

BROOD ECOLOGY AND
POPULATION DYNAMICS
OF KING EIDERS

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By

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ABSTRACT

Birth and death processes and the extent of dispersal directly affect population dynamics. Knowledge of ecological factors that influence these processes provides insight into natural selection and understanding about changes in population size. King eiders (*Somateria spectabilis*) breed across the arctic region of North America and winter in polar oceanic waters of the western and eastern regions of the continent. Here I studied a local population of King Eiders at Karrak Lake, Nunavut, where I used analysis of naturally-occurring stable isotopes (^{13}C , ^{15}N) from feathers, in conjunction with banding data, to investigate the extent of dispersal among winter areas and the influence of winter area on subsequent breeding. In addition, I used capture-mark-recapture methods to (1) investigate the relative contributions of survival and recruitment probabilities to local population dynamics, and (2) to test hypotheses about the influence of specific ecological factors on those probabilities or their components, e.g., nest success, duckling survival. Isotopic data suggested that female King Eiders were not strongly philopatric to wintering areas between years. Individuals that wintered in western seas initiated nests earlier and had slightly larger clutch sizes during early nest initiation relative to females that wintered in the east. Female condition during incubation did not vary by winter area.

Female King Eiders of known breeding age were at least 3-years-old before their first breeding attempt. Age of first successful breeding attempt did not appear to be influenced by body size. However, after reaching breeding age, larger females apparently experienced greater breeding propensity. Adult survival rate (1996-2002) was estimated as 0.87 and recapture probabilities varied with time and ranged from 0.31 to 0.67. There is no evidence of survival advantages related to larger size. Population growth for this local study area was high, estimated at 20%/year with larger females contributing more to the population growth than smaller females. With continued population growth, density-dependent effects on components of recruitment appeared to

emerge; the proportion of the female population that nested successfully declined with increasing

population size. The probability of breeding successfully did not correlate with Mayfield estimates of nest success.

To gain insight into King Eider brood ecology I, respectively, monitored 111 and 46 individually-marked ducklings from broods of 23 and 11 radio-marked King Eiders during 2000 and 2001. Total brood loss accounted for 84% of all duckling mortality with most brood loss (77%) less than 2 days after hatch. Estimated apparent survival rates of ducklings to 22 days of age were 0.10 for those that remained with radio-marked females, 0.16 for all ducklings, including those that had joined other broods, and 0.31 for broods. Ducklings brooded by larger females experienced higher survival than those brooded by smaller females, and ducklings that hatched earlier in the breeding season survived at higher rates. Overland brood movements of 1 km or more occurred in both years, and survival was greatest for ducklings that dispersed from Karrak Lake to smaller ponds than on Karrak Lake itself, the central nesting area. Estimates of duckling survival, combined with relative contributions to the population by adults, suggest that ecological factors such as body size can influence population growth. Furthermore, low duckling survival and delayed maturity, emphasize the need of high adult survival for population growth to occur. These data, in combination with evidence of dispersal among wintering areas have helped contribute to a broader understanding of North American King Eider demographics.

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1. GENERAL INTRODUCTION

1.1 POPULATION DYNAMICS AND THE INFLUENCE OF LIFE HISTORY ATTRIBUTES

The aim of population ecology is to understand which factors are most influential to life history traits (i.e., birth, death, dispersal, and migration) and how these factors affect changes in population size over time and space. Knowledge about ecological processes that affect population size is essential to ultimately understand *why* populations change through time. Research from this thesis was motivated by the desire to gain a greater understanding of such factors that might influence population change in King Eiders, a sea duck that occupies the northern extreme of the waterfowl continuum. Understanding life history traits for species that experience different selection pressures help to provide the ecological framework to better understand how various life histories have evolved.

Inferences about population ecology are influenced by the spatial scale of study. Changes in population size are primarily determined by birth and death (meta-population level), or they can be defined by smaller subunits (local or sub-populations) where immigration and emigration directly affect local population size (Endler 1977, Slatkin 1987, Berryman 2002). Therefore, a convenient metric (λ) for characterizing temporal change in spatially-defined populations is the number of individuals in the population (N) from one year (i) to the next ($i+1$), as expressed by $\lambda = N_{i+1}/N_i$. Such changes in population size, $N_{t+i} = \lambda_i N_i$, result from the sum of population additions, through births (B_i) and immigration (I_i), minus the number of losses through death (D_i) and emigration (E_i). The number of births and deaths from one year (i) to the next ($i+1$) depend on the number of individuals (N_i) alive in the population at time i . Consequently, these processes are most often expressed as per capita change in numbers; $B_i = (b_i)(N_i)$, $D_i = (d_i)(N_i)$, $E_i = (e_i)(N_i)$, and $I_i = (g_i)(N_i)$ where b_i , d_i , e_i , and g_i equal the change in numbers between time i and $i+1$, resulting from birth, death, emigration and immigration rates,

respectively (Williams et al. 2002). Accordingly, the annual rate of population change, λ_i , equals the sum of the four per capita rates, $b_i + d_i + e_i + g_i$.

If research attention is focused on a single subpopulation without knowledge about other subpopulations, as in this study, then permanent emigration from the focal subpopulation is confounded with death rate (Nichols 1992), and birth rates confounded with immigration (Nichols et al. 2000). Sampling marked individuals through time allows for unbiased estimates of individual vital rates and their contributions to λ because this approach also simultaneously estimates detection probability (p), or the probability that an individual is observed on a study area given that it is present (Nichols 1992, Nichols et al. 2000). Unless all individuals are observed ($p_i = 1$), estimation of p is necessary to calculate both population size and individual vital rates. For example, estimation of population size requires a count (C) of the number of individuals in a given area. However, a complete count of all free-ranging individuals present is seldom possible because some individuals are inevitably present but undetected, i.e., $p_i < 1$. If detection probabilities remained constant through time, counts could serve as an index to population size. However, p_i generally varies with environmental conditions, animal behavior, and among observers (Nichols 1992, MacKenzie and Kendall 2002). Therefore, unbiased estimates of population size (N) must account for changes in both, C and p , as expressed by: $N = C / p$.

Estimates of true survival require the recovery of marked dead individuals (Seber 1970, Brownie et al. 1985) because without these recoveries, mortality is confounded with permanent emigration. When marked recoveries are not possible, apparent survival, ϕ_i , can be estimated in lieu of true survival, where ϕ_i is the product of the probability that an individual survives (S) and the complement of permanent emigration, or philopatry (F) to the study area (Cormack, 1964, Jolly 1965, Lebreton et al. 1992). Fundamentally, without marked individuals that are re-encountered through time, estimates of p remain unknown and all estimates of vital rates will likely be biased. When based on mark-recapture data, ecologically-based variation in vital rates can be estimated, leading to knowledge of processes relevant to population change. These changes can affect any portion of the life-cycle (Figure 1.1).

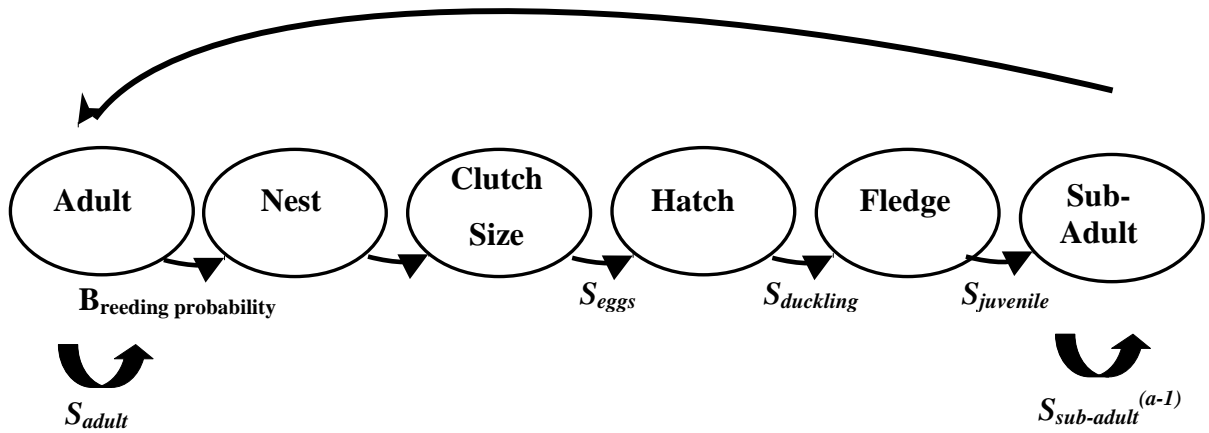


Figure 1.1. Conceptual life-cycle for King Eiders, where S = probability of survival and a = age at first breeding. *In situ* recruitment equals the product of all components of the life cycle.

In long-lived species, adult survival has the greatest impact on population size because adult survival ultimately determines how often individuals will breed over a lifetime (Rockwell et al. 1997, Nichols et al. 2000, Crone 2001). However, recruitment is more variable than adult survival, especially in long-lived species, and can often have the greatest influence on fluctuations in population size (Coulson 1984, Gaillard et al. 1998, Cooch et al. 2001). Differential variation in contributions of adult survival and recruitment to population growth are consistent with *Fisher's fundamental theorem*, which states that an increase in fitness (i.e., greater contribution to population growth) is equal to the genetic variance (as demonstrated by greater fluctuations) of fitness at that time (Falconer and Mackay 1989).

Current information about factors that influence survival, recruitment and resulting population dynamics of ducks are primarily from relatively short-lived and readily hunted species such as Northern Pintails *Anas acuta* (Flint et al. 1998), Mallards *Anas platyrhynchos* (Dufour and Clark 2002, Hoekman et al. 2002), and Canvasbacks *Athya valisineria* (Anderson et al. 1997, Anderson et al. 2001). Far less is known about estimates of such population parameters in sea ducks (tribe Mergini), a group characterized by higher adult survival and delayed maturity. Discrepancies in information available for these groups of species are due to (1) use of habitats by prairie-nesting waterfowl that are relatively easily accessed by researchers, (2) early breeding at one to two years of age that offers a continuous opportunity to collect data from pre-fledgling to adult stage, and (3) reliable band returns from hunter-killed birds that allow for the estimation of true survival (Barker 1997).

1.2 STUDY SPECIES

King Eiders (*Somateria spectabilis*) breed across the arctic region of North America and winter in northern waters of the western and eastern regions of the continent. Unlike most avian species, King Eiders remain at polar latitudes throughout the annual cycle (Bellrose 1976) where they rely heavily on stored nutrients during both the non-breeding (Frimer 1994) and breeding periods (Kellett and Alisauskas 2000). King Eiders exhibit seasonal monogamy (Suydam 2000), with pairs forming before spring migration occurs (Parmelee 1967).

Theoretically, larger individuals should show advantages in thermoregulation, proportionally greater storage of fat reserves, and greater fasting endurance relative to smaller conspecifics (Kendeigh 1969, Kendeigh 1970, Fretwell 1972, Calder 1974). Thus, King Eiders represent an appropriate species for studying the interplay between nutrition, body size, survival and recruitment because they are near the extremes of the waterfowl continuum in severity of climate and reliance on nutrient reserves. In addition, King Eiders have high adult survival and do not breed until they are at least 3 years old (this study). Harsh polar environments may create a threshold, where only older females with ample nutrient reserves are able to breed (Kellett and Alisauskas 2000). King Eiders have a relatively small clutch size ($\bar{x} = 5.4$; Kellett and Alisauskas 1997) and arctic environments produce boom and bust years for reproduction (Coulson 1984; Gaillard et al. 1998). Therefore, recruitment is likely to rely heavily on high adult survivorship to produce enough young over a lifetime for population growth to occur (see Crone 2001).

King Eiders that breed in North America are thought to be from two separate populations, defined by their use of discrete wintering areas (Atlantic and Pacific; Suydam 2000). However, recent analyses of King Eider population genetics show no phylogeographic structure, suggesting that regular gene flow occurs among these populations (Pearce et al 2004). The extent and timing of population mixing are unknown. Because population estimates are based on count surveys at key migration corridors (Suydam et al. 1997), if individuals are not philopatric to wintering areas and the respective migration corridors, this would likely bias population estimates and population trends. Importantly, King Eider populations appear to have declined (Suydam et al. 1997) despite high probability of annual survival among adults (~ 0.87 , this study) and high nest success (50%; Moitoret et al. *in* Suydam 2000, 48.5%; Kellett et al. 2003). Juvenile survival may, therefore, be a limiting factor to population growth (Coulson 1984), emphasizing the potential importance of the brood-rearing period to population dynamics.

I set out to estimate and test ecological predictions about population dynamics, recruitment and survival in a local population of King Eiders nesting at Karrak Lake, Nunavut, in Canada's central arctic. I was particularly interested in the relative

contributions of survival and recruitment probabilities on local population dynamics, and on ecological factors that influence those probabilities or their components, i.e., duckling survival.

1.3 STUDY OBJECTIVES

To define the local King Eider population of study, in reference to the North American King Eider population(s) (Suydam 2000), and to investigate the extent of movement among wintering areas, I combined capture-mark-recapture techniques with analysis of naturally occurring stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). Isotope analysis allowed me to delineate the local population by wintering area (western or eastern seas)

In this thesis, I also address the influence of recruitment toward dynamics of this local population of King Eiders. Recent techniques of reverse-time capture models (Pradel 1996, Nichols et al. 2000) offer opportunities to estimate and assess relative contributions of survival and recruitment to changes in population size. I used a long-term data set to model vital rates that contributed to King Eider population growth. I also consider some aspects of variation in annual survival of breeding King Eider females. Specifically, I estimated the relationship between body size and survival probability. However, most of my research was focused on the influence of ecological variables on specific components of recruitment, with special attention to sources of variation in adult and duckling survival. Many aspects of annual variation in nesting success have been addressed elsewhere (Kellett and Alisauskas 1997, 2000, Kellett et al. 2002), but I used a novel approach for comparing breeding success through use of multistate analysis. I also estimated the survival of ducklings before fledging using radio-telemetry, and examined ecological sources of variation in such survival probabilities.

The specific objectives of this study were:

1. Delineate eastern and western populations of King Eiders using naturally occurring $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope ratios.
2. Estimate repeatability and heritability of external morphology in King Eider females.
3. Estimate female survival and recruitment into the breeding population, in relation to body size.

4. Investigate reproductive patterns of breeding females to determine if the probability of successful nesting affects the breeding success during the following year.
5. Investigate patterns of female condition during multiple years.
6. Investigate factors that may influence duckling and brood survival.

2. TO WINTER EAST OR WEST? HETEROGENEITY IN WINTER PHILOPATRY IN A CENTRAL ARCTIC KING EIDER POPULATION

2. 1 INTRODUCTION

Extent of dispersal defines the spatial boundaries of a population (Berryman 2002). Therefore, estimates of philopatry, or the probability that individuals use the same area in sequential years, are necessary to understand population boundaries. When pairs form on breeding areas alone, the amount of emigration influences estimates of breeding philopatry. However, pair formation by waterfowl occurs on wintering areas (Rohwer and Anderson 1988), so philopatry to both breeding and wintering areas can influence mixing between areas (Cooke et al. 1975, Rockwell and Barrowclough 1987, Cooke et al. 2000). Shifts in areas used by birds can have profound effects on interpretations about population trends and overall demography because changes in area use could be misinterpreted as changes in population size if inferences are drawn from unmarked birds (Mosbech and Boertmann 1999, Suydam et al. 2000).

Linkage between breeding and wintering areas is also important for understanding population dynamics because weather and habitat conditions encountered by birds during the winter can cause severe mortality (Fournier and Hines 1994, Dierschke 1998) or influence subsequent breeding success (Alisauskas 2002). Individuals from the same breeding area often share wintering areas, so entire cohorts could be affected by ecological factors on either of these areas (Esler 2000). Thus, knowledge of linkages between wintering and breeding areas will improve understanding of population biology over a species' annual cycle (Webster et al. 2002).

King Eider (*Somateria spectabilis*) populations in North America are presumably of two distinct groups that winter in either Northern Atlantic or Northern Pacific regions (Suydam 2000). Lack of genetic differentiation between these eastern and western populations suggests that these populations may interbreed (Pearce et al. 2004). Band

recoveries from hunter-killed birds indicate that individuals from the Pacific and Atlantic populations share the same breeding grounds within the central Arctic (Bird Banding Laboratory, Canadian Wildlife Service, Quebec, Canada, unpubl. data). However, the extent and timing of population mixing remain unknown.

Previous isotopic analyses of zooplankton indicated an east-west gradient in the incidence of ^{15}N and ^{13}C in the arctic marine environment of North America, with the Bering and Chukchi Seas more enriched relative to the arctic waters of eastern North America (Dunton et al. 1989, Schell et al. 1998). Because eiders grow body feathers on their wintering areas (Suydam 2000), and isotopic ratios within feathers reflect the food webs where they were grown (Hobson 1999), stable-isotope ratios are useful in identifying the wintering locations of King Eiders. Naturally occurring stable isotopes from King Eider head feathers have proven successful in stratifying western and eastern winter King Eider populations based on known winter origin (99% and 94% correct classification for western and eastern seas, respectively; Mehl et al. 2004). Head feathers provided the best discrimination over other feather tracts (Mehl et al. 2004). Here my objective was to use naturally occurring stable isotope values from head feathers of individually marked female King Eiders to evaluate extent of winter philopatry. Secondly, to understand if winter choice of influenced breeding biology, I tested whether nest initiation date, clutch size, and body condition differed for individuals that wintered in Pacific compared to Atlantic waters. This study was motivated by apparent declines in King Eider populations (Suydam et al. 2000) and the need for a better understanding of linkages between breeding and wintering areas.

2.2 METHODS

2.2.1 Feather Collection and Isotopic Analysis

During 2001 and 2002, I systematically searched for King Eider nests on islands in Karrak and Adventure Lakes ($67^{\circ}14'\text{N}$, $100^{\circ}15'\text{W}$; Figure 2.1), about 60 km south of Queen Maud Gulf, Nunavut, Canada. These islands support one of the highest known densities of breeding King Eiders (Kellett et al. 2003; see Kellett 1999 for detailed descriptions of the study area). I began nest searches in mid-June and revisited nests



Figure 2.1 Study area of Karrak Lake and Adventure Lakes, Nunavut, Canada, where incubating female King Eider feathers were collected for stable isotope analysis during 2001 and 2002. King Eiders wintered in either the northern Pacific (Chukchi or Bering Sea) or northern Atlantic, including the Labrador Sea.

every 4 to 7 days to determine clutch size, egg attrition rate, and nest fate. I calculated nest initiation dates by backdating from known laying dates, or from incubation stages estimated by candling eggs (Weller 1956), assuming an incubation length of 23 days (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973). I captured nesting female King Eiders during late incubation (≥ 16 days incubation) using either mist nets placed over nesting females or with self-triggered bow nets. I marked females with standard Canadian Wildlife Service–U.S. Fish and Wildlife Service leg bands and weighed each with a Pesola spring scale to the nearest 10g. I also recorded the following measurements (twice for each female): head and tarsus length using dial calipers to the nearest 0.1 mm, and flattened wing chord using a flat ruler (Dzubin and Cooch 1993). Mean measures were used to obtain indices of size. I also collected 3–10 feathers from the crown, and stored feathers from each bird in separate paper envelopes.

Feathers were rinsed in a 2:1 chloroform:methanol solution and allowed to air dry. Weighed (1 mg), dry feather samples were then placed into tin cups and each was combusted in a RoboPrep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific, Crewe, UK; Hobson and Schell 1998). All stable isotope values are reported in δ notation relative to Pee Dee Belemnite (PDB) and atmospheric air standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements, respectively. Measurement precision, based on thousands of measurements of albumen lab standard, is estimated to be $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ measurements and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ measurements.

2.3 STATISTICAL ANALYSES

I classified individuals as wintering in eastern or western areas using predictive equations derived from quadratic discriminant function analysis (QDFA) based on isotope-ratios of eider feathers of known winter origin (Mehl et al. 2004). Using chi-square analysis, I investigated possible local breeding segregation by testing if observed nesting locations (islands and lakes) of King Eiders that wintered in eastern and western seas differed from expected ratios. I grouped individuals by year and assessed the proportion of individuals that were estimated to have wintered in eastern or western seas during the preceding winter. I then compared those results with the proportion of

individuals that wintered in eastern and western seas, as indicated by band recoveries (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data), to determine possible differences in hunting pressure between wintering areas. I calculated 95% CI for wintering-area classifications based on random binomial variance (Zar 1999). I assessed the proportion of individuals that returned to the same area during consecutive winters based on breeding females captured in both 2001 and 2002, and from band recoveries for birds whose previous year's wintering area I had inferred from stable-isotope analysis. Estimates of philopatry were contingent upon classification probabilities in both 2001 and 2002. When an individual was judged to have switched to an alternate wintering site during the second year, I calculated a classification probability for the switch among wintering areas as the product of both annual winter-area classification probabilities for that individual.

I estimated (1) body condition during incubation, (2) nest initiation date, and (3) clutch size for females classified as having wintered in eastern compared to western seas during the preceding winter. I used principal components analysis (PCA) with mean body measurements to establish an index of female size (Rising and Somers 1989, Alisauskas and Ankney 1990). I regressed eider weight on the size index (PC1), incubation stage at capture, and nest initiation date to adjust these parameters (Kellett and Alisauskas 2000) and then used residuals as an index of body condition (Weatherhead and Brown 1996). I tested for differences in female condition and nest initiation date using separate ANOVAs, by comparing models with single effects of year and wintering area, an additive model with year and area effects, and a global model that included the year * wintering area interaction. I confirmed that variances associated with nest initiation dates and body condition were normally distributed, based on the most saturated model using the Shapiro-Wilk statistic (Zar 1999). I chose the most parsimonious of four candidate models for each response variable using Akaike's Information Criterion corrected for sample size (AIC_c ; Akaike 1985, Burnham and Anderson 1992). I did not correct for overdispersion as each observation was based on a separate individual female and therefore not likely affected by overdispersion (Burnham and Anderson 2002). I estimated mean condition and nest initiation date, along with associated 95% CI adjusted for year and wintering area, using least-squared means in

PROC GLM (SAS Institute 1996).

