AGE-SPECIFIC SURVIVAL ESTIMATES OF KING EIDERS DERIVED FROM SATELLITE TELEMETRY

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

[1]*Department of Biology and Wildlife, 211 Irving 1, University of Alaska, Fairbanks, AK 99775-6100*
[2]*U.S. Geological Survey, Alaska Cooperative Fish & Wildlife Research Unit, and Institute
of Arctic Biology, 209 Irving I., University of Alaska, Fairbanks, AK 99775-7020*

Abstract. Age- and sex-specific survival and dispersal are important components in the dynamics and genetic structure of bird populations. For many avian taxa survival rates at the adult and juvenile life stages differ, but in long-lived species juveniles' survival is logistically challenging to study. We present the first estimates of hatch-year annual survival rates for a sea duck, the King Eider (*Somateria spectabilis*), estimated from satellite telemetry. From 2006 to 2008 we equipped pre-fledging King Eiders with satellite transmitters on breeding grounds in Alaska and estimated annual survival rates during their first 2 years of life with known-fate models. We compared those estimates to survival rates of adults marked in the same area from 2002 to 2008. Hatch-year survival varied by season during the first year of life, and model-averaged annual survival rate was 0.67 (95% CI: 0.48–0.80). We did not record any mortality during the second year and were therefore unable to estimate second-year survival rate. Adults' survival rate was constant through the year (0.94, 95% CI: 0.86–0.97). No birds appeared to breed during their second summer. While 88% of females with an active transmitter (*n* = 9) returned to their natal area at the age of 2 years, none of the 2-year old males (*n* = 3) did. This pattern indicates that females' natal philopatry is high and suggests that males' higher rates of dispersal may account for sex-specific differences in apparent survival rates of juvenile sea ducks when estimated with mark–recapture methods.

Key words: adult survival, hatch-year survival, King Eider, natal philopatry, satellite telemetry, Somateria spectabilis.

Estimados de la Supervivencia Específicos de la Edad Derivados Mediante Telemetría Satelital en

Resumen. La supervivencia y dispersión específicas de la edad y el sexo son componentes importantes de la dinámica y la estructura genética de las poblaciones de aves. En muchos taxones de aves, las tasas de supervivencia difieren entre aves adultas y jóvenes, pero estudiar la supervivencia de las aves jóvenes en especies longevas es logísticamente desafiante. Con base en datos de telemetría satelital, presentamos los primeros estimados de las tasas de supervivencia anual de individuos dentro del primer año desde la eclosión para un pato marino, *Somateria spectabilis*. Entre 2006 y 2008, equipamos a individuos de esta especie antes de que emplumaran con transmisores satelitales en áreas de cría en Alaska y estimamos las tasas de supervivencia anual durante sus primeros dos años de vida con base en modelos de destino conocido. Comparamos esos estimados con las tasas de supervivencia de adultos marcados en la misma área entre 2002 y 2008. La supervivencia dentro del primer año de eclosión varió entre las temporadas durante el primer año de vida y el estimado de la tasa de supervivencia anual promediado entre modelos fue de 0.67 (IC del 95%: 0.48–0.80). No registramos mortalidad durante el segundo año, por lo que no estuvimos en capacidad de estimar la tasa de supervivencia para el segundo año. La tasa de supervivencia de los adultos fue constante a lo largo del año (0.94, IC del 95%: 0.86–0.97). Ningún ave pareció reproducirse durante su segundo verano. Mientras que el 88% de las hembras con transmisores activos (*n* = 9) regresaron a su área de nacimiento a la edad de dos años, ninguno de los machos de dos años de edad (*n* = 3) lo hizo. Este patrón indica que la filopatría natal de las hembras es alta y sugiere que las mayores tasas de dispersión de los machos podrían explicar las diferencias entre sexos en la tasa de supervivencia aparente de los patos marinos jóvenes, estimada mediante métodos de marcado y recaptura.

INTRODUCTION

Understanding how basic demographic rates vary with age is essential for understanding the population dynamics of long-lived vertebrates. Survival rates of different age classes often differ, and age-specific survival estimates are an important factor in population models of long-lived birds with delayed breeding (Martin 1995, Spendelow et al. 2002, Lake et al. 2006). Sea ducks are generally long-lived, and their sexual maturity is delayed, but for most species knowledge about variation in survival rates by age class is absent.

