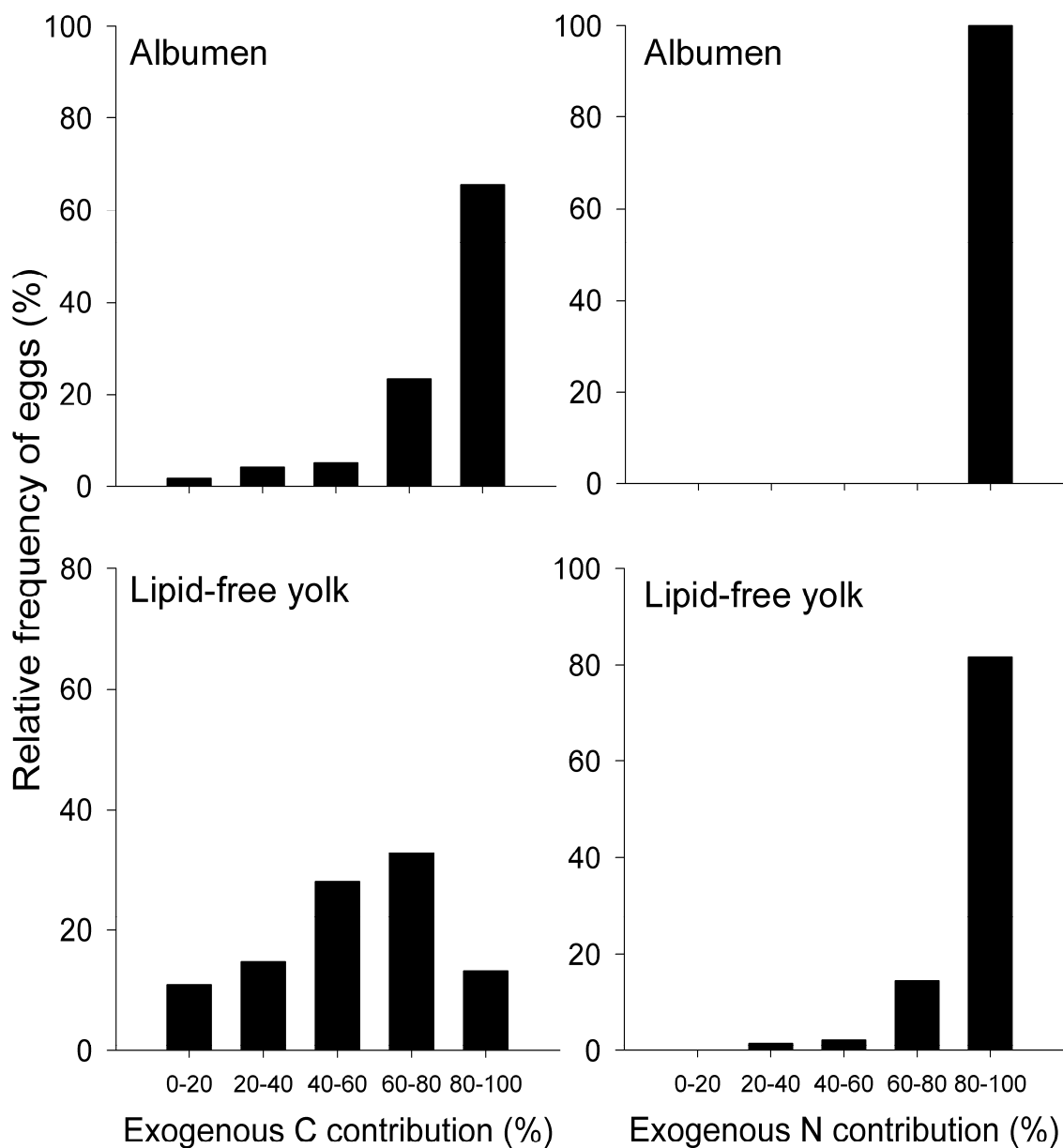
Figure 5.1. Relative frequency of exogenous carbon (left) and nitrogen (right) contribution to lipid-free yolk and albumen in King Eider eggs collected in northern Alaska, 2005–2007. Eggs for which mixing model results exceeded 100% were included in the 80-100% category.
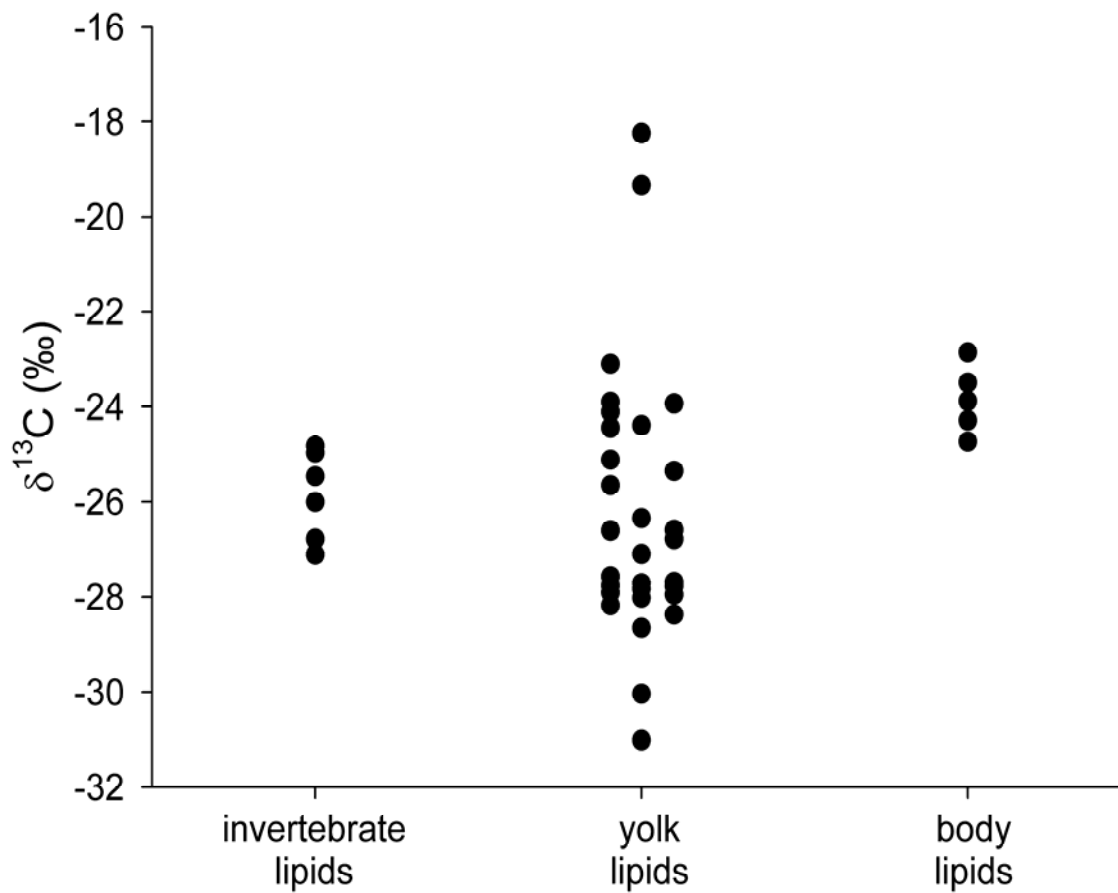
Figure 5.2. Carbon stable isotope values (δ^{13}C) for yolk lipids were extremely variable in King Eider eggs. Half of the analyzed samples ($n = 30$) were depleted compared to lipids from freshwater invertebrates, and 75% were depleted compared to King Eider adipose tissue reserves.
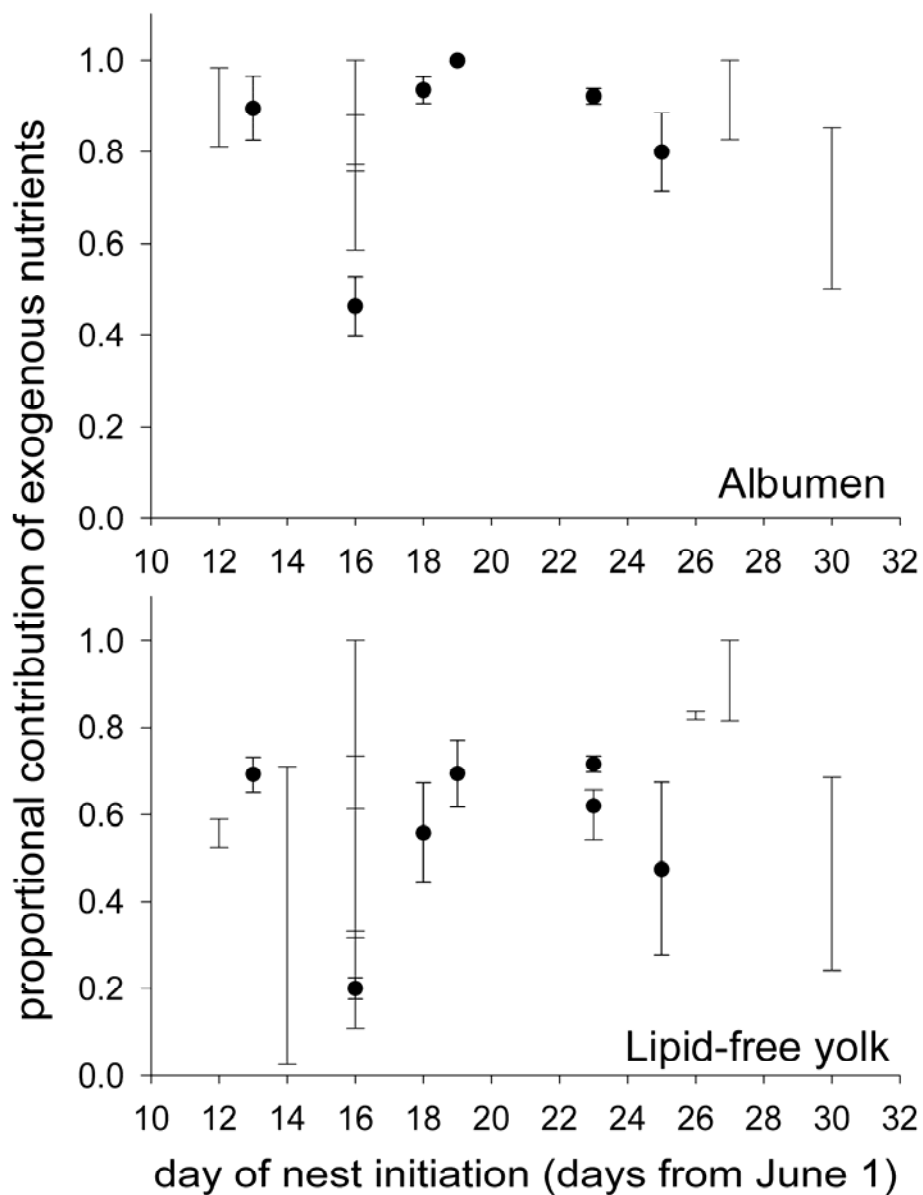
Figure 5.3. Proportional contribution of exogenous carbon to albumen (top) and lipid-free yolk (bottom) in eggs of 16 King Eider nests in relation to nest initiation date. Points represent averages (± SE) from clutches with >2 eggs, lines represent range in clutches from which only 2 eggs were analyzed.
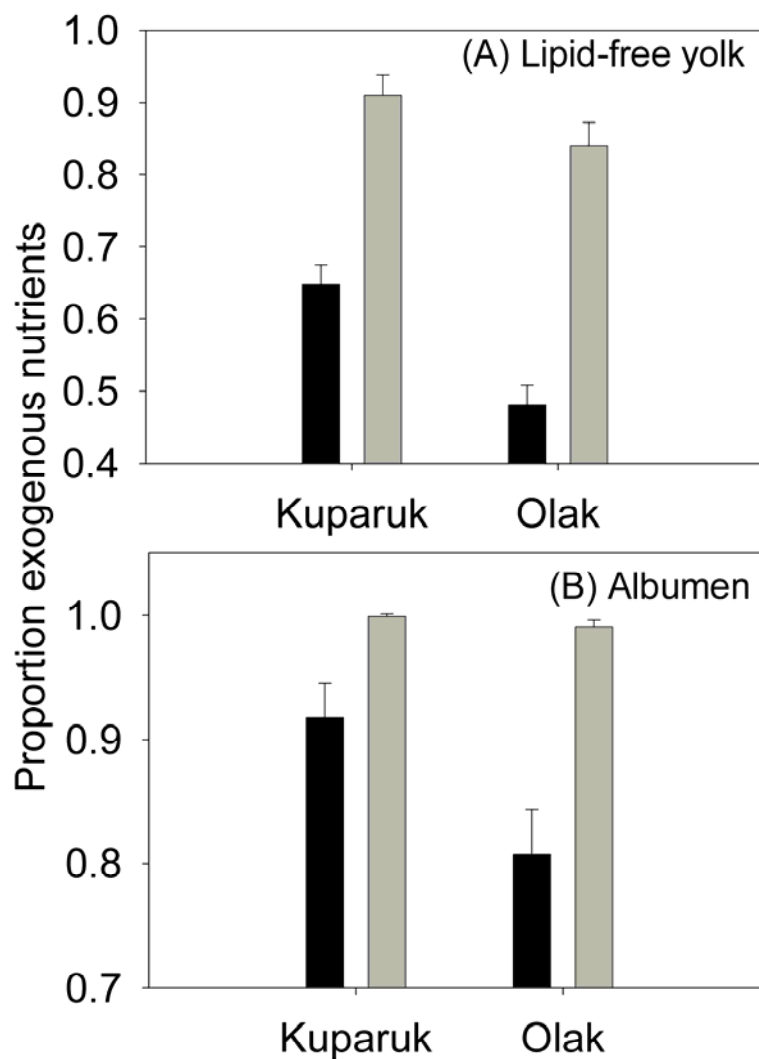
Figure 5.4. Site-specific average (± 95% confidence interval) proportional use of exogenous nutrients for (a) lipid-free yolk and (b) albumen in King Eider eggs calculated from a δ^{13}C isotope mixing model (black bars) and a δ^{15}N mixing model (gray bars). Eggs were collected at two different sites, Olak and Kuparuk, in northern Alaska, 2005–2007.
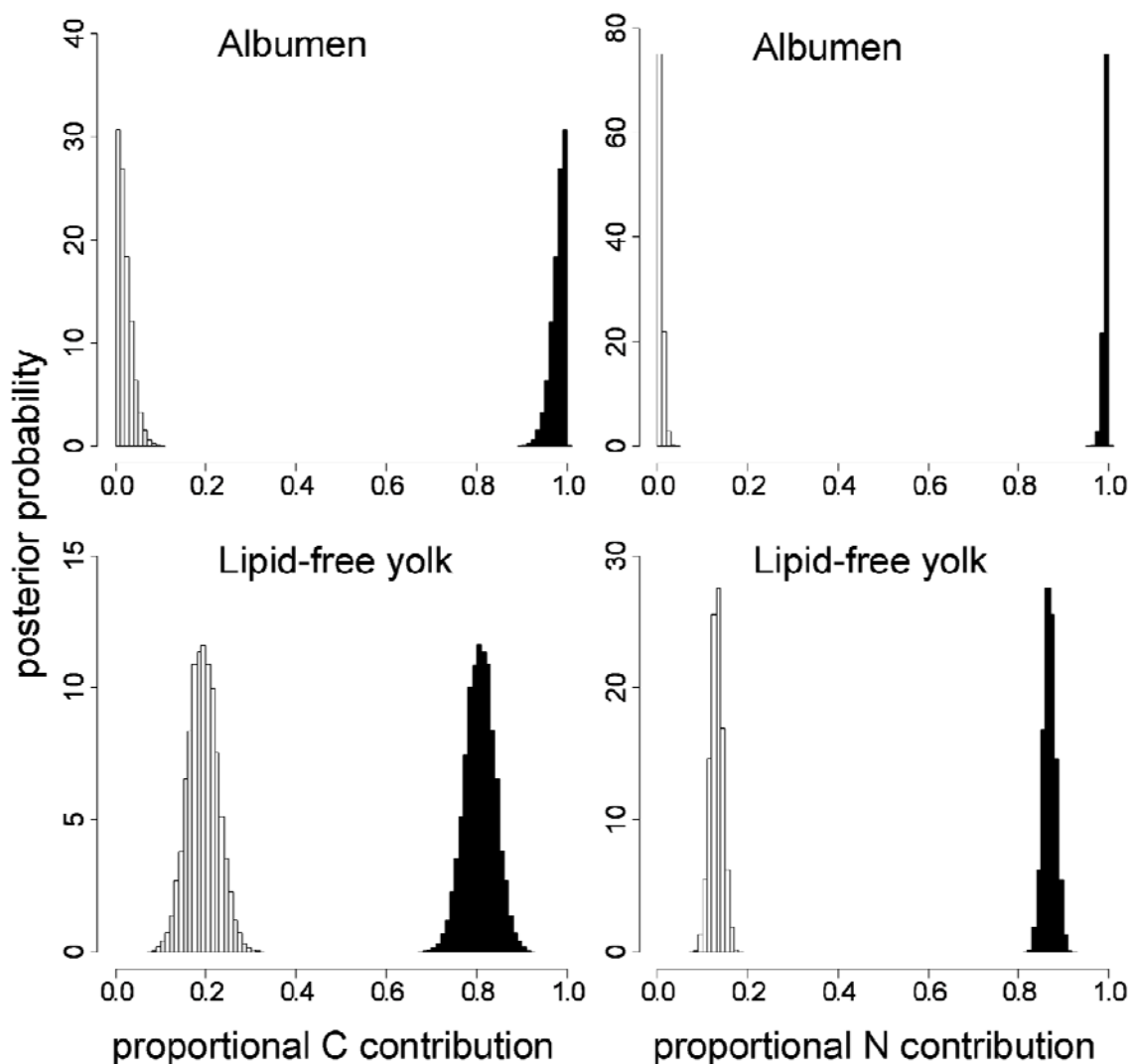
Figure 5.5. Posterior probability distribution of exogenous (white) and endogenous (black) nutrient contribution to King Eider eggs collected in northern Alaska, 2005–2007, calculated with a Bayesian isotope mixing model at the population level taking uncertainty in endpoints and discrimination factors into account. Carbon (left) and nitrogen (right) contributions to albumen (top) and lipid-free yolk (bottom).