I compared clutch size between years and wintering area using an analysis of covariance (ANCOVA), with nest initiation date as a continuous covariate. I tested for normal distribution of variances associated with clutch size using the most saturated model with the Shapiro-Wilk statistic (Zar 1999). Log-transformed clutch size resulted in normally distributed variances and was used for all clutch size analyses. Clutches with more than six eggs are likely the result of nest parasitism (Anderson 2000), so I considered two sets of ANCOVA models, each with eight candidate models: one set that included all clutch sizes and another that included only clutches of less than seven eggs. Candidate models included interactions of nest initiation date * year, wintering area * year, and nest initiation date * wintering area. I chose the most parsimonious models using AIC_c (Akaike 1985, Burnham and Anderson 1992), and estimated 95% CI of mean clutch size adjusted for nest initiation date, year, and wintering area during early, middle, and late nest initiation dates using the ESTIMATE option in PROC GLM (SAS 1996). Estimates of early, middle, and late nest initiation date included only those dates when individuals that wintered in both areas nested simultaneously. I did not compare estimates of nest success for birds between wintering areas because capture of individuals and subsequent acquisition of feather samples was only possible in late incubation periods, after which most nest failures had already occurred (Kellett et al. 2003).

2.4 RESULTS

2.4.1 Delineation of Breeding Population by Winter Area

I collected feathers from 85 and 82 female King Eiders during 2001 and 2002, respectively. Based on QDFA classification, about 69% (117 of 167; 95% CI = 63–77%) of these individuals wintered to the west, in Pacific waters, and 31% (51 of 167; 95% CI = 24–38%) wintered to the east, in Atlantic waters. The estimated proportion of individuals wintering to the west was slightly higher during 2002 (73%; 60 of 82; 95% CI = 52–82%), relative to 2001 (66%; 56 of 85; 95% CI = 56–77%). Precision around the classification estimates was greater during 2002, with 87% (71 of 82) of all individuals having >90% probability of wintering in the respective eastern or western

areas, compared with 71% (60 of 85) of individuals with >90% probabilities during 2001 (Figure 2.2). In contrast, about half (56%, 5 of 9) of hunter-killed King Eiders (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data) marked at Karrak Lake were recovered in eastern wintering areas. Wintering area did not appear to influence local breeding locations, as King Eiders at Karrak Lake nested among islands ($\chi^2_{25} = 23.0, P = 0.58$) and lakes ($\chi^2_1 = 0.9, P = 0.35$) independently of wintering area.

2.4.2 Winter Philopatry

Based on stable isotope values from feathers of individuals captured during both 2001 and 2002 ($n = 20$), I calculated that six females may have switched between eastern and western wintering areas among years, and that at least four females probably did so (Table 2.1). Classification probabilities for wintering area varied among years and individuals (Table 2.1). I collected feather samples from four of eight King Eiders banded at Karrak Lake that were eventually shot by hunters. Based on classification results from isotope data, three of these individuals were shot in the same wintering area as they predicted to have wintered during the previous year. The remaining individual was classified as wintering in the west during 2001 (91% classification probability) but was shot near the Greenland coast the following winter. Collectively, these two data sets indicated that up to 29% (7 of 24; 95% CI = 11–47%) of King Eiders switched among wintering areas. Only 13% (3 of 24; 95% CI = 0–26%) of females had >80% classification probability of having switched between western and eastern wintering areas. I collected feather samples from only one mother-daughter pair and both individuals were classified as having wintered in the east during the previous winter (79% and 91% classification probability, respectively).

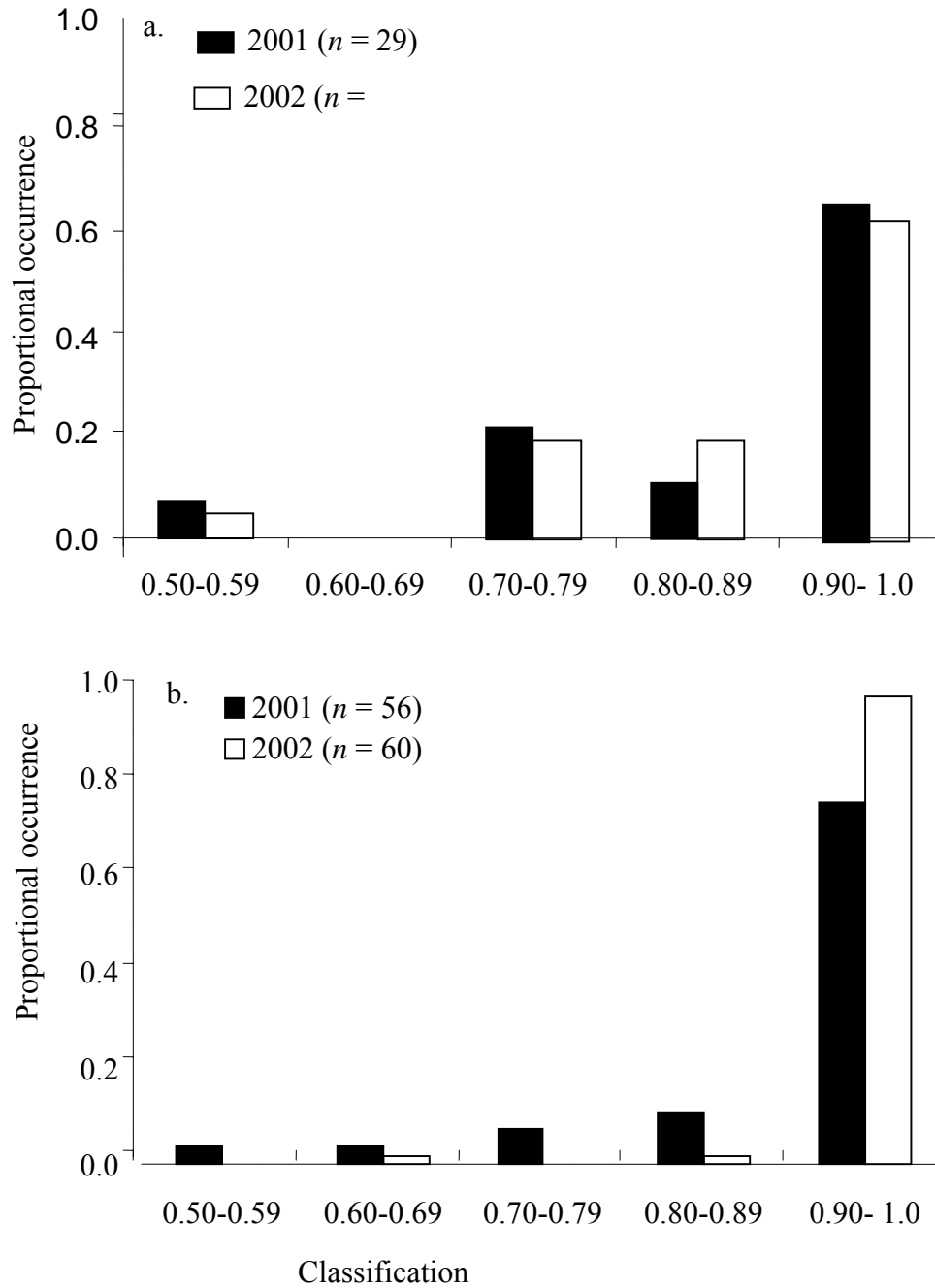


Figure 2.2 Proportional occurrence of classification probabilities for adult female King Eiders breeding at Karrak and Adventure Lakes, Nunavut, Canada, and wintering in the eastern (a) and western seas (b) during 2001 and 2002. Classification probabilities were based on predictive equations derived from Mehl et al. (2004) and reflect the probability that an individual King Eider wintered in that region.

Table 2.1 Based on 20 female King Eiders analyzed in both 2001 and 2002, six were classified as wintering in different areas among years. Differing degrees of classification probability among individuals and between years yielded variable confidence but at least four eiders appeared to have a high likelihood of switching wintering areas between years. Classification was based on quadratic discriminant function analysis of stable-isotope ratios for female eiders nesting at Karrak Lake, Nunavut, Canada. Classification probability of switching among wintering areas was defined as the product of annual winter classification probabilities.

Individual	2001		2002		Classification probability of switching among winter areas
	Classification Probability	Winter Location	Classification Probability	Winter Location	
1	0.93	East	0.95	West	0.88
2	0.88	West	0.94	East	0.83
3	0.78	East	0.87	West	0.68
4	0.66	West	0.89	East	0.59
5	0.56	West	0.73	East	0.41
6	0.76	West	0.51	East	0.39

2.4.3 Affects of Winter Area on Breeding Performance

PC1 accounted for 51% of variation in structural size, with loadings of 0.76, 0.52, and 0.43 for head, tarsus, and wing lengths, respectively. Size accounted for half of the variation in body mass ($F_{3,168} = 76.7$, $r^2 = 0.50$, $P < 0.01$). AIC_c model weight (0.53) suggested that female condition varied more between years than between wintering areas (Table 2.2) but the 95% CI of all four estimates of relative size overlapped (mean PC1 scores [95% CI]: 2001, western area: -5.1 [-25.2 to 15.1]; eastern area: -8.2 [-36.5 to 20.1]; 2002, western area: 7.8 [95% CI = -11.6 to 27.3]; eastern area: -7.8 [-39.7 to 24.1]).

Nest initiation date varied by both winter location and year (Table 2.3). During 2002, nest initiation date was 3.4 days earlier for females that wintered to the west (95% CI [Julian dates]: western area: 169.3 – 171.7 ; eastern area: 171.9 – 175.9), with overlapping confidence intervals during 2001 (western area: 169.3 – 171.8 ; eastern area: 168.8 – 172.4). When I included all clutches in analyses, models showed support for clutch-size variation among wintering area, timing of nest initiation, and years (Table 2.4). Clutch size was greater for females that wintered in the west, but these differences existed only during the early initiation period when nest parasitism (i.e., clutches with >6 eggs) was more frequent (Figure 2.3). Estimated mean clutch size and associated 95% CI adjusted for nest initiation date during early, middle, and late nest initiation dates are shown in Figure 2.3. When considering only clutch sizes with <7 eggs, clutch size models supported similar effects of year, timing of nest initiation, and wintering area, with support for nest initiation * year and nest initiation date * winter location ($\Delta AIC_c < 2$; Burnham and Anderson 1992; Table 2.5). Estimated mean clutch sizes and 95% CI for clutches smaller than 7 eggs, adjusted for nest initiation date, are shown in Figure 2.3 for each of the three nest initiation categories.

2.5 DISCUSSION

Use of stable-isotopic measurements from head feathers of King Eiders offer a useful method of distinguishing wintering areas (Mehl et al. 2004). When combined with local banding efforts, this technique provided insight into winter philopatry not otherwise

Table 2.2 Akaike's Information Criterion (AIC_c) values for all candidate models explaining condition of incubating female King Eiders. Models are based on ANOVA with female condition as the dependent variable and winter location (determined from stable-isotope analysis) and year as independent variables. Values are based on 163 females nesting at Karrak and Adventure Lakes, Nunavut, Canada during 2001 and 2002. AIC_c weight reflects the relative support of each model given the model set, and sums to one.

Model	RSS ^a	No. of parameters	ΔAIC_c^b	AIC_c weight
Year	922143	3	0.00	0.53
Location year	918748	4	1.84	0.21
Location	950778	3	2.19	0.18
Location year location*year	917396	5	3.86	0.08

^aRSS = Residual sums of squares from ANOVA.

^bLowest AIC_c value was 624.46.

Table 2.3 Akaike's Information Criterion (AIC_c) values for all candidate models explaining nest initiation dates for King Eiders. Models are based on ANOVA with nest initiation date as the dependent variable and winter location (determined from stable-isotope analysis) and year as independent variables. Values are based on 165 females nesting at Karrak and Adventure Lakes, Nunavut, Canada during 2001 and 2002. AIC_c weight represents the relative support of each model given the model set, and sums to one.

Model	RSS ^a	No. of parameters	ΔAIC_c^b	AIC_c weight
Location	3851	3	0.00	0.45
Location year	3815	4	1.42	0.22
Location year location*year	3719	5	1.73	0.19
Year	3983	3	2.42	0.14

^aRSS = Residual sums of squares from ANOVA.

^bLowest AIC_c value was 231.90.

Table 2.4 Akaike's Information Criterion (AIC_c) values for all candidate models explaining King Eider clutch size, including all clutch sizes. Models are based on analysis of covariance with clutch size as the dependent variable adjusted for nest initiation date, winter-site location (determined from stable-isotope analysis), and year. Values are based on 165 clutches for females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC_c weight represents relative support of each model given the model set, and sums to one.

Model	RSS ^a	No. of parameters	ΔAIC_c^b	AIC_c weight
Initiation, location, year, initiation*location, initiation*year	11.6	7	0.00	0.39
Initiation, location, initiation*location	12.2	6	1.65	0.17
Initiation, year, initiation*year	12.2	6	1.65	0.17
Initiation, location, year, initiation*location, initiation*year, location*year	11.6	8	2.20	0.13
Initiation, location	13.4	4	3.25	0.08
Initiation, location, year	13.2	5	5.25	0.03
Initiation, year	13.8	4	5.96	0.02
Initiation, location, year, location* year	13.2	6	7.33	0.01

^aRSS = Residual sums of squares from ANOVA.

^bLowest AIC_c value was -175.63.

Table 2.5 Akaike's Information Criterion (AIC_c) values adjusted for small sample size for all candidate models explaining King Eider clutch size, including only clutch sizes with <7 eggs (i.e., nests in which brood parasitism was unlikely). Models are based on analysis of covariance with clutch size as the dependent variable adjusted for nest initiation date, winter-site location (determined from stable-isotope analysis), and year. Values are based on 143 clutches for females nesting at Karrak and Adventure Lakes, Nunavut, Canada, during 2001 and 2002. AIC_c weight represents relative support of each model given the model set, and sums to one.

MODEL	RSS ^a	No. of Parameters	ΔAIC_c	AIC_c weight
Initiation, location, year, initiation*year	6.9	6	0.00	0.45
Initiation, location, year, initiation*location, initiation*year	6.9	7	1.35	0.23
Initiation, location	7.9	4	3.35	0.08
Initiation, location, year, initiation*location, initiation*year, location*year	6.8	8	3.49	0.08
Initiation, location, year, initiation*location	7.4	6	3.89	0.06
Initiation, location, year	7.7	5	4.33	0.05
Initiation, location, year, location* year	7.7	6	6.38	0.02
Initiation, year	8.3	4	6.42	0.02

^aRSS = Residual sums of squares from ANOVA.

^bLowest AIC_c value was -175.27.

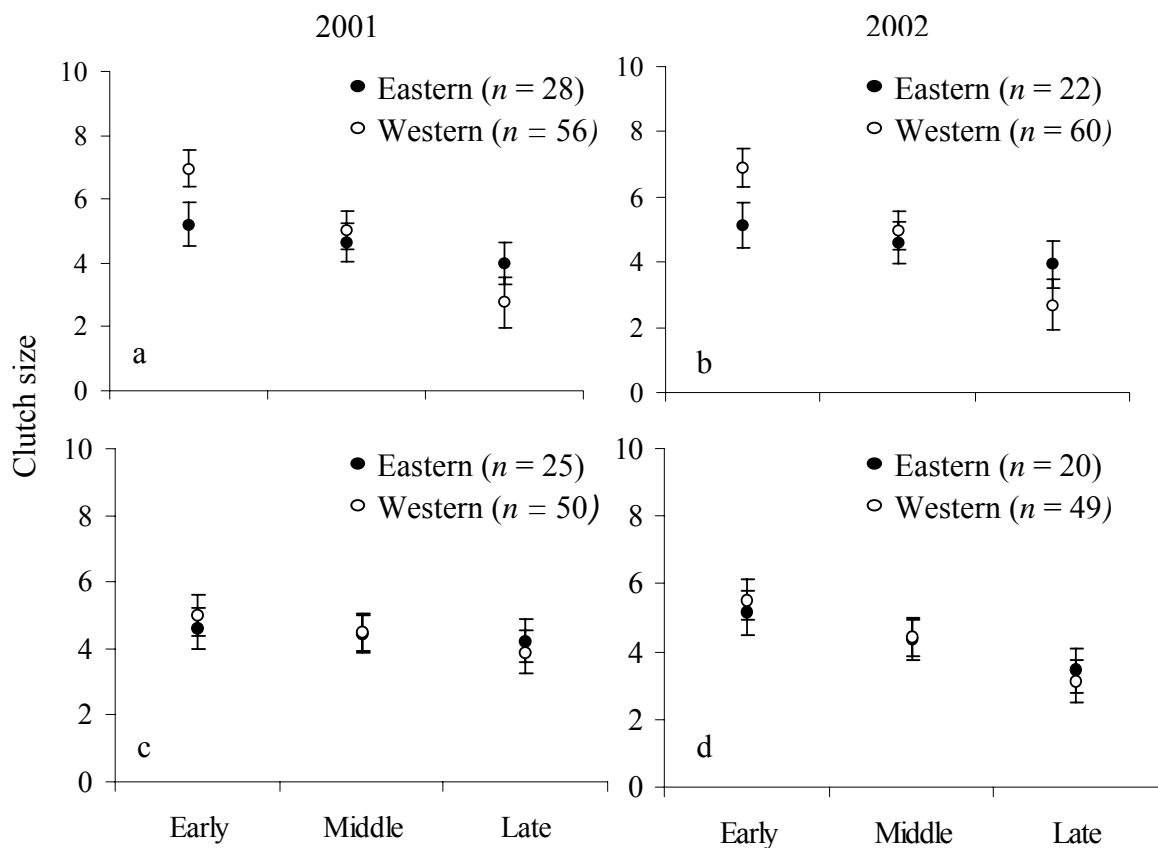


Figure 2.3 ANCOVA estimates of mean clutch size (95% CI) scaled to midpoints of the early (14 June), middle (20 June), and late (27 June) incubation periods for female King Eiders that nested at Karrak and Adventure Lakes during 2001 and 2002 and were predicted to have wintered within western (Pacific) or eastern (Atlantic) seas during the winter preceding that breeding season. Estimates are for nests of all clutch sizes, including those where (a, b) more than one female likely contributed to the overall clutch size and (c, d) for only those clutches with <7 eggs.

possible by more conventional approaches. Alternative methods, such as resighting color-marked individuals on wintering areas, is difficult because King Eiders winter at sea several kilometers from shore (Mosbech and Johnson 1999, Suydam 2000), battery lifespan for satellite transmitters is too short to allow for estimates of philopatry among years, and differential hunting pressures among regions can bias band recovery data (Robertson and Cooke 1999). My results suggest that inference about winter distributions based on band recoveries from hunters was biased for King Eiders. Isotope analyses showed that most King Eiders at Karrak Lake wintered in the Pacific (66–73%), whereas limited band recoveries for the same breeding population suggested that only about 44% wintered there. I suggest that intensive hunting along the coast of Greenland (Christensen and Falk 2001) resulted in more band recoveries from that area.

Some female King Eiders switched between wintering areas, and must have used completely different migration pathways among years. This suggests that winter philopatry among King Eiders is low, despite high rates of philopatry to breeding areas (Kellett 1999). Benefits and consequences of philopatry and dispersal are generally assessed relative to breeding areas (Greenwood 1980, Rohwer and Anderson 1988). Unlike most birds, waterfowl are thought to exhibit female-biased breeding philopatry (Greenwood 1980, Rohwer and Anderson 1988, but see Doherty et al. 2002). Robertson and Cooke (1999) suggested that in waterfowl, the normal avian pattern of male-biased philopatry was likely selected for on wintering, as opposed to breeding areas, due to the tendency for waterfowl to form pairs during winter. However, there have been few studies of winter philopatry in waterfowl, leaving hypotheses largely untested (Robertson et al. 1999). Nevertheless, low philopatry to wintering areas could lead to increased gene flow (Cooke et al. 1975, 2000), and even if male King Eiders exhibit high winter philopatry (Robertson et al. 1999), winter dispersal by females alone would provide ample gene flow for population mixing to occur (see Slatkin 1987). This may explain lack of phylogeographic structure among eastern and western populations (Pearce et al. 2004).

Dispersal by female King Eiders among wintering areas may be facilitated by gregarious behavior and group migration. Females congregate on breeding areas before fall migration; I observed such flocks of up to 46 females at Karrak Lake during late

summer. King Eiders migrate in groups (Suydam 2000), so individuals from one wintering area may follow those of another to an alternate wintering site. Potential benefits of female philopatry include familiarity with local food resources and predators (Anderson et al. 1992). Winter philopatry may be less important to female King Eiders if flocking during winter (Suydam 2000) allows for information exchange on productive foraging areas (Brown 1988) and if lack of predators in open oceanic waters lessens the need for familiarity with local predators (Rohwer and Anderson 1988).

Dispersal among areas is most likely if movement is favorable in both directions (Bull et al. 1987); otherwise, geographic variation in selection can partially block gene flow (Barton 1983). Although my results show benefits in the form of earlier nest initiation and larger clutches for females that wintered in the west, these benefits are likely not consistent among years and thus may not constitute a strong force of selection. For instance, differences in nest initiation dates likely reflect differential spring conditions among western and eastern seas and the availability of open water along migration routes (Abraham and Finney 1986, Suydam 2000). Late springs generally result in lower nest densities because a greater number of females are suspected to forgo breeding opportunities (Coulson 1984). I suspect that a late eastern spring during 2002 may have delayed spring migration and hence nesting attempts and decreased breeding probability for eastern birds, compared to 2001. If so, western seas are also likely to experience late seasons, as trends in diminished sea ice indicate similar long-term (18-year) trends for both eastern (Labrador Sea, Davis Strait) and western (Bering and Chukchi Seas) wintering areas (Parkinson 2000).

Females that wintered in the Pacific appeared to reap increased benefits with larger clutch sizes, but they also showed a greater prevalence for apparent nest parasitism compared to females from the Atlantic. However, high frequency of apparent nest parasitism during early nest initiation may counter these benefits if parasitism leads to decreased egg success or offspring survival (Eadie and Anstey 1999). Unfortunately, I was unable to test for differences in nest success with respect to preceding wintering area. Assuming that lack of winter philopatry by female King Eiders results in population mixing between eastern and western populations, increased nest parasitism by individuals that wintered in the west should not reflect genetic differences between

these local populations. Without genetic analysis of young, identification of parasitic females, and hence their winter origin (west or east) remains unknown.