Populations of several sea ducks have declined over the past decades (Stehn et al. 1993, Gratto-Trevor et al. 1998, Suydam et al. 2000, Merkel 2004, Žydelis et al. 2009). The causes of population declines are poorly understood, but the declines could be a consequence of changes in prey availability at sea and resulting effects on survival rates (Lovvorn et al. 2003, 2009, Richman and Lovvorn 2003, Grebmeier et al. 2006). Assessing whether such environmental changes may affect survival, especially of young and inexperienced birds, is hindered by the lack of information about survival rates of different age groups. Therefore, estimates of survival rates for adult and young birds are urgently needed for the mechanisms of population dynamics to be understood.

In sea ducks, population dynamics are strongly influenced by adult survival, but juvenile survival and recruitment are also critical components of population dynamics (Coulson 1984, Johnson et al. 1992, Wilson et al. 2007). Several studies have determined that survival rates of adult sea ducks are generally very high (Flint and Grand 1997, Flint et al. 2000b, Wilson et al. 2007, Hario et al. 2009) and that high mortality of ducklings before fledging significantly limits annual reproductive output (Flint and Grand 1997, Christensen 1999, Flint et al. 2006, Mehl and Alisauskas 2007, Lehikoinen et al. 2008b, Öst et al. 2008). However, survival of birds during their first and second years of life (hereafter referred to as hatch-year and second-year, respectively) is very poorly known in sea ducks, and logistical difficulties have limited studies to particular seasons or study areas (Flint et al. 2000a, Regehr 2003, Boyd et al. 2009).

Survival rates for sea ducks have so far been studied with capture–mark–recapture approaches. For species and life stages in which rates of dispersal are high, such studies are poorly suited to estimating survival rates without a geographically broad effort toward recovery to reduce the possibility of permanent emigration from the study area (Paradis et al. 1998, Blums et al. 2003, Regehr 2003). Hatch-year and second-year sea ducks are generally believed to disperse at rates higher than adults (Anderson et al. 1992), and to reliably estimate survival rates of young birds during their first 2 years of life, dispersal must be taken into account (Blums et al. 2003, Breton et al. 2006). In the past decade, the use of satellite transmitters has advanced the knowledge of many aspects of sea ducks' life history, and robust modeling tools are now available for satellite tracking data to be used for the estimation of survival rates (Murray 2006).

In this study we addressed three main questions critical for understanding the population dynamics of sea ducks: (1) What is the survival rate of males and females in their first and second years? (2) Within a species, are annual survival rates of hatch-year and second-year birds different from those of adults? (3) What proportion of birds surviving the first 2 years of life return to their natal breeding area in their second spring? We addressed these questions by tracking hatch-year and second-year King Eiders (*Somateria spectabilis*) with satellite transmitters to estimate their survival rate and describe their dispersal from natal areas. Similarly, we estimated adult survival rates over several years on the basis of information from satellite transmitters attached to adults. These data provide the first estimates of rates of hatch-year survival and second-year dispersal in eiders and will be invaluable for building population models for species of conservation concern.

METHODS

STUDY SPECIES

The King Eider is a large (~1500–2000 g) sea duck that breeds in arctic tundra around the world (Suydam 2000). The birds nesting in northern Alaska migrate from breeding grounds through the Beaufort and Chukchi seas to molting and wintering areas in the Bering Sea (Phillips et al. 2006, Oppel et al. 2008), where they remain from October through April. In April and May they return via staging areas in the Chukchi and Beaufort seas to breeding grounds in Alaska (Phillips et al. 2007, Oppel et al. 2009). While estimates of nest survival (Kellett et al. 2003, Bentzen et al. 2008) and duckling survival (Mehl and Alisauskas 2007) are available, for the western arctic population of the King Eider survival rates of neither adults nor younger age classes are known (Suydam 2000).