Table 5.1. Ratios of stable carbon and nitrogen isotopes of relevant sources of nutrients, body tissues, and egg tissues of King Eiders in northern Alaska.

	$\delta^{13}C$					$\delta^{15}N$				
	n	mean	sd	min	max	*n*	mean	sd	min	max
King Eider body tissues										
breast muscle	*8*	-17.8	0.5	-18.4	-16.9	*8*	14.5	0.8	13.5	15.6
red blood cells (pre-nesting)	*21*	-19.5	0.8	-20.7	-18.3	*21*	14.5	0.6	13.4	15.5
abdominal lipids	*5*	-23.9	0.8	-24.7	-22.9	*5*	11.6	1.6	9.4	13.8
plasma (pre-nesting)	*19*	-23.1	2.0	-26.9	-19.8	*19*	11.4	2.2	9.1	16.6
Food on breeding grounds										
invertebrates	*59*	-26.6	3.5	-33.0	-20.3	*59*	4.8	2.3	0.0	9.9
invertebrate lipids	*7*	-25.9	0.9	-27.1	-24.8	*7*	3.0	0.8	2.1	4.5
plants (*Cyperaceae*)	*15*	-28.3	1.2	-30.0	-26.4	*15*	-0.3	5.6	-12.9	10.9
King Eider egg tissues										
eggshell membrane	*262*	-21.2	2.1	-26.8	-14.60	*262*	9.2	1.3	5.5	12.9
albumen	*117*	-22.9	2.1	-28.8	-18.1	*117*	7.9	1.2	4.3	12.0
lipid-free yolk	*142*	-22.1	2.2	-29.1	-16.4	*142*	9.9	1.6	6.2	15.7
whole yolk	*20*	-24.0	2.4	-26.9	-17.9	*20*	9.2	1.4	7.2	12.1
yolk lipids	*30*	-26.4	2.8	-31.0	-18.2	*30*	2.1	1.6	-0.9	5.6

Appendix 5.1. Ratios of stable sulfur isotopes of King Eider blood samples and egg tissues collected in northern Alaska in 2006. Egg yolk and albumen samples were analyzed for sulfur isotope ratios at the Stable Isotope Ratio Facility for Environmental Research (University of Utah, Salt Lake City). Plasma and red blood cell samples were analyzed for sulfur at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff). The analytical error was estimated to be less than ±0.3‰ for sulfur in bovine liver standards run concurrently with samples.

		δ^{34}S			
	n	mean	sd	min	max
King Eider body tissues					
red blood cells (pre-nesting)	*14*	15.1	1.2	13.0	16.6
plasma (pre-nesting)	*14*	12.5	4.4	1.5	16.7
King Eider egg tissues					
albumen	*91*	11.3	1.8	4.0	14.3
lipid-free yolk	*102*	12.0	2.0	4.4	16.0
whole yolk	*30*	9.8	2.3	3.8	13.8

6. Assigning King Eiders to Wintering Regions in the Bering Sea using Stable Isotopes of Feathers and Claws[1]

6.1. Abstract

Identification of wintering regions for birds sampled during the breeding season is crucial to understand how events outside the breeding season may affect populations. In this study, we assigned king eiders captured on breeding grounds in northern Alaska to three broad geographic wintering regions in the Bering Sea using stable carbon and nitrogen isotopes obtained from head feathers. Using a discriminant function analysis of feathers obtained from birds tracked with satellite transmitters we estimated that 88% of feathers were assigned to the region in which they were grown. We then assigned 84 birds of unknown origin to wintering regions based on their head feather isotope ratios, and tested the utility of claws for geographic assignment. Based on the feather results we estimated that similar proportions of birds in our study area use each of the three wintering regions in the Bering Sea. These results are in close agreement with estimates from satellite telemetry and show the usefulness of stable isotope signatures of feathers to assign marine birds to geographic regions. The use of claws is currently limited by incomplete understanding of claw growth rates. Data presented here will allow managers of eiders, other marine birds, and marine mammals to assign animals to regions in the Bering Sea based on stable isotope signatures of body tissues.

Key Words: Geographic assignment, Stable isotopes, Bering Sea, King eider, 13C, 15N, Feather

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6.2. Introduction

Events outside the breeding season can not only affect population numbers (Votier et al. 2005), but also influence the physical condition of migratory birds, and thus have the potential to affect their population dynamics (Webster et al. 2002, Newton 2006). For instance, events during the winter have been shown to affect the body condition and the reproductive performance of migratory birds (Marra et al. 1998, Norris et al. 2003, Bearhop et al. 2004). It is therefore important to identify the wintering areas of migratory birds to investigate such carry-over effects. Winter locations are difficult to determine for birds that use remote areas at sea.

Stable isotope analysis of tissues has advanced the ability to investigate the migratory connectivity of breeding and wintering areas for several bird species (Hobson 1999, Webster et al. 2002, Gómez-Díaz and González-Solís 2007). This technique relies on the assumption that birds incorporate the isotopic signature of the geographic area in which they forage during tissue formation. For biochemically inert keratin-based tissues, such as feathers and claws, the isotope signature does not change after growth is completed (Mizutani et al. 1992, Hobson 2005).

Sea ducks nesting in the Arctic generally winter in marine environments, where many grow body feathers of the alternate (breeding) plumage (Madge and Burn 1988). Stable isotope analyses have been applied to infer the geographic location of wintering and molting areas of North American sea ducks (Mehl et al. 2005, Knoche et al. 2007). Managers require reliable techniques to identify molting and wintering regions of duck populations that are monitored during the breeding season because recent declines in sea duck populations may be associated with changes on wintering grounds (Lovvorn et al. 2003, Grebmeier et al. 2006).

The king eider, *Somateria spectabilis*, is the most abundant Arctic sea duck, but populations in western North America have declined substantially between the 1970s and 1990s (Suydam et al. 2000). King eiders from breeding grounds in northern Alaska and

western Canada migrate to wintering areas in the Bering Sea (Suydam 2000, Phillips et al. 2006), and population declines are presumably linked to ecosystem changes in the Bering Sea (Grebmeier et al. 2006). There are at least three distinct winter regions used by king eiders in the Bering Sea, among which there is little or no movement of individuals during mid-winter (Oppel et al. 2008, Chapter 1; Fig. 6.1). These three regions differ in their physical properties, proximity to breeding areas, and extent of human use. Regional differences may therefore result in differing physical condition or survival of individuals during winter. To examine breeding performance of individuals wintering in different regions, it is necessary to assign individuals to one of the wintering regions based on samples that can be obtained from breeding birds.

Spatial differences of stable isotope values exist in Bering Sea sediments (Naidu et al. 2000), benthic organisms (Dunton et al. 1989), zooplankton (Schell et al. 1998), and in king eider primaries (Knoche et al. 2007). As king eiders forage on sessile benthic organisms by diving to the sea-floor, isotopic differences inherent in a regions' food web are likely to be reflected in king eider tissues. We hypothesized that the three regions used by king eiders in winter may be distinct in carbon and nitrogen isotope ratios of tissues grown in these regions.

Stable isotope ratios of head feathers, which are assumed to be grown on wintering areas, have been used to discern whether king eiders winter in the Atlantic or Pacific Ocean (Mehl et al. 2004, Mehl et al. 2005). Molt of head feathers in king eiders is believed to start as early as October and might be completed by November (Suydam 2000). In this paper, we establish a method to geographically assign birds to one of the three wintering regions in the Bering Sea using stable isotope ratios of head feathers. We used information obtained from satellite-tracked king eiders to isotopically delineate the three main regions in the Bering Sea. We then assigned feathers of birds not tracked with satellite transmitters to regions using their stable isotope signatures.

A vital component for the application of stable isotope analysis of feathers to infer geographic origin is a clear understanding of the molt cycle of the species in question. Recent analyses of satellite-tracked king eiders show that fall migration schedule is

extremely variable, and that some king eiders may not arrive on their wintering grounds before they have completed their body molt (Oppel et al. 2008, Chapter 1). It is thus possible that head feathers carry the isotopic signature of a molting or staging area, which may result in an incorrect assignment of birds to wintering areas based on their head feather isotopic signature. In contrast, claws grow continuously and claw tips may provide isotopic information from several months prior to collection (Bearhop et al. 2003, Bearhop et al. 2004). Our second objective in this paper was to explore whether claw tips collected from birds on the breeding grounds can be used as an alternative tissue that reflects the isotopic signature of the wintering region.

6.3. Materials and methods

6.3.1. Study area

We captured king eiders on breeding grounds on the Arctic coastal plain of Alaska at two study locations (Fig. 6.1): (1) near Teshekpuk Lake (70° 26' N, 153° 08' W), and (2) in the Kuparuk oilfield (70°20' N, 149°45' W). From extensive satellite telemetry of 94 adult king eiders tracked from Alaska between 2002 and 2006, we found three discrete wintering regions in the Bering Sea: (1) the northern Bering Sea; (2) Southwest (SW) Alaska; and (3) the Kamchatka coastline (Fig. 6.1, Oppel et al. 2008, Chapter 1). Each of these regions is a broad geographic unit that contains several localities where king eiders winter. Because movements of king eiders occurred within each region a finer spatial resolution was not practical.

6.3.2. Choice and collection of tissues

King eiders annually undergo complete flight feather molt, as well as two almost complete molts of body plumage. Flight feather molt is simultaneous and renders birds

flightless for several weeks during August – October (Suydam 2000; Phillips et al. 2006). Timing and distance of migration to wintering sites after flight feather molt is highly variable (Oppel et al. 2008, Chapter 1). Body feathers of the alternate plumage, which is worn through the breeding season in the following year, are molted some time after flight feathers, with high individual variation in both timing and extent of the molt (Suydam 2000). Claws grow continuously, and thus can provide an isotopic signal of a point in time prior to sampling that depends mostly on the length of the claw and its growth rate (Bearhop et al. 2003). Data on claw growth rates for sea ducks are currently unavailable, but experimentally determined claw growth rates for three species of captive waterfowl (mallard, Anas platyrhynchos, pintail A. acuta, lesser scaup, Aythya affinis) ranged from 0.06 to 0.13 mm/day (R. G. Clark, Canadian Wildlife Service, unpublished data). For king eider claws of 9-10 mm in length, these growth rates would result in isotopic information at the distal end (~1 mm) of the claw from a time 70-170 days prior to capture. Claws from king eiders captured in June and early July would thus yield isotopic information from late December through early April. None of 94 satellite tracked king eiders wintering in the Bering Sea moved between wintering regions during this time period (Oppel et al. 2008, Chapter 1). Isotopic discrimination between food and tissue is similar for feathers and claws; claws may therefore provide a similar isotope ratio as feathers if they were grown from the same diet and in the same region (Bearhop et al. 2003). We therefore chose head feathers to determine wintering regions of king eiders, and used the isotope ratio of claws to evaluate whether claw tips reflected the same region as head feathers.