Despite apparent differences in clutch size and nest initiation date, female condition of breeders was similar among individuals that wintered in eastern and western areas. Such similarities are likely related to a minimum threshold of endogenous nutrients, which females must exceed as a precondition for breeding (Kellett and Alisauskas 2000). Given that a greater proportion of this local population of female King Eiders wintered in the west despite the longer migration distances, there may be greater benefits to wintering in the west, as opposed to the eastern seas. Adult survival may also differ among wintering areas due to differential hunting pressures. However, data that incorporate isotope analysis with mark-recapture methods collected over a longer term than that of this study period, are needed before movement and subsequent survival probabilities can be estimated directly (Lindberg et al. 1995).

2.6 CONCLUSION

Collection and isotopic analysis of feathers has recently gained the attention of many ecologists (Webster et al. 2002, Smith et al. 2003). My results show that isotope analysis of feathers can be of further use when combined with local banding efforts and that these data allow for broad-scale inferences useful for modeling demography. This method also offers a means of monitoring potential for gene flow directly through dispersal and subsequent breeding success. Evidence for movement among wintering areas and lack of segregation on the breeding area according to winter distribution suggest that King Eiders wintering in Atlantic and Pacific seas may behave as one population rather than two (see Berryman 2002). These data also emphasize the need to use caution when interpreting band recoveries for purposes of movement and dispersal due to differences in hunting pressures among areas. Finally, I hope that this study will encourage researchers to incorporate, where appropriate, stable-isotope analysis with local banding efforts. Future work should incorporate similar isotope and banding studies, particularly near the eastern and western limits of the species' breeding areas.

3. LOCAL KING EIDER SURVIVAL AND POPULATION GROWTH: POTENTIAL INFLUENCE OF BODY SIZE

3.1 INTRODUCTION

Fisher's fundamental theorem predicts that traits closely connected to fitness have low heritability, as fitness benefits would reduce additive genetic variance and lead to evolutionary equilibrium (Price and Schluter 1991). In contrast, variation in body size often correlates with variation in life-history traits (Sauer and Slade 1984, Blanckenhorn 2000, Rotella et al. 2003) despite high heritability of external morphological traits (Boag 1983, Boag and Grant 1978, Grant and Grant 1994). Price and Schuller (1991) suggest that most support for Fisher's fundamental theorem has come from low heritability of life-history traits (i.e., survival and fecundity) and that such low heritability would occur regardless of evolutionary equilibrium because environmental and nonadditive genetic variance has a greater influence on life-history traits than on morphological traits. For example, nonadditive genetic characters, and factors such as weather (Davidson 1981) and predation (Sargent et al. 1984) can largely influence survival.

Here, I was interested in the influence of body size and its contributions to population growth. If benefits to body size exist, it is likely that the magnitude of benefits vary geographically. For example, larger-bodied birds are generally able to withstand cooler temperatures, store proportionately more fat reserves, and fast for longer periods of time relative to smaller conspecifics because of lower body surface area to volume ratios, and greater feather insulation (Kendeigh 1969, Kendeigh 1970, Calder 1974). However, overall nutrient demands, risk of heat stress, and juvenile growth periods also increase with body size (Kendeigh 1969, Blanckenhorn 2000). Additionally, larger body size may reduce agility, leaving larger individuals more susceptible to predation (Blanckenhorn 2000, Rotella et al. 2003). Thus, there can exist increased costs, as well as benefits, with increased body size and such costs can act as

partial stabilizing mechanisms that impede the achievement of exceptionally large body size. Given such cost and benefits, Fretwell (1972) hypothesized that larger body size would be favored in the presence of (1) limited breeding resources, (2) cold temperatures, (3) reduced photoperiod, and (4) consumption of foods that are difficult to digest. Therefore, species that breed and winter in polar regions should benefit the most from larger size compared to species with more temperate provenances.

King Eiders are a suitable study species for assessing effects of body size because they breed in arctic regions and, unlike most arctic-breeding species, which migrate to southern latitudes during the nonbreeding period, King Eiders remain in northern latitudes throughout the annual cycle (Bellrose 1976). Winter foraging is primarily during daylight of reduced duration and intensity (Frimer 1994). In addition, King Eiders do not breed until they are at least 3 years old (this study) and breeding females rely heavily upon stored nutrients, losing an average of 30% of their pre-incubation body mass during incubation (Kellett and Alisauskas 2000). Lastly, King Eider diets include about 50% bivalves with non-digestible shells (Frimer 1997), which likely requires a longer gut system. In accordance to Fisher's fundamental theorem, with body size being highly heritable (Appendix D), I predicted that if size benefits exist, these benefits would have the greatest influence on recruitment as opposed to survival, because recruitment contributes less to population growth (i.e., fitness) relative to survival (Rockwell et al. 1997, Crone 2001).

3.2 METHODS

3.2.1 Study Area and Data Set

This study was conducted on islands in Karrak and Adventure Lakes and mainland habitats near these lakes (67° 14' N, 100° 15' W). Kellett and Alisauskas (2000) provided detailed descriptions of the study area. Islands at Karrak (1995-2002) and Adventure Lakes (1996-2002) were systematically searched for King Eider nests beginning in mid-June. King Eider nest initiation dates were calculated by back-dating from known laying dates, or from estimated incubation stages by candling eggs (Weller 1956), assuming an incubation length of 23 days (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973). About 7 days before predicted hatch,

female King Eiders were trapped by placing mistnets over nesting females or by use of self-triggered bow-nets. Captured females were marked with standard CWS/USFWS leg bands and morphometric measurements (± 1.0 mm) of head length and tarsus using dial calipers, and wing chord using a flat ruler (Dzubin and Cooch 1993) were recorded. In addition, uniquely numbered web-tags and plasticine-filled metal bands (Blums et al. 1994) were used to mark ducklings at nests. Information gained from marked ducklings allowed me to obtain age of first breeding and heritability estimates for body size among parent and offspring.

3.3 STATISTICAL ANALYSES

I used principal components analysis (PCA) of the correlation matrix of mean metric measurements of individual females to establish indices of female structural size (PC1) (SAS Institute Inc. 1996). I did not include mass in my measurement of size, as mass is known to vary among years (Johnson et al. 1985, Alisauskas and Ankney 1990). I assessed measurement error (%ME), i.e., proportion of measurement variation due to observers, assuming that individual structural size was constant, by using repeated measurements for the same individuals over multiple years (Lessells and Boag 1987, Loughheed et al. 1991). I used general linear models (GLM) to test for age related size effects. Although this method lacks robustness due to small sample size ($n = 24$ adult females of known size and breeding age), given our data set, this was the only method available to examine potential age and size effects.

I investigated the influence of body size on population dynamics using both Pradel seniority models (Pradel 1996) and Cormack-Jolly-Seber models (CJS; Lebreton et al. 1992) within Program MARK (White and Burnham 1999). Pradel models use forward capture histories to estimate apparent survival ($\hat{\phi}_i$); the probability that a female survived from year i to $i+1$, and returned to the study area, and recapture probability (\hat{p}_i); the probability that a marked female alive in year i was captured in year i . In addition, Pradel models also use reverse order capture histories to estimate seniority ($\hat{\gamma}_i$) or the probability that an individual in the population at time i was also in the population during the previous year, $i-1$ (Pradel 1996, Nichols et al. 2000). Because of the

relationship of ϕ and γ to population growth (λ), I was able to estimate $\hat{\lambda}_i$ using the following equation:

$$\hat{\lambda}_i = \frac{\hat{\phi}_i}{\hat{\gamma}_{i+1}} \quad (3.1)$$

and recruitment (\hat{f}_i) by:

$$\hat{f}_i = \hat{\phi}_i \left(\frac{1 - \hat{\gamma}_{i+1}}{\hat{\gamma}_{i+1}} \right). \quad (3.2)$$

Whereas $\hat{\gamma}_{i+1}$ represents the probability that an individual was a member of the population during the previous period, this value can be interpreted as the relative, proportional contribution of adult survival to $\hat{\lambda}_i$ and therefore $(1 - \hat{\gamma}_i)$ is the proportional contribution of new recruits to the population. For these estimates to be unbiased, the study area in which individuals are marked must remain constant throughout the study (Pradel 1996, Nichols et al. 2000). Work at Karrak Lake was expanded in 1996 to include islands within Adventure Lake. Therefore, I restricted seniority analyses to include data collected only during 1996-2002. Lastly, I also estimated $\hat{\phi}_i$ and \hat{p}_i using all data from 1995-2002 in CJS models.

Because estimates of $\hat{\phi}_i$ are the product of true survival and fidelity, and because I was only able to capture breeding birds, I was unable to distinguish among probabilities of (1) permanent emigration from the study area, (2) movement to permanent nonbreeding status or (3) death. Additionally, captures took place during late incubation, so, in this study, skipped or failed breeding was indistinguishable from temporary emigration. Therefore, \hat{p}_i represents a capture probability of successful breeders that had not permanently emigrated from the study area.

I used individual encounter histories with PC1 scores as individual-level covariates to examine if larger females survived at higher rates, were captured more frequently, or if larger individuals tended to contribute proportionately more to $\hat{\lambda}_i$ (i.e., effects of PC1 on $\hat{\gamma}_{i+1}$), relative to smaller conspecifics. I used the following three forms of models to test these relationships: (1) linear, where that effects of body size changed at a constant

rate $[\beta_0 + \beta_1(x_1) + \dots + \beta_n(x_n)]$, (2) quadratic, where an intermediate size benefits $[\beta_0 + \beta_1(x_1) + \beta_2(x_1^2) + \dots + \beta_n(x_n) + \beta_{n+1}(x_{n+1}^2)]$, or (3) pseudothreshold, where size effects increase at a constant rate to a point at which the effects of size approach, but do not reach, an asymptote $[\beta_0 + \beta_1 \ln(x_1 + 4.0) + \dots + \beta_n \ln(x_n + 4.0)]$. For each, β_0 is the intercept, and x_i is the body size covariate. To adjust for negative and zero values in pseudothreshold models, I added 4.0 to PC1 scores before multiplying each value by the natural log. I used the logit link function when testing covariates and the sine link for non-covariate models (White and Burnham 1999). I was interested in overall structural size, so I did not incorporate univariate measurements as covariates in my models.

3.3.1 Model Selection

I tested goodness-of-fit of the most general CJS model using the parametric bootstrap method in Program MARK (White and Burnham 1999). I adjusted the variance inflation factor (\hat{c}) to account for lack of model fit (Burnham and Anderson 2002). The adjusted \hat{c} (1.08) was calculated by dividing the deviance of the most general model by the mean deviance from 1,000 bootstrap iterations (White and Burnham 1999). I assumed $\hat{c} = 1$ for Pradel Survival and Seniority Models in Program MARK because Pradel model estimates are conditioned on the full encounter history, rather than portion following the first capture (Franklin 2001), therefore use of CJS estimates for \hat{c} are inappropriate for this method (White and Burnham 1999). I chose the most parsimonious model(s) using quasi-likelihood Akaike's Information Criterion (QAIC_c) adjusted for sample size (Akaike 1985, Burnham and Anderson 2002).

I considered 13 candidate CJS models for $\hat{\phi}_i$ and \hat{p}_i (Table 3.1). I began model selection by first reducing the number of parameters for the most general, fully time-dependent model beginning with time constraints on \hat{p}_i . For seniority models, I began model selection by initially adding time constraints to $\hat{\gamma}_{i+1}$, followed by \hat{p}_i , and then $\hat{\phi}_i$. After obtaining the most parsimonious model without covariates, I added body size covariates to the model and tested for interactions between body size and year. I

Table 3.1 Candidate models used to investigate the influence of body size (BS) on apparent survival (ϕ), and recapture probability (p) of 264 breeding King Eider females at Karrak Lake, Nunavut, from 1996 - 2002. Parameter estimates included full time effects, where time varied annually (t), linear trend with time (T), and no time variation (.). Covariates included linear effects of body size (BS), body size as pseudothreshold relationship (BS_{ln}), and as quadratic relationship (BS_{TT}) with the estimated parameters. Models are ranked in accordance to QAIC_c values and are denoted as additive (+) or interaction (*) models.

Number\	Model	Δ QAIC _c	QAIC _c Weight	No. of Parameters	QDeviance
1	$\phi(.) p(T+BS_{ln})$	0.00	0.27	4	870.73
2	$\phi(.+BS_{ln}) p(T)$	1.26	0.15	4	871.98
3	$\phi(.) p(T+BS)$	1.29	0.14	4	872.02
4	$\phi(.+BS_{ln}) p(T+BS_{ln})$	1.93	0.10	5	870.61
5	$\phi(.) p(T)$	2.08	0.10	3	874.84
6	$\phi(.+BS) p(T)$	2.44	0.08	4	873.17
7	$\phi(.) p(T+BS_{TT})$	3.08	0.06	5	871.76
8	$\phi(.) p(t+BS)$	3.81	0.04	9	864.20
9	$\phi(.+BS_{TT}) p(T)$	4.40	0.03	5	873.08
10	$\phi(.) p(t)$	4.83	0.02	8	867.31
11	$\phi(t) p(t)$	9.38	0.00	13	861.32
12	$\phi(.) p(t*BS)$	10.84	0.00	15	858.48
13	$\phi(t) p(.)$	18.35	0.00	8	880.83

^aLowest QAIC_c value was 878.82.

considered 16 candidate models for Pradel seniority models (Table 3.2). Influence of body size was based on Akaike model weights (Burnham and Anderson 2002). I also used model-averaged estimates based on Akaike weights (Burnham and Anderson 2002) of $\hat{\phi}_i$ and $\hat{\gamma}_{i+1}$ from Pradel candidate models to calculate $\hat{\lambda}_i$ for the defined Karrak Lake population and to estimate the relative contribution of adult survival and recruitment to overall population growth.

3.3.2 Analysis For Trap Dependent Behavior

Lastly, seniority is estimated using \hat{p} of marked animals and when $\hat{\gamma}$ is applied to population growth of both marked and unmarked animals, these estimates are likely to introduce biases if a permanent trap response behavior exists for some individuals (Nichols et al. 2000). Robustness of such models are therefore conditional on equal capture probabilities among marked and unmarked individuals. I tested for potential trap response behavior among female King Eiders captured in my sample, using the two-tailed *Goodness-of-fit* (GOF) test in U-CARE (Pradel et al. 2003). GOF tests for differences in capture probabilities between the animals captured and not captured at the previous occasion, conditional on presence at both occasions. Values of $X^2 < 0$ represent trap-happiness whereas, values of $X^2 > 0$ represent trap-shyness (Pradel et al. 2003).

3.4 RESULTS

3.4.1 Captures and Body Size

The data consisted of 264 individual adult female King Eiders from 1995 to 2002. Captures included one mainland nesting female during 2001, all other captures occurred on islands (Table 3.3). Captures from 1995 to 2003 included 25 individuals of known breeding age, 8 of which were 3 years old when first captured as adults, 14 individuals were 4 years old, 2 individuals were 5 years old, and one female was 6 years old. Twenty-four of these offspring were measured, in which 20 had measurements recorded from their putative mothers. Results suggest no trap-dependent behavior among female King Eiders $X^2 = -1.85$, $P = 0.06$. Percent ME for body size

Table 3.2 Candidate models used to investigate the influence of body size (BS) on apparent survival (ϕ), recapture probability (p), and seniority (γ) of breeding King Eider females at Karrak Lake, Nunavut from 1996- 2002. Parameter estimates included full time effects, where time varied annually (t), linear trend with time (T), and no time variation (.). Body size was considered to affect parameters linearly (BS), in a pseudothreshold relationship (BS_{ln}) and in a quadratic relationship (BS_{TT}). Models are ranked in accordance to QAIC_c values and are denoted as additive (+) or interaction (*) models.

Number\Model	Δ QAIC _c	QAIC _c	No. of Parameters	QDeviance
1 $\phi(.) p(t+BS_{ln}) \gamma(.+BS_{TT})$	0.00	0.27	12	1862.27
2 $\phi(.) p(t+BS_{ln}) \gamma(.)$	0.85	0.18	10	1867.31
3 $\phi(.) p(t) \gamma(.+BS_{TT})$	1.97	0.10	11	1866.34
4 $\phi(.) p(t+BS) \gamma(.)$	2.20	0.09	10	1868.66
5 $\phi(.) p(t) \gamma(.+BS)$	2.60	0.07	10	1869.07
6 $\phi(.) p(t) \gamma(.)$	2.61	0.07	9	1871.16
7 $\phi(t) p(T) \gamma(.)$	3.45	0.05	4	1882.30
8 $\phi(.) p(t+BS_{TT}) \gamma(.)$	4.01	0.04	11	1868.38
9 $\phi(.) p(t) \gamma(.+BS_{ln})$	4.05	0.04	10	1870.52
10 $\phi(.+BS_{ln}) p(t) \gamma(.)$	4.26	0.03	10	1870.73
11 $\phi(.+BS) p(t) \gamma(.)$	4.69	0.03	10	1871.16
12 $\phi(.+BS_{TT}) p(t) \gamma(.)$	6.21	0.01	11	1870.58
13 $\phi(t) p(t) \gamma(.)$	7.20	0.01	14	1865.23
14 $\phi(.) p(t*BS) \gamma(.)$	8.63	0.00	16	1862.39
15 $\phi(t) p(t) \gamma(t)$	12.38	0.00	18	1861.83
16 $\phi(.) p(.) \gamma(.)$	16.49	0.00	3	1897.37

^bLowest AIC_c value was 1886.93.

Table 3.3 Number of King Eider nests found and number of adult female King Eiders and ducklings (both sexes) banded during 1995 to 2002 on islands within Karrak Lake and Adventure Lake, Nunavut.

Year	No. of nests found	No. of adult females marked	Adult females captured (%)	No. of ducklings marked
1995	41 ^a	25	61.0%	0
1996	100 ^b	63	63.0%	23
1997	123	62	50.4%	185
1998	146	60	41.1%	193
1999	191	71	37.2%	260
2000	191	56	29.3%	175
2001	208	91	43.8%	186
2002	221	84	38.0%	174

^aKellett and Alisauskas 1997

^bKellett et al. 2003 (1996-2001)

when calculated annually (1995 to 2002) was 17% (repeatability = 83%). My index of size (PC1) accounted for 53% of variation in body measures, with PC1 loadings of 0.72, 0.76, 0.71 for head length, tarsus, and wing, respectively. Body size was unrelated to age ($F_{3,23} = 0.96$, $r^2 = 0.12$, $P = 0.43$) and did not appear to affect age of first capture (Figure 3.1). Mean measurements for head length was 106.3mm (95% CI = 106.5 to 106.0), mean tarsus was 47.1mm (95% CI = 47.3 to 46.9), and mean wing length was 275.6 mm (95% CI = 276.4 to 274.8)

3.4.2 Apparent Survival, Capture Probability and Seniority

Results from CJS models suggest that $\hat{\phi}$ remained stable and \hat{p} decreased linearly through time from 1995 to 2002 (Table 3.1). In contrast, with the exclusion of 1995 from the data set, Pradel 1996-2002 models suggested that \hat{p} varied non-linearly with time (Table 3.2). Model average estimate of $\hat{\phi}$ during 1996-2002 from Pradel seniority models was 0.87 (95% CI = 0.81 to 0.91), \hat{p} varied with time (range = 0.31 to 0.67), and $\hat{\gamma}$ was 0.72 (95% CI = 0.67 to 0.77). Based on model averaged estimates of $\hat{\gamma}$, contribution of survivors to the Karrak Lake population of breeding females was 72%, meaning that local survival within the population was 2.6 times more important to the annual population growth than was the addition of new recruits. Average $\hat{f}_{1996-2002}$ for the Karrak Lake population was estimated at 0.34 (95% CI = 0.27 to 0.40) and $\hat{\lambda}_{1996-2002}$ at 1.20 (95% CI = 1.05 to 1.36). Low sample size of known maternal female and locally-produced offspring precluded separation of recruitment into ‘*in situ* recruits’ and immigrants.

Relationship of body size to $\hat{\phi}$ and \hat{p} were similar among CJS and Pradel models. Based on the candidate set of models used, I found no relationship between $\hat{\phi}$ and body size. However, I did find a pseudothreshold trend in the effects of body size on \hat{p} , and a quadratic trend with $\hat{\gamma}$ and body size (Figure 3.2). Based on model weights, body size had the greatest influence \hat{p} and the greatest precision relative to other parameters.

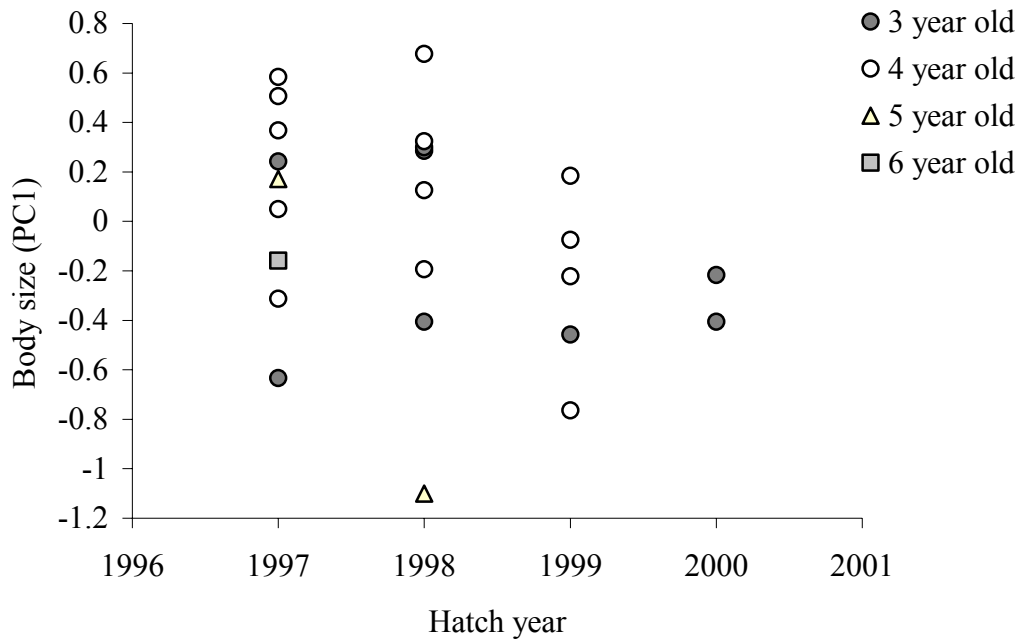


Figure 3.1 Age of first capture relative to body size and hatch year for female King Eiders of known breeding age. Females were marked as ducklings and later recaptured as breeding adults at Karrak Lake, Nunavut 1997-2003.