MARKING AND TRACKING EIDERS

We studied King Eiders at three locations on the arctic coastal plain of Alaska and captured 100 adult birds (52 females, 48 males) in early June 2002–2005 and late August 2006–2008 by using mist nets erected in ponds on the breeding grounds (Oppel et al. 2009). We captured hatch-year birds as almost fully grown ducklings in late August approximately 5 days prior to fledging. We captured nine ducklings in family groups in the Kuparuk Oilfield (70° 20′ N, 149° 45′ W) in 2006 and a total of 48 ducklings in an aggregated brood at an unnamed lake south of Teshekpuk Lake (70° 26′ N, 152° 34′ W) in 2007 (*n* = 42) and 2008 (*n* = 6). We erected funnel traps along the shoreline and mist-net arrays in shallow water and, using kayaks, herded flightless ducklings into traps or nets.

Following standard surgical methods (Korschgen et al. 1996, Mulcahy and Esler 1999), we equipped each bird with an intra-abdominal satellite transmitter (42 g PTT, approximately 3.5% of body weight, Microwave Telemetry, Inc., Columbia, MD). We released the birds where captured 2 hr after surgery. All birds were handled under the Institutional Animal Care and Use Committee protocol 05–29 of the University of Alaska, Fairbanks. More details regarding the capture, marking, and satellite tracking of these King Eiders was reported by Phillips et al. (2006), Oppel et al. (2008), and Oppel et al. (2009).

All transmitters contained a battery and temperature sensor, and because transmitters were implanted into the bird's abdominal cavity we were able to assess whether a bird was

alive or dead from the temperature the sensor transmitted. We considered a bird dead if the temperature of the transmitter sensor fell below 35 °C for at least two transmission periods. If transmissions ended and the last transmissions indicated that the bird was still alive we considered that bird's encounter history unknown ("censored") for the time after the last transmission (Bunck et al. 1995).

ANALYSIS OF SURVIVAL RATES

We analyzed survival rates of birds captured as ducklings and adults separately. Because the temperature sensor of implanted satellite transmitters allowed us to verify whether an animal was dead or alive we used known-fate models to estimate survival rates (Murray 2006). We used the Kaplan–Meier product-limit estimator in the known-fate-model routine in program MARK (White and Burnham 1999) to estimate monthly survival rates. We used a sine-link function and normal error distribution to generate estimates of regression coefficients and their sampling variances and covariances in MARK. Known-fate models assume that marking does not affect an individual's fate, that fates of individuals are independent, and that censoring is unrelated to mortality (White and Burnham 1999). We excluded four hatch-year females and two adult males from analysis because their failure to migrate and subsequent death suggested that marking may have affected their survival. As all other birds moved away from the site of capture and dispersed widely at sea (Phillips et al. 2006, Oppel et al. 2008, Oppel et al. 2009), we are confident that the assumption of independent fates was met.

We were not able to independently assess whether the assumption that censoring was unrelated to mortality was met in our study. We believe that the assumption was true because most transmitters (91%, $n = 103$) in which transmissions ended while the bird was still alive showed battery voltage drastically declining prior to the last transmission, indicating that a dying battery was the main cause of censoring. Esler et al. (2000) also found censoring to be unrelated to mortality in the Harlequin Duck (*Histrionicus histrionicus*), a species wintering in an environment similar to the King Eider's, further supporting our assumption that the mortality of censored individuals was not higher.

We estimated survival rate on a monthly basis and compared different models to assess what time scale of variation in survival rate was best supported by the data. For birds marked as ducklings we compared the following models: (1) survival rate varying monthly through the first 2 years of life; (2) survival rate varying seasonally in fall (September–November), winter (December–March), and summer (April–August); (3) survival rate varying seasonally during the first year but remaining constant during the second year of life; (4) survival rate constant during the first year and different but constant during the second year of life; and (5) survival rate constant from fledging until return to breeding grounds 2 years later. Because survival rates differing by sex have been described

TABLE 1. Candidate models explaining variation in monthly survival rate of hatch-year and second-year King Eiders, ranked by AIC_c and ordered by the difference in AIC_c for each model in relation to the most parsimonious model (ΔAIC_c).