We collected head feathers and claws of adult king eiders in June and early July 2005 – 2007 by capturing birds in nesting areas using mist-nets. We collected head feathers from an additional 12 females during brood rearing in mid-August 2006 and 2007. We did not collect claws from birds captured after 20 July each year, as the claw tip isotope signature after that date would be unlikely to reflect wintering grounds. We plucked one head feather and clipped the apical 2 mm section of the central forward claw

of either foot using a dog nail clipper. All tissues were collected under the Institutional Animal Care and Use Committee protocol #05-29 of the University of Alaska Fairbanks.

6.3.3. Stable isotope analyses

We removed surface contaminants from all claws and feathers by rinsing them repeatedly in ethanol and scrubbing with cotton swabs (Knoche 2004). We removed the most apical section of the claw (~0.5 – 1 mm) that provided sufficient sample weight for isotopic analysis (0.2 – 0.4 mg). Claw material was homogenized and ground to a fine powder in an electrical mill. We analyzed claws and feathers for C and N stable isotope ratios at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks using a continuous flow stable isotope-ratio mass spectrometer with a precision of ±0.14‰ and ±0.06‰ for C and N, respectively. Results of isotopic analyses are reported as ratios in delta notation relative to international standards (PeeDee Belemnite for C, atmospheric air for N) according to the following equation:

$$\delta X = ([R_{sample}/R_{standard}]-1) \times 1000$$

where X denotes either ^{13}C or ^{15}N, and R represents the ratio of ^{13}C /^{12}C or ^{15}N /^{14}N, respectively. We report all isotope ratios as mean ± standard deviation (SD).

6.3.4. Isotopic delineation of regions

We equipped 32 of the sampled adult king eiders (13 males, 6 females in 2005, 6 females in 2006, 7 females in 2007) with satellite transmitters, enabling us to track their movements throughout the following year (see Oppel et al. 2008, Chapter 1 for detailed description of methods). Male and female eiders use identical winter regions (Phillips et al. 2006, Oppel et al. 2008) and consume very similar diets at sea (Bustnes and Erikstad 1988, Frimer 1997, Bustnes et al. 2000, Merkel et al. 2007a). We therefore did not expect

isotope ratios of winter-grown feathers to differ by sex, and tested this assumption by comparing isotope ratios of head feathers between sexes within each winter region (see Results, Table 6.1).

We determined the location of each bird during winter using the data provided by satellite transmitters. Feathers sampled from satellite tracked birds were grown in the year before we tracked the birds. Hence, in order to relate the isotopic information of feathers to geographic regions we implicitly assume winter region fidelity between years. This assumption is realistic due to the large size ($>10^5$ km^2) of the regions we distinguish (Robertson and Cooke 1999). Further, king eiders display fidelity to molting areas (Phillips and Powell 2006), and winter region fidelity has so far been found in all individuals in which the battery of the satellite transmitter lasted long enough to track birds for two subsequent winters (n = 4, Oppel, unpub. data). Thus, we considered feathers collected from satellite-tracked birds to be of 'known origin'. We assigned stable isotope values of head feathers to one of the three regions in the Bering Sea where the bird was recorded during winter. We delineated the three main regions by separating clusters of data points from feathers assigned to the same region using a discriminant function analysis (DFA) with the stable isotope ratios of C and N of 32 head feathers (one per tracked bird) as predictor variables. We conducted DFA in SPSS^{TM} 11.0, setting prior probabilities equal among regions. We present classification results as the number of feathers of known origin correctly classified in a jacknife cross-validation procedure, where each feather is tested for correct classification predicted from a DFA model constructed without that feather (Gómez-Díaz and González-Solís 2007). We compared isotope ratios among the three regions using Kruskal-Wallis tests and $\alpha = 0.05$.

6.3.5. Geographic assignment of tissues of unknown origin

The origin of feathers and claws was unknown for 94 birds (94 head feathers, 62 claws) captured on breeding grounds but not equipped with a satellite transmitter. We

assigned the tissues of unknown origin to one of the three regions in the Bering Sea using the discriminant functions and the isotopic data for each tissue. Each tissue of unknown origin was assigned to the region for which it had the highest probability of membership. To increase confidence in assignments and reduce misclassifications we used an exclusion threshold of 75% on the posterior probability of membership, and excluded any tissue with a lower level of geographic assignment probability for each of the three regions (Wunder et al. 2005, Rocque et al. 2006). Based on head feather assignment, we calculated the proportion of birds wintering in each region. To assess the utility of claws as an indicator of wintering region, we compared winter region inferred from claw and head feather isotope ratios for individuals from which we had both claw and head feather with a >80% assignment probability.

6.4. Results

6.4.1. Feathers of known origin

We analyzed one winter-grown head feather from each of the 32 king eiders we tracked with satellite transmitters. C and N isotope ratios did not differ between male and female feathers in each winter region (all $p > 0.6$, Table 6.1), and we pooled feathers from both sexes for further analysis. Feathers from birds that subsequently wintered in SW Alaska were enriched in ^{15}N compared to feathers from birds wintering near Kamchatka and in the northern Bering Sea ($H = 16.12$, $p < 0.001$; Table 6.1). In contrast, feathers from Kamchatka were enriched in ^{13}C compared to feathers from SW Alaska and the northern Bering Sea ($H = 16.39$, $p < 0.001$, Table 6.1). A reliable assignment of a feather to one of the three regions would thus not be possible when using isotope ratios of only a single element (Fig. 6.2).

A discriminant function analysis provided an accurate classification of these 32 feathers to the three major regions in the Bering Sea using two discriminant functions

explaining 94.1% and 5.9% of the variance, respectively. The standardized canonical discriminant function coefficients for the two discriminant functions were -1.047 and 0.589 for δ^{13}C, and 1.070 and 0.545 for δ^{15}N, respectively. We classified 87.5% ($n = 28$) of the 32 feathers of known origin correctly in jacknife cross-validation by using two discriminant functions. Four feathers were assigned to a geographic region different than the one used by the respective bird in the subsequent winter. These feathers had classification probabilities of <60% to any region. Applying an exclusion threshold of 75% classification probability resulted in the exclusion of 6 feathers (19%), and correct classification of all remaining feathers ($n = 26$). Parameters required to reconstruct this model and apply it to data of unknown origin are available from the authors upon request.

6.4.2. Feathers and claws of unknown origin

We analyzed 94 head feathers and 62 claws from 94 birds of unknown origin. We assigned each feather and claw to one of the three regions in the Bering Sea using their δ^{15}N and δ^{13}C and the two discriminant functions (Table 6.2, Fig. 6.2). Ten head feathers (11%) and 9 claws (15%) had classification probabilities of <75% to any region and were excluded from further analysis.

Based on reliably assigned head feathers of 84 birds, 27% of king eiders wintered in SW Alaska, 45% in the northern Bering Sea, and 27% along the coastline of Kamchatka. For 48 of these birds (6 males, 42 females) we were able to compare the geographic assignment to a wintering region based on reliable assignments from claws and head feathers. Claws and head feathers were assigned to identical regions for 33 birds (69%). In 15 birds the claw was either assigned to a region farther south ($n = 5$, 10%), or to a region farther north than the head feather ($n = 10$, 21%).

6.5. Discussion

Our study provides evidence that the three main regions used by king eiders in the Bering Sea can be distinguished based on $\delta^{13}C$ and $\delta^{15}N$ of feathers grown in these regions. A spatial pattern of $\delta^{13}C$ and $\delta^{15}N$ has been shown to exist for sediments (Naidu et al. 2000), benthic organisms (Dunton et al. 1989), zooplankton (Schell et al. 1998), and king eider flight feathers (Knoche et al. 2007) in the Bering and Chukchi Seas. There is, however, substantial overlap among the three regions used by king eiders in both $\delta^{13}C$ and $\delta^{15}N$ of feathers, and we suggest that both elements are required to accurately assign feathers of unknown origin to a specific region. Previous approaches of feather geographic assignment of king eiders using only $\delta^{15}N$ (Mehl et al. 2005) would have assigned 20% of our samples to the Atlantic Ocean, which is an extremely unlikely wintering region for birds from our study area (Phillips et al. 2006, Oppel et al. 2008). Besides using two isotopic dimensions, the application of an assignment probability threshold also increased the accuracy of our geographic assignments. Mehl et al. (2004) did not exclude feathers with ambiguous assignment probabilities, and may have erroneously assigned 4 of 6 king eiders with <75% assignment probability to wintering areas in a different ocean (Mehl et al. 2004). The choice of an appropriate assignment probability threshold depends on the number of distinct regions examined (Wunder et al. 2005), and requires careful consideration. While choosing a higher threshold (e.g. >90% probability) will increase the accuracy of assignments, it will decrease the number of samples that can be assigned with above-threshold assignment probability (Wunder et al. 2005, Rocque et al. 2006). In our study, 13% of all samples could not be accurately assigned to either of the three regions. This trade-off between accuracy and the proportion of samples retained for inference needs to be carefully considered in studies applying the approach presented here.

Claws can be a useful tissue to trace king eiders to wintering grounds, but the amount of information gained in comparison with head feathers is limited. By using claw

data we found that in 10% of birds, head feathers were likely grown before the birds migrated from molting to wintering regions. The use of claws as an alternative to feathers is currently handicapped by limited information on claw growth rates. In 20% of birds the claw was assigned to an area farther north than the head feather, indicating that the sampled portion of the claw may have grown during spring migration and not during winter. Interpreting potential causes for discrepancies between feather and claw assignments is complicated by our lack of knowledge of the time of tissue synthesis, and a better understanding of claw growth rates is clearly needed. Experimental data on claw growth rates and discrimination ratios would be useful before isotope ratios of claw tips alone can be reliably employed to infer geographic origin at certain times of the annual cycle (Bearhop et al. 2003).

The isotopic composition of feathers and claws represents the isotopic composition of the bird's diet during the time of tissue growth plus some discrimination factor (Mizutani et al. 1992). The diet of king eiders in the Bering Sea is poorly known, but likely consists of a variety of benthic and epibenthic macro-invertebrates (Frimer 1997, Suydam 2000, Merkel et al. 2007b). Potential prey items in the south-eastern Bering Sea range from -19‰ to -17‰ in δ^{13}C and 12 to 17‰ in δ^{15}N (Dunton et al. 1989). This is consistent with the range of king eider feathers we assigned to this region (δ^{13}C: -18‰ to -16‰, δ^{15}N: 16‰ to 20‰) if we apply general diet-feather discrimination factors of +1.4‰ for δ^{13}C and +3.6‰ for δ^{15}N (Becker et al. 2007). Similarly, feather isotope ratios from the northern Bering Sea show a range of 13.5-16‰ in δ^{15}N, which agrees well with the δ^{15}N-range (9.5-11.5‰) of the most common bivalves and crustaceans in this region (Lovvorn et al. 2005). Potential prey items in the northern Bering Sea show a wide range in δ^{13}C (-22‰ to -17‰, Lovvorn et al. 2005), and this offers an explanation for the wide δ^{13}C range we found in king eider feathers grown in this region.

Isotopic differences among the three wintering regions could result from differences in diet composition and/or a different structure of respective food webs. Little

is known about king eider diet composition in the Bering Sea (Suydam 2000). However, the isotopic composition of benthic prey differs across the Bering Sea partly due to differences in the importance of particulate organic matter as the primary nutrient source for benthic organisms (Dunton et al. 1989, Hobson et al. 1995, Lovvorn et al. 2005). The depletion of δ^{13}C in feathers grown along the coast of Alaska could result from freshwater inflow from rivers, as freshwater is depleted in ^{13}C compared to sea water (Peterson and Fry 1987). This could potentially lead to misclassifications if birds in other regions molt feathers in the immediate vicinity of freshwater discharge areas. Overall, differences we report for feathers are consistent with currently known isotopic patterns across the Bering Sea, but more research is required to determine causes of large-scale regional differences in isotope ratios of higher trophic level consumer tissues.

Based on geographic assignment of head feathers we estimated fairly equal proportions of king eiders wintering in the three regions of the Bering Sea. This result is similar to the wintering distribution of king eiders tracked via satellite transmitters from the same breeding location (Phillips et al. 2006, Oppel et al. 2008). Together these studies support the conclusion that king eiders breeding in Alaska winter in different areas of the Bering Sea, and that migratory connectivity is diffuse. The approach presented here offers a simple and cheap alternative to support conclusions derived from satellite telemetry, and thus increases confidence in population inference (Lindberg and Walker 2007).

Results presented here for head feathers might also be applicable to other feathers grown in the same regions in the Bering Sea, as diet-tissue discrimination factors are similar for different feather tracts (Mizutani et al. 1992, Thompson and Furness 1995, Bearhop et al. 1999). At the population level, king eiders use the same regions in the Bering Sea in which they winter for their annual flight feather molt (Phillips et al. 2006). Therefore, δ^{13}C and δ^{15}N of flight feathers such as primaries could be used to assign king eiders to a molting region in the Bering Sea using our DFA model. We evaluated this approach by applying our model to an external data set of isotope ratios from king eider

primaries collected in 2003 (Knoche et al. 2007). We were able to reliably (>75%) assign 11 out of 12 feathers (92%), and 10 of these feathers (90%) were correctly assigned to the region where the bird was recorded during wing molt one year later. This shows that our model performs well with data from a different feather type.

The use of multiple tissues such as primaries, head feathers, and claws from the same bird captured on breeding grounds may enable an assessment of the migration strategy of an individual by assigning tissues to their respective molting and wintering regions (Yerkes et al. 2008). Our model provides a suitable framework for all feathers grown in the Bering Sea. However, some female king eiders may molt flight feathers in freshwater ponds on breeding grounds (Knoche 2004), and some females breeding in the western Canadian Arctic may molt flight feathers in the eastern Beaufort Sea (2 of 51 birds tracked with satellite transmitters, D.L. Dickson, Canadian Wildlife Service, unpublished data). Both freshwater ecosystems and the eastern Beaufort Sea are known to be relatively depleted in ^{13}C (Peterson and Fry 1987, Dunton et al. 1989, Schell et al. 1998), and feathers grown there are distinct from feathers grown in the Bering Sea. We urge researchers and managers to carefully consider the migration and molt schedules of their study species before using our model. Feathers grown outside the Bering Sea should not be classified with the discriminant function model presented here.

We demonstrated that king eider tissues can be assigned to a region in the Bering Sea with high accuracy. This approach could also be applied to a variety of birds and mammals using the Bering Sea and feeding on similar prey as king eiders, such as other sea ducks, loons, gulls, walrus (*Odobenus rosmarus*) or gray whales (*Eschrichtius robustus*). We recommend that the model presented here is validated by analyzing prey items across large spatial and temporal scales to establish isotopic baselines of the geographic regions in the Bering Sea (Inger and Bearhop 2008). Isotope analysis of sea duck feathers can then be used to estimate remote molting and wintering locations and explore whether breeding performance varies for sea ducks wintering in different regions. Knowing wintering regions for sea ducks is essential for evaluating causes of changes in population size or developing management actions to recover populations.

