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Does winter region affect spring arrival time and body mass of king eiders in northern Alaska?

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Abstract Events during the non-breeding season may affect the body 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*) arrival time and body mass upon arrival at breeding grounds in northern Alaska were affected by their choice of a winter region in the Bering Sea. We captured birds shortly after arrival on breeding grounds in early June 2002–2006 at two sites in northern Alaska and determined the region in which individuals wintered using satellite telemetry or stable isotope ratios of head feathers. We used generalized linear models to assess whether winter region explained variation in arrival body mass among individuals by accounting for sex, site, annual variation, and the date a bird was captured. We found no support for our hypothesis that either arrival time or arrival body mass of king eiders differed among winter regions. We conclude that wintering in different regions in the Bering Sea is unlikely to have reproductive consequences for king eiders in our study areas.

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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 non-lethal 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 (Bearhop et al. 2004; Gunnarsson et al. 2006; Marra et al. 1998; Norris et al. 2003). Many waterfowl species breeding in the Arctic rely on stored nutrient reserves for reproduction, either to produce eggs or to fuel metabolism during incubation (Gauthier et al. 2003; Parker and Holm 1990). These body reserves can be accumulated during the preceding winter or during spring migration, and arctic-nesting waterfowl are therefore subject to potentially long-term carry-over effects (Alisauskas 2002; Drent et al. 2007; Yerkes et al. 2008). 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.

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 may affect body mass and reproductive success (Lehikoinen et al. 2006; Lovvorn et al. 2003; Petersen and Douglas 2004). While female eiders require body reserves for incubation (Bentzen et al. 2008b; Kellett and Alisauskas 2000; Parker and Holm 1990), males forage very little on breeding grounds (Holcroft-Weerstra and Dickson 1997) and may require body reserves for mate guarding (Hario and Hollmén 2004; Hipes and Hepp 1995; Steele et al. 2007). Wintering in different oceans has been shown to affect nest initiation dates and clutch sizes of king eiders (*S. spectabilis*) nesting in the central Canadian Arctic (Mehl et al. 2004). Thus it is possible that due to carry-over effects between winter and breeding areas the body condition and the arrival time of king eiders returning to breeding areas depends on the region used during the previous winter.

King eiders nesting in western North America winter in three discrete regions in the Bering Sea (Fig. 1; Oppel et al. 2008) and migration routes, distances, and migration time differ among individuals migrating to each one. The three regions differ in their oceanographic properties, with the northern Bering Sea region 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). Recent changes to benthic communities in the northern Bering Sea may have reduced the quality of available food sources in that region (Grebmeier et al. 2006b; Lovvorn et al. 2005; Richman and Lovvorn 2003). This change may alter the quality of this region and thus affect the body condition of king eiders wintering there. We explored whether body mass as an indicator of body condition of king eiders breeding in northern Alaska differed among birds using different winter regions in the Bering Sea. We captured king eiders shortly after arrival on breeding grounds in June and assigned them to a winter region using either stable isotope ratios of head feathers or satellite telemetry. We further examined whether arrival time on breeding grounds differed among birds wintering in different regions, as earlier arriving birds often achieve higher reproductive success (Gunnarsson et al. 2006; Kokko 1999). Our study thus provides insights into the potential fitness consequences of wintering strategies in king eiders.

Material and methods

Study area and field methods

We captured king eiders in the first half of June 2002–2006 at two sites on the Arctic coastal plain of Alaska: (1) near Teshekpuk Lake (site “Olak”, 70°26′N, 153°08′W); and (2) in the Kuparuk oilfield (site “Kuparuk”, 70°27′N, 149°41′W). Both areas consist of flat tundra with numerous ponds, lakes, and wetland complexes.