Model	K^a	ΔAIC_c	w_i^b	Likelihood[c]
S (season_y1 + constant_y2)[d]	3	0.00	0.58	1.00
S (season_y1 × sex + constant_y2)	4	0.65	0.42	0.72
S (year)	2	16.10	0.00	0.00
S (season)	3	16.41	0.00	0.00
S (year × sex)	4	19.65	0.00	0.00
S (season × sex)	6	21.42	0.00	0.00
S (month)	22	26.84	0.00	0.00
S (constant)	1	29.34	0.00	0.00
S (constant × sex)	2	31.13	0.00	0.00
S (month × sex)	44	71.91	0.00	0.00

[a]Number of estimable parameters.
[b]AIC_c model weight.
[c]Evidence ratio.
[d]Minimum $AIC_c = 147.5$.

for hatch-year birds in other sea ducks (Regehr 2003, Boyd et al. 2009), we also investigated whether males' and females' survival rates differed by including models with sex-specific survival parameters at each of the five scales of temporal variation (Table 1). Because the focus of our study was to provide time- and sex-specific estimates of survival parameters, we entered sex as a group variable and coded the parameter-index matrix in program MARK to achieve the desired level of variation among monthly survival estimates.

For adult birds we considered the following three models: (1) survival rate constant, (2) survival rate varying seasonally with different rates for migration and breeding (April–October) and winter (November–March), and (3) survival rate varying monthly. As for hatch-year and second-year birds, we tested for sex-specific survival rates by including sex as a group variable at every level of temporal variation (Table 2).

For each age group we averaged estimates of survival-rate parameters on basis of the best approximating models

TABLE 2. Candidate models explaining variation monthly survival rate in adult King Eiders ranked by AIC_c.

Model	K^a	ΔAIC_c	w_i^b	Likelihood[c]
S (constant)[d]	1	0.00	0.56	1.00
S (constant × sex)	2	1.97	0.21	0.37
S (season)	2	1.99	0.20	0.36
S (season × sex)	4	5.75	0.03	0.06
S (month)	24	28.52	0.00	0.00
S (month × sex)	40	58.52	0.00	0.00

[a]Number of estimable parameters.
[b]AIC_c model weight.
[c]Evidence ratio.
[d]Minimum $AIC_c = 114.0$.

(Burnham and Anderson 2002) and present mean estimates and 95% confidence intervals of real parameter estimates for survival rates at the appropriate time scale.

ANALYSIS OF DISPERSAL RATE

For all second-year birds alive at the beginning of their second spring and summer (May–July 2 years after capture) we assessed whether they returned to their natal site by using the locations provided by the satellite transmitter. We received location data from Service ARGOS and filtered them for unreasonable locations by using the SAS ARGOS filter algorithm with a maximum redundancy distance of 10 km and a travel rate of 60 km hr^{-1} (Douglas 2006). This algorithm selected the best location per duty cycle on the basis of the location class provided by ARGOS and the distance, angle, and rate to previous and subsequent locations (Kenow et al. 2002).

On the basis of the accepted locations, we estimated the distance between the location of original capture and the nearest location during the summer 2 years later. Adult female King Eiders are faithful to breeding sites (Phillips and Powell 2006); we also provide the mean distance that adult females nested away from the lake of capture in the year after they were marked. This information serves as a reference scale of the distances at which females nest away from the lake where they joined the brood-rearing aggregation that provided the hatch-year birds in our sample. We calculated the proportion of all second-year birds returning to their natal site as the number of birds recorded near the lake where they were captured, divided by the total number of birds of that age group alive and actively transmitting at that time. We considered second-year birds to have dispersed to another breeding area if they were recorded on land within the breeding range of the King Eider (Suydam 2000). We defined a nesting attempt as a period of >10 days between mid-June and mid-July when the bird was stationary within the known breeding range (Petersen et al. 2006).

RESULTS

Of 53 marked hatch-year birds surviving the period immediately after capture (25 females, 22 males, 6 of undetermined sex), 17 died during the time that their transmitter was active (females 40%; males 27%). We excluded four hatch-year females that did not move >10 km from the capture location and died within 6 weeks after implantation. These four females were on average >200 g lighter at capture (body mass 1015 ± 230 g) than all other hatch-year birds (1230 ± 150 g, $W = 33.5$, $P = 0.035$). For adults, we recorded six deaths out of 98 marked birds surviving the post-capture period (females 6%, $n = 52$; males 7%, $n = 46$). We excluded two males from analysis that died <3 weeks after transmitter implantation.