6.6. Acknowledgements

6.7. Literature cited

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Table 6.1. Mean isotope ratios (± standard deviation) of head feathers of 32 king eiders tracked with satellite transmitters from breeding grounds in northern Alaska to wintering regions in the Bering Sea. Geographic assignment of feathers to regions is based on the assumption of between-year site fidelity of satellite-tracked birds. See Figure 1 for extent of regions.

Geographic Region	sex	*n*	δ^{13}C (‰)	δ^{15}N (‰)
North Bering Sea	male	*5*	-17.3 ± 0.4	14.9 ± 1.0
	female	*9*	-16.8 ± 1.2	15.1 ± 0.7
SW Alaska	male	*3*	-16.9 ± 0.6	17.3 ± 1.0
	female	*3*	-17.0 ± 0.7	17.6 ± 2.0
Kamchatka	male	*5*	-14.9 ± 0.6	13.9 ± 1.1
	female	*7*	-15.1 ± 1.0	14.3 ± 1.1

Table 6.2. Mean isotope ratios (± standard deviation) of head feathers and claw tips of 84 king eiders captured on breeding grounds in northern Alaska. Feathers and claw tips were assigned to geographic regions using a discriminant function analysis based on feather samples presented in Table 6.1. All tissues presented here were assigned with a probability >75%. See Figure 1 for extent of regions.

Geographic Region	head feather			claw tip		
	n	δ^{13}C (‰)	δ^{15}N (‰)	*n*	δ^{13}C (‰)	δ^{15}N (‰)
North Bering Sea	*38*	-17.1 ± 0.7	14.9 ± 0.6	*30*	-17.4 ± 0.8	14.9 ± 0.6
SW Alaska	*23*	-17.4 ± 0.5	17.0 ± 0.5	*8*	-17.1 ± 0.9	17.4 ± 0.7
Kamchatka	*23*	-15.0 ± 0.6	14.6 ± 0.9	*15*	-15.2 ± 0.3	14.1 ± 0.7
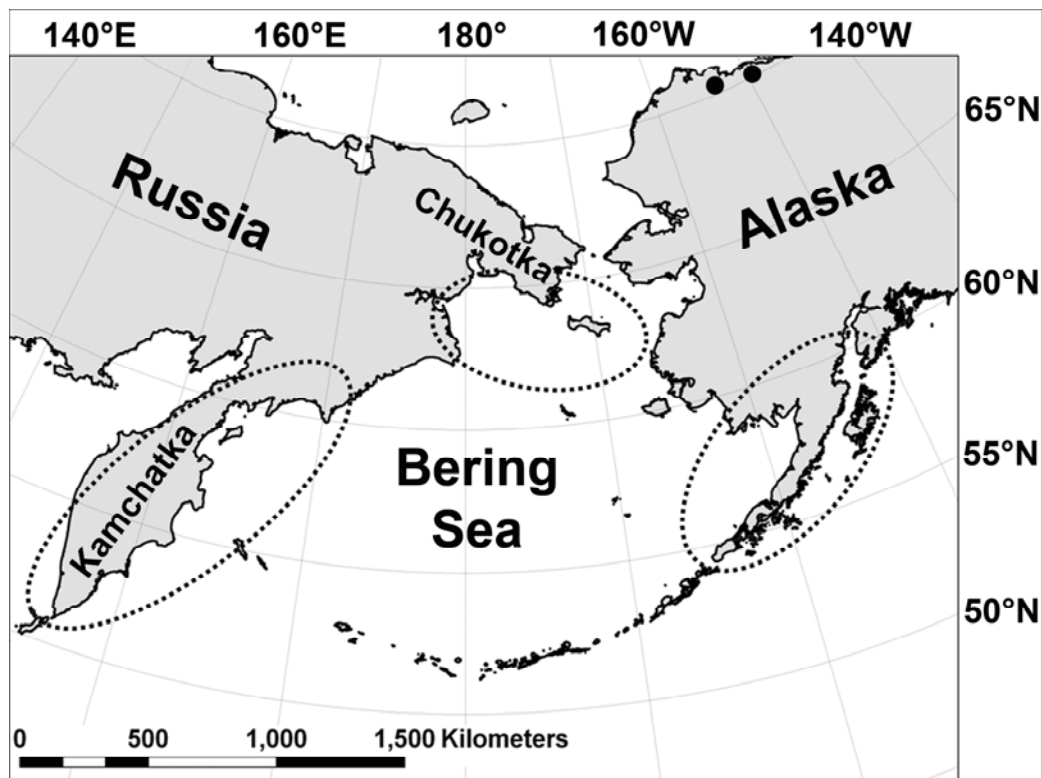
Fig. 6.1. Location of three distinct regions (dashed ovals) used by wintering king eiders (*Somateria spectabilis*) in the Bering Sea as derived from satellite telemetry of 95 adult king eiders between 2002 and 2007. Capture locations on breeding grounds are indicated by black circles.
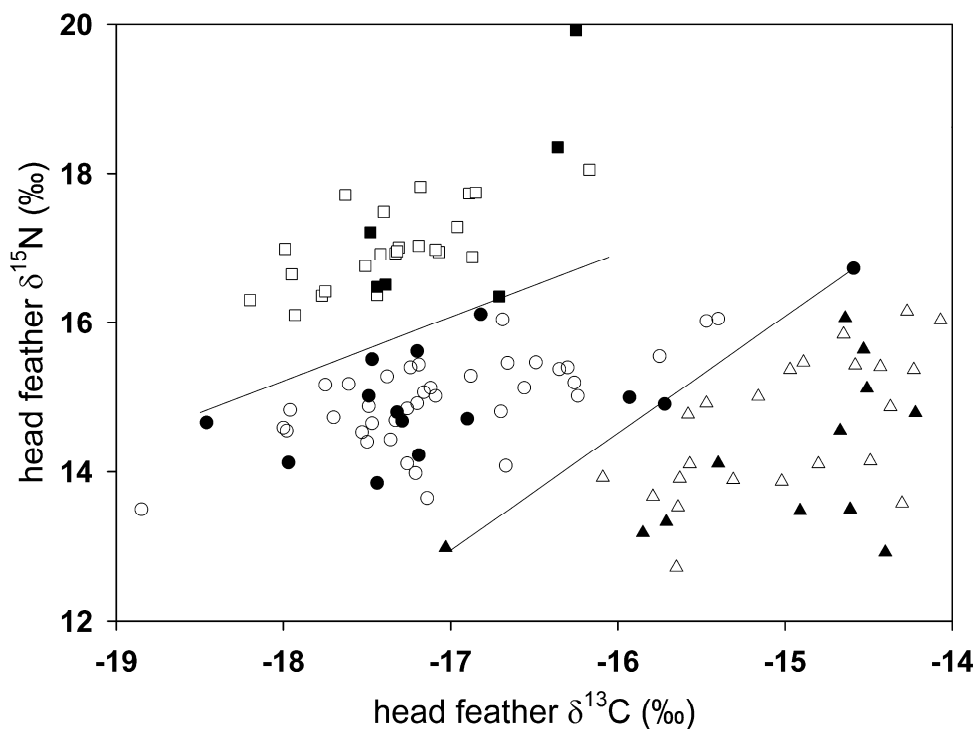
Fig. 6.2. Stable carbon and nitrogen isotope ratios of king eider head feathers collected from birds captured on breeding grounds in northern Alaska. Filled symbols represent feathers from birds tracked with satellite transmitters, open symbols represent tissues of unknown origin assigned to one of the three regions in the Bering Sea with >75% probability using a discriminant function analysis. Solid lines represent the discriminant functions used for classification; squares represent SW Alaska, circles represent the northern Bering Sea, triangles represent the coast of Kamchatka; see Fig. 6.1 for geographic extent of regions.

7. Does winter region affect nest survival of king eiders in northern Alaska? [1]

7.1. Abstract

Events during the non-breeding season may affect the condition of migratory birds and influence performance during the following breeding season. Migratory birds nesting in the Arctic often rely on endogenous nutrients for reproductive efforts, and are thus potentially subject to such carry-over effects. We tested whether king eider (*Somateria spectabilis*) nest survival in northern Alaska was affected by their choice of a winter region in the Bering Sea. We monitored nest survival at two sites in northern Alaska in 2005-2007. The region in which a nesting female spent the previous winter was determined by using stable isotope ratios of head feathers. We used generalized linear models to assess whether winter region explained variation in daily nest survival rates between 10 days after the start and until the end of incubation. We found little support that female king eiders who had wintered in the northern Bering Sea ($n = 29$) had different rates of daily nest survival than king eiders wintering in more southern parts of the Bering Sea (n = 36). We conclude that wintering in different regions in the Bering Sea has only a minor influence on nest survival of king eiders in our study areas.

Keywords Bering Sea – carry-over effect – king eider – migration – nest survival – stable isotopes – winter region

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7.2.   Introduction

The physical condition of migratory birds during the breeding season may be affected not only by habitat quality in the breeding area, but also by habitats used during previous seasons. Such interactions between seasons are known as carry-over effects, defined as nonlethal residual effects of habitat choice in one season on the fitness of an individual in a later season (Norris and Marra 2007). For example, habitat choices made during the winter period have been shown to affect body condition of some migratory birds, resulting in reduced reproductive output in the following breeding season (Marra et al. 1998, Norris et al. 2003, Gunnarsson et al. 2006). Many waterfowl breeding in the Arctic rely on stored nutrient reserves for reproduction, either to produce eggs or to fuel metabolism during incubation (Parker and Holm 1990, Gauthier et al. 2003). These body reserves can be accumulated during the preceding winter or during spring migration. Arctic-nesting waterfowl are therefore subject to potentially long-term carry-over effects (Alisauskas 2002, Drent et al. 2007). As a result of these seasonal interactions, the performance of waterfowl during the breeding season may be susceptible to changes in winter and staging habitats (Klaassen et al. 2006). Thus, predicting the demographic consequences of changing winter and staging habitats requires an understanding of the strength of seasonal carry-over effects.

Breeding success of arctic-nesting ducks has been positively related to foraging conditions in winter (Lehikoinen et al. 2006, Guillemain et al. 2008). Examining carry-over effects requires identifying the areas used by individuals over multiple seasons (Norris et al. 2006). Satellite tracking can provide this information, but is usually limited to small sample sizes. Stable isotope analysis of feathers grown outside the breeding season can be used to assign migratory birds captured on breeding grounds to areas or habitats used during the time the feathers were grown (Hobson 2005). This allows fitness parameters estimated during the breeding season to be related to habitat use during the non-breeding season (Norris et al. 2006, Hebert et al. 2008, Yerkes et al. 2008).

Eiders (*Somateria* spp.) are the largest ducks nesting in the Arctic. They migrate to north-temperate and sub-arctic marine wintering areas, where they forage on benthic invertebrates by diving to the sea floor. Winter foraging conditions have been linked to reproductive success in common eiders (*S. mollissima*) in Europe (Lehikoinen et al. 2006), and have been assumed to be related to population changes of spectacled eiders (*S. fischeri*) in Alaska (Lovvorn et al. 2003, Petersen and Douglas 2004). Eiders rely on body reserves for reproduction (Parker and Holm 1990), but there is currently little information on how regional winter conditions affect eider reproductive success, and how the effects of climate change on winter habitat could influence reproductive output of eiders.

King eiders (*S. spectabilis*) nesting in western North America winter in three discrete regions in the Bering Sea (Fig. 7.1, Oppel et al. 2008). These three regions differ in their oceanographic properties and their proximity to breeding grounds. The northern Bering Sea region is characterized by a rich benthic fauna resulting from cold, nutrient-rich waters transported north from the continental shelf-break by the Anadyr current (Dunton et al. 2005, Grebmeier et al. 2006a). By contrast, the two continental shelf regions, one along the coast of southwestern Alaska and one along the Kamchatka peninsula, are less nutrient rich and have a lower benthic biomass (Grebmeier et al. 2006a). This difference in food abundance could be expected to affect body condition of eiders and reduce reproductive output (Lovvorn et al. 2003, Richman and Lovvorn 2003). King eiders rely on stored body reserves to maintain very high levels of incubation constancy (Kellett and Alisauskas 2000, Bentzen et al. 2008b). Depleted body reserves can force incubating females to take recesses to forage during incubation that leave the eggs vulnerable to predators (Kellett et al. 2003, Bentzen et al. 2008a). In addition, migration distance to breeding grounds in Alaska is 20-30% longer from the two winter regions with low benthic biomass (Oppel et al. 2008, Chapter 1). The additional cost of migration could further deplete stored reserves from birds wintering in these regions. Thus, we hypothesized that king eiders who had wintered in the northern Bering Sea would benefit from a shorter migration route and a more abundant food supply in winter, and achieve higher productivity in the following breeding season.

We examined whether daily nest survival of king eiders breeding in northern Alaska was related to the winter region used by individual females during the previous winter. We tested this hypothesis by capturing nesting female king eiders, assigning them to a wintering region using stable isotope ratios of head feathers, and monitoring nest survival. To our knowledge this is the first examination of carry-over effects in arctic-nesting eiders that were individually assigned to a winter region.

7.3.   Material and methods

7.3.1. Study area and field methods

We studied nesting king eiders in late June and July 2005–2007 at two sites on the Arctic coastal plain of Alaska: (1) near Teshekpuk Lake (70°26' N, 153°08' W); and (2) in the Kuparuk oilfield (70°27' N, 149°41' W). Both areas have intermediate densities (~1-2 nests km^{-2}) of nesting king eiders on flat tundra with numerous ponds, lakes, and wetland complexes. We systematically searched suitable wetland habitat for king eider nests. Age and initiation date of nests was assessed by candling eggs on the first nest visit (Weller 1956). Nests were visited every 3–6 days to monitor status and nesting success by observing females from a distance without flushing them from nests, except during a single capture event. We considered nests as successfully hatched if we found remaining eggshell membranes in the nest after a minimum of 23 days of incubation.

To obtain morphological measurements and collect feathers we captured females on the nest after at least 10 days of incubation. We used either a mist-net carried by two persons and dropped over the incubating female or a remotely triggered clap-trap to capture females on their nest. We measured the flat wing chord to the nearest 1mm using a metal ruler, and plucked one head feather from each female. We handled females for less than 10 minutes, released them within 20 m of their nest, and left the nest area quickly after capture to reduce nest abandonment (Criscuolo 2001). Three nests were abandoned within two days of capture and were excluded from the analysis presented

here. The treatments described here were approved by the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks (#05-29).

