

Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck

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Summary

1. 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.
2. 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.
3. 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.
4. We found extremely high individual variability in winter movement decisions by king eiders, and the individual bird was the most important variable followed by location, date, and sea ice concentration.
5. We conclude that individual strategies exist that interact with environmental conditions to form multiple movement patterns.
6. 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

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 & Cooke 1999; 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 (Terrill & Ohmart 1984), nonpasserines (Ruiz *et al.* 1989; Berthold *et al.* 2002), and especially arctic nesting waterfowl wintering at temperate or sub-arctic latitudes (Haila 1980; 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 sea ducks spend the winter in marine environments in temperate or sub-arctic latitudes where they live in social congregations and forage for invertebrate prey by diving to the sea floor (Madge & Burn 1988). While some species have been shown to remain within a small discrete area throughout winter (Petersen & Douglas 2004; Iverson & 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 & 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).

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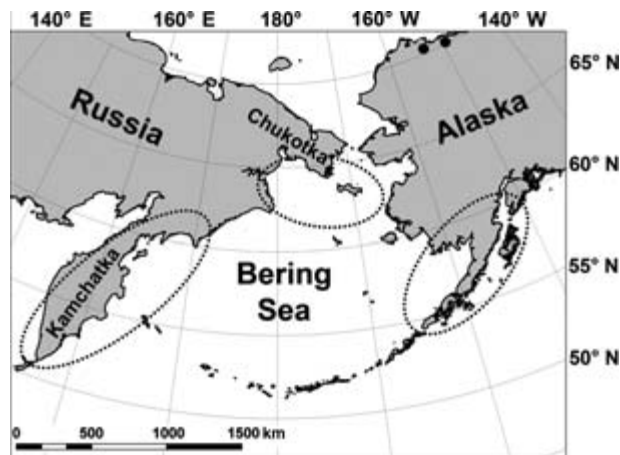


Fig. 1. Main wintering regions (North Bering Sea, south-west Alaska, Kamchatka) of king eiders tracked from breeding areas in western North America (North America) to the Bering Sea (after Oppel *et al.* 2008).

King eiders (*Somateria spectabilis*, L.) in the Bering Sea winter over a large latitudinal range, from 50° N to 65° N (Suydam 2000; Phillips, Powell & Rexstad 2006) (Fig. 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, Powell & Dickson 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 for wintering king eiders to move away from a wintering site should increase with (i) increasing sea ice cover (Vaitkus 1999; Bump & Lovvorn 2004), (ii) decreasing food abundance (Guillemette, Reed & Himmelmann 1996; Lindberg *et al.* 2007), and (iii) decreasing day length (Systad, Bustnes & Erikstad 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.

Materials and methods

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 (38 g PTT with

external whip antenna, Microwave Telemetry Inc., Columbia, MD, USA). We captured birds in early June 2003–05 near Teshekpuk Lake, Alaska (70°26' N, 153°08' W), in June 2002–05 in the Kuparuk oil-field, Alaska (70°20' N, 149°45' W), and in June 2003–04 on Victoria Island, Northwest Territories (70°21' N, 110°30' W). We measured wing chord length of each bird using a ruler, body mass using a spring scale accurate to 10 g, 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 2 h after surgery where they were caught. Transmitters were programmed to different duty cycles throughout the year, with shorter duty cycles (4–6 h of transmission every 1–4 days) from June through November, and longer duty cycles (6 h 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). 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 between sexes (Oppel *et al.* 2008), and therefore pooled the data for the present study.

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 programme 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 & Imboden 1972). We imported all locations into ARCGIS 9.1 on a Lambert Azimuthal projection centred on 65° N and 165° W, and overlaid all locations with layers containing environmental information (see below).

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).

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 & Esler 2006; Merkel *et al.* 2006).