The annual survival rate in the first year of life (0.67, 95% CI: 0.48–0.80, $n = 49$) differed markedly from that in the second (1.0, $n = 21$) and was best described by seasonally varying survival rates in the first year and a constant survival

rate in the second year (Table 1). Confidence in estimates of survival rate during the second year is low, however, because we did not record any mortalities and therefore lacked the data to estimate survival rates. We also found support for the model assuming that males' and females' survival rates during the first winter differed (Table 1). According to this model, males' mean survival rate during the first winter was approximately 12% higher than that of females. For hatch-year females, monthly survival rates during the winter months (December–March, 0.94, 95% CI: 0.89–0.97) and during the first fall (September–November, 0.94, 95% CI: 0.90–0.96) were similar, whereas those of hatch-year males were slightly higher during winter (0.97, 95% CI: 0.91–0.98) than during fall (0.94, 95% CI: 0.90–0.96).

For adults, the model with monthly survival rate constant over the year received the most support from our data (Table 2). There was little evidence that adults' survival rates differed by season, and monthly survival rates in winter (0.98–1.0) were indistinguishable from those during migration and breeding (0.98–1.0). Likewise, we found little support for a difference in annual survival rates between adult females and adult males (Table 2). On average, adults' annual survival rate (0.94, 95% CI: 0.86–0.97, $n = 98$) was 1.4 times higher than that of hatch-year birds but appeared to be very similar to that of second-year birds.

Twelve second-year birds (9 females, 3 males) provided reliable location information during their second spring and summer. Among the females, eight (88%) were recorded on the tundra within 25 km of the lake on which they were captured as ducklings 2 years earlier (Fig. 1, Table 3). The remaining female was recorded in lagoons and river deltas along the coastline of the Chukotka Peninsula, one of the King Eider's most important molting and wintering areas (Phillips and Powell 2006, Phillips et al. 2006, Oppel et al. 2008). None of the 2-year-old females appeared to nest, as suggested by late arrival (late June to mid July, Table 3), early departure (mid-July), and roaming while on the breeding grounds. None of the three males was recorded on land; they remained at sea during their second summer, with one male migrating to Siberia (Fig. 1). Of the adults, all of the females ($n = 28$) but only one of the males ($n = 26$) returned to breeding sites in Alaska in the year after they were captured there (Phillips and Powell 2006, Oppel et al. 2008). The adult females captured together with ducklings at the lake where they reared their broods returned to breeding areas on average 8 km (range 0.5–16 km) away from the lake in the year following capture ($n = 12$).