7.3.2. Stable isotope analysis and winter region assignment

Stable isotope ratios of head feathers have been used successfully to assign king eiders to wintering regions (Mehl et al. 2004, Oppel and Powell 2009). We used this approach to assign king eiders captured on nests to the region used during the previous winter in the Bering Sea. To conduct stable isotope analysis we first removed surface contaminants from all feathers by rinsing them repeatedly in ethanol and scrubbing with cotton swabs. We cut one whole head feather (~0.3 mg) per female into small pieces for stable isotope analysis. We analyzed feathers for carbon and nitrogen stable isotope ratios at the Alaska Stable Isotope Facility using a continuous flow stable isotope-ratio mass spectrometer. We assigned all feathers to one of three regions in the Bering Sea using the isotope data and a discriminant function developed with feathers of known origin (Oppel and Powell 2009, Chapter 6). Each feather was assigned to the region with the highest probability of membership. To increase confidence in the assignment we excluded any individual bird with a feather having <75% assignment probability to any region (Rocque et al. 2006, Kelly et al. 2008). Details of the stable isotope analyses can be found in Oppel and Powell (2009, Chapter 6). Since we had no *a priori* hypothesis that nest survival would differ between birds wintering in southwestern Alaska and Kamchatka ($n = 36$), we pooled these two regions and contrasted them together against birds wintering in the northern Bering Sea ($n = 29$).

7.3.3. Nest survival analysis

To quantify the strength of support for hypotheses explaining variation in nest success, we constructed generalized linear models of daily nest survival (Dinsmore et al. 2002,

Rotella et al. 2004) and evaluated their relative support using an information–theoretic approach (Burnham and Anderson 2002). Individual nests only contributed to daily nest survival rates from the time of capture to hatch or failure. Nests that failed prior to capture were not included in our analysis because we could not determine winter region for these females.

Nest and duckling survival of king eiders have been shown to vary by year, nest age, study site, observer effects, and size of the female (Mehl and Alisauskas 2007, Bentzen et al. 2008a). We created a set of three biologically plausible candidate models that all incorporated variation associated with site, year, and nest age. Based on previous information (Bentzen et al. 2008a), we included a year $\times$ site interaction term in one model and an observer effect in the remaining two models. In one of the two latter models we also included wing length as an indicator of body size. We estimated each model with and without winter region as an explanatory variable, resulting in a candidate set of six models (Table 7.1).

Nest age was calculated as number of days since the first day of the nesting season. We defined the first day of our season as the first day on which we captured a female on any nest (28 June). We incorporated observer effects by estimating daily survival rate depending on whether or not a nest was visited on a given day (Rotella et al. 2004).

We used generalized linear models with a logit link function and binomial error distribution in the 'nest success' module of program MARK version 5.1 (White and Burnham 1999) to estimate daily nest survival rate and generate maximum likelihood estimates of regression coefficients (Dinsmore et al. 2002, Rotella et al. 2004). We evaluated the relative support for our candidate models using AIC corrected for small sample sizes (AIC$_c$, Burnham and Anderson 2002). We interpreted logit-scale regression coefficients only if their 95% confidence intervals did not overlap zero. We present estimates and unconditional standard errors for coefficients averaged across all models with ΔAIC$_c$ <2 (Burnham and Anderson 2002).

7.4.   Results

We captured 74 females on nests during the study period, and reliably (>75% probability) assigned 65 birds to a winter region in the Bering Sea, including the northern Bering Sea ($n = 29$, successful nests: 19), southwestern Alaska ($n = 20$, successful nests: 15), and along Kamchatka ($n = 16$, successful nests: 11).

For all three model combinations, the model containing winter region as additional explanatory variable had a higher AIC_c score than the corresponding model without winter region (Table 7.1). Winter region was included in one of the three top models with $\Delta AIC_c < 2$. The cumulative Akaike weights for winter region were 0.42.

Nest age was the only covariate with parameter estimate 95%-confidence intervals not overlapping zero ($\beta = 0.12 \pm 0.05$). Winter region had a parameter estimate <0 ($\beta = -0.47 \pm 0.22$), but due to large uncertainty daily nest survival rates were not different between females that wintered in different regions (Fig. 7.2).

7.5.   Discussion

Our models of daily nest survival rate indicated that nest survival increased with increasing nest age, a pattern that has been found in many recent waterfowl studies (Rotella et al. 2004, Blums et al. 2005). We also found annual variation in nest survival to differ between our two study sites (Bentzen et al. 2008a). Annual variation in nesting success of arctic-nesting waterfowl is well documented, and results primarily from weather variability (Skinner et al. 1998, Madsen et al. 2007), or predator and lemming abundances (Sittler et al. 2000, Bêty et al. 2001).

The region where king eider females spent the previous winter did not have a major effect on their daily nest survival rate. Females wintering in the northern Bering Sea tended to have slightly lower nest survival than females wintering elsewhere in the Bering Sea, but this effect was very small and is unlikely to have demographic

consequences. Nonetheless, the direction of the effect was contrary to our prediction. The northern Bering Sea has experienced a regime shift in recent decades, leading to changes in primary productivity as well as trophic interactions among consumers (Grebmeier et al. 2006b, Mueter and Litzow 2008). This may have led to a general decrease in prey availability for eiders (Bluhm and Gradinger 2008), as well as to a shift in prey species composition resulting in the dominance of less profitable species in the northern Bering Sea (Lovvorn et al. 2003, Richman and Lovvorn 2003). It is thus possible that the northern Bering Sea today is not as beneficial for wintering eiders as it used to be two decades ago, and may not differ from other regions in the Bering Sea. Alternatively, king eiders may not winter in the northern Bering Sea by choice, but rather due to poor body condition, which does not allow them to migrate farther south. Birds in better body condition may trade-off the more benign environmental conditions at lower latitudes against the costs of migration and wintering in poorer quality habitat (Brodersen et al. 2008). If this was the case, birds wintering in the northern Bering Sea would be expected to have poorer body condition and lower nest survival.

Carry-over effects that have been found in other bird species may not be evident if king eiders are able to compensate for deficits in body condition on highly productive spring staging grounds. King eiders do not migrate directly from the Bering Sea to nesting areas in northern Alaska, but stage in the Eastern Chukchi and Beaufort Seas during spring migration (Phillips et al. 2007, Oppel et al. 2008, Chapter 8). The eastern Chukchi Sea is a highly productive region (Dunton et al. 2005), and this staging area could be where fat depots are accumulated for nesting. If foraging and fat deposition rates are not density dependent in this area, then even birds arriving late or in poor body condition may be able to fully compensate for residual effects of winter region choice. Furthermore, if lower nest attendance due to poor body condition does not affect nest survival (Bentzen et al. 2008a), then carry-over effects would be very difficult to detect.

The low support for an effect of winter region on nest survival could also be a result of the subset of females that we sampled. Due to logistic constraints, feather sampling of nesting females was not possible before mid-incubation. Thus, females that

failed early during incubation were not included in our sample. This explains the fairly high rates of nest survival we report in comparison with other studies (Kellett and Alisauskas 1997, Kellett et al. 2003, Bentzen et al. 2008a). In addition, females in poor body condition may forego nesting in any one year (Coulson 1984), and may therefore not be included in our sample. However, if birds wintering in a specific region were more likely to fail early, or not nest at all, we would expect to find very few birds from that winter region in our sample. We concurrently used satellite telemetry to track female king eiders captured prior to nesting on the same study sites (Oppel et al. 2008, Chapter 1). The proportions of those females wintering in each of the three regions in the Bering Sea were similar to those in this study (χ^2-test, $P = 0.64$). We therefore conclude that our sampling strategy did not bias our estimate of the effect of winter region on nest survival.

Our study suggests that migration to different wintering regions does not have a large effect on nest survival of king eiders breeding in northern Alaska. In long-lived species like eiders reproductive output accounts only for a small proportion of variation in population growth rates (Wilson et al. 2007). Population declines documented in recent decades (Suydam et al. 2000) may result primarily from changes in adult survival rates. Future studies need to determine whether king eider survival rates differ among the wintering regions in the Bering Sea. We also recommend long-term monitoring of nest survival to determine whether reproductive performance of king eiders responds to continuing changes of conditions in wintering regions.

7.6.　Acknowledgements

7.7.   References

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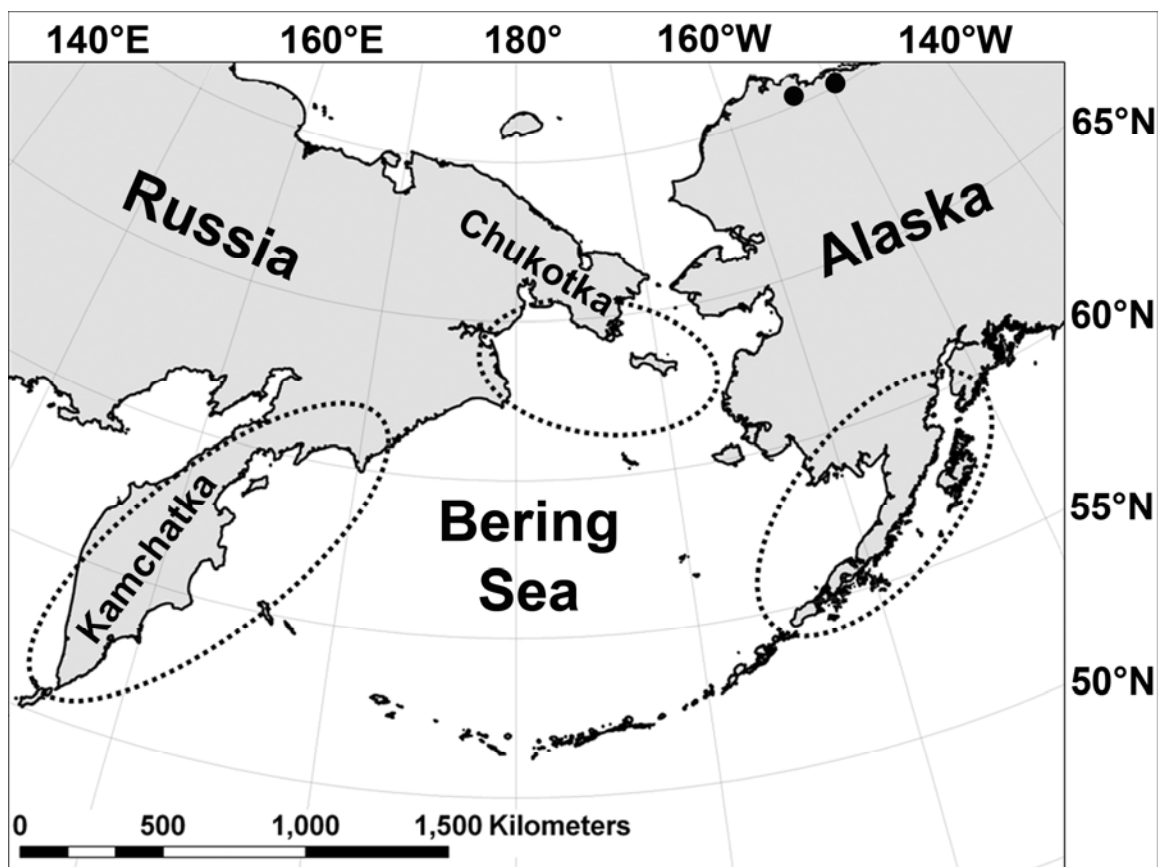
Figure 7.1. King eider nest survival study sites in northern Alaska (black circles), and winter regions used by king eiders in the Bering Sea (broken lines).
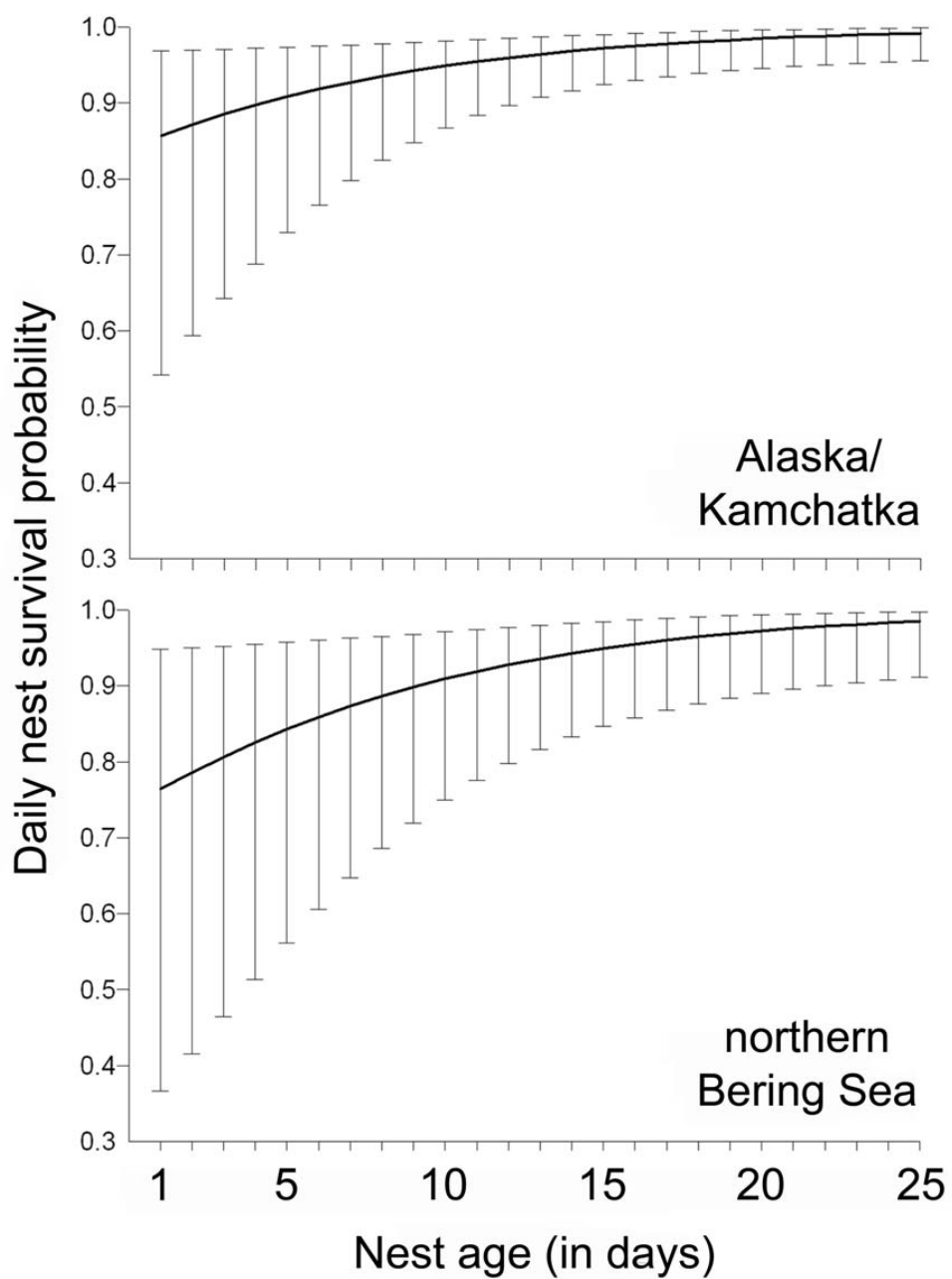
Figure 7.2. Daily nest survival probability of king eiders breeding in northern Alaska. Shown for females that spent the previous winter southwestern Alaska or Kamchatka (top panel), and in the northern Bering Sea bottom panel).