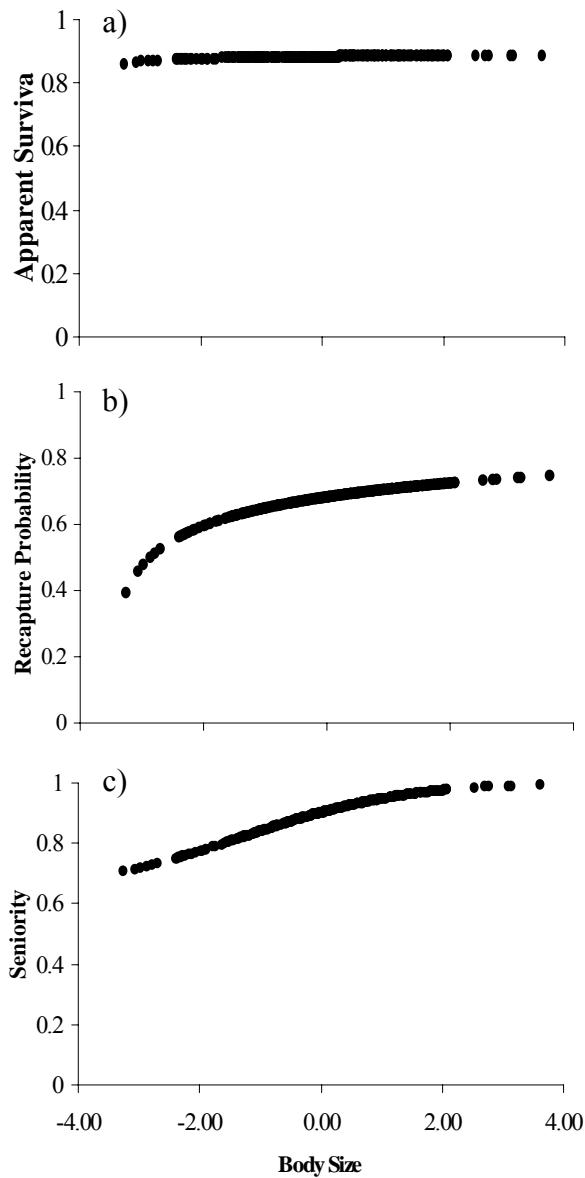


Figure 3.2 Predicted influence of body size on apparent survival (a), recapture probability (b), and seniority (c) of female King Eiders returning to breed at Karrak and Adventure Lakes, Nunavut. Values shown have been backtransformed from the logit function. Slope estimates are based on weighted model averaged estimates are as follows: 1) $\hat{\phi} : \hat{\beta}_{femalesize_{in}} = 0.09$ (95%CI= -0.17 to 0.36); 2) $\hat{p} : \beta_{femalesize_{in}} = 0.21$ (95%CI=0.01 to 0.42), and 3) $\hat{\gamma} : \beta_{femalesize_{TT}} = 0.14$ (95%CI=-0.05 to 0.32) + 0.14 (95%CI=-0.03 to 0.30).

3.5 DISCUSSION

My results suggest that body size had little influence on apparent survival of adult female King Eiders once they have successfully bred for the first time. Ideally, I would have measured individuals at hatch and followed their survival from fledging through all breeding attempts. Female King Eiders are 3-5 years of age before they nest successfully, so selection against the smallest individuals may have occurred before the sampling period. For example, early mortality of smaller-sized young occurs in Ross's geese (*C. rossii*; Slattery and Alisauskas 2002) and Ruddy Ducks (*Oxyura jamaicensis rubiada*; Pelayo 2001). If the smallest individuals died during the first 3-5 years of life, or failed to be recruited into the breeding population, the remaining measured breeding individuals may already have been above a minimum threshold of larger body size (Hill et al. 2003).

Several factors may have contributed to differences in recapture probabilities between small and large-bodied females. Female King Eiders rely heavily on endogenous reserves for breeding (Kellett and Alisauskas 2000), and if larger individuals are more efficient at using these reserves due to lower surface area to volume ratio (Calder 1974), these individuals may be in better condition relative to smaller conspecifics. Several studies have documented positive relationships between female condition and nest success (Gloutney and Clark 1991, Mallory and Weatherhead 1993, Kellett and Allisauskas 2000). Most King Eider nest failures occur during early incubation (Kellett and Allisauskas 2000); short arctic breeding seasons and heavy reliance on stored nutrient reserves likely prevent renesting after nest loss in the same season (Korschegeen 1977, Suydam 2000). Therefore, if smaller individuals nested less successfully than larger individuals, the probability of capturing smaller individuals would have been reduced. Furthermore, intermittent breeding can be extensive among eiders (Coulson 1984). If larger individuals are more efficient at using nutrient reserves, this may enable these individuals to breed more regularly, whereas smaller females may refrain from breeding during some years. Alternatively, smaller individuals may have flushed from nests more readily than large individuals, and therefore smaller females

may have simply been more difficult to capture than large individuals, which generally have higher incubation constancy (Skutch 1962, Afton and Paulus 1992). Regardless, lower recapture probability for smaller females is consistent with a positive influence of larger size on breeding effort.

Estimation of $\hat{\gamma}$ using Pradel models provided additional insights. Effects of body size on $\hat{\gamma}$ suggest that larger individuals contributed more to growth of the local population than smaller individuals. In other words, the likelihood of being a previous member of the population increased with body size. Given that my sample of marked birds was restricted to breeding female eiders, the relationship between seniority and body size suggests that large females show greater consistency from year to year in being members of the breeding cohort than did smaller females. Estimation of seniority was conditional on detection or capture probability, suggesting that higher capture probability estimated from CJS models were related more to increased breeding probability rather than to any direct influence of body size on likelihood of capture given presence.

Influence of body size appears to have the greatest influence on $\hat{\gamma}$ for small and medium-sized individuals, with a threshold-type relationship where $\hat{\gamma}$ remains relatively constant for individuals larger than medium body size (Figure 3). Annual entry into the breeding population was greater for smaller females and I suggest this is because smaller individuals show less consistency in membership in the breeding population, with higher frequency of leaving and re-entering this cohort. Contributions of both large and small-bodied individuals to growth of the breeding population (quadratic time trend) may likely act to maintain body size variation within the population. Furthermore, benefits of body size may fluctuate under variable conditions. For instance, during spring, King Eiders rely on nutrient-rich leads in the ice and polynyas with limited open water in which to feed. Natural closures of these areas can leave King Eiders unable to forage during critically low temperatures (Fournier and Hines 1994). Therefore, selection pressures on body size may be most pronounced during these periods, as larger individuals should be more efficient at using stored reserves and withstand fasting for longer duration (Kendeigh 1969, Kendeigh 1970, Calder 1974). However, large size

requires increased energy requirements to meet daily energetic maintenance (Kendeigh 1969), so if individuals are forced to fast before nutrient reserves are acquired, then smaller-bodied individuals may be at an ecological advantage. This may help to explain the large variability in recorded body size of breeding female King Eiders, as selection for an optimal size should deplete genetic variance (Gibson and Bradley 1974).

Ideally, study populations should have low immigration rates of individuals exposed to different selection pressures (Larsson et al. 1998). Results from isotope analysis of King Eider feathers indicate that individuals from this population winter in both western and eastern seas and that nest initiation dates and clutch size varied by wintering area, suggesting that variable selective pressures may occur among wintering sites (Mehl et al. 2004). However, I suggest that these selection pressures vary through time and are likely not consistent among sites. I also acknowledge that body size is likely a polygenic trait and that selection may act on other correlated or unmeasured traits such as heavier feather insulation, hormone actions, or enzyme systems (see Kendeigh 1969).

3.6 CONCLUSION

In conclusion, model-averaged estimates suggest that larger individuals show higher probability of previous membership in the breeding cohort of King Eiders at Karrak Lake, and have greater fitness from more frequent successful nesting attempts.

Population growth for the study area was high, with an estimated overall growth of 20%. These growth rates were similar to those exhibited by Common Eiders (*Somateria mollissima*), where most of the growth seemed to occur in a step-wise growth pattern attributed to boom and bust production years (Coulson 1984). Assuming that King Eiders also follow a step-wise growth pattern, some years may allow successful production unconstrained by size and thus, maintain a high degree of phenotypic plasticity and heritability within the population. Lastly, caution should be taken when interpreting local estimates of population growth. Overall population trends indicate declining abundance of King Eiders throughout much of their range (Suydam et al. 2000). My data did not allow separation of immigration and *in situ* recruits and, at the metapopulation level, local areas such as Karrak Lake may exhibit population increases while other areas simultaneously decline. Furthermore, my estimates λ may be biased

high if a large proportion of young recruits has recently shifted the age-structure toward recruits (Cooch et al. 2001). Studies need to focus on marking young at nests to establish a marked population of known breeders. Such data are necessary to separate contributions to the population by *in situ* recruits from contributions through immigration, and to better understand factors that contribute to fitness benefits. In addition, similar studies to that presented here are needed to establish comparison data at local sites throughout the species' range so that we can begin to understand geographical variation in local rates of population growth.

4. KING EIDER NEST SUCCESS AND BREEDING CONDITION: RELATIONSHIPS BETWEEN FUTURE SURVIVAL AND BREEDING

4.1 INTRODUCTION

Natural selection is a consequence of differences in fitness (e.g., reproductive effort and longevity). It is through such fitness differences that the evolution of trade-offs between various life history traits evolved (Williams 1966, Renzick 1985, Stearns 1992, Cooch et al. 2002). For instance, allocation of resources for reproduction may reduce future reproductive efforts if body reserves are depleted to such a degree that survival or future breeding attempts are diminished (Clutton-Brock et al. 1982), via increase vulnerability to disease (Korschgen et al. 1978, Wobeser 1981) or if breeding leads to increased likelihood of mortality from predation (Sargeant et al. 1984, Dufour and Clark 2002). For species that rely heavily on nutrient reserves for breeding, individuals with lower relative nutrient reserves may incur greater costs to future reproductive efforts, relative to those individuals in better condition. The presence of such trade-offs may not be ubiquitous (Tuomi et al. 1983, Harris and Wanless 1995, Cam et al. 1998). However, if present, detection of such trade-offs is an important step toward understanding ecological pressures and the evolution of life-history traits.

Relative nest initiation date is often linked to components of recruitment, where recruitment is greatest for nests of early relative hatch date (Cook et al. 1984, Dawson and Clark 2000, Reed et al. 2003). If such trade-offs exist, relative nest initiation date may also influence the magnitude of trade-offs among life history traits. For instance, in seasonal environments, annual median nest initiation dates reflect differential spring conditions and habitat availability (Suydam 2000, Reed et al. 2003). For species that rely heavily on nutrient reserves for successful breeding, delayed nest initiation due to late onset of spring conditions may cause individuals to deplete their stored nutrients before breeding begins, resulting in fewer birds nesting during late breeding years

(Chapter 2). Therefore, reproductive costs to individuals that breed in late years may be greater relative to early years, in terms of reduced survival or probability to breed during the subsequent year.

Multistate models are useful tools to understand ecological pressures that shape life history traits, as these models allow ecologists to estimate costs of reproduction in terms of survival or future reproductive efforts, and provide insights into time variation in such costs (Nichols et al. 1994, Nichols and Kendall 1995). Life history traits vary over space and time, therefore, if trade-offs among life history traits exist, such trade-offs may vary with factors such as environmental fluctuations (Franklin et al. 2000), resource availability (Nichols and Kendall 1994), and population density (Frederiksen et al. 2001).

Here I use multistate models to investigate annual patterns in nest success and breeding condition of female King Eiders (*Somateria spectabilis*) in relation to (1) costs of reproduction and relative nutrient reserves, and (2) measure the effects of annual nest initiation on breeding success and nutrient reserves. King Eiders are a good study species to test costs associated with reproduction and nutrient reserves as they are a long-lived (Chapter 3), breed and winter in northern latitudes (Suydam 2000), and rely heavily on stored nutrients for reproduction, losing about 30% of their pre-incubation body mass during incubation (Kellett and Alisauskas 2000). I predict that nesting attempts and nutrient reserves during incubation pose few costs to survival, as females with nutrient reserves below an adaptive threshold required for nesting likely forego breeding attempts or abandon nests (see Kellett and Alisauskas 2000). Furthermore, arctic habitats and the occurrence of island nesting likely to pose few predation threats to incubating females (Sargeant and Raveling 1992). Heterogeneity in quality among individuals is important underlying factor to population dynamics (Cooch et al. 2002). To my knowledge, this is the first use of multistate models to investigate such factors of female quality.

4.2 METHODS

4.2.1 Study Area and Captures

This study took place on island habitats within Karrak and Adventure Lakes and mainland habitats near these lakes, located about 60 km south of the Queen Maud Gulf, Nunavut (67° 14' N, 100° 15' W). Kellett and Alisauskas (1997) provide detailed descriptions of the study area.

Islands on Karrak Lake (1995-2002) and Adventure Lake (1996-2002) were systematically searched for King Eider nests beginning in mid-June. King Eider nests on the mainland were found opportunistically when females flushed during research activities with Lesser Snow Goose (*Chen caerulescens*) and Ross's Goose (*C. rossii*) (Kellett et al. 2003). Nest initiation dates were calculated by back-dating from known laying dates, or from incubation stage by candling eggs (Weller 1956), assuming a laying interval of one egg per day (Lamothe 1973) and incubation of 23 days (Parmelee et al. 1967). Nesting female King Eiders were captured within about 7 days of predicted hatch, using mistnets or self-triggered bownets. Captured females received standard metal leg bands, each was weighed using a Pesola scale (+10g), and measurements of head length, and tarsus recorded using dial calipers (± 1.0 mm), and wing chord (± 1.0 mm) recorded using a flat ruler (Dzubin and Cooch 1993).

4.3 STATISTICAL ANALYSES

4.3.1 Body Condition

I used the correlation matrix of mean annual metric measurements for each individual as an index of female structural size (PC1; SAS Institute Inc. 1996). I excluded body weight from this index, as body mass can be highly variable among and within years (Johnson et al. 1985, Alisauskas and Ankney 1990). I used general linear models (GLM) to regress body weight on PC1 and incubation stage at capture, and used residuals as an index of adult female condition. Condition indices thus, represent body weight corrected for structural size (PC1) and incubation stage at capture (Alisauskas and Ankney 1990, Hochachka and Smith 1991). I used general linear models to test if clutch size has varied over time, assuming that annual correlations may exist between female condition and clutch size (Alisauskas and Ankney 1990),

4.3.2 Patterns in and Costs to Nest Success and Condition

I used multistate models in Program MARK (Brownie et al. 1993, White and Burnham 1999), where encounter histories were coded by the different states that an individual occupied at time of capture (i.e., successful or failed nester and good or poor condition; Brownie et al. 1993, Nichols et al. 1994). To examine potential costs and patterns in nest success data, I organized encounter histories of nesting females such that each capture was coded according to nest success after capture. Females with hatched nests were coded as successful (S), while those with failed nesting attempts after capture were coded as failures (F). To investigate costs and patterns in female condition, I reorganized encounter histories to reflect females that were in good (G) or poor (P) condition, relative to other individuals captured during the same year. Residuals of the condition index >0 , represented those individuals in good condition, and residuals < 0 represented individuals in poor condition. I used multistate models to estimate the following: (1) apparent survival, ϕ_i^{rs} , the probability that an individual alive and in state r at time i was alive in state s at time $i+1$ and did not emigrate permanently from the study area; (2) recapture probability, p_i^r , the probability that an individual was recaptured at time i and was in state r , provided that the individual was alive and in the study area at time i ; and (3) movement or transition probability, Ψ_i^{rs} , the probability that a female in state r at time i changed to state s at $i+1$ (Brownie et al. 1993, Nichols et al. 1994). The probability that an individual did not change states (i.e., Ψ_i^{rr}) is equal to $1 - \Psi_i^{rs}$. For all nest success analyses, females marked with transmitters during 2001 were censored from the analysis ($n = 29$), as transmitters during this year lead to high nest loss (Appendix A).

4.3.3 Model Selection

I tested goodness-of-fit of nest success and condition models using U-CARE (Pradel et al. 2003) and calculated Quasi-Akaike's Information Criterion (QAIC_c) from AIC_c

using a variance inflation factor $\hat{c} = \frac{\chi^2}{df}$ to correct for small sample size and over-

dispersion (Akaike 1985, Burnham and Anderson 2002). I considered 26 candidate models for patterns of nest success ($\hat{c} = 1.30$; see Table 4.1 for top 10 candidate models) and 34 candidate models to investigate patterns in female condition ($\hat{c} = 1.82$; see Table 4.2 for top 17 candidate models). I investigated models for temporal variation or constancy for each estimated parameter and chose the most parsimonious models using QAIC_c (Akaike 1985, Burnham and Anderson 2002). After obtaining the most parsimonious time constrained model, I added median annual nest initiation directly into the PIMs as an annual-level covariate (White and Burnham 1999). Median nest initiation date was scaled so that the year with the earliest median nest initiation date was equal to one. Scaled annual, median nest initiation dates ranged from 1 – 10, as median nest initiation varied by up to 10 days among years.

4.3.4 Model Assumptions

Because most nest failure occurs during the laying period (Kellett et al. 2003) and my sample of female King Eiders was comprised of females captured during mid- to late incubation, encounters of King Eiders were biased toward successful nesters. Despite these biases, inclusion of recapture probability within multistate models still allows for non-biased estimates in regards to the costs of reproduction if the data meet the following assumptions (Brownie et al. 1993, Nichols et al. 1994): 1) All individuals nest successfully at least once (i.e., there are no individuals that are not available for capture because they are never successful); 2) individuals within the same state have equal recapture probability (i.e., all females that were in good condition were equally available for capture); and 3) costs of reproducing at time i occurred during the subsequent interval before the next encounter ($i+1$).

Table 4.1 Top 10 of 26 candidate models used to investigate nest success terms of apparent survival (ϕ), recapture probability (p), and transition probability (ψ) for female King Eider that nested successfully or failed in their breeding attempts at Karrak Lake, Nunavut, from 1996 - 2002. Models included group affects where parameters varied with nest success (g) or held constant (\cdot), and time effects, where time varied annually (t), linear trend with time (T), or with no time variation (\cdot). Covariates included annual median nest initiation date. Models are ranked in accordance to QAIC_c values and are denoted as additive (+) or interaction (*) models.

Model Number/Name	ΔQAIC_c	ΔQAIC_c Weight	No. of Parameters	Deviance
1 $\phi(\cdot) p(g) \psi(g*T)$	0.00	0.45	6	672.18
2 $\phi(g) p(g) \psi(g*T)$	1.92	0.17	7	672.01
3 $\phi(\cdot) p(g+T) \psi(g*T)$	2.03	0.16	7	672.12
4 $\phi(\cdot) p(g*T*\text{initiation}) \psi(g*T)$	3.65	0.07	8	671.63
5 $\phi(g) p(g+T) \psi(g*T)$	4.01	0.06	8	671.99
6 $\phi(g) p(g) \psi(g*\text{initiation})$	6.71	0.02	7	676.80
7 $\phi(\cdot) p(g*T*\text{initiation}) \psi(g+\text{initiation}*T)$	7.11	0.01	10	670.84
8 $\phi(\cdot) p(g*T*\text{initiation}) \psi(g*T*\text{initiation})$	7.25	0.01	10	670.97
9 $\phi(g) p(g+T) \psi(g+T)$	7.69	0.01	8	675.67
10 $\phi(g) p(g+T) \psi(g*t)$	9.23	0.00	13	666.46

*Lowest QAIC_c value = 684.46

Table 4.2 Top 17 of 34 candidate models used to investigate effects of female body condition on apparent survival (ϕ), recapture probability (p), and transition probability for female King Eider that nested successfully or failed in their breeding attempts at Karrak Lake, Nunavut, from 1996 - 2002. Models included group effects where parameters varied among females in good and poor condition (g) or remained constant (\cdot), and time effects, where time varied annually (t), linear trend with time (T), or with no time variation (\cdot). Covariates included annual median nest initiation date. Models are ranked in accordance to QAIC_c values and are denoted as additive (+) or interaction (*) models.

Model Number/Name	ΔQAIC_c	Weight	No. of Parameters	Deviance
1 $\phi(\cdot) p(\cdot+\text{initiation}) \psi(\cdot)$	0.00	0.29	5	614.06
2 $\phi(\cdot) p(\cdot+\text{initiation}) \psi(\cdot)$	0.26	0.26	4	616.38
3 $\phi(g,\cdot) p(\cdot+\text{initiation}) \psi(g)$	1.84	0.12	6	613.83
4 $\phi(g,\cdot) p(\cdot+\text{initiation}) y(\cdot+\text{initiation})$	1.91	0.11	6	613.90
5 $\phi(g,\cdot) p(g+\text{initiation}) \psi(\cdot)$	2.07	0.10	6	614.06
6 $\phi(g,\cdot) p(g*\text{initiation}) \psi(\cdot)$	3.58	0.05	7	613.49
7 $\phi(g,\cdot) p(\cdot+\text{initiation})$ $\psi(g+\text{initiation})$	3.72	0.05	7	613.62
8 $\phi(g,\cdot) p(\cdot+\text{initiation}) \psi(g*\text{initiation})$	5.81	0.02	8	613.62
9 $\phi(g,\cdot) p(\cdot+\text{initiation}) \psi(g*t)$	13.90	0.00	18	600.02
10 $\phi(g,\cdot) p(g+\text{initiation}) \psi(g*t)$	15.84	0.00	19	599.72
11 $\phi(g,\cdot) p(g*t) \psi(g*t)$	17.65	0.00	25	587.78
12 $\phi(g,\cdot) p(g*\text{initiation}) \psi(g*t)$	17.73	0.00	20	599.35
13 $\phi(g,\cdot) p(g*t) \psi(g+T)$	18.37	0.00	18	604.49
14 $\phi(\cdot) p(g*t) \psi(g*T)$	19.63	0.00	18	605.75
15 $\phi(g+T) p(g*t) \psi(g*t)$	19.94	0.00	26	587.73
16 $\phi(g,\cdot) p(g*t) \psi(g*T)$	20.38	0.00	19	604.26
17 $\phi(\cdot,\cdot) p(g*t) \psi(g*t)$	20.52	0.00	25	590.65

*Lowest QAIC_c value = 624.24

4.3.5 Annual trends in nest success and condition

I estimated (1) the number of females that nested successfully and (2) the number of individuals in good condition (\hat{N}_i^r) based on:

$$\hat{N}_i^r = \frac{m_i^r}{\hat{p}_i^r} \quad (4.1)$$

where m_i^r is the number of individuals captured in state r (i.e., number of captures where females nested successfully or were in good condition at capture) at time i , divided by the corresponding recapture probability (\hat{p}_i^r). I used estimates of state-specific capture probabilities based on the top model to calculate the approximate variance of the proportion of the population that nested successfully (Nichols et al. 1994). I did not use parameter estimates from weighted model averages to calculate these variances because (1) QAICc weight for this model was relatively high ($\omega = 0.45$ out of 1.0), and (2) the variance approximation is already biased high when recapture probabilities vary among states (Nichols et al. 1994). For the proportion of the population in good condition, I calculated the variance based on model average equal capture probabilities among condition states as outlined by Nichols et al. (1994). Mark-recapture do not provide recapture probabilities for the first year of any study (White and Burnham 1999), therefore, for the above population proportions, I used the annual patterns denoted by my models to project recapture rates for 1995.