DISCUSSION

Our results offer the first estimates of annual survival for hatch-year and adult King Eiders and show that survival is on average 20–30% lower in hatch-year birds than in adults. After surviving their first winter, second-year King Eiders appeared to suffer no higher mortality rates than adults. We
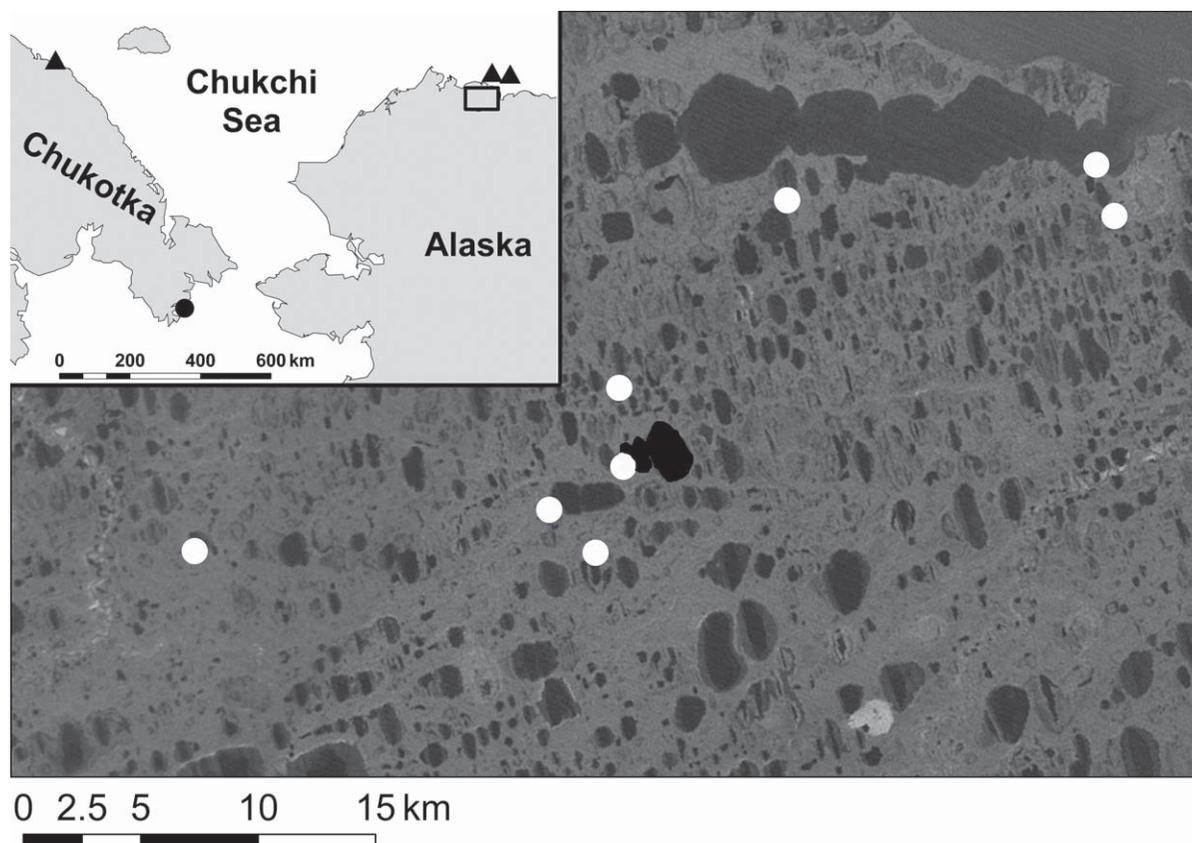
FIGURE 1.   Infrared satellite image showing locations of second-year female King Eiders (white circles) during their second summer in June and July 2009 closest to their site of origin. The lake where individuals were captured as flightless ducklings in August 2007 is shown in black. Inset map shows location of one female (circle) and three males (triangles) that remained at sea during their second summer. The location of the natal area is indicated by the black rectangle.

TABLE 3.   Dispersal distances of individual second-year King Eiders between the lake in northern Alaska where they were caught as ducklings and the nearest location where they were recorded by satellite transmitters during the summer 2 years later.

Sex	Date	Distance to brood lake (km)
female	12 June	0
female	27 June	3
female	27 June	5
female	4 July	6
female	12 June	12
female	30 June	21
female	29 June	21
female	13 July	22
female	23 June	1036
male	23 June	100
male	25 June	108
male	30 June	1208

also found that >85% of second-year females returned to the breeding area from where they originated. Under the assumption that those females will breed at that location in the future, our results indicate high natal philopatry in female eiders.

For most sea ducks, rates of hatch-year survival are unknown. The model-averaged mean estimate of hatch-year survival of King Eiders during our study period was 26% lower than the long-term average survival rates of hatch-year female Common Eiders (*S. mollissima*) from an island colony in the Dutch Wadden Sea (Kats et al. 2007). That study found marked annual variability, with survival rates similar to those we found in 2 of the 11 years of the study but >0.93 during the remaining 9 years (Kats et al. 2007). We could not explore annual variation in hatch-year survival rates because most of our hatch-year birds were marked in a single year (2007). It is possible that the birds at that Dutch colony had higher survival rates in most years because of their nonmigratory lifestyle and more benign environment than the King Eiders we studied.