Table 7.1. Candidate models of king eider daily nest survival in northern Alaska, 2005-2007 ($n = 64$ nests) ranked by AICc. Table reports the difference in AICc for each model in relation to the most parsimonious model (ΔAIC_c), AIC$_c$ model weight (ωAICc), the number of estimable parameters (k), and the deviance.

Model	k	ΔAICc	ωAICc	Deviance
nest age + year + site + site*year	5	0.00	0.02	107.00
winter region + nest age + year + site + site*year	6	0.65	0.22	105.60
nest age + year + site + observer effect	6	1.68	0.13	106.62
winter region + nest age + year + site + observer effect	7	2.52	0.09	105.40
nest age + year + site + observer effect + wing chord length	6	4.21	0.04	109.16
winter region + nest age + year + site + observer effect + wing chord length	7	4.69	0.03	107.58

8. International importance of the eastern Chukchi Sea as a staging area for migrating king eiders[1]

8.1.   Abstract

The evaluation of habitats used by arctic birds on migration is crucial for their conservation. We explored the importance of the eastern Chukchi Sea (ECS) as a staging area for king eiders (*Somateria spectabilis*) migrating between breeding areas in Siberia and western North America and wintering areas in the Bering Sea. We tracked 190 king eiders with satellite transmitters between 1997 and 2007. In late summer, 74% of satellite-tracked king eiders migrating south staged in the ECS for 13 ± 13 (SD) days between late June and early November. During spring migration, all king eiders staged in the ECS between mid-April and early June for 21 ± 10 days. All birds migrating to breeding grounds in western North America ($n = 62$), and 6 of 11 males migrating to breeding grounds in Siberia used this area for at least one week during spring migration. The importance of this staging area renders it possible that industrial development could adversely affect king eider populations in both Siberia and North America.

Keywords industrial development, king eider, migration, satellite telemetry, staging, *Somateria spectabilis*.

8.2.   Introduction

Migratory birds depend on a variety of habitats throughout their annual life cycle, and recent evidence suggests that there are strong seasonal interactions between different life-history stages that affect the fitness of individuals and the demography of migratory populations (Newton 2006, Norris and Marra 2007). Rapid changes to an environment used by migratory birds during one season may therefore affect the fitness of individuals in subsequent seasons. In staging areas, where birds accumulate body reserves for migration and other energetically costly life-history events, changes in habitat quality may result in reduced body condition of migrants, which in turn may decrease reproductive output (Klaassen et al. 2006b, Drent et al. 2007).

Many sea duck populations migrate from arctic breeding grounds to lower latitude wintering areas at sea. For large sea ducks, like eiders (*Somateria* spp.), seasonal carry-over effects are assumed to be relatively strong (Parker and Holm 1990, Meijer and Drent 1999). Changes to habitats on wintering grounds or along migration routes are therefore believed to be a potential cause of recent population declines for some species (Lovvorn et al. 2003, Grebmeier et al. 2006b). King eiders (*S. spectabilis*) breed around the circumpolar arctic. The population breeding in western North America declined between the 1970s and the 1990s (Suydam et al. 2000). King eiders in western North America migrate from breeding grounds in Alaska and western Canada through the Beaufort and Chukchi Seas to wintering areas in the Bering Sea (Suydam 2000, Oppel et al. 2008, Chapter 1). While the distribution and habitat use of king eiders in the western Beaufort Sea has been analyzed (Phillips et al. 2007), there is currently little information on king eider distribution and use of the Chukchi Sea.

The Chukchi Sea (Fig. 8.1) is a shallow sea with a broad continental shelf that supports a high abundance of benthic organisms due to the influx of nutrients from the Bering Sea (Feder et al. 1994, Dunton et al. 2005). The high abundance of both plankton and benthic organisms provides a reliable food source for consumers at higher trophic

levels, which renders the eastern Chukchi Sea an important habitat for large populations of sea birds (Springer et al. 1984) and marine mammals (Miller et al. 1986, Gilbert 1989).

The Chukchi Sea has been of interest for oil and gas exploration since the 1980s (Dees 1991). The shelf regions of the Chukchi Sea are estimated to hold between 1-14 billion barrels (Bbbl) of crude oil (Dees 1991, Sherwood et al. 2001), with 1 Bbbl currently being considered as a minimum threshold for economically feasible development (Minerals Management Service 2007). In recent years, receding sea ice cover and decreasing sea ice thickness as well as technological advances have facilitated exploration of arctic seas, including the Chukchi Sea (Kerr 2002, Khain and Polyakova 2006). In February 2008, the Minerals Management Service, the federal institution that regulates offshore oil exploration in the USA, sold 1.1 million hectares of lease area in the Chukchi Sea to oil companies (Minerals Management Service 2008). The final environmental impact statement (EIS) for the Chukchi Sea planning area highlighted that a lack of knowledge of natural resources in the area limited the credibility of any potential effects assessment (Minerals Management Service 2007). It conceded that there "is a high potential for marine and coastal birds to experience disturbance and habitat alteration. However, little recent site-specific data are available on habitat and use patterns, routes, and timing of specific species using the arctic environment" (Minerals Management Service 2007: p. ES-4).

In this study we estimate the proportion of king eiders tracked to wintering areas in the Bering Sea that uses the eastern Chukchi Sea as a staging area during spring and fall migration. We further delineate core areas and annual windows during which the area is used by king eiders, and thus provide data that can be used to estimate the potential effects of oil and gas exploration activities on migratory eiders.

8.3.   Materials and methods

8.3.1. Study area

We defined the eastern Chukchi Sea (ECS) as the part of the Chukchi Sea between Cape Thompson and Barrow, Alaska, within 150 km from the shoreline. We chose this distance based on prior information from satellite telemetry which indicated few locations outside this area (Oppel et al. 2008, Chapter 1). We included all locations from satellite tracked king eiders that fell into an area bounded by 68.09° N in the south, 72.05° N in the north, 169.84° W in the west, and 156.65° W in the east (Figure 1). The area included all active lease blocks currently being leased for exploration and future development (Minerals Management Service 2008).

8.3.2. Satellite telemetry

Between 1997 and 2007, we trapped 208 King Eiders: 103 adult and 51 juvenile king eiders in Alaska, USA (50 adult females, 53 adult males, 27 juvenile females, 18 juvenile males, 6 juveniles of unknown sex), and 54 adults (25 females, 29 males) in Northwest Territories, Canada (Table 8.1). All birds were captured just prior to the breeding season (June) from 1997 to 2005, and during brood-rearing in late August 2006 and 2007. Each bird was equipped with an intra-abdominal satellite transmitter (38g PTT with external whip antenna, Microwave Telemetry Inc., USA) following standard surgical methods (Korschgen et al. 1996, Mulcahy and Esler 1999). We released the birds where they were caught two hours after surgery. Transmitters before 2006 were programmed to different duty cycles throughout the year, with shorter duty cycles (4-6 hrs of transmission every 1-4 days) during fall migration, and longer duty cycles (6 hrs every 3-7 days) during spring migration (see Oppel et al. 2008, Chapter 1 for details). In 2006 and 2007 we programmed transmitters to 6 hours on and 5 days off throughout their lifetime. All birds

were handled under the Institutional Animal Care and Use Committee protocol #05-29 of the University of Alaska Fairbanks, and Canadian Wildlife Service Animal Care Committee permit #PNR007.

We received location data from Service ARGOS and filtered them for unreasonable locations using the SAS ARGOS Filter algorithm (Douglas 2006). This algorithm selected the best location per duty cycle based on the location class provided by ARGOS, and the distance, angle, and rate to previous and subsequent locations (Kenow et al. 2002). Further details on capture and tracking methods are presented elsewhere (Phillips et al. 2006, Oppel et al. 2008). Due to transmitter failure and mortality we lost 18 birds (9 adult males, 5 adult females, 4 juvenile females) prior to fall migration. We had information from 83 adult king eiders during spring migration, of which 15 did not provide reliable information to calculate staging times.

8.3.3. Calculations of Staging Pattern and Spatial Distribution

We calculated arrival, departure, and residency times (hereafter referred to as staging pattern) and spatial distribution for two seasons, the southward migration in summer and fall, and the northward spring migration. We refer to the southward migration to molting and wintering areas as fall migration. We considered a king eider staging in the ECS if the bird was recorded at least once in the study area during the respective season. For each season, we calculated the residency time in the ECS for each individual bird by calculating the difference between the first and the last location in the study area. As the exact arrival and departure times are unknown, we added the length of one duty cycle to the residency time to account for uncertainty in arrival and departure times (Petersen et al. 2006). If a transmission period before or after locations in the ECS did not provide a reliable location, we added the length of half a duty cycle for each skipped transmission period to the residency time. If there was a gap of 10 days or more between the first or last location in the ECS and the previous or subsequent location outside the ECS, we

excluded that bird from calculations of staging patterns in the ECS (7 birds during fall, 15 during spring migration).

We calculated the average arrival, departure, and residency times separately for males and females in both seasons, and for adult and juvenile birds during fall migration. We calculated the proportion of individuals with at least one location in the study area based on the total number of live birds with active transmitters during each season. This represents a minimum estimate of birds using the ECS, as staging periods shorter than one duty cycle could have gone undetected. For fall migration we analyzed birds captured in Alaska and Canada separately. During spring migration, we divided the actively transmitting birds into those that migrated to breeding grounds in Canada, Alaska, and Siberia, and calculated staging parameters for each group separately. Because female king eiders show high breeding site fidelity (Phillips and Powell 2006), we were not able to track females to breeding grounds in Siberia. King eiders form pair bonds in winter or early spring and the pair migrates north together (Rohwer and Anderson 1988, Suydam et al. 2000). Male migration patterns can therefore be assumed to reflect the migration patterns of the females they accompany. We calculated the distance flown to breeding grounds as the cumulative distance of all travel steps along the migration route from the last location in the ECS until the bird was recorded on land or reversed its heading to migrate south.

To describe the spatial distribution of king eiders staging in the ECS we estimated core use areas using fixed kernel density home ranges. We used Hawth's Tools for GIS v. 3.27 (Beyer 2004) to calculate 50% volume contours with a single parameter smoothing factor of $h = 10\ 000$, a grid cell size of 10 000m, and a bivariate normal kernel function (Laver and Kelly 2008). We plotted king eider locations in ArcGIS 9.2 and calculated the distance of each recorded location ($n = 623$ for fall, and $n = 371$ for spring migration) to the coastline, as well as the proportion of locations within the area currently being leased for industrial development (Minerals Management Service 2007). Further, we used available bathymetry maps (National Ocean Service 1997) to describe water depths used by king eiders during staging.

We report all times, distances, and depths as mean ($\bar{x}$) ± standard deviation (SD). We compared times, distances, and depths among age, sex, and geographic groups using two-tailed non-parametric Mann-Whitney U-tests or Kruskal-Wallis tests with $\alpha = 0.05$.

8.4.   Results

8.4.1. Fall Migration

King eiders migrated southward through the ECS from 21 June through 8 November (Table 8.2), with the exception of one adult non-breeding male which arrived on 5 June. Of a total of 190 king eiders alive and transmitting during fall migration we recorded 140 (74%) in the ECS between June and November. Staging in the ECS was more common among adults (79%, $n = 143$) than juveniles (59%, $n = 47$), and slightly more common for Canadian (81%, $n = 43$) than Alaskan birds (71%, $n = 147$). Most of the adult females equipped with a satellite transmitter in June did not nest successfully in the year they were tracked. Of 13 adult females captured in late August while accompanying young (presumably females that nested successfully in the tracking year) only two (15%) used the ECS on fall migration.

The staging pattern in fall differed between birds migrating from Alaska and western Canada, with adult males from Canada arriving later and staging for a shorter period than those from Alaska (Table 8.2). Adult females from Canada also arrived later than those from Alaska, but females from both regions staged for similar periods in the ECS. For adults, males migrated through the ECS earlier than females. Males from Alaska remained in the ECS on average more than twice as long as all females, but males from Canada remained on average only a day longer than all females (Table 8.2). We did not record any adult king eider that moved <20 km in 3 weeks in the ECS. Such

restricted movement would be indicative of flight feather molt (Phillips et al. 2006, Guillemette et al. 2007).

Juveniles were tracked only from Alaskan breeding grounds, and they migrated later than all adult females (Table 8.2). The majority (75%) of juveniles arrived in the ECS after successfully nesting adult females had departed from the ECS ($n = 2$; 20 September,). Arrival, departure, and residency times were the same for male and female juveniles. Juveniles of both sexes remained in the ECS on average 2 weeks longer than adult females, and only slightly longer than adult males (Table 8.2).

Within the ECS, king eiders occurred in highest concentrations near Point Lay, Icy Cape, and Peard Bay (Fig. 8.1). Adults staged at an average distance of 13.7 ± 11.4 km from the shoreline in waters 20 ± 10 m deep, and farther offshore and in deeper water than juveniles (Table 8.3). Among juveniles, males and females were on average the same distance from the coast ($P = 0.51$, $n = 101$), and in waters equally deep ($P = 0.40$, $n = 101$). Among adults, females were farther offshore than adult males, but not in deeper water than adult males (Table 8.3). We recorded no king eider locations within the area recently leased for oil and gas exploration and possible future development (Fig. 8.1).

8.4.2. Spring Migration

Adult king eiders returned to the ECS in mid-April and remained through early June before continuing migration to their breeding grounds (Table 8.4). In addition, 9 of the 25 first-year birds we tracked through spring returned to the Chukchi Sea in their first spring, but none migrated to the ECS before July. We tracked 11 males to breeding grounds in Siberia, of which 6 (55%) used the ECS for an average of 24 days (Table 8.4). All of the 56 birds migrating to North American breeding grounds used the ECS. We excluded 15 birds from calculations of residency and departure times because the transmitter failed during staging in the ECS. One adult male left the ECS but did not migrate to a breeding area, and returned to the ECS after two weeks in the Beaufort Sea. Three birds (2 males, 1 female) flew from the ECS >250 km into the Beaufort Sea in

May, returned to the ECS less than a week later for a second staging period, and then continued spring migration. We subtracted the time spent in the Beaufort Sea from the spring staging time of these birds, but used the last location date in the ECS as departure date.