Table 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 turning 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 20 (1–312)
SEX	Sex of the individual, male or female
YEAR	Year of capture, 2002–05
BIOM	Model-predicted benthic biomass [g wet weight/m ²]
DAY_HRS	Day length [h]
CULMEN	Length of culmen [mm]
WING	Length of wingchord [mm]
MASS	Body mass of bird at the time of capture in the previous spring [g]
TARSUS	Length of full tarsus [mm]
BIRD	Individual

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 7 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: (i) no other bird moved simultaneously, (ii) all other birds moved simultaneously, or (iii) 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. 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, Battles & Benning 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 before 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).

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 12 environmental and six bird-specific predictor variables (Table 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 & 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 & 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, Iverson & Liaw 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, Hornik & Zeileis 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 & 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 2.6.1 (<http://www.r-project.org/index.html>) with the add-on package 'party' (Hothorn, Hornik & Zeileis 2006a).

We used the following predictor variables (Table 1): individual identity, sex, indicators of the structural body size of each bird (wing length, tarsus length, and culmen length), body mass as an indicator of body condition (Schamber, Esler & Flint 2009), the bird's location (latitude and longitude), the broad geographical region (northern Bering Sea, eastern Bering Sea around Bristol Bay, Alaska, and western Bering Sea along the coast of Kamchatka, Russia, Fig. 1), date, day length calculated for every location as a function of date and latitude, sea ice cover at each location before 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 & 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 & 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 modelled 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.

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

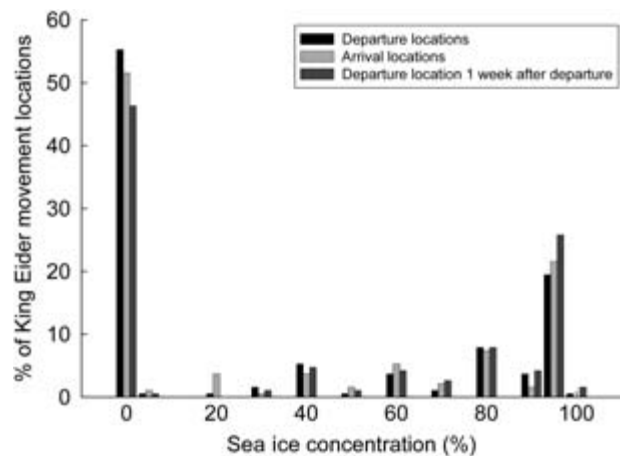


Fig. 2. Relative frequency of locations associated with king eider winter movements in relation to sea ice concentration in the Bering Sea from 2002–06; black columns represent departure locations before departure, white columns represent arrival locations, and gray columns represent departure locations at the time when king eiders were recorded at the arrival location.

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). 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).

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).

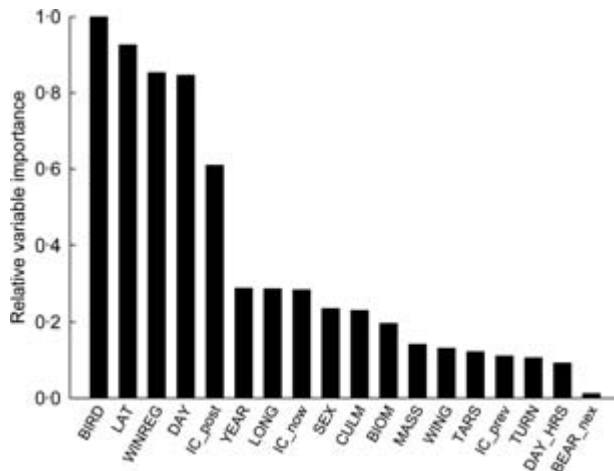


Fig. 3. Importance of environmental and bird-related predictor variables in order of their relevance to increase accuracy of a random forest model predicting under what conditions individual king eiders depart from a wintering site in the Bering Sea. The importance is scaled to 1 for the most important variable. See Table 1 for explanation of variables.

The individual bird was the most important variable in explaining movement decisions (Fig. 3). Almost equally important were a group of three variables including latitude and region of the location, and date. 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 60–64° N (Fig. 4a). Date predicted that movements were unlikely before the end of October, and fairly uncommon through January (Fig. 4b). 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. 4c). All other variables were relatively unimportant (~20% of individual bird, Fig. 3).