I investigated trends in nest success and female condition using linear regressions weighted by the variance⁻¹ of population proportion that nested successfully and in good condition. I used the slope as the best linear unbiased estimate for annual trends (SAS 1996). Lastly, I used Pearson correlation coefficients to test for correlations between the proportion of the population that nested successfully and estimates of Mayfield nest success during the same time period. Nest success data were based on that of Kellett et al. (2003). Costs associated with nest success or condition were calculated as the difference between probabilities of remaining in the same state and changing states (i.e., $\hat{\Psi}^{rr}$ vs $\hat{\Psi}^{sr}$; Nichols et al. 1994).

All results are reported as \pm SE and all parameter estimates reflect weighted model average estimates (Burnham and Anderson 2002) unless otherwise noted.

4.4 RESULTS

Encounter histories for multistate analysis of annual nest success and female condition consisted of 244 and 239 individually marked King Eider females, respectively. Annual median nest initiation appeared to decline with time. Scaled median nest initiation dates were 1, 6, 6, 9, 10, 7, 8, respectively, for 1996 to 2002. Based on the estimated number of females in each state, the proportion of Karrak Lake King Eiders that nest successfully has declined somewhat with time ($\beta_{\text{NS}} = -0.06 \pm 0.02$, $F_{1,7} = 9.1$, $P = 0.02$, $r^2 = 0.60$). Temporal patterns in the proportion of the population that nested successfully was not correlated with temporal patterns of Mayfield nest success estimates ($r^2 = 0.25$, $P = 0.20$; Figure 4.1). Similar to nest success, the proportion of the population in good condition has also apparently declined over time ($\beta_{\text{COND}} = -0.07 \pm 0.02$, $F_{1,7} = 6.0$, $P < 0.01$, $r^2 = 0.74$; Figure 4.2) during which time clutch size has remained constant ($F_{7,516} = 131$, $r^2 = 0.02$, $P = 0.24$).

4.4.1 Nest success and condition

Nest success models (Table 4.1) suggest $\hat{\phi}$ was similar for females that nested successfully ($\beta_{\text{S}} = 0.92$; 95% CI = 0.82 to 0.97) relative to those that failed ($\beta_{\text{F}} = 0.91$; 95% CI = 0.80 to 0.96). In contrast, \hat{p} varied by state of nest success, with trends toward higher recapture rates for successful nesters ($\beta_{\text{S}} = 0.92$; 94% CI = 0.32 to 0.99) relative to failed nesters ($\beta_{\text{F}} = 0.20$; 94% CI = 0.03 to 0.64). Transition probabilities among nest success states indicated a linear time trend, with interactions between state specific transition probabilities (Table 4.1). Parameter estimates from the top model indicated that $\hat{\Psi}_{\text{S} \rightarrow \text{F}}$ increased linearly by 0.37 (± 0.09) each year, whereas $\hat{\Psi}_{\text{F} \rightarrow \text{S}}$ declined linearly ($\beta_{\hat{\Psi}_{\text{F} \rightarrow \text{S}}} = -0.16 \pm 0.13$). Costs, in terms of future reproductive efforts, appeared to increase over time, as the probability of females that failed their nesting attempt in year i tended toward greater nesting success during the subsequent year than

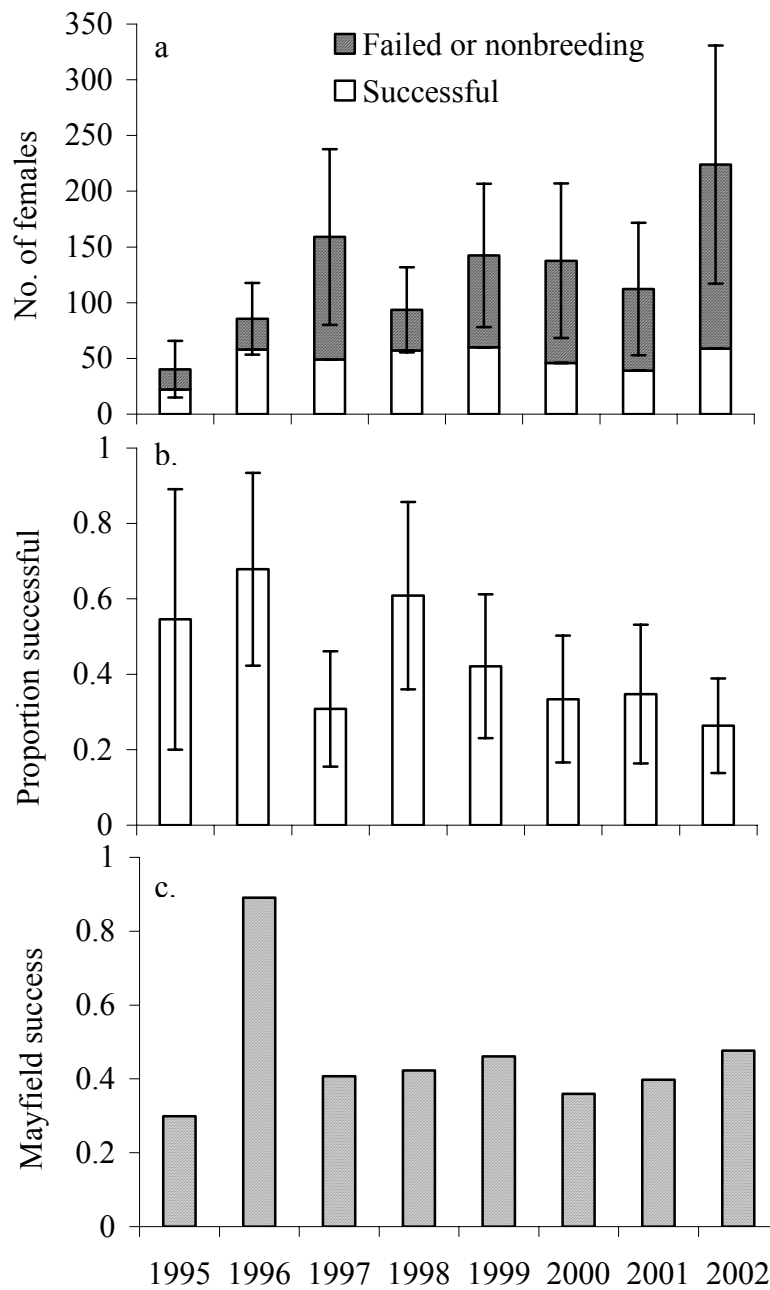


Figure 4.1 Estimated number (\pm 95% CI) of King Eider resident females to have successful breeding attempts at Karrak Lake, Nunavut during 1995 – 2002, relative to those that failed or did not breed (a), proportion of the population estimated to be successful (b), and relative to Mayfield nest success estimates for the same population during this period (c). Nest success estimates are from Kellett et al. (2003; 1995-2001) and Alisauskas, unpubl. data (2002).

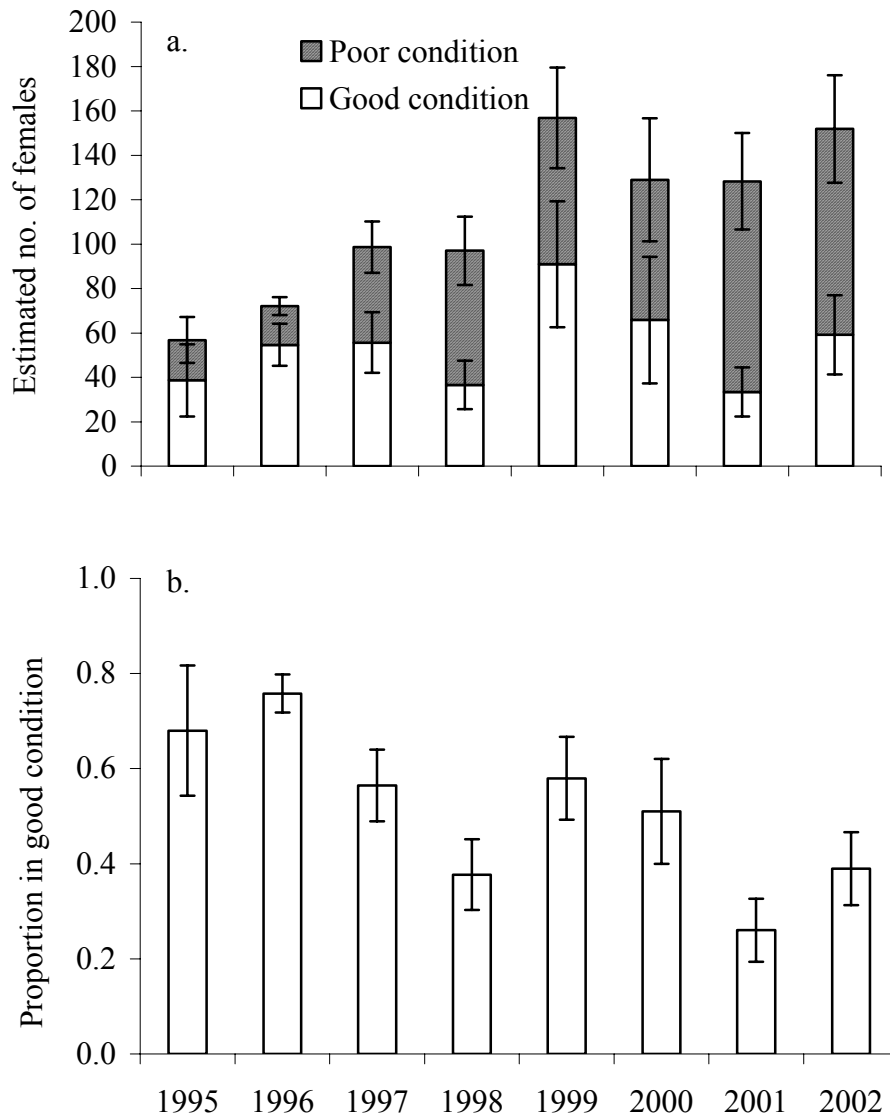


Figure 4.2 Estimated number (\pm 95% CI) of nesting King Eider resident females to have been in relative good or poor body condition at Karrak Lake, Nunavut during 1995 – 2002 (a) and the annual variability in the proportion of the population estimated to be in good condition (b).

were females that nested successfully during the previous year (Figure 4.3). Annual median nest initiation date had no apparent effect on nest success state for any of the modeled parameters ($QAIC_c > 3$; Burnham and Anderson 1992).

Weighted model averages from models for female condition (Table 4.2) suggest $\hat{\phi}$ did not differ for females in good ($\beta_G = 0.95$; 95% CI = 0.84 to 0.99) and poor condition ($\beta_P = 0.88$; 95% CI = 0.75 to 0.95). Similarly, models suggest that \hat{p} did not differ among state of condition, with \hat{p} declining in years of late nest initiation ($\beta = -0.26$; 95% CI = -0.10 to -0.41). Transition probabilities among states of body condition was constant across time and states, ($\beta_{G \rightarrow P, P \rightarrow G} = 0.31$; 95% CI = 0.23 to 0.42), such that females in good condition tended to remain in good condition and those in poor condition tended to be in poor condition during subsequent captures ($1 - \hat{\Psi} = 0.69$ probability of remaining in the same state).

4.5 DISCUSSION

I did not detect either reduced survival or increased permanent emigration that resulted from successful nesting by King Eiders. However, the data suggest that successful nesters bred more frequently or, at least experienced more frequent success, as indicated by higher recapture probabilities. Part of the difference in capture probabilities between successful and failed nesters likely resulted from nest failure before capture. Other studies have shown that individuals with higher reproductive effort are likely higher quality individuals, with no phenotypic costs associated with increased reproductive effort (Meadow voles *Microtus pennsylvanicus*, Nichols et al. 1994; Common Guillemots *Uria aalge*, Harris and Wanless 1995; Black-legged Kittiwake *Rissa tridactyla*, Cam et al. 1998; Common Eiders *Somateria mollissima*, Yoccoz et al. 2002). Moreover, if survival costs associated with reproduction do exist, such costs may reflect environmental pressures (Price and Schluter 1991). For example, in ground-nesting prairie waterfowl, the greatest annual mortality risk is generally predation during the nesting period (Sargent et al. 1984). In order for long-lived species to have adapted high survival, mortality risks during the breeding season

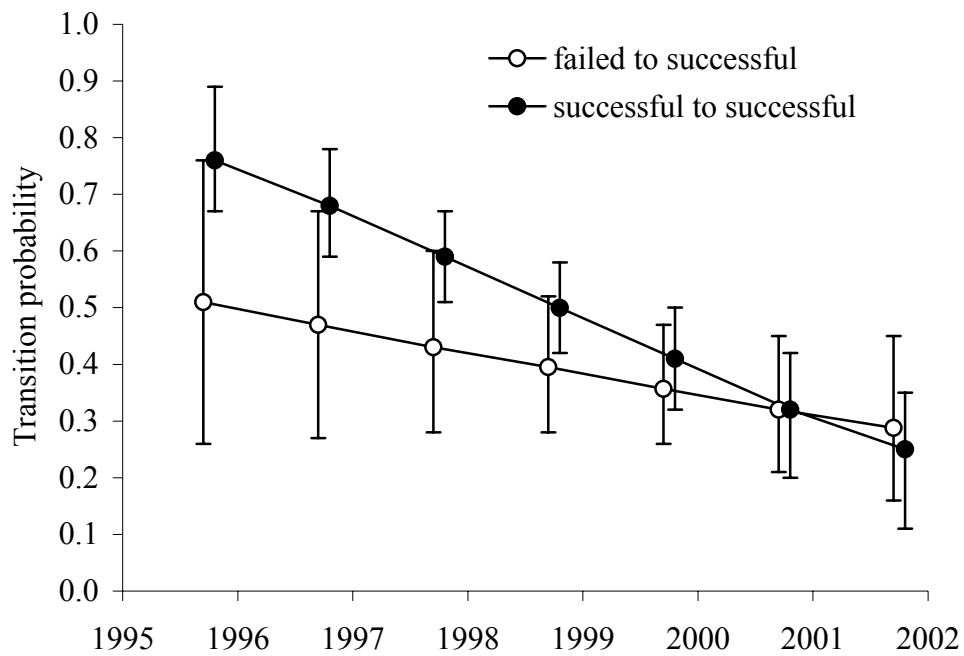


Figure 4.3 Probability (\pm 95% CI) that successful and failed nesters at Karrak Lake, Nunavut during 1995 – 2002, were able to nest successfully during the subsequent year. As long as the probability of remaining a successful breeder is \geq probability of moving from failed to successful breeding status, there are assumed to be no costs in terms of future reproductive efforts incurred (Nichols and Kendall 1994).

must be low. Accordingly, King Eiders in this study nested primarily on islands where mortality risks to females and their nests are low relative to mainland areas where probability of encounters by mammalian predators are higher (Kellett et al. 2003). However, caution must be used when applying these results to other nesting populations, as King Eider nesting populations elsewhere are thought to nest primarily on mainland habitats (Suydam 2000).

The probability that successful nesters became unsuccessful in the next year increased during the course of this study, while the probability that failed nesters became successful declined. As a result, a smaller proportion of the population nested successfully each year. Over the same period of study, local population size of nesting females (defined as those that ever nested but may have temporarily emigrated) grew by about 20% (Chapter 3). Thus, the increasing propensity of previously successful nesters to become unsuccessful, and a decrease in the proportion of the population nesting successfully is consistent with density-dependence. Such density dependent costs may occur, for example, if higher densities lead to greater conspicuousness of the nests to predators (Anderson and Titman 1992), or decreased nest success resulting from brood parasitism (Eadie and Anstey 1999). Alternatively, decreased proportional nest success may represent a shift in age-structure. If a larger proportion of the population has shifted toward younger individuals that are less successful at nesting (Raveling 1981, Aldrich and Raveling 1983). Importantly, temporal patterns of Mayfield nest success estimates (probability of successful nesting given that an individual tried to nest) did not coincide with the declining probability of successful nesting, given that an individual had not permanently emigrated (i.e., product of breeding probability and nest success). Current population projection studies incorporate Mayfield nest success and not proportional breeding (Flint et al. 1998, Hoekman et al. 2002). These results emphasize the importance of incorporating multistate approaches into projection models (Fujiwara & Caswell 2002), specifically, the importance of accounting for the proportion of breeders breeding individuals as this would have a greater effect on recruitment and population dynamics than Mayfield nest success alone.

Nest initiation date had no apparent effect on state of nest success or apparent nutrient reserves, as the proportion of individuals moving from failed nest success or poor condition did not improve in years of earlier breeding. Late arctic springs generally result in reduced nest densities (Coulson 1984, Babcock et al. 2002). Recapture probability for female condition models was lowest in years when nest initiation was delayed and I suggest this resulted from either early nest failure or a greater number of individuals forgoing breeding attempts in these years, either of which would leave fewer marked birds available for capture. Conversely, recapture probability for states of nest success varied more among success states than with annual nest initiation dates, inferring that successful nesting had a greater influence on local breeding probability (or fidelity) during the following year than did late spring conditions.

I found that apparent survival and recapture probabilities were similar among females of good and poor condition, implying no condition-related phenotypic costs. However, if females of poorest condition abandon their nests during laying or early incubation, or forgo breeding attempts altogether, my indices of poor and good condition would more accurately represent females in average and above average condition. Regardless, the probability of remaining in the same relative body condition among years was more than double that of changing condition states, suggesting variations in individual quality. I discount that varying condition is due to wintering regions, as most individuals from the local population winter in the west and condition indices did not differ by wintering area even when nest initiation dates did (Mehl. et al. 2004).

Finally, these results provided insight on density dependent nest success and have shown the usefulness of multistate analysis to investigate patterns of individual variation, and the need to account for these patterns when addressing demographics. Intermittent breeding can be extensive within populations and its occurrence can have a profound influence on population dynamics (Coulson 1984, Cam et al. 1998). Future work is needed to identify heterogeneity of failed nesters. Use of memory models are data hungry and although data presented here are too sparse for use in such models, longer-term data collected with these methods in mind are important if we are to

understand if long-term changes are a function of individual heterogeneity (Cooch et al. 2002). In addition, use of permanent individual markers that allow for resighting individuals without recapture, or use multiple captures within the same season (i.e., robust design), are needed to directly estimate breeding propensity and assess breeding propensities with prior nest success (Kendall et al. 1997, Anderson et al. 2001, Cooch et al. 2002).

5. KING EIDER BROOD ECOLOGY: INFLUENCE OF ABIOTIC AND BIOTIC FACTORS

5.1 INTRODUCTION

Knowledge of survival, movements and habitat requirements of waterfowl broods is essential, as duckling survival constitutes an important component of recruitment (Johnson et al. 1992, Sedinger 1992). After nest success, duckling survival is typically the most limiting factor on recruitment (Johnson et al. 1992, Cowardin and Blohm 1992) because, despite successful nesting, entire broods may be lost (Ringelman and Longcore 1982, Mauser et al. 1994, Korschgen et al. 1996). Consequently, the brood-rearing period may act as an important bottleneck in annual productivity (Flint et al. 1998).

Estimation of probabilities for transition between sequential states in an organism's life cycle, including up to recruitment into the breeding cohort, is important for understanding population dynamics of long-lived species, as this parameter can contribute greatly to population growth (Coulson 1984). Adult survival constitutes the greatest proportion of annual rate of population change in long-lived species (Rockwell et al. 1997, Crone 2001), but long-lived species tend to show constant adult survival (Coulson 1984, Gaillard et al. 1998, Harris and Wanless 1995). Moreover, retrospective analyses indicate that high variability in recruitment rates can be the underlying cause of fluctuations in population size (Coulson 1984, Gaillard et al. 1998, Cooch et al. 2001).

Several abiotic and biotic factors are correlated with pre fledgling survival of precocial young, to include weather (Mendenhall 1979), hatch date (Cooke and Findlay 1982), dispersal distance of broods (Ball et al. 1975, Sedinger 1992), and offspring and female attributes such as size and condition (Afton and Paulus 1992,

Christensen 1999). Previous research has focused on these relationships in terms of only a few correlates at once, and was restricted to pooling survival estimates from multiple weeks to establish composite estimates for the brood-rearing period (Dzus and Clark 1997, Flint et al. 1997). Capture-mark-resight (CMR) methodologies permit greater flexibility when modeling survival estimates, and allow partitioning the amount of variation in survival that can be attributed to each of these potential correlates (White and Burnham 1999, Pelayo and Clark 2003). Furthermore, if data are sampled appropriately, these techniques provide estimates of variable daily survival rates (Lebreton et al. 1992).

My objectives were to use CMR techniques, combined with radio-telemetry, to investigate potential covariates of King Eider offspring survival. By following radio-marked females and resighting individually-marked ducklings, I gained insight about the importance of brood-rearing habitats on brood survival and, in turn, the influence of brood loss on residency in such habitats by females with young and those without. Based on previous observations, I predicted that offspring mortality would be greatest during the first week after hatch, and that females with young would disperse from the study area by using the rivers to reach the sea before fledging (Parmelee et al. 1967).

5.2 STUDY AREA

The study was conducted on Karrak and Adventure Lakes and on freshwater habitats surrounding these lakes. The study area is about 60 km south of the Queen Maud Gulf, Nunavut, Canada (67° 14' N, 100° 15' W). Karrak and Adventure Lakes support the highest known density of nesting King Eiders (Kellett and Alisauskas 1997). Karrak Lake averages about 1.2 m in depth, with an area of 16.1 km² and contains 2.5 km² of various-sized islands; Adventure Lake is about 300m east of Karrak Lake, and averages about 2.5 m in depth, is 8.8 km² in size and contains 0.2 km² of islands (Kellett and Alisauskas 2000). Surrounding wetland habitats vary in size, with most nearby wetlands being smaller than either Karrak or Adventure Lakes. A weather station at the Karrak Lake research camp recorded daily maximum and minimum ambient temperatures, precipitation, and wind speed.