There were no differences in timing or duration of staging between males and females migrating to Alaska and Canada (all $P > 0.1$). All adult females returned to the breeding area where they had been caught initially, thus we did not track any females migrating to Siberia.

The timing of spring migration differed among birds depending on their final breeding destination (Table 8.4). Birds subsequently migrating to all three regions (Alaska, Canada, Siberia) arrived in the ECS at similar times. Birds migrating from the ECS to Canada departed earliest, and had the shortest residency time in the ECS. The residency time was highly variable, ranging from 3 days to 6 weeks, and was longest for birds migrating to Alaska (Table 8.4). The distance to the final breeding destination for birds migrating to Siberia was much longer than for birds migrating to Alaska or Canada (Table 8.4).

In spring, king eiders occurred in highest concentrations in Ledyard Bay near Point Lay, and offshore near Kasegaluk Lagoon and Peard Bay (Fig. 8.2). Both adult males and females staged farther offshore (28.6 ± 16.7 km) in spring than during fall migration, and in deeper water (23 ± 7 m, Table 8.3). In spring, there was no difference between sexes in either distance to coast or water depth. There was annual variation in the distance from shore, ranging from 22.6 ± 13.7 km (95% confidence interval $20.0 - 25.2$ km) in 2003 ($n = 111$) to 32.3 ± 18.9 km (95% CI $28.8 - 35.7$ km) in 2005 ($n = 117$). We recorded no king eider locations within the area recently leased for oil and gas exploration and possible future development (Fig. 8.2).

8.5.   Discussion

The eastern Chukchi Sea is a crucial staging area for king eiders on both fall and spring migration. During spring migration the area served as a staging ground for all marked birds migrating to North American breeding grounds and more than half of the marked birds migrating to Siberian breeding areas. The ECS is therefore important to king eiders that breed over half of the circumpolar range. The ECS was used by king eiders continuously from mid-April through early November, with fall migration of some (presumably non-breeding) males starting before spring migration was fully completed, and first-year birds using the area during summer.

8.5.1. Fall migration

Fall migration occurred over a five month period with marked differences among age and sex classes. Despite some long staging times by adults, king eiders do not appear to molt in the ECS. This is in contrast to the congeneric spectacled eider (*S. fischeri*), which uses the ECS as a regular molting area (Petersen et al. 1999). The king eiders we tracked molted mainly along the Chukotka Peninsula and farther south in the Bering Sea (Phillips et al. 2006). In late summer, the ECS is probably used for staging and foraging to accumulate energy for molting and further migration. During this time, males seem to rely on resources in the ECS to a greater extent than females, as they remained longer on average.

Females from breeding areas in northern Alaska primarily use the Beaufort Sea as a pre-migratory staging area in late summer (Phillips et al. 2007). Similarly, adult males from Canadian breeding areas stopover in the Amundsen Gulf and the Beaufort Sea (Dickson and Gilchrist 2001), and thus arrive later and remain shorter in the ECS than adult males from Alaska. Competition for high quality molting areas may exert selective pressure on adult birds migrating to molting areas (Hohman et al. 1992). This could reduce stopover times to a minimum required to successfully complete migration, and

explain the shorter residency time of later migrating adults. Juveniles, which do not molt flight feathers in their first summer (Suydam 2000), migrated later than adults, but showed the longest staging times in the ECS.

8.5.2. Spring migration

We did not find different migration schedules for male and female king eiders during spring migration in the ECS. King eiders are assumed to pair on wintering grounds or during spring migration, and migrate mostly in pairs from the Chukchi into the Beaufort Sea in spring (Suydam et al. 2000). It is therefore unlikely that sexes migrate on different schedules after pair formation has occurred. Phillips et al. (2007) reported that female king eiders migrated through the Beaufort Sea later in spring than males. However, most of the males in that study migrated to breeding areas in Canada, while all females returned to breeding areas in Alaska (Phillips and Powell 2006). Our study shows that birds of both sexes migrating to breeding grounds in Canada left the ECS about 10 days earlier than birds migrating to breeding grounds in Alaska. We thus believe that the different staging pattern described by Phillips et al. (2007) was an effect of breeding destination rather than sex. King eiders nesting in Canada use the eastern Beaufort Sea as an important staging area in spring (Alexander et al. 1997, Dickson and Gilchrist 2001). This may reduce their need to accumulate reserves in the ECS, thus allowing them to shorten their staging time there. Birds migrating to Siberia left the ECS later than birds migrating to Canada, despite a considerably longer distance to breeding grounds. This suggests that there may be few other reliable staging areas between the ECS and breeding areas in Siberia. Thus, king eiders migrating west from the ECS may have to acquire sufficient reserves prior to departure from the ECS to complete spring migration.

King eiders require body reserves not only for migration but also for successful reproduction (Kellett 1999, Kellett and Alisauskas 2000). The ECS is the closest staging area to Alaskan nesting areas and thus the most likely area where body reserves are accumulated (Klaassen et al. 2006a). While we were able to track only males to Siberian

nesting areas, it is highly likely that those males accompanied females (Rohwer and Anderson 1988). Hence, our study suggests that females breeding in Siberia may also depend on body reserves accumulated in the ECS. Alteration of this habitat and disturbances of king eider spring migration schedules could have negative consequences for reproductive success and population dynamics of this species, not only in North American but also in Siberian populations.

The spatial distribution of king eiders in the ECS differed slightly between fall and spring migration, with most spring locations being farther offshore and slightly farther south. During spring migration coastal ice prevents king eider foraging in nearshore areas, and open water exists only in polynyas in the pack ice. The location of the polynya depends on ocean currents and wind conditions, and varies among years (Ahlnäs and Garrison 1984). Variation in sea ice probably accounts for annual variation in the distance from shore that king eiders use for staging during spring migration.

8.5.3. Importance of the ECS and potential threats to eiders

Besides king eiders, the ECS is also a crucial staging area for common (*S. mollissima*) and spectacled eiders (M. Petersen, US Geological Survey, Anchorage, pers. comm.). It is an important molting area for the North American spectacled eider population (Petersen et al. 1999). Some of the Steller's eiders (*Polysticta stelleri*) nesting in Alaska also use the region during fall migration (P. Martin, U.S. Fish and Wildlife Service, Fairbanks, pers. comm.). Thus, the area is important for all four eider species, and alteration of habitat and increases in disturbance levels may have negative consequences for several species of sea ducks, including two species (Steller's and spectacled eider) listed as 'Threatened' under the U.S. Endangered Species Act.

The international importance of the ECS to eiders requires consideration when evaluating proposals for industrial development. The current EIS estimates that over the life of development and production of oil and gas facilities in the Chukchi Sea, the chance of a large spill ≥ 1000 barrels (≈ 140 tons) of oil is within a range of 33–51%

(Minerals Management Service 2007). An oil spill in the ECS could potentially cause high mortality of eiders and have long-term adverse effects on eider populations (Peterson et al. 2003). The areas already leased for oil and gas exploration and possible development in the ECS are >70 km offshore (Minerals Management Service 2008), and production facilities would thus be unlikely to fall within the areas most heavily used by eiders for foraging. However, king eiders use the entire area between the coast and the offshore development area, and will potentially be affected by air and ship traffic connecting land-based and offshore facilities (Mosbech and Boertmann 1999, Agness et al. 2008). Man-made structures and activities at sea may also affect sea birds during migratory flights (Wiese et al. 2001, Garthe and Hüppop 2004, Fox et al. 2006). Eiders are generally heavy ducks with high wing loading and poor maneuverability (Raikow 1973). They tend to avoid man-made structures at sea, but fatal collisions occur in low visibility during peak migration (Mallory et al. 2001, Larsen and Guillemette 2007). Development of industrial facilities near major flyways of eiders could lead to additional mortality or costly detours resulting in negative fitness consequences. While many North American eiders may migrate close enough to the coast to bypass structures in the current lease sale area, king eiders flying from the ECS to Siberia may have to cross the currently leased areas and are thus potentially affected by industrial structures.

Another potential threat to eiders in the ECS are environmental changes. Sea ice is receding from Arctic seas due to increases in water temperature (Stroeve et al. 2008). Elevated water temperatures facilitate northward range expansion of some species (Vermeij and Roopnarine 2008) and may lead to changes in benthic invertebrate community structure and abundance (Dunton et al. 2005, Grebmeier et al. 2006a, Bluhm and Gradinger 2008). Such changes detrimentally affected food sources for eiders in the Bering Sea (Lovvorn et al. 2003), and may in the future reduce prey availability for eiders in the ECS. Changes in prey abundance or distribution could be compounded with increasing anthropogenic disturbances to substantially decrease the profitability of the ECS as a staging area on migration. Reductions in sea ice may also enable sea ducks to winter in the ECS in the near future, thus potentially extending their exposure to harmful

effects from industrial developments. The potential interactions between climate change and direct anthropogenic impacts have not been adequately addressed in the Chukchi Sea. More research is required to determine current food sources of sea ducks and possible future changes in the abundance of prey organisms. This research is essential for predicting and mitigating possible future impacts of industrial development in the region.

8.6.   Acknowledgements

8.7.　　　References

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Table 8.1. Locations in western North America where king eiders were captured and equipped with satellite transmitters. Birds were captured before nesting in June from 1997 to 2005 and during brood-rearing in late August 2006 and 2007.

Site	*n* birds	Latitude	Longitude	capture years
Victoria Island, Canada	*44*	70° 21' N	110° 30' W	1997, 1998, 2003, 2004
Prudhoe Bay, Alaska	*10*	70° 10' N	148° 35' W	1999
Banks Island, Canada	*10*	72° 23' N	125° 05' W	2000
Kuparuk Oilfield, Alaska	*74*	70° 20' N	149° 45' W	2002-2006
Teshekpuk Lake, Alaska	*20*	70° 26' N	153° 08' W	2003-2005
Trap Lake, Alaska	*50*	70° 26' N	152° 34' W	2007

Table 8.2. King eider staging times during fall migration in the eastern Chukchi Sea as revealed by satellite telemetry from adult birds captured on breeding grounds in Alaska or Canada, and hatch year birds captured in Alaska. Arrival is the first recorded location of a bird after migration from the Beaufort Sea, departure is the last recorded location prior to migration towards the Bering Sea, and residency time is the difference between the arrival and departure dates plus the time of one complete duty cycle of the satellite transmitter. All times are given ± standard deviation (in days).

| | adult | | | | hatch year | | | | | |
| | male | | female | | male | | female | | unknown | |
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Alaska	(*n* = 46)		(*n* = 34)		(*n* = 12)		(*n* = 12)		(*n* = 4)	
arrival	9 July	12	19 Aug	17	23 Sept	15	27 Sept	11	22 Sept	5
departure	24 July	7	22 Aug	16	10 Oct	15	14 Oct	12	5 Oct	19
total range	5 Jun - 14 Aug		8 Jul - 29 Oct		5 Sept - 8 Nov		5 Sept - 30 Oct		17 Sept - 29 Oct	
residency time (days)	17	10	6	11	22	20	23	15	18	16
Canada	(*n* = 14)		(*n* = 14)							
arrival	4 Aug	8	30 Aug	14						
departure	9 Aug	7	3 Sept	15						
total range	28 Jul - 22 Aug		17 Aug - 17 Oct							
residency time (days)	9	4	6	4						

Table 8.3. Depth and distance to coast of king eider staging locations during fall and spring migration in the eastern Chukchi Sea. All sample sizes reflect locations recorded by satellite transmitters.

| | adult | | | | | hatch year | | | | |
| | male | | female | | | male | | female | | unknown | |
	mean	SD	mean	SD		mean	SD	mean	SD	mean	SD
fall migration	(n = 353)		(n = 146)			(n = 49)		(n = 52)		(n = 23)	
distance to coast (km)	12.4	10.1	16.7	13.6		5.6	12.6	4.8	7.2	5.8	10.4
water depth (m)	-20.2	10.7	-21.1	8.6		-9.7	6.8	-10.8	7.2	-8.9	7.2
spring migration	(n = 193)		(n = 178)								
distance to coast (km)	28.5	17.5	28.7	16.0							
water depth (m)	-23.1	7.1	-23.4	6.0							

Table 8.4. King eider staging times during spring migration in the eastern Chukchi Sea as revealed by satellite telemetry from adult birds. Birds are grouped into geographic regions of their final destination on spring migration, and average distance to breeding site is given for birds where the final destination of spring migration could be determined. Arrival date represents the first recorded location of a bird after migration north from the Bering Sea, departure date represents the last recorded location prior to migration towards the breeding grounds, and residency time is the difference between the arrival and departure dates plus the time of one complete duty cycle of the satellite transmitter. All times are given ± standard deviation (in days).