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, Houston & McNamara 2004) have recently been recognized to be widespread across many taxa and behaviours, including movement decisions (Roshier, Doerr & Doerr 2008b). Individual differences in behaviour have therefore been successfully incorporated in a variety of ecological models (DeAngelis & 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

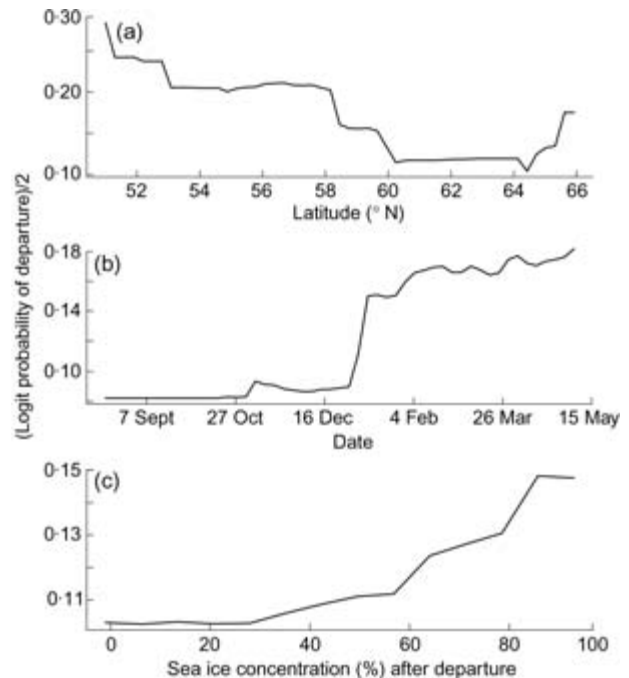


Fig. 4. Partial dependence plots for three important variables predicting movement rates of king eiders in the Bering Sea. (a) Latitude, (b) date, and (c) sea ice concentration at a location 1 week after the bird was last recorded there. The y-axis is half the logit of the predicted probability of departure from a wintering site, for more information see Cutler *et al.* (2007).

differences in behaviour may be prevalent in many aspects of annual routines and need to be considered for management and conservation (Festa-Bianchet & 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, Burton & Metcalfe 1992). 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 (Brodersen *et al.* 2008). Our measure of body condition, which was taken in the previous spring, explained very little of winter movement decisions. 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 age and the social status of tracked birds. The wintering strategy may change during the lifetime of long-lived species like king eiders, and may thus vary with age (Ezard, Becker & Coulson 2007). In a species pairing on wintering grounds (Robertson & Cooke 1999), social status may motivate especially males to travel large distances in search of a partner. Future investigations need to focus on these individual traits as potentially motivating factors for winter bird movements.

Despite the large individual variation, our multivariate algorithmic model identified four 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. Furthermore, 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). The nonlinear relationships of latitude 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, Asmus & Klaassen 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 [*Somateria fischeri* (Brandt, 1847)] wintering in the northern Bering Sea, which rarely leave sites even when ice cover is extreme (Petersen & Douglas 2004). As has been predicted for spectacled eiders at a smaller scale (Bump & 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 (Petersen & 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 (*Somateria 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, Esler & Boyd 2007). King eiders generally forage in deeper water than surf scoters and common eiders (Bustnes & Erikstad 1988) where prey depletion may be less likely (Larsen & 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, Ramos & Winker 1989; Ruiz *et al.* 1989). While among territorial forest songbirds the wanderer strategy was inferior (Rappole *et al.* 1989), 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 alternative 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 & 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 & Templeton 2002; Dall *et al.* 2005). Environmental fluctuations causing freeze up of polynyas used on spring migration have resulted in mass-mortality events in king eiders (Barry 1968; Fournier & 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 conspecifics 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 conspecifics as an indicator of the quality of a site (Beauchamp, Belisle & Giraldeau 1997) 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 into 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.

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