5.3 METHODS

5.3.1 Nest Search and Trapping

I systematically searched islands within Karrak and Adventure Lakes for King Eider nests beginning in mid-June. Islands were searched 2-3 times to increase my odds of finding most nests. I calculated nest initiation date, defined as the date the first egg was laid in a nest, by back-dating from known laying dates or from estimated incubation stages by candling eggs (Weller 1956), assuming an incubation length of 23 days (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973). About 4-7 days before predicted hatch dates, I trapped nesting female King Eiders by laying mist nets over incubating females or by use of self-triggered bow nets. Upon capture, I marked females with standard CWS/USFWS leg bands, and weighed each with Pesola scale (+10g). I recorded (twice for each female) morphometric measurements of head length, and tarsus using dial calipers (± 1.0 mm), and wing chord (± 1.0 mm) using a flat ruler (± 1.0 mm) (Dzubin and Cooch 1993). I attached subcutaneous anchored transmitters (Advanced Telemetry SystemsTM; Mauser and Jarvis 1991) to a subset of captured females ($n = 30$, every 2nd captured female in 2000; $n = 29$ every 3rd capture in 2001) and using surgical sutures attached a uniquely colored combination of nasal tags through the nares for individual identification. Use of dissolving sutures permitted nasal tags to break away from the nares before winter. Before releasing newly radio-marked females, I removed all eggs from nests, and replaced them with an equal number of color-dyed chicken eggs. I administered 1-1.5 ml Propofol in the tarsal vein of the female to reduce nest abandonment after radio-attachment (Machin and Caulkett 2000). King Eider eggs were artificially incubated in a portable incubator at camp. At hatch, I weighed ducklings using a digital scale (± 0.1 g), recorded head length and tarsus measurements (twice each) using digital calipers (± 0.5 mm), and marked each with a plasticine leg band (Blums et al. 1994) and a uniquely-colored nape-marker (Taber 1949, Gullion 1951, Pelayo 2001). I then returned marked ducklings to their original nests loosely wrapped in a paper-towel envelope so that they would remain in the nest until the female returned (Korschgen et al. 1996).

Nests of 6 radio-marked females were depredated in 2000, and one nest was abandoned before ducklings could be returned to nests. I divided ducklings from the 6 failed nests among 4 different radio-marked females whose broods had hatched on the same day, artificially increasing brood size for 4 of 23 radio-marked females. Brood enlargements consisted of 3, 5, 6, and 7 extra ducklings for a total brood size of 5, 10, 11, and 11, respectively. Six radio-marked females abandoned their nests in 2001, and another 12 nests were depredated before duckling hatch. I did not manipulate brood size of radio-marked females in 2001.

I located radio-marked females and associated ducklings once every 2-days over a 24-day period and recorded total number of adult female King Eiders present, number of ducklings and corresponding color codes of nape tags, status of brood (amalgamated or not), and habitat type (pond [$<1\text{km}^2$], lake [$>1\text{km}^2$], or river). To minimize observer disturbance to broods that would lead to possible gull predation, I did not attempt to record nape tag colors when foraging gulls (*Larus* spp.) were near broods. To better understand differences in habitat use and movements of brood and non-brood females, I also monitored radio-marked females that had failed their nesting attempt or had experienced total brood loss.

The Animal Care Committee - University of Saskatchewan approved methods on behalf of the Canadian Council on Animal Care.

5.4 STATISTICAL ANALYSES

5.4.1 Covariates for Survival Analyses

I used principal component analysis (PCA) of the correlation matrix of mean individual measurements to establish an index of structural size (SAS Institute Inc. 1996). I used residuals from general linear models (GLM) to obtain indices of (1) adult female body weight corrected for structural size ($\text{PC1}^{\text{adult}}$), and incubation stage at capture, and (2) duckling weight corrected for duckling size ($\text{PC1}^{\text{duckling}}$) and hatch date (Alisauskas and Ankney 1990, Hochachka and Smith 1991). I tested for brood size variation among years and hatch dates using GLM. To examine if larger females produced larger, better-conditioned ducklings, I assessed correlations between duckling size and condition with female size. I also used PCA to derive indices of

weather ($PC1^{weather}$, $PC2^{weather}$) from the correlation matrix of mean maximum relative humidity, minimum ambient temperature, and maximum wind speed for first 7 days after hatch.

I considered the following effects as sources of variation in survival: year, hatch date (adjusted for median hatch of the colony in a given year), brood size, natal female size and condition, duckling size and condition, PC scores of weather, and distance traveled from the nest site during the first week after hatch. In addition, I investigated presence of an optimal hatch date and brood size using quadratic relationships of these covariates with survival and investigated pseudothreshold relationships among other covariates (excluding weather and body condition). I assessed correlations of female size and hatch date, using hatch date relative to median hatch date among years in my analyses. Models that assessed survival of ducklings that remained with radio-marked females included all 16 covariates above. Survival models based on all ducklings, including those that joined other broods, did not include covariates of brood movements, brood size, or natal female, as these covariates would theoretically have no affect on ducklings that did not remain with the natal brood ($n = 8$ covariates). Brood-level models excluded individual-level covariates of duckling size and condition ($n = 13$ covariates).

5.4.2 Modeling Apparent Survival

I estimated apparent survival (ϕ_i) and recapture probability (p_i) of marked ducklings using Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999). I was unable to obtain estimates of true survival (S), because I could not locate all ducklings at specific intervals due to early transmitter failure and because I did not record all nape tag colors in the presence of foraging gulls. Therefore, my estimates of $\hat{\phi}_i$ represent the product of true survival and fidelity to study area during brood-rearing. I confirmed identities of radio-marked females with failed transmitters, by observing nasal-tag combinations. I modeled $\hat{\phi}_i$ and \hat{p}_i for (1) marked ducklings that remained with radio-marked females, and for (2) all marked ducklings, including ducklings that joined other broods. Fates among broodmates

likely were not independent because of complete brood loss, so I also modeled (3) brood-level survival for all broods associated with radio-marked females. Nape-markers were placed too low on necks of ducklings from 2 broods ($n=1$ brood/year), rendering color-combinations unreadable. Hence, these ducklings were excluded from analyses of individual duckling survival.

I tested model fit using the global time dependence model ($\hat{\phi}_i, \hat{p}_i$) and the parametric bootstrap method in Program MARK (White and Burnham 1999). I adjusted the variance inflation factor (\hat{c}) to account for lack of model fit by dividing the deviance of the most general model by the mean deviance from 1000 bootstrap iterations (Burnham and Anderson 2002). All models were chosen subsequently based on parsimony using quasi-likelihood Akaike's Information Criterion (QAIC_c) to correct for small sample size and lack of fit due to overdispersion (Akaike 1985, Burnham and Anderson 2002).

In addition to my global, time dependence model, I considered models with constancy in resighting and survival probabilities. I chose the most parsimonious model without covariates and used this model to investigate age trends with survival. Age trends included survival modeled as (1) a linear function and (2) natural log of a linear relationship (pseudothreshold model) of duckling age, whereby offspring survival increased with age, eventually approaching but not reaching 100%. After obtaining the model with the most parsimonious trend in survival with age, I considered possible covariates as tests of specific hypotheses. I then verified the significance of the slope ($\hat{\beta}_1$) for each covariate. When the 95% CI encompassed zero, I considered the precision of the estimator to be poor and did not re-enter the covariate back into the model. I entered each covariate singularly and combined with other covariates. I tested for interactions between univariate variables, and interactions of all covariates with age. I considered the following 6 covariates important (i.e., 95% CI did not encompass zero) to survival of ducklings that remained with radio-marked females: (1) hatch date, (2) pseudothreshold hatch date, (3) duckling size, (4) pseudothreshold duckling size, (5) female size, and (6) pseudothreshold female size.

I observed radio-marked females only once during each two-day period, so survival estimates represent a combined two-day $\hat{\phi}$ rate. Lastly, to account for model uncertainty, I used model-averaging with QAIC_c weights to estimate survival and recapture probabilities for the study period (Burnham and Anderson 2002). Apparent survival for the duration of my study was defined as the product of the 11 two-day intervals between 12 observational periods, based on weighted averages. Variances for model-averaged estimates were calculated using the delta method to account for covariance between estimates across survival periods. Parameter estimates represent the maximum-likelihood and corresponding 95% CI based on the SIN (identity matrices) and logit link function (non-identity matrices) in Program MARK (White and Burnham 1999). Covariates were scaled $[(x_i - \bar{x}) / SD]$ automatically by Program MARK.

5.4.3 Survival and Movements Among Habitats

To assess how dispersal and habitat use influenced survival, I used multi-state models (Lebreton et al. 1999) where encounters were classified as one of two states: (K) Karrak or Adventure Lake, where most ducklings were hatched, or (O) all other habitats, such as lakes, ponds, or rivers away from Karrak or Adventure Lakes. Probabilities estimated from multistate models included: (1) apparent survival, ϕ_i^r ; (2) resighting probability, p_i^r ; and (3) conditional transition probability, Ψ_i^{rs} (Brownie et al. 1993, Nichols et al. 1994).

I tested goodness-of-fit of habitat models using U-CARE (Pradel et al. 2003) and calculated Quasi-Akaike's Information Criterion (QAIC_c) from AIC_c to correct for small sample size using a variance inflation factor $\hat{c} = \frac{\chi^2}{df}$ to correct for over dispersion (Akaike 1985, Burnham and Anderson 2002). Model selection proceeded as above, by first adding time constraints to resighting probabilities, then transition probabilities, and lastly time constraints to survival. I did not model multistate data with covariates. Finally, to compare habitat use between females with and without

broods, I examined frequency of habitat use by both groups of females using χ^2 analysis weighted by sample size for each group.

5.5 RESULTS

5.5.1 Marked Individuals and Brood Size

I monitored 111 and 46 individually-marked ducklings from broods of 23 and 11 radio-marked King Eiders in 2000 and 2001, respectively. I encountered individually-marked ducklings 252 and 128 times and radio-marked broods 86 and 50 times in 2000 and 2001, respectively. I also encountered radio-marked females following total brood loss 119 and 54 times and radio-marked females with failed nesting attempts 30 and 138 times in 2000 and 2001, respectively.

Brood size did not vary among years or hatch dates ($F_{10,32} = 1.77$, $P = 0.13$). Brood size, to include artificially enlarged broods, ranged from 3-11 in 2000, and 3-6 in 2001. Median hatch date for the nesting colony was 2 days earlier in 2001 ($n = 176$ nests) than in 2000 ($n = 164$ nests). Marked ducklings represented mostly early and mid-hatched nests (Figure 5.1).

Brood amalgamations occurred within 2 days of hatch ($n = 5$ broods in 2000; 3 broods in 2001) with a mean of 3 females and 9 ducklings, and 4 females and 7 ducklings in 2000 and 2001, respectively. Amalgamated broods ranged from 2 females:7 ducklings to as large as 10 females:29 ducklings. Amalgamations appeared to remain stable through time (i.e., broods did not group together and later disband), although females with recorded total brood-loss, appeared to join broods temporarily. I also observed temporary brood abandonment. In this case, I returned three individually-marked ducklings to one radio-marked female. This specific female had no young during the first two observations after hatch. However, on the 3rd observation, she was accompanied by three young, only one of which hatched from her nest. One other marked duckling from this female was observed in a separate brood with a non-marked female. I never observed more than one marked duckling in unmarked broods.

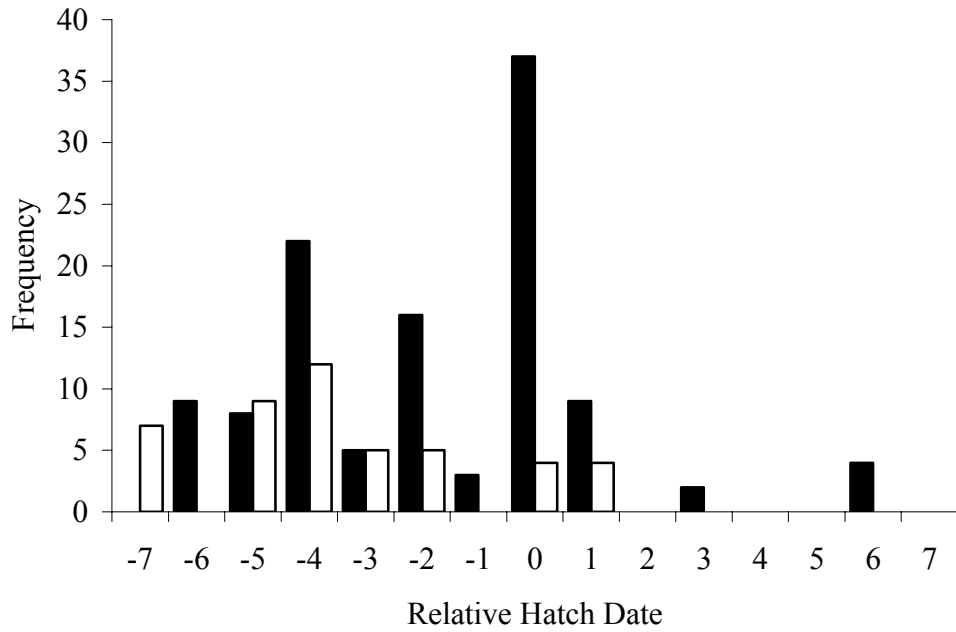


Figure 5.1 Frequency distribution of relative hatch dates of King Eider broods marked on Karrak and Adventure Lakes, Nunavut during 2000 (solid bars) and 2001 (open bars). Hatch dates are relative to the median hatch date for a given year.

5.5.2 Covariates of Duckling Survival

My index of duckling size ($PC1^{\text{duckling}}$) accounted for 73% of variation in body measures, with PC1 loadings of 0.86 for both head and tarsus. Adult female size ($PC1^{\text{adult}}$) accounted for 66% of the variation in female body measures, with loadings of 0.80, 0.78, 0.84 for head length, tarsus, and wing, respectively. Larger structural size was positively correlated with body weight of both ducklings ($F_{2,156} = 15.82$, $r^2 = 0.17$, $P < 0.01$) and adults ($F_{2,33} = 15.50$, $r^2 = 0.50$, $P < 0.01$). Larger adult female size correlated with hatch of larger ducklings ($r = 0.36$, $n = 157$, $P < 0.01$) and ducklings of better condition ($r = 0.17$, $n = 157$, $P = 0.03$), but nests of larger females did not hatch earlier ($n = 34$, $P > 0.73$).

Weather ($PC1^{\text{weather}}$) accounted for 57% of the variation in maximum relative humidity, minimum ambient temperature, and maximum wind speed for the first week of hatch, with respective loadings of -0.82 , 0.90 , and 0.49 . Positive $PC1^{\text{weather}}$ scores represented drier, warmer and blustery days, while negative scores represented damper, cooler and calmer days. $PC2^{\text{weather}}$ accounted for an additional 31% of total variation in weather data, i.e., 88% cumulative variation for $PC1^{\text{weather}}$ and $PC2^{\text{weather}}$, with loadings of 0.43 , -0.08 , and 0.86 for maximum relative humidity, minimum temperature, and maximum wind speed, respectively. Thus, positive $PC2^{\text{weather}}$ scores represented damp, windy days, while negative scores represented dry, calm days.

5.5.3 Variation in Apparent Survival of Ducklings and Broods

Bootstrap results suggest that duckling and brood encounter data were overdispersed, so I applied variance inflation factors (\hat{c}) to models for respective groups of analyses. I considered 40 candidate models ($\hat{c} = 1.34$) for ducklings accompanied only by radio-marked females (Table 5.1), 24 models ($\hat{c} = 1.27$) for all ducklings, including those associated with non-natal females (Table 5.2), and 30 models ($\hat{c} = 1.35$) for analyses of brood survival (Table 5.3). I also considered 17 multistate models for estimation of movement and survival probabilities between habitat types ($\hat{c} = 1.51$; Table 5.4). Model results suggested that estimates of both duckling and brood survival were

Table 5.1 Top 14 of 40 candidate models used to investigate covariates to apparent survival (ϕ) and resighting probability (p) of King Eider ducklings at Karrak Lake, Nunavut in 2000 and 2001. Models are based on observations of marked ducklings brooded by radio-females. Parameter estimates included year and age effects, where time varied annually and with age (yr,t), linearly with age (T), in a pseudothreshold relationship with age (T_{ln}), and no time or year variation (.). Model covariates included: hatch date (hd), brood size (bs), duckling body size (ds), duckling condition (dc), female size (fs) and female condition (fc), distance moved from the nest during the first week (dist), and principal components of weather during the first week after hatch (w1, w2). Hatch date, distance moved, brood size, and female and duckling size were also entered as a pseudothreshold relationship (X_{ln}), and hatch date and brood size in a quadratic relationship (X_{TT}). Models are ranked in accordance QAIC_c values and are denoted as additive models (+) or models with interaction (*).

Number/Model	ΔQAIC_c^a	QAIC _c Weights	No. of Parameters	QDeviance
1 $\phi(., T_{ln} fs_{ln} * hd_{ln}) p(yr, t)$	0.00	0.57	23	578.84
2 $\phi(., T_{ln} + fs_{ln} * hd_{ln} + dc) p(yr, t)$	0.96	0.36	24	577.55
3 $\phi(., T_{ln} fs_{ln} + hd_{ln}) p(yr, t)$	4.32	0.07	22	585.39
4 $\phi(., T_{ln} + fs_{ln}) p(yr, t)$	12.69	0.00	21	595.98
5 $\phi(., T_{ln} + fs) p(yr, t)$	12.88	0.00	21	596.17
6 $\phi(., T_{ln} + fs_{ln} + dc) p(yr, t)$	13.63	0.00	22	594.69
7 $\phi(., T_{ln} * fs) p(yr, t)$	14.61	0.00	22	595.68
8 $\phi(., T_{ln} + fs_{ln} * dc) p(yr, t)$	15.51	0.00	23	594.35
9 $\phi(., T_{ln} + hd_{ln}) p(yr, t)$	16.11	0.00	21	599.39
10 $\phi(., T_{ln} + hd_{ln} * dc) p(yr, t)$	17.68	0.00	23	596.52
11 $\phi(., T_{ln} + hd) p(yr, t)$	18.14	0.00	21	601.42
12 $\phi(., T_{ln} * hd) p(yr, t)$	20.15	0.00	22	601.22
13 $\phi(., T_{ln} + dist) p(yr, t)$	24.82	0.00	21	608.10
14 $\phi(., T_{ln} * ds_{ln}) p(yr, t)$	25.28	0.00	22	606.35

^alowest QAIC_c value = 627.52

Table 5.2 Top 14 of 24 candidate models used to investigate covariates to apparent survival (ϕ) and resighting probability (p) of King Eider ducklings at Karrak Lake, Nunavut in 2000 and 2001. Models are based on observations of individually marked ducklings that remained with radio-marked females and marked ducklings that mixed with non-radio-marked broods. Parameter estimates included year and age effects, where time varied annually and with age (yr,t), linearly with age (T), in a pseudothreshold relationship with age (T_{ln}), and no time or year variation (.). Model covariates included: hatch date (hd), duckling body size (ds), duckling condition (dc), and principal components of weather during the first week after hatch (w1, w2). Hatch date and duckling size were also entered as a pseudothreshold relationship (X_{ln}), and hatch date in a quadratic relationship (X_{TT}). Models are ranked in accordance QAIC_c values and are denoted as additive models (+) or models with interaction (*).

Model Number/Name	$\Delta QAIC_c^a$	QAIC _c Weights	No. of Paramters	QDeviance
1 $\phi(., T_{ln} * dc + hd_{ln}) p(yr, t)$	0.00	0.46	23	755.00
2 $\phi(., T_{ln} + hd_{ln} + dc) p(yr, t)$	0.81	0.31	22	758.04
3 $\phi(., T_{ln} + hd_{ln} * dc) p(yr, t)$	2.69	0.12	23	757.69
4 $\phi(., T_{ln} + hd_{ln}) p(yr, t)$	3.97	0.06	21	763.40
5 $\phi(., T_{ln} + hd) p(yr, t)$	6.74	0.02	21	766.18
6 $\phi(., T_{ln} + * dc) p(yr, t)$	7.09	0.01	22	764.31
7 $\phi(., T_{ln} + dc) p(yr, t)$	7.48	0.01	21	766.92
8 $\phi(., T_{ln} * hd) p(yr, t)$	8.82	0.01	22	766.05
9 $\phi(., T_{ln}) p(yr, t)$	10.71	0.00	20	772.35
10 $\phi(., T_{ln} + w2) p(yr, t)$	12.28	0.00	21	771.72
11 $\phi(., T_{ln} + hd_{TT}) p(yr, t)$	12.29	0.00	21	771.73
12 $\phi(., T_{ln} + w1) p(yr, t)$	12.84	0.00	21	772.28
13 $\phi(., T_{ln} + dist_{ln}) p(yr, t)$	12.86	0.00	21	772.30
14 $\phi(., T_{ln} + dist) p(yr, t)$	12.90	0.00	21	772.33

^alowest QAIC_c value = 803.62

Table 5.3 Top 14 of 30 candidate models used to investigate brood-level apparent survival (ϕ) and resighting probability (p) of King Eiders at Karrak Lake, Nunavut in 2000 and 2001. Models are based on observations of marked broods with radio-marked females. Parameter estimates included year and age effects, where time varied annually and with age (yr,t), linearly with age (T), in a pseudothreshold relationship with age (T_{ln}), and no time or year variation (.). Model covariates included: hatch date (hd), brood size (bs), female size (fs) and female condition (fc), distance moved from the nest during the first week (dist), and principal components of weather during the first week after hatch (w1, w2). Hatch date, distance moved, brood size, and female size were also entered as a pseudothreshold relationship (X_{ln}), and hatch date and brood size in a quadratic relationship (X_{TT}). Models are ranked in accordance QAIC_c values and are denoted as additive models (+) or models with interaction (*).