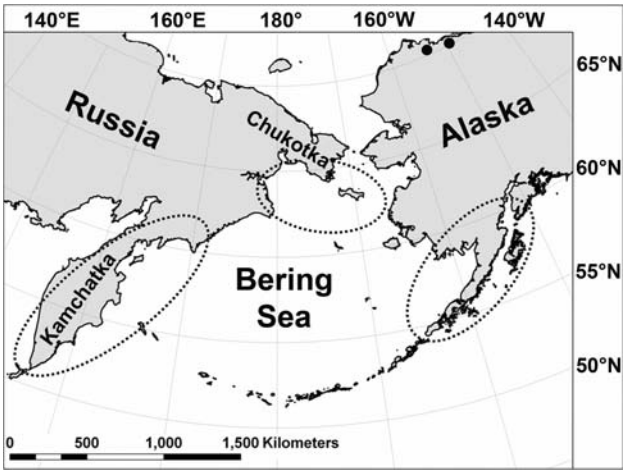

Fig. 1 King eider study sites on breeding grounds in northern Alaska (*black circles*), and winter regions used by king eiders in the Bering Sea (*broken lines*)

We used mist-net arrays and decoys to capture adult king eiders on ponds in the study areas. We measured body mass of each captured bird using spring scales accurate to 10 g, and assume that body mass was positively correlated with body condition (Schamber et al. 2009). From 2002 through 2005 we implanted birds with satellite transmitters to follow their movements for 12 months after capture (Oppel et al. 2008; Phillips et al. 2006). In 2006 we plucked one head feather from each bird and used carbon and nitrogen isotope ratios of the head feather to assign individuals to the winter region in which the feather had been grown (Oppel and Powell 2008). The treatments described here were approved by the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks (#05-29).

Winter region assignment

For birds tracked with satellite transmitters we determined the location of each bird during winter using the data provided by satellite transmitters. This analysis yielded information on the winter region used in the winter after capture; hence, in order to relate spring arrival body mass 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 (Iverson et al. 2004; 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 adult individuals in which the battery of the satellite transmitter lasted long enough to track birds for two subsequent winters ($n = 11$, S. Oppel, unpubl. data).

In 2006 we used stable isotope ratios of head feathers to assign king eiders to the region used during the previous winter in the Bering Sea (Mehl et al. 2005; Oppel and Powell 2008). 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 bird into small pieces for stable isotope analysis. We analyzed feathers for carbon and nitrogen stable isotope ratios at the Alaska Stable Isotope Facility using continuous flow stable isotope-ratio mass spectrometry; further details of the stable isotope analyses can be found in Oppel and Powell (2008). 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 2008). 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 (Kelly et al. 2008; Rocque et al. 2006). At this level of probability all feathers of known origin were correctly classified in cross-validation (Oppel and Powell 2008).

Arrival time estimation

Twenty-eight female king eiders equipped with a satellite transmitter returned to breeding grounds in northern Alaska in the year after instrumentation with a functional transmitter, and thus enabled us to estimate arrival time on breeding grounds. We considered the first location provided by the satellite transmitter on the study area following spring migration as arrival time on breeding grounds, and related arrival time of individuals to the winter region used in the previous winter as recorded via satellite telemetry. Due to limited sample size we were not able to control for annual and spatial variation in arrival time. We compared arrival times of birds from different wintering regions using a nonparametric Kruskal–Wallis test, and present 95% confidence intervals of arrival time for each winter region.

Statistical analysis of arrival body mass

We expected body mass upon arrival on breeding grounds to vary among sexes (Suydam 2000), between study sites (Bentzen et al. 2008a), among years, and depending on the date on which a bird was captured. We used generalized linear models with a Gaussian error distribution in R 2.8.0 to account for the variation in king eider body mass as a result of these variables. We used an information-theoretic approach to find the most parsimonious model out of a candidate set of 12 models containing plausible combinations of sex, study site, year, and date of capture (Table 1). We then added our variable of interest, the winter region used by the individual bird, as explanatory variable to the most parsimonious model and evaluated the support for this model by using Akaike's information criterion corrected for small sample size (Burnham and Anderson 2002).