In Canada, Boyd et al. (2009) found that apparent survival of hatch-year Barrow's Goldeneyes (*Bucephala islandica*), estimated by mark–recapture, was much higher for females (0.68)

than for males (0.35). Using radio-telemetry, Regehr (2003) found that during the six winter months in Prince William Sound, Alaska, the local survival rate of hatch-year female Harlequin Ducks (0.84) was higher than that of hatch-year males (0.58). In the King Eider, by contrast, we did not find that females had higher survival rates during the first winter than males but rather that females' survival may have been slightly lower. In sea ducks, males tend to be more mobile than females (Phillips and Powell 2006, Pearce and Petersen 2009). Therefore, obtaining good estimates of true survival from recapture or resighting data is inherently more difficult for males than for females. Previous studies based on band records or local radio-telemetry may have underestimated male survival because of permanent emigration from the study areas (Regehr 2003, Robertson 2008, Boyd et al. 2009).

Capture-related mortality among the hatch-year birds we studied was limited to females, and the four females that died prior to migration were about 200 g lighter at capture than the remaining birds. While we cannot evaluate whether mortality was a consequence of capture and surgery, it is possible that lighter birds suffer stronger effects from implantation. Sexual size dimorphism is generally pronounced in sea ducks (Livezey 1995), and male King Eiders are usually larger and heavier than females (Suydam 2000); when we captured them, however, hatch-year male King Eiders (mass = 1280 ± 110 g) were not heavier than hatch-year females (1210 ± 150 g, $W = 241.5$, $P = 0.14$).

Survival of females lower than that of males has also been found in eider ducklings (Swennen et al. 1979, Lehikoinen et al. 2008b), possibly as a result of a difference in size (Anderson and Alisauskas 2001) or higher susceptibility of females to disease and parasites (Bize et al. 2005). Although the biological mechanism of hatch-year mortality differing by sex is unknown, the slightly elevated mortality of females during the pre- and post-fledging periods could account for a surplus of adult males in populations of waterfowl (Blums and Mednis 1996, Donald 2007, Lehikoinen et al. 2008a).

In contrast to those of hatch-year birds, survival rates of male and female adult King Eiders did not differ. However, our sample size of recorded mortalities was small, so the power to detect differences between the sexes was low. Annual survival rates estimated from studies of banded adult Common Eiders range from 0.82 to 0.98 (Kats et al. 2007, Wilson et al. 2007, Hario et al. 2009). Our estimates and confidence intervals of adult survival rate are similar to that range and not confounded by permanent emigration from a particular study area. This result highlights the value of estimates of survival rates derived from satellite telemetry, and we encourage researchers using this technology for tracking migration to estimate survival rates and provide critical components for population models.

Equally important for future population models is the apparent lack of nesting by second-year King Eiders, which agrees with data from other sea ducks found to breed first at the age of 3 years (Boyd et al. 2009). We recorded arrival times of 2-year-old females on breeding grounds up to 6 weeks after adults (Oppel et al. 2008, Oppel and Powell 2010), indicating that females returning to their natal area in their second summer may have been prospecting. Prospecting by immature birds is known in cavity-nesting sea ducks (Eadie and Gauthier 1985, Zicus and Hennes 1989) and colonial sea birds (Halley et al. 1995, Dittmann and Becker 2003) and may influence future choice of a breeding area. While information on the precise time at which King Eiders enter the breeding population is lacking, future population models should assume a minimum age of 3 years as the age of first reproduction.

Despite the lack of evidence for breeding in their second year, most females returned to their site of origin, which suggests that natal dispersal of females may be very low. The King Eider has little spatial genetic structure, despite distinct wintering areas in the North Atlantic and Pacific oceans (Pearce et al. 2004). Possible mechanisms for the lack of a spatial genetic structure include insufficient time for genetic divergence (Pearce et al. 2004), diffuse migratory connectivity of adult birds leading to sufficient gene flow between populations wintering in the Atlantic and Pacific (Mehl et al. 2004, Oppel et al. 2008), or dispersal of second-year birds to breeding areas away from their natal area. Our study provides some evidence that natal dispersal of females may not contribute much to genetic mixing, and suggests that dispersal of both adult and subadult males may account for most nuclear gene flow among geographic areas.

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