Model Number/Name	$\Delta QAIC_c^a$	QAIC _c	No. of Weights Parameters	QDeviance
1 $\phi(., T_{ln}+fs) p(.,.)$	0.00	0.10	4	236.06
2 $\phi(., T_{ln}) p(.,.)$	0.05	0.10	3	238.21
3 $\phi(., T_{ln}+fs_{ln}) p(.,.)$	0.56	0.08	4	236.62
4 $\phi(., T_{ln}+hd_{ln}) p(.,.)$	0.89	0.07	4	236.95
5 $\phi(., T_{ln}+hd) p(.,.)$	1.19	0.06	4	237.25
6 $\phi(., t) p(.,.)$	1.39	0.05	7	231.01
7 $\phi(., T_{ln}+fc) p(.,.)$	1.40	0.05	4	237.46
8 $\phi(., T_{ln}+w2) p(.,.)$	1.51	0.05	4	237.57
9 $\phi(., T_{ln}*w2) p(.,.)$	1.58	0.05	5	235.52
10 $\phi(., T_{ln}*fs) p(.,.)$	1.92	0.04	5	235.86
11 $\phi(., T_{ln}+hd_{TT}) p(.,.)$	2.10	0.04	4	238.17
12 $\phi(., T_{ln}+bs) p(.,.)$	2.11	0.04	4	238.18
13 $\phi(., T_{ln}+bs_{ln}) p(.,.)$	2.12	0.04	4	238.19
14 $\phi(., T_{ln}+bs_{TT}) p(.,.)$	2.12	0.04	4	238.19

^alowest QAIC_c value = 244.30

Table 5.4 Top 9 of 17 candidate models used to investigate apparent survival (ϕ), resighting probability (p), and movement (Ψ) of marked King Eider broods that moved from Karrak Lake, the primary brood area, to other lakes, ponds, or rivers away from Karrak Lake. Models are based on observations of marked broods resighted with radio-marked females at Karrak Lake, Nunavut in 2000 and 2001. Parameter estimates included year and full time effects where time varied annually and with duckling age (yr,t), linearly with time (T), in a pseudothreshold relationship with time (T_{ln}) and no time or year variation (.). ϕ and p were estimated for ducklings observed on Karrak Lake (K) or on other habitats (O) and movement of ducklings from Karrak to other habitats (K-O) or movements back to Karrk Lake (O-K). Models are ranked in accordance QAIC_c values and are denoted as additive models (+) or models with interaction (*).

Model Number/Name	$\Delta QAIC_c^a$	QAIC _c	No. of Parameters	QDeviance
1 $\phi K(., T_{ln}) \phi O(., t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	0.00	0.52	30	197.93
2 $\phi K(., t) \phi O(., t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	1.30	0.27	34	189.93
3 $\phi K(., t) \phi O(yr, t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	3.46	0.09	35	189.72
4 $\phi K(., T) \phi O(., t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	4.05	0.07	30	201.98
5 $\phi K(yr, t) \phi O(yr, t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	7.09	0.01	38	186.22
6 $\phi K(yr, t) \phi O(yr, t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, 2000t, 2001.)$	7.09	0.01	38	186.22
7 $\phi K(., T_{ln}) \phi O(., t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	7.95	0.01	30	205.88
8 $\phi K(., t) \phi O(., t) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	8.79	0.01	34	197.41
9 $\phi K(., T_{ln}) \phi O(., T_{ln}) pK(yr, t) pO(., t) \Psi K-O(yr, t) \Psi O-K(yr, t)$	9.19	0.01	31	204.81

^alowest QAIC_c value = 611.84

similar among years. Total brood loss was detected in 65% of 34 broods and accounted for 84% of 126 ducklings. Most (77%) of the total brood loss occurred within two days of hatch (Figure 5.2). No mortality occurred after 14 days of age, but, due to high mortality of very young ducklings, composite survival to 24 days of age was estimated as 0.10 (95%CI = 0.05 to 0.15) for ducklings accompanied by radio-marked females, 0.16 (95%CI = 0.12 to 0.22) for all ducklings, and 0.31 (95% CI=0.13 to 0.50) for broods. My data set included 6 ducklings that were abandoned by their putative mothers, and fostered by other females with broods. In addition, I resighted four marked ducklings ($n = 3$ broods) that had joined other broods, but whose putative mothers continued to accompany siblings of the fostered ducklings.

Resighting probability of ducklings, \bar{p}^d , varied between years, and among duckling ages. For ducklings that remained with radio-marked females, $\bar{p}^d = 0.63$ (95%CI=0.42 to 0.80) in 2000, and 0.75 (95%CI=0.53 to 0.92) in 2001 (Figure 5.3). For all ducklings, $\bar{p}^d = 0.57$ (95%CI=0.37 to 0.73) in 2000, and 0.73 (95%CI=0.53 to 0.90) in 2001. Resighting probability of broods was similar among age and years, $\bar{p}^b = 0.76$ (95%CI=0.66 to 0.83).

For analyses of ducklings that remained with radio-marked females, the best model (QAIC_c weight ≈ 1.0) included combined additive effects of female size and hatch date, and interactions between these covariates, as important contributors to variation in duckling $\hat{\phi}$ (Table 5.1). In general, ducklings brooded by larger females tended to have higher survival ($\hat{\beta}_{fsize} = 0.54$, 95% CI = 0.19 to 0.90), as did ducklings that hatched earlier ($\hat{\beta}_{hatchdate} = -0.33$, 95% CI = 0.00 to -0.65; Figure 5.4). Models also suggested ducklings that hatched in better condition survived at a higher rate ($\Delta QAIC_c < 2$; Table 5.1); however, model-averaged estimates were less precise because of model uncertainty, and thus lacked precision ($\hat{\beta}_{ducklingcondition} = 0.06$, 95%CI=-0.15 to 0.28). Hence, I did not consider this to be an overwhelming influence on duckling survival. For analyses of all duckling resightings, which excluded effects of adult attributes, the top three models that included combined effects of hatch date and duckling condition

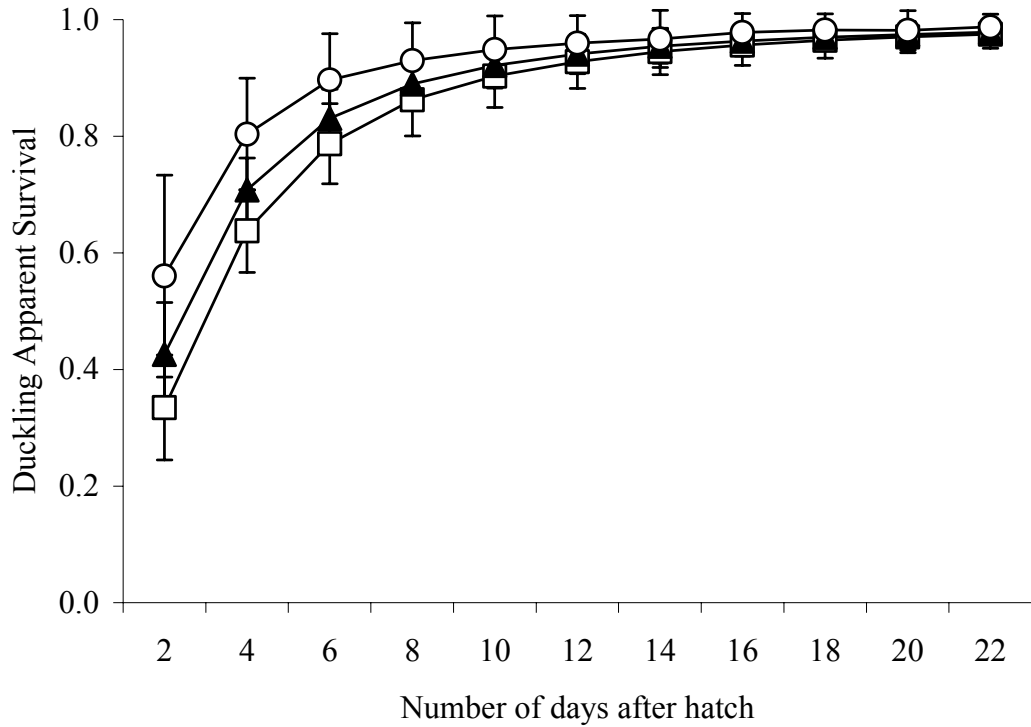


Figure 5.2 Estimates of apparent survival and 95% CI for King Eider duckling and broods marked on Karrak Lake and Adventure Lakes, Nunavut, during July and August, 2000 and 2001. Values were calculated using the logit-link function and are the weighted averages based on candidate models. Averages were weighted according to QAICc values. Open circles = brood survival, closed triangles = survival of marked ducklings, including those associated with non-natal females, and open squares = duckling survival for ducklings that remained with radio-marked females.

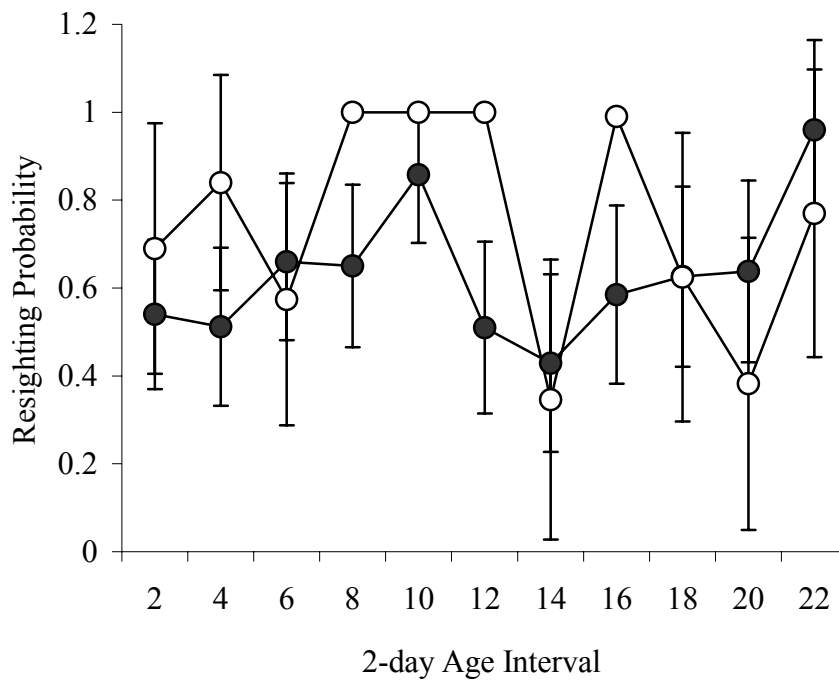


Figure 5.3 Age dependent resighting probability and 95% CI based on weighted model averages for ducklings that were marked on Karrak and Adventure Lakes, Nunavut during summers of 2000 (solid circles) and 2001 (open circles), and resighted with radio-marked females.

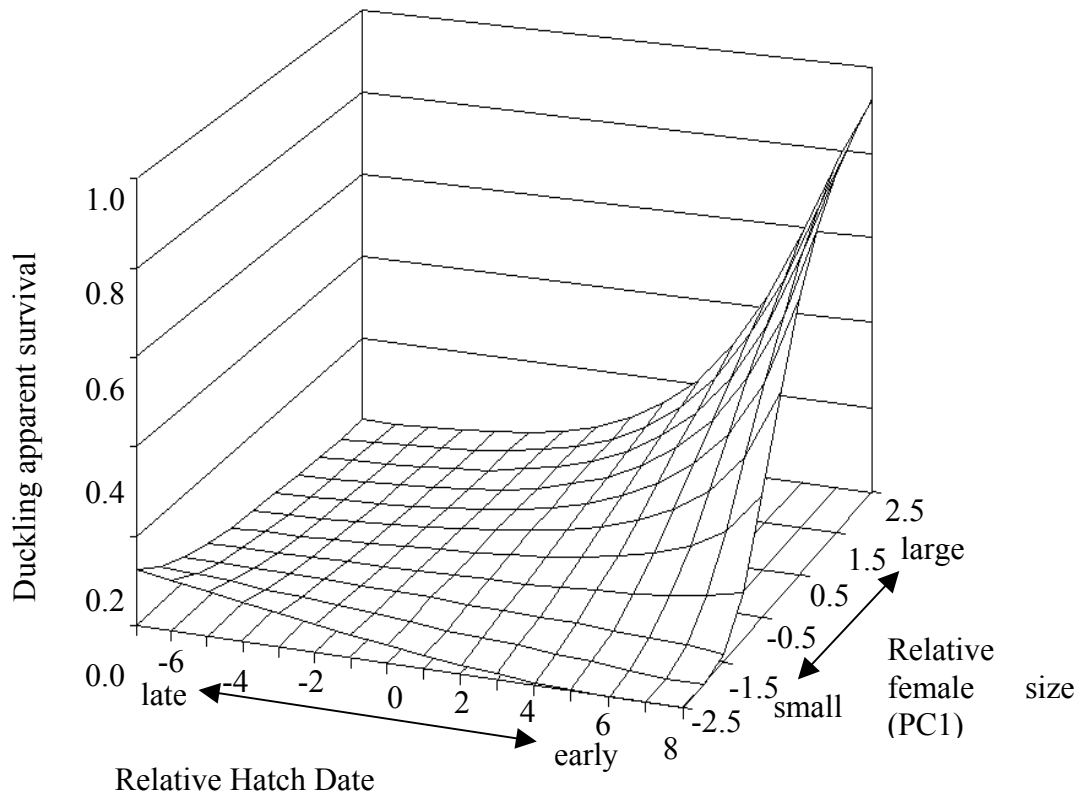


Figure 5.4 Influence of female size and hatch date on duckling apparent survival as predicted by models for ducklings that remained with radio-marked females for the first 24 days after hatch at Karrak Lake, Nunavut during 2001 and 2002. The relationship is based on weighted model averages and expresses the interaction between female size and hatch date, additive among age categories. Data are backtransformed from a logit scale ($\hat{\beta}_{femalesize_{in}} = 0.54$ [95%CI = 0.19 to 0.90], $\hat{\beta}_{hatchdate_{in}} = -0.33$ [95%CI = -0.65 to 0.00], $\hat{\beta}_{femalesize_{in} * hatchdate_{in}} = -0.48$ [95%CI = -0.03 to -0.92]).

accounted most of the model weight (weight = 0.88; Table 5.2). Model-averaged estimates suggested improved survival with increasing duckling condition ($\hat{\beta}_{\text{ducklingcondition}} = 0.41$, 95%CI = -0.06 to 0.88), but these lacked precision in predicting interactions with duckling condition with age ($\hat{\beta}_{\text{ducklingcondition} * T_{\text{in}}} = -0.21$, 95%CI = -0.75 to 0.33). There was a negative influence of late hatching dates on survival ($\hat{\beta}_{\text{hatchdate}_{\text{in}}} = -0.34$, 95%CI = -0.08 to 0.61), an inference, although weak, was similar to that from analyses of ducklings that remained with radio-marked females. Brood-level models showed some support for female size and hatch date ($\Delta\text{QAIC}_c < 2$); however, 95% CI for slope estimates of all covariates included zero (Table 5.3).

5.5.4 Dispersal and Duckling Survival

Brood movements ≥ 1 km overland, i.e., no direct water link from the main lake to the destination ponds, occurred in both years. Mean distance moved from nest locations during the first week was similar between years ($\bar{x} = 2.0$ km, range = 0.1 – 4.2 km, $n = 9$ broods 2000; $\bar{x} = 2.3$ km, range = 0.7 – 4.6 km, $n = 6$ broods 2001). Model-averaged estimates from multistate models suggested higher survival for broods that moved to habitats away from Karrak Lake (0.81, 95%CI = 0.60 to 1.02) than those that remained on Karrak Lake (0.09, 95%CI = -1.70 to 1.88). All marked broods that nested on Adventure Lake moved to Karrak Lake ($n = 7$) or other habitats ($n = 2$) within 2 days after hatch; no broods, marked or unmarked, were observed using Adventure Lake thereafter. Despite higher survival when using other habitats (Figure 5.5), most ducklings remained on Karrak Lake ($\bar{\Psi}_{\text{Karrak-Other}} = 0.05$, 95%CI = -0.04 to 0.13) and those that moved from Karrak Lake tended to remain on small ponds ($\bar{\Psi}_{\text{Other-Karrak}} = 0.04$; 95%CI = -0.01 to 0.09) more often than they returned to Karrak Lake. Movement to other habitats generally occurred during the early part of brood rearing. Lastly, radio-marked females with broods tended to use ponds or lakes other than Karrak or Adventure Lakes more often (35% [30/86; 2000, $\chi^2 = 5.03$, $P = 0.02$] 20%

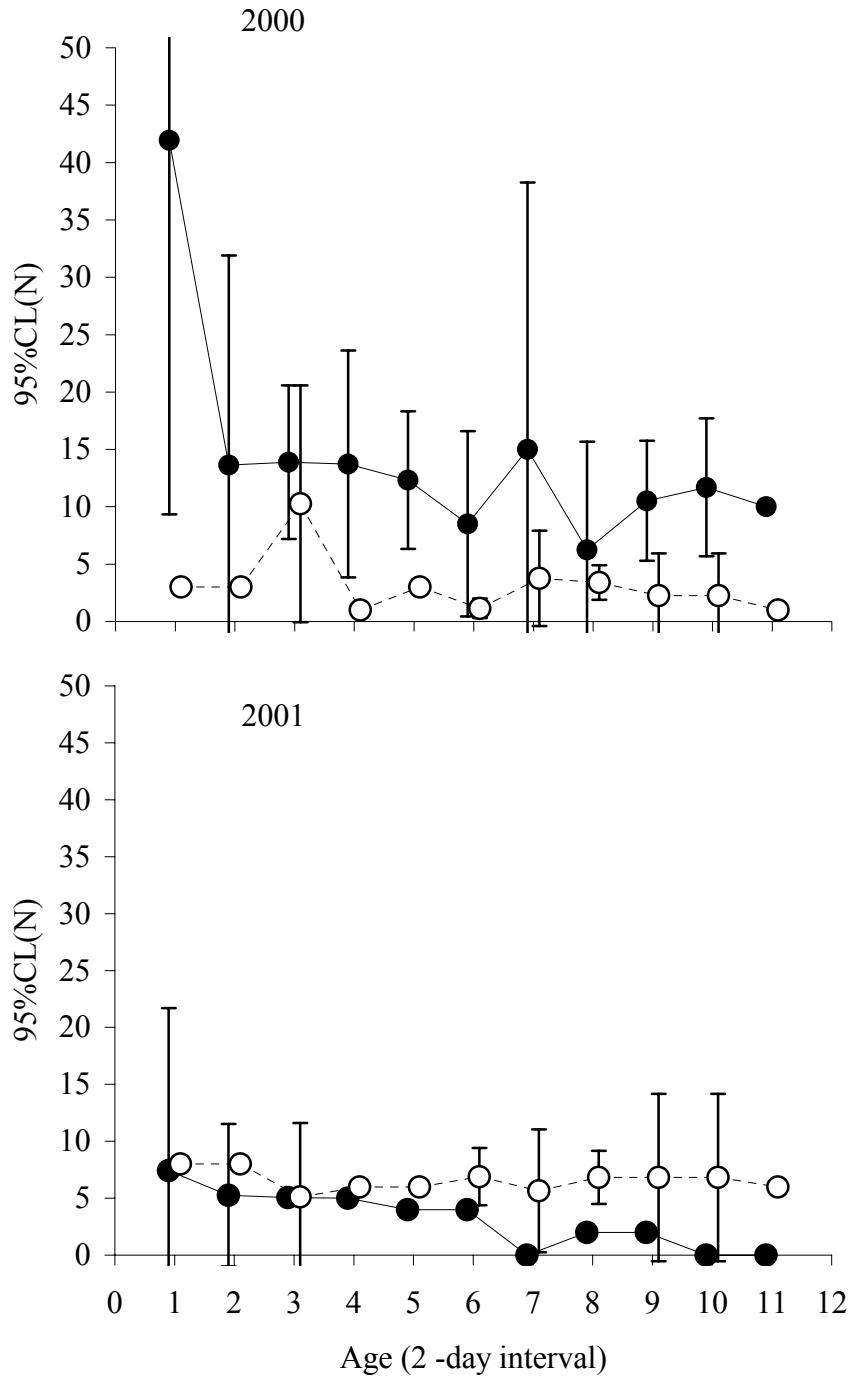


Figure 5.5 Estimated number of individually marked King Eider ducklings surviving by age for broods that remained at Karrak Lake, Nunavut (solid circles) and those that moved to smaller freshwater ponds and other nearby habitats (open circles) during 2000-2001.

[10/50;2001, $\chi^2 = 129.92$, $P < 0.01$] of brood resightings) than females that experienced total brood loss (22% [26/119;2000] and 3% [2/54;2001] of resightings) or failed nesters (12% [7/30;2000] and 11% [15/138;2001]of resightings). Nest failure and total brood loss resulted in females leaving the study area before those with surviving ducklings (Table 5.5).

5.6 DISCUSSION

These estimates are the first for duckling survival in King Eiders, which were similar to survival rates reported for closely-related Common Eiders *Somateria mollissima* (17 yr \bar{x} =10%, Mendenhall and Milne 1987; 1 yr estimate = 19%, Flint et al. 1998). Most duckling mortality in King Eiders occurred shortly after hatch and was largely the result of total brood loss, as is common in most waterfowl (Campbell 1975, Talent et al. 1983, Orthmeyer and Ball 1990, Mauser et al. 1994). Comparatively, King Eider duckling survival was considerably lower than that estimated for Spectacled Eider ducklings *Somateria fischeri* in Alaska (3 year estimate = 34%; Flint and Grand 1997). Such differences may reflect fluctuations in annual productivity rates, in that some years yield considerable higher fledging rates relative to other years (Mendenhall 1974, Coulson 1984, Mendenhall and Milne 1985). As well, predator communities likely differ between areas and may contribute to differences in duckling survival. Similar to Common Eiders (Campbell 1975, Mawhinney and Diamond 1999), gull predation (*Larus hyperboreus*, *Larus argentatus*) was likely the greatest cause of mortality for King Eider ducklings. King Eider ducklings inhabit tundra lakes with no emergent aquatic vegetation in which to escape predators. This leaves diving by ducklings, or active defense of broods by attending females, as the only means of escape from or deterrence to foraging gulls. Duckling motor skills are least developed shortly after hatch (Anderson 2000), rendering the youngest ducklings most vulnerable to predation (Campbell 1975, Mendenhall and Milne 1985). Survival to fledging may be lower than that reported in this study if mortality continued to occur after 24 days following hatch. However, as in most other studies of duckling survival (Orthmeyer and Ball 1990, Mauser et al. 1994, Flint and Grand 1997), I found that most mortality occurred

Table 5.5 Mean number of days after hatch or nest failure that radio-marked female King Eiders at Karrak Lake, Nunavut, were resighted during 2000-2001.