	Alaska ($n = 23$)			Canada ($n = 33$)			Russia ($n = 6$)		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
arrival	*23*	4 May	10	*33*	30 Apr	6	*6*	28 Apr	5
departure	*23*	24 May	11	*33*	14 May	6	*6*	18 May	11
total range	*23*	18 Apr - 8 Jun		*33*	18 Apr - 24 May		*6*	20 Apr - 5 Jun	
residency time (days)	*23*	25	13	*33*	18	5	*6*	24	9
distance to breeding site (km)	*20*	697	387	*16*	1553	420	*5*	2969	638

Figure 8.1. Spatial distribution of king eiders in the eastern Chukchi Sea during fall migration from 5 June through 8 November. Bold black lines indicate high use areas (50% fixed kernel volume contours), light gray points represent king eider locations (*n* = 623) as recorded by satellite transmitters, and dark gray blocks are active leases for oil and gas exploration and development. Inset map shows general location of study area.
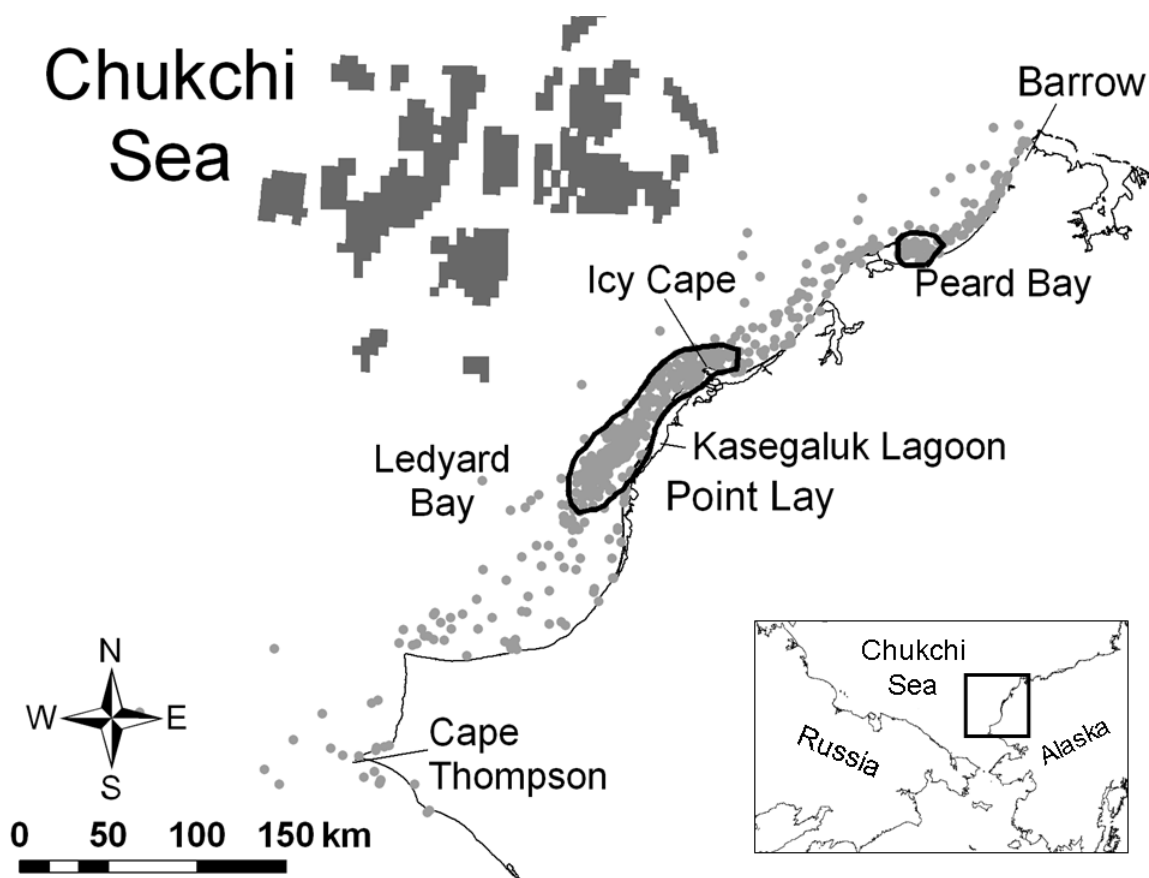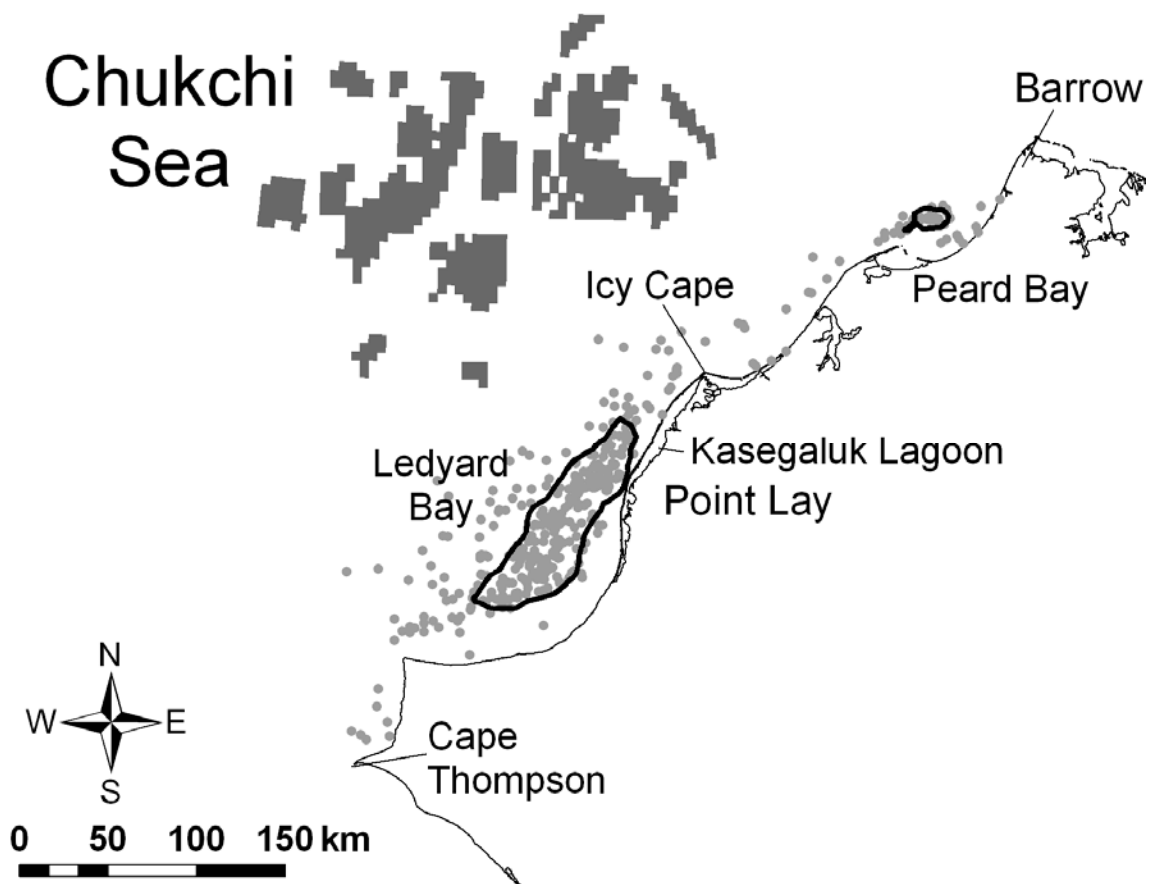
Figure 8.2. Spatial distribution of king eiders in the eastern Chukchi Sea during spring migration from 18 April through 8 June. Bold black lines indicate high use areas (50% fixed kernel volume contours), light gray points represent king eider locations ($n = 371$) as recorded by satellite transmitters, and dark gray blocks are active leases for oil and gas exploration and development.

Conclusions

Four species of eider inhabit Arctic marine and coastal ecosystems around the world. Two of these, Steller's (*Polysticta stelleri*) and Spectacled (*Somateria fischeri*) eiders, are limited in their distribution to certain regions of the Arctic, are comparatively rare, and listed as 'vulnerable' under international criteria (BirdLife International 2008). The two larger eider species, Common (*S. mollissima*) and King Eiders (*S. spectabilis*), have a circumpolar distribution and are more abundant, with recent estimates for the world's King Eider population close to one million birds (Wetlands International 2006). King Eiders are not only the most abundant eider species in the Arctic, they are also genetically homogenous, and show virtually no spatial genetic structure among different continents (Pearce et al. 2004). In contrast, Common Eiders show distinct genetic structuring, and many of the 17 sub-species are genetically isolated from one another (Goudie et al. 2000). My research has helped to elucidate why King Eiders are a successful and widespread inhabitant of Arctic ecosystems, do not show spatial genetic variation, and may be better adapted than other eider species to cope with future challenges resulting from climate-driven changes to their arctic environments.

A common theme throughout my research is individual variability in virtually all aspects of King Eider life history, a topic that has recently received increased attention in ecology (Dall et al. 2004, Sih et al. 2004, Roshier et al. 2008). I have shown that the timing and distance of annual migrations (Chapter 1), behavior and movements during the winter period at sea (Chapter 2), and food consumption and nutrient investment strategies on breeding grounds (Chapter 5) all vary widely among individuals. It is generally acknowledged that arctic ecosystems show tremendous annual variability, which I have also found with respect to nest survival (Chapter 7). Part of the reason why King Eiders are a common and widespread species of the arctic environment may be their flexibility, whether at the individual level or as a species, so that in any given year, under any given conditions, at least some birds will be able to survive and breed successfully. The variability in migration and winter movements I described (Chapters 1 and 2)

suggests that King Eiders are very successful in exploring marine environments to find suitable habitat over a large spatial range. In an annually highly variable environment like the arctic and subarctic seas where King Eiders winter, this strategy could be more successful than wintering in a single, spatially limited area. Once suitable areas are encountered, individuals may use these areas for many years. Female King Eiders show very high site fidelity to geographic areas used during energetically expensive stages of the annual cycle, namely the breeding season and the wing molt period (Phillips and Powell 2006). We currently do not know how those areas are chosen initially, but familiarity with the environment may enhance success for females during stages of the annual cycle during which they are most vulnerable to predation (Hakkarainen et al. 2001).

The variability in movements and wide distribution during the non-breeding season make it likely that King Eiders may be able to respond to changes in their marine habitat better than other eider species. As sea ice recedes and benthic communities change, some of the areas that currently offer abundant food and open water during the winter may become less suitable, most notably areas in the northern Bering Sea around the coast of Chukotka (Grebmeier et al. 2006, Bluhm and Gradinger 2008, Mueter and Litzow 2008). In turn, other areas that have so far been inaccessible during the winter may become available. Polynyas in the Chukchi Sea, which until recently often closed during the winter (Stringer and Groves 1991), may remain open even during times of maximal annual ice extent in the near future and offer King Eiders new wintering areas. In January and February 2008, villagers in Point Lay reported having seen brown ducks in leads that remained open throughout the winter (R. Suydam, pers. comm.), indicating that this change may be already under way. This area in the eastern Chukchi Sea that may in the future become an important new wintering area is now the most important spring staging area (Chapter 8).

While King Eiders may benefit from their flexibility and ability to rapidly exploit new areas, the eastern Chukchi Sea may not be a safe haven in the future. Oil and gas exploration is proceeding in this region, and anthropogenic disturbance will likely

increase dramatically in this region over the next decades (Chapter 8). Equally important, but to date completely unknown, may be effects of prey depletion by sea ducks. In Chapter 8 I presented data that show that the entire western North American population of King Eiders uses the eastern Chukchi Sea during spring migration. This population is currently estimated around 500,000 birds (Suydam et al. 2008). Additional birds migrating to breeding grounds in Siberia, as well as an unknown number of first-year or non-breeding birds, also use this area in spring and summer, thus increasing the total number of ducks foraging in the eastern Chukchi Sea in spring. The eastern Chukchi Sea is also used extensively during late summer, and moreover serves as an important molting and staging area for Spectacled and Common Eiders – all of which presumably forage on similar prey items as King Eiders. It is currently unknown whether eiders, in concert with some marine mammal species also foraging on benthic invertebrates such as Walrus (*Odobenus rosmarus*) or Gray Whales (*Eschrichtius robustus*), have the capacity to significantly deplete benthic biomass. If they do, then an extended period of use – through an increasing number of King Eiders wintering in the Chukchi Sea – may reduce the carrying capacity of this region at other times of the year. As King Eiders seem, again, very flexible in their choice of prey (Bustnes and Erikstad 1988, Frimer 1997, Merkel et al. 2007), they may be able to use this area when it becomes less attractive for other species. In this respect it is interesting to note that Steller's Eiders, the smallest of the four eider species, do not seem to use the eastern Chukchi Sea in spring at all (P. Martin, unpubl. data). The cause for the absence of Steller's Eiders is unknown, but their absence may be due to leads that form in water too deep for this species, or competition from larger species. Much needs to be learned about eider foraging at sea, and the potential for prey depletion deserves more attention as prey depletion may become an acute problem in the near future.

It is not surprising that foraging habits of eiders at sea are poorly understood, as the logistical challenges of any study in marine areas covered by sea ice are considerable. The foraging habits of eiders on the tundra, however, are even less known (Holcroft-Weerstra and Dickson 1997). In this thesis I have shown that foraging in tundra ponds

provides a large part of the nutrients that are used for egg synthesis (Chapter 5). As was the case in movement behavior, I also found high individual variation in nutrient allocation strategies among females. A similar variation may exist in breeding propensity, although I was not able to test this in my thesis. Low breeding propensity has recently been shown in Lesser Scaup (*Aythya affinis*) in interior Alaska (Martin 2007), and is known from Common Eiders in some years (Coulson 1984). The high individual variation in nutrient allocation strategies among King Eiders may lead to some birds being able to nest in any given year, so that all strategies are maintained in the population due to the variable and unpredictable environment in which they nest. Again, the flexibility in the amount of body reserves used for egg production would make King Eiders a successful inhabitant of the Arctic and may be part of the reason why this species is abundant and widespread. The species breeds at higher latitudes than most other sea ducks (Bellrose 1976), and birds nesting at higher latitudes may show a narrower range of nutrient allocation strategies with a higher reliance on endogenous reserves. Future research could examine nutrient allocation patterns at the northern margin of King Eider's breeding range, as well as individual variation in breeding propensity over several years.

Despite the large variation in nutrient allocation to eggs, the use of an income strategy changes the old paradigm that all eiders are capital breeders. Thus, seasonal interactions between spring migration and breeding season are lower than expected. Despite their reliance on tundra nutrient sources for egg formation, King Eiders may still rely on stored body nutrients to fuel metabolism during incubation (Kellett and Alisauskas 2000, Bentzen et al. 2008b). These nutrients may be accumulated at marine staging areas, which play a vital role in allowing King Eiders to prepare for reproduction and successfully incubate a clutch and raise offspring. If King Eiders do not attain a threshold body condition that enables them to maintain high incubation constancy, their nesting attempts may fail (Bentzen et al. 2008a). We currently do not know in what geographic region King Eiders accumulate body reserves, but results from Chapter 7

indicate that the winter region is probably not the most important area for the accumulation of body reserves critical for breeding.

In Chapter 7 I showed that annual, seasonal, and site effects influence variability in daily nest survival rates of King Eiders in northern Alaska, but that the region where a nesting female spent the previous winter was unimportant. This could either indicate that the winter regions in the Bering Sea are equivalent, or that interactions between winter and breeding season are confounded by events along the migratory route. As Chapters 1 and 8 showed, the eastern Chukchi Sea is probably the most likely area where body reserves are accumulated, and residual effects from the winter may be amalgamated during the staging time in the eastern Chukchi Sea.

In conclusion, we now know that King Eiders are behaviorally variable ducks that cope with the arctic environment through a number of different and individually flexible strategies. This flexible life-style may offer resilience against future climatic changes and King Eiders may be able to adjust to a changing arctic environment to a certain degree. Nonetheless, more research on energy budgets, demographic consequences of individual strategies, and consequences of habitat changes on land and at sea are needed to fully understand what the future will bring for King Eider populations in Alaska and around the world.

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