Table 1 Candidate models explaining variation in king eider spring arrival body mass in northern Alaska, 2002–2006 ($n = 87$) ranked by AIC*c*

Model	k	ΔAICc	ωAICc	Evidence ratio
Day + sex	4	0.00	0.26	1.00
Site + sex	4	1.01	0.16	1.66
Day + sex + site	5	1.62	0.11	2.25
Day	3	2.00	0.09	2.72
Sex	3	2.51	0.07	3.51
Site	3	2.81	0.06	4.07
Sex + year	4	3.08	0.06	4.66
Site + year + sex	5	3.16	0.05	4.85
Day + site	4	3.38	0.05	5.43
Day + year + day × year	5	3.79	0.04	6.65
Site + year	4	4.85	0.02	11.28
Year	3	5.04	0.02	12.43

Table reports the difference in AIC*c* 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 evidence ratio

Results

Body mass of king eiders arriving on breeding grounds in northern Alaska ranged from 1,150 to 2,140 g. Body mass was on average 80 g higher for females than for males (Table 2), and birds captured in the Kuparuk oilfield were on average 75 g lighter than birds captured at Olak (Table 2).

The most parsimonious model describing variation in king eider body mass contained date of capture and sex, with body mass decreasing at a rate of 13 g day^{-1} (±6 g day^{-1} standard error) during the first 3 weeks of June. An alternative model containing sex and study site as explanatory variables received similar support (Table 1). Adding the variable winter region to either of those two models did not increase the explanatory power, and both models containing winter region as explanatory variable received very little support (Table 3). We conclude that after accounting for variation in body mass as a result of sex, study site, and date of capture there was no difference in king eider body mass among the winter regions used by individuals in the Bering Sea.

Arrival time of king eiders on breeding grounds did not differ between Olak and the Kuparuk oilfield ($H = 0.21$, $p = 0.65$), and we pooled samples from both sites for subsequent analysis. Birds arrived on breeding grounds at similar

Table 2 Body mass (mean ± standard deviation in grams) of adult king eiders captured in the first half of June 2002–2007 at two sites (Olak, Kuparuk) on breeding grounds in northern Alaska

Winter region	Females						Males					
	Olak			Kuparuk			Olak			Kuparuk		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
SW Alaska	5	1,788	156	7	1,689	280	3	1,715	126	11	1,579	120
Northern Bering Sea	6	1,669	271	6	1,655	156	10	1,669	165	9	1,572	99
Kamchatka	4	1,735	318	9	1,656	216	3	1,617	186	14	1,593	93

Birds were assigned to a winter region in the Bering Sea using either satellite telemetry or stable isotopes of winter-grown head feathers

Table 3 Most parsimonious models explaining variation in king eider spring arrival body mass in northern Alaska, 2002–2006 ($n = 87$) with and without the effect of winter region

Model	*k*	ΔAIC*c*	*ω*AIC*c*	evidence ratio
Day + sex	4	0.00	0.55	1.00
Site + sex	4	1.01	0.33	1.66
Day + sex + winter region	6	4.28	0.07	8.49
Site + sex + winter region	6	4.90	0.05	11.57

Table reports the difference in AIC*c* for each model in relation to the most parsimonious model (ΔAIC_c), AIC_c model weight (*ω*AIC*c*), the number of estimable parameters (*k*), and the evidence ratio

times after wintering in the northern Bering Sea (95% CI 9–16 June, $n = 10$), southwestern Alaska (8–17 June, $n = 10$), or Kamchatka (6–13 June, $n = 8$; $H = 2.24$, $P = 0.32$).

Discussion

The region where king eiders spent the previous winter did not affect their body mass or arrival time on breeding grounds in northern Alaska. Instead, body mass varied with the date of capture, sex, and study site. Females were on average slightly heavier than males, presumably because females require body reserves for incubation (Bentzen et al. 2008b; Kellett and Alisauskas 2000). Body mass declined with date of capture for both sexes during the month of June, and may reflect lower body mass of later-arriving birds (Drent et al. 2003). Higher body mass in earlier arriving individuals has been found in several migratory bird species, and may reflect the need for additional body reserves required by early arriving individuals to safeguard against harsh weather conditions and food shortages during the early season (Brown and Bomberger Brown 2000; Forstmeier 2002; Ninni et al. 2004). As neither body mass nor arrival time varied among winter regions, we conclude that wintering in different regions does not affect the relevant fitness parameters on breeding grounds, rendering carry-over effects unlikely at the spatial resolution of our study.

Mehl et al. (2004) described that in some years nest initiation dates of king eiders breeding in the central Canadian Arctic may vary among birds having wintered in either the Atlantic or the Pacific Ocean. They attributed this pattern to annually differing ice conditions along respective migratory routes. Such a pattern is unlikely in our study as all birds from the three winter regions we distinguished use the same migration route through the Chukchi and Beaufort Seas back to our study areas (Oppel et al. 2008, 2009). Hence, variable ice conditions during spring migration would affect birds from all three regions equally and differences in arrival time would not be expected unless winter region had an effect on the onset and speed of spring migration.

Our analysis of arrival time and arrival body mass was partly based on the assumption of winter region fidelity. While we are confident that this assumption was met in our study, it is possible that some king eiders may not winter in the same region every year (Mehl et al. 2004). We therefore examined whether our conclusions would be vulnerable to a violation of the winter region fidelity assumption by randomly permuting the winter region of 20–60% of individuals in our study. The results were identical to the results presented above in that there was no support for winter region to have affected either arrival time or body mass. We are therefore confident that our conclusions are robust even if some individuals did not use the same winter region 2 years in a row.

We are not able to determine the mechanism by which king eiders wintering in different regions in the Bering Sea achieve similar body masses upon arrival on breeding grounds. Despite the oceanographic differences among the three regions (Grebmeier et al. 2006a), food may not be limiting in either region, and body mass may therefore not be affected. Alternatively, even if habitat quality was sufficiently different among the three regions, king eiders may acquire a critical body mass regardless of habitat quality by increasing foraging effort (Bond and Esler 2006).

The differences in migration distance to the different winter regions may be compensated by more severe environmental conditions at higher latitudes. Higher thermoregulatory costs due to colder temperatures, and shorter day lengths limiting the time available for foraging (Systad and Bustnes 2001) may affect body mass of individuals wintering in the northern Bering Sea equally as migrating to more southern areas (Mason et al. 2006). During spring migration, the additional cost of a longer migration from more southerly winter regions could be compensated by an earlier start of migration. From published estimates of flight costs (Pelletier et al. 2008) and flight speeds (Day et al. 2004) in eiders we estimate that ca. 6,000–7,500 kJ of energy are required to travel the additional 1,150 km from winter regions in Kamchatka or southwestern Alaska. If the energy required for this flight is derived from lipids, king eiders would lose ca. 150–190 g of body fat (Battley et al. 2001; Battley and Piersma 2005; McWilliams et al. 2004). Accumulating this amount of body fat would take ca. 12–15 days based on average fuel deposition rates of eight species of waterfowl (Drent et al. 2007; Lindström 2003). King eiders wintering in southern areas in the Bering Sea start spring migration 11–29 days earlier than birds wintering in the northern Bering Sea (Oppel et al. 2008). Thus, these birds may be able to compensate for additional migration costs without affecting their arrival time or body condition on breeding grounds.

Compensation for body condition deficits during spring migration may also explain why we did not find carry-over effects that have been found in other bird species. 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 (Oppel et al. 2009; Phillips et al. 2007). The eastern Chukchi Sea is a highly productive region (Dunton et al. 2005), and this staging area could be where fat depots for nesting are accumulated (Oppel et al. 2009). 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.

In summary, our study shows that it is unlikely that wintering in different regions has reproductive consequences for king eiders nesting in Alaska. The maintenance of different wintering strategies in the population indicates that there is either no consistent long-term benefit for any one strategy, or no heritability of winter region choice. Environmental stochasticity may incur fitness benefits in some years, and disadvantages in others, thus enabling the persistence of different heritable strategies within the population. Alternatively, if winter region choice has no heritable component, different strategies could potentially persist in a population despite the presence of a selection gradient (van Noordwijk et al. 2006). Little is known about the heritability of migration strategies in sea ducks. Future studies need to explore whether winter strategies are heritable and whether adult survival differs among winter regions in order to examine the evolutionary implications of different migratory strategies in king eiders.

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