Status	2000		2001	
	Mean (<i>n</i>)	95% CI	Mean (<i>n</i>)	95% CI
Brooding females	25 (9)	22 - 26	22 (4)	15-27
Females with total brood loss	16 (14)	14 - 17	17 (8)	15-20
Failed nesters	10 (7)	5 - 14	15 (17)	12-17

early during the brood-rearing period and I observed no mortality between 14 and 24 days of duckling age. Moreover, ducklings closely resembled adults on the water and did not dive or try to elude gulls by the end of the study period.

Ducklings brooded by larger females survived at a higher rate than ducklings brooded by smaller females. I suggest such size related advantages were due to a composite of different factors, to include (1) more efficient use of reserves (Kendeigh 1969, Kendeigh 1970, Calder 1974) that enabled larger females to spend less time foraging (Goudie and Ankney 1986) and more time in vigilance to detect impending gull attacks; (2) a correlation with greater physical strength and increased maneuverability, improving the success of larger females at defending against predation attempts by gulls; or (3) an indirect effect of size related to the tendency for larger females to be more experienced breeders. Previous breeding experience has been linked with increased breeding success (Raveling 1981, Aldrich and Raveling 1983) and greater breeding propensity by larger females, suggests these individuals breed more often, relative to smaller females (Chapter 3). However, I observed no correlation between hatch date and female size, suggesting that, if larger females are more experienced breeders, then experience does not influence nest initiation date. Finally, these data suggest that advantages of female size may be reduced if nesting is delayed (Figure 5.4). I suggest that larger females may have greater success at defending against gull predation and that this has the greatest impact on offspring survival earlier in the season when gull attacks are fewest (Bedard and Munro 1976). I also consider that advantages of female size may, in part, be due to maternal effects if King Eiders exhibit natal philopatry to brood-rearing sites. For instance, larger adult size may have been due to use of nutrient rich brood-rearing areas during the early stages of life and, the return of females to raise their own broods in these nutrient rich areas may lead to higher duckling survival (Sedinger et al. 1995, Cox et al. 1998).

Alternatively, larger females may have been more likely to brood their own young, relative to smaller females. Such abandonment by smaller females may have increased mortality among their ducklings until acceptance by foster females and their broods. However, observations of marked ducklings that had mixed with non-marked broods, while natal females continued to independently care for marked siblings, suggest that

accidental brood mixing is likely to occur. Brood amalgamation among King Eiders was relatively uncommon compared to that observed in Common Eiders (Bedard and Munro 1976) and White-winged Scoters *Melanitta fusca deglandi* (Brown and Brown 1981, Traylor 2003). Although the significance of amalgamations remains unclear, my data did not provide evidence that King Eiders abandon their young entirely to the care of others. Rather, evidence for temporary abandonment suggests that King Eider females may leave their broods for short periods of foraging or in search of better brood-rearing areas (see Afton and Paulus 1992). During periods of temporary abandonment, ducklings may join with other broods that share the same habitat and, if female-young recognition is not developed, brood mixing may lead to some natal females brooding young other than their own, as suggested by observations of one female caring for the correct number of ducklings, but where only one was her own. Total brood loss by a natal female, in the presence of marked ducklings that had joined other broods, may give the false impression of abandonment. If so, estimates of duckling survival for those that remained with radio-marked females are likely to be most accurate.

I found that King Eider broods remain on freshwater habitats throughout the first 24 days of the brood-rearing period, contrary to movements by coastal-nesting conspecifics toward marine habitats after hatch (at sea ~15 days after hatch; Parmelee et al. 1967). Residents on local freshwater ponds may realize benefits from familiarity with local predators and safe roosting sites (Greenwood 1980). I did not continue observations until the fledgling stage, so females and broods may have used rivers to reach marine habitats after my observations ceased. Data suggest that females without young leave breeding areas earlier than those females with young, suggesting that unsuccessful females may have moved toward ocean habitats (~60 km) to molt (Suydam 2000). In contrast, I observed brood females molting on freshwater habitats.

Brood movements away from the main nesting lakes resulted in increased duckling survival, because smaller freshwater ponds (1) provided improved foraging (see Cox et al. 1998), (2) had lower densities of foraging gulls than Karrak or Adventure Lakes, or (3) provided sheltered areas from the wind, as winds on larger lakes may separate broods and aid in gull attacks (see Gilchrist et al. 1998, Traylor 2003). With such

disadvantage in remaining on large lakes, I wonder why more broods did not disperse to ponds. However, most overland movements to ponds occurred soon after hatch when duckling motor skills were least developed, so overland movement may have increased mortality (see Ball et al. 1975). Nevertheless, once broods reached ponds, they survived at a far greater rate than on either Karrak or Adventure Lake.

5.7 CONCLUSION

My results suggest that adult female body size can have an important influence on duckling survival. Use of individually-marked ducklings and nesting hens, and use of models that account for detection probability provided a useful approach to estimation of survival while accounting for brood abandonment. Furthermore, use of radio-telemetry allowed continued detection of ducklings that had dispersed to smaller ponds away from the primary nesting by King Eiders. Otherwise, my estimates of true duckling survival would have been seriously biased low if my attention remained focused solely on the large lakes from which ducklings hatched. Without complete ability to detect live ducklings that had dispersed from Karrak and Adventure Lakes, disappearance of ducklings from the study area due to brood dispersal would have been considered as mortality. Research that combines these approaches is needed to provide unbiased estimates for which proper inferences about variation in offspring survival can be drawn. Future studies that incorporate cross-fostering experiments are needed to help tease apart maternal effects on covariates to survival.

6. SYNTHESIS

My main research objectives were to examine (1) population dynamics and (2) brood ecology of King Eiders in order to better understand factors responsible for growth of a local population. The study focused on: 1) linking breeding and wintering areas in an effort to understand cross-seasonal effects of winter area on subsequent breeding success; 2) estimating female adult survival and assessing the influence of survival and recruitment on population growth; 3) examining potential costs to breeding; and lastly, 4) estimating duckling and brood survival and investigating factors that influence this vital parameter.

At the start of this research, there was little information available about the breeding ecology of King Eiders, other than estimates of nest success (Kellett and Alisauskas 1997, 2000, Kellett et al. 2003). Estimates of other vital rates are critical prerequisites for understanding apparent declines in range-wide abundance of North American breeding populations (Suydam et al. 2000, Mosbech and Boertmann 1999). Improved knowledge about factors that influence population growth, or its component vital rates, permits prediction about population response to future ecological change (Berryman 2002). The goal of this research therefore, was to evaluate ecological processes underlying observed dynamics of a free-ranging population, using empirically based models from which prescriptions for conservation and management of King Eiders could be drawn.

Information on movements among wintering areas is imperative to understand King Eider population boundaries and thereby, population demographics (Berryman 2002, Pulliam 1988). In chapter 2, I discuss migration patterns and winter philopatry of female King Eiders breeding in the central arctic and demonstrate the implications to North American King Eider populations. King Eiders that breed in North America are currently thought to be from two separate breeding populations whose boundaries are

based on discrete wintering areas in the Northern Pacific and Northern Atlantic regions (Suydam 2000). However, analyses of King Eider population genetics suggest that these populations are not genetically distinct, implying that population mixing occurs (Pearce et al 2004), but the timing and extent of mixing remained unknown.

I found that female King Eiders do not exhibit strong philopatry to wintering areas and show about 30% dispersal among winter areas annually. Pair formation by King Eiders occurs on the wintering areas (Suydam 2000), and evidence of dispersal are consistent with lack of phylogeographic structure between Atlantic and Pacific populations. Consequently, I suggest that North American King Eiders that winter in Atlantic and Pacific seas be treated as one metapopulation rather than two (see Berryman 2002). Low winter philopatry suggests that familiarity with local food resources and predators (Bustnes and Erikstad 1993, Anderson et al. 1992) are not as important for female eiders. Higher dispersal may be mediated by gregarious flocking behavior during winter (Suydam 2000) which may be adaptive if such flocks serve as information-centers about productive foraging areas (Brown 1988, Dall 2002). Analysis of stable isotopes in feathers, combined with banding efforts, offer a method of monitoring gene flow directly through dispersal and subsequent breeding success thus, allowing for broad-scale inferences useful for understanding population demography.

In Chapter 3, I discuss results from mark-recapture data from Karrak Lake, Nunavut, during 1995-2002. Based on recaptures of female King Eiders of known breeding age, King Eiders were at least 3-5 years old at the time of their first breeding attempt. Such delayed maturity places greater importance on adult survival for population growth and stability as it creates a lag time for recruitment (Rockwell et al. 1997, Crone 2001). Thus, if populations decline, recovery periods are slower relative to species with early maturity. Despite apparent population declines across North America, my study population of individually-marked females grew by about 20% year⁻¹ from 1995-2002 (Chapter 3). For most long-lived species, adult survival probability represents a greater fraction of population growth rate than does recruitment/female partly because adult survival governs how often individuals will breed over a lifetime (Rockwell et al. 1997, Nichols et al. 2000, Crone 2001). I found

that King Eider adult survival was high (87%) and was a greater component (72%) of population growth rate than was recruitment (28%). I found no evidence that body size influenced survival or age of first successful breeding. However, survival was a greater contributor to population growth rate in larger individuals than it was in smaller conspecifics, suggesting that larger individuals tend to remain in the population with greater consistency than did smaller birds. In contrast, smaller individuals are likely to show greater probability of recruitment. I suggest that contributions to population growth by larger sized females may reflect more frequent and successful breeding attempts, as recapture rates were highest for larger females. Because I was only able to capture females on the nest during mid-late incubation, failed or missed nesting attempts led to lower recapture rates.

Given that an individual decides to breed, life-history theory assumes that trade-offs exist between various traits. For instance, increased breeding effort is assumed to decrease survival (Williams 1966, Renzick 1985, Stearns 1992). In Chapter 4, I investigated patterns in King Eider nest success and female breeding condition related to potential reproductive costs and investigated the influence of annual median nest initiation on parameter estimates. I used annual nest initiation dates as these dates act as a surrogate to annual weather patterns (Schamel 1977, Abraham and Finney 1986, Suydam 2000). I found no evidence that nest initiation influenced transition to successful state or greater probability of being in good condition. Also, I found no evidence for reproductive costs in terms of future survival. However, I did find that successful nesters were easier to capture. Because I captured individuals only during mid-late incubation, nonbreeding or early nest failure were confounded, either of which can be viewed as temporary emigration from those available for capture. Consequently, I suggest that individuals that nested successfully bred more frequently or, at least were more frequently successful relative to failed nesters. In addition, I found that the proportion of the population that nested successfully declined over the course of the study. Given population growth rate of 20% (Chapter 3) over the same period, these declines are consistent with density-dependence or possible changes in local population age-structure. Moreover, temporal patterns in Mayfield nest success (defined as the probability of nesting successfully given that an attempt was made)

differed from the proportion of the population that nested successfully. This has important implications to population dynamics, as the proportion of successful nesters affects recruitment directly. This suggests that Mayfield nest success estimates currently used in population projections (Flint et al. 1998, Hoekman et al. 2002) may not reflect proportional success. These results emphasize the importance of incorporating multi-state approaches to population models (Fujiwara & Caswell 2002) in order to account for the proportion of breeders and ultimately, lead to a better understanding of demographics.

Lastly, brood ecology may be a key component of population dynamics because this period is an important to recruitment (Johnson et al 1992, Sedinger 1992). Thus, in chapter 5, I modeled duckling and brood survival to gain a better understanding of factors that affect this component of the life cycle. As found in most waterfowl studies, mortality (84%) was largely the outcome of total brood loss (Ringelman and Longcore 1982, Mauser et al 1994, Korschgen et al 1996). Furthermore, 77% of complete brood losses occurred within 2 days of hatch. Relatively few (about 10-16%) King Eider ducklings fledged. Nevertheless, such low levels of duckling survival may still be sufficient to result in local population growth with comparatively high probabilities of annual adult survival (Mendenhall and Milne 1987). In general, ducklings brooded by larger females had higher survival than did ducklings from earlier hatching nests. I suggest that if larger females successfully breed more frequently (see Chapter 2), they would have greater experience and experience may increase their likelihood of fledging young. Unfortunately, the two years of data from this study supply little information on temporal variation in duckling survival. Therefore, longer-term studies are necessary to better understand this variation. In addition, increased effort to mark ducklings at the nest and at the juvenile stage are required for improved estimation of juvenile survival and *in situ* recruitment.

In conclusion, results from this study have contributed to a more comprehensive understanding of waterfowl demography in general, and of King Eider ecology in particular. I combined banding data with isotope analysis to address theories on waterfowl dispersal patterns, and link breeding and wintering areas. This information is crucial to understand demography of King Eider, as it provided evidence of changes

in migration pathways, in turn leading to gene flow among populations. This study also uncovered key information on adult survival and proportional contributions (survival and recruitment) to growth of a local population. I was able to address theories concerning benefits of size in northern climates (Fretwell 1978). Such knowledge is important as it provides insight into selection pressures. In addition, I demonstrated the occurrence of potential nonbreeding and showed trends in declining probabilities of nesting successfully, as well as declining proportion of individuals in good condition. This information is of special importance as it has implications to density-dependent regulation, and it emphasizes the need to account for proportions of individuals breeding if we are to better understand population dynamics. Lastly, my data about duckling survival and habitat use offered insight about events that affect King Eider productivity. For example, I found benefits to larger maternal body size in terms of duckling production and show the importance of habitat choice on duckling survival. Overall, my study emphasizes the complexities of population dynamics and provided insight into ecological pressures that have helped to shape King Eider ecology. My data indicate that larger females have a higher frequency of successful nesting and that ducklings raised by larger females, provided a relative early hatch date, survive at a higher rate. This suggests some support for Fretwell's body size hypothesis, that larger size is favored; however, such fitness benefits occur through recruitment only, with recruitment contributing fewer overall benefits to fitness, relative to that of survival. Fitness benefits incurred only through recruitment would have lower selection pressure and this may partially explain the maintenance of high heritability of this trait.

Future information needs for conservation of King Eiders include gaining more precise estimates of trend data specifically, monitoring population growth at multiple breeding colonies to establish comparison data at local sites elsewhere. Data from multiple colonies can provide data on immigration rates (Nichols et al. 2000) while continued efforts to mark young at the nest site are important to separate *in situ* recruitment from immigration, and understand those factors that ultimately affect recruitment. Lastly, dispersal among eastern and western populations and the importance of adult survival to population growth highlights the need for management

efforts to monitor adult mortality through careful regulation of hunting and other factors that may limit adult survival rates throughout the population.

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APPENDIX A. INFLUENCE OF SUBCUTANEOUS MOUNT TRANSMITTERS AND USE OF PROPOFOL ON NEST SUCCESS OF BREEDING FEMALE KING EIDERS

A.1 INTRODUCTION

Radio telemetry is an effective tool useful for understanding movements and survival rates. Information gained from its use can lead to less biased results when estimating survival, if marked individuals undertake permanent movements to habitats where they would otherwise be unobserved (see Lebreton et al. 1992). Telemetry can also be essential in obtaining reliable estimates of habitat use (Drake et al. 2001). However, information gained from these studies is useful only if radio-marks do not change individual behavior during time of data collection (White and Garrott 1990).

Subcutaneous anchor-mount transmitters (Mauser and Jarvis 1991) are beneficial because they are easy to apply, cost effective, require only local anesthesia and sutures, and transmit over greater distances than transmitter implants (Rotella et al. 1993; Paquette et al. 1997). However, their use has led to some question over their effects on reproduction and subsequent survival for prairie-nesting Mallards (*Anas platyrhynchos*; Paquette et al. 1997).

Use of propofol for temporary sedation of newly transmitter-marked individuals may reduce potential negative effects (Machin and Caulkett 2000), but its use has not been widely evaluated. Here I evaluate effects of subcutaneous anchor-mount transmitters and use of propofol on nesting effort of King Eiders (*Somateria spectabilis*) in the central Arctic. This evaluation was motivated by my use of subcutaneous anchor-mount transmitters to study brood ecology in this species. I also evaluate effects of possible covariates to nest success, such as incubation stage at capture and female specific attributes for various treatment groups.

King eiders are long-lived sea ducks and differences in life history traits, relative to previously-evaluated transmitter effects on shorter-lived prairie nesting species, may lead to differences in nesting behavior after transmitter attachment. For instance, long-lived species typically lay smaller clutches and re-nest less frequently within the same season. Thus, relative to shorter-lived species, each individual nesting attempt contributes less to overall life-time reproductive success. Females with less relative annual investment, may abandon individual nesting attempts more readily, if disturbance is perceived as a mortality risk.

A.2 METHODS

The study took place during the summers of 2000 – 2001 at Karrak and Adventure Lakes, Nunavut (67° 14' N, 100° 15' W), located within the Queen Maud Gulf Bird Sanctuary. See Kellett and Alisauskas (2000) for detailed descriptions of the study area.

A.2.1 Captures

About 7-10 days before predicted hatch dates, I trapped nesting female King Eiders by laying mist nets over them. Predicted hatch dates were based on known laying dates or estimated incubation stage by candling eggs (Weller 1956), assuming a 23-day incubation period (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973). I banded all captured females with standard metal leg bands and weighed each with a Pesola spring scale (± 10 g). I measured and recorded twice for each female: head length and tarsus length using dial calipers (± 0.1 mm), and flattened wing chord using a flat ruler (Dzubin and Cooch 1993). I later used the average of both measurements to obtain indices of structural size.

During 2000 I attached subcutaneous anchor-mount transmitters (Advanced Telemetry Systems™; Mauser and Jarvis 1991) to every other captured female. I injected 0.1-0.2 ml of Bupivacaine subdermally at several sites around the area of anchor attachment before implanting the transmitter anchor subcutaneously. Transmitters were secured with 3 sutures (3-0 Prolene). I then sedated transmitter-marked females with 1.5 ml of propofol, via tarsal vein, before placing her near her

nest. At capture, eggs of transmitter-marked females were replaced with an identical number of non-fertile chicken eggs, and natural eggs were artificially incubated using portable air-circulating incubators. Upon hatch, I replaced chicken eggs with newly hatched and individually marked natal ducklings. During 2001 I attached subcutaneous anchor-mount transmitters, sedated each with propofol and artificially incubated eider eggs as noted above, to every 3rd captured female. In addition, I created a control group of females captured subsequent to transmitter-marked individuals. For the control group, I artificially incubated eider eggs and sedated captured females with propofol but did not affix transmitters. The 3rd group, females captured subsequent to controls, were banded and released without transmitter attachment or use of propofol. Birds within the band and release group were allowed to naturally incubate their own eggs. I recorded handling time for all captures during 2001.

A.3 STATISTICAL ANALYSIS

I established an index of female structural size using principal component analysis (PCA) based on the correlation matrix of head length, wing length, and tarsus (SAS Institute Inc. 1996). I regressed body weight on structural size (PC1) and incubation stage at capture and used the residuals from general linear models (GLM) as an index to female condition (Alisauskas and Ankney 1990, Hochachka and Smith 1991).

I evaluated transmitter and propofol effects on nesting effort by estimating nest success of captured females in Program MARK (White and Burnham 1999, Dinsmore et al. 2002). I considered a total of 15 candidate models (Table A.1) to assess nest success based on the following attribute groups from 2001: (1) nasal-marked females with transmitters and sedated with propofol (transmitter-marked group), (2) nasal-marked females sedated with propofol but not marked with transmitters (propofol control group), and (3) nasal-marked females banded and released without transmitter attachment or use of propofol (band/release group). I also modeled nest success among years for groups 1 and 3, above, based on a set of 19 candidate models (Table A.2). For both analyses I began model selection using time constant models because nest success

Table A.1 Candidate models used to investigate influence of subcutaneous anchor-mount transmitters and use of propofol at Karrak and Adventure Lakes, Nunavut, 2001. Nest success was modelled for female King Eiders (1) fitted with subcutaneous anchor-mount transmitters and sedated with propofol (transmitter group), (2) sedated with propofol without transmitter attachment (control group), and (3) females captured, banded and released without transmitter attachment or use of propofol (release group). Parameters were modelled as time constant using the following covariates: relative nest initiation date (initiation), clutch size, female body size, female condition (cond), incubation stage at capture (inc), handling time from capture to time of release (handling), and if the individual was a recapture from previous years (recap). Models are ranked in accordance AICc values and are denoted as additive models (+) or models with interaction (*).

Model Number/Name	ΔAIC_c^a	AIC _c	No. of Weights	Deviance Parameters
1 (control-transmitter, release)+inc+cond	0.00	0.18	4	172.62
2 (control-transmitter, release)+inc	0.23	0.16	3	174.95
3 (control-transmitter, release)	0.61	0.14	2	177.41
4 (control-transmitter, release)+cond	0.71	0.13	3	175.43
5 (control-transmitter, release)+initiation	1.65	0.08	3	176.37
6 (control, transmitter, release)	1.74	0.08	3	176.47
7 (control-transmitter, release)+handling	2.08	0.06	3	176.80
8 (control-transmitter, release)+clutch size	2.55	0.05	3	177.27
9 (control-transmitter, release)+female size	2.62	0.05	3	177.35
10 (control-release, transmitter)	2.72	0.04	2	179.52
11 (control-transmitter, release)*initiation	2.81	0.04	4	175.44
12 (control-transmitter, release)* handling	4.07	0.02	4	176.70
13 (control-transmitter, release)*clutch size	558.4	0.00	4	731.02
14 (control-transmitter, release)*recap	568.1	0.00	3	742.79
15 (control-transmitter, release)+recap	952.4	0.00	2	1129.15

^alowest AICc = 180.87

Table A.2 Top 15 candidate models used to investigate the combined effects of subcutaneous anchor-mount transmitters and propofol on annual nesting success of female King Eiders captured and banded at Karrak and Adventure Lakes, Nunavut, during 2000 and 2001. Nest success was modelled for females marked with transmitters and sedated with propofol (group T) and for females banded and released without transmitter attachment or use of propofol (group R). All parameter estimates were modeled as time constant within a season. Nest success was allowed to vary among years (00, 01) and held constant (00-01). Models considered the following as covariates to nest success: relative nest initiation date, clutch size, female body size, female condition, incubation stage at capture, and if the individual was a recapture from previous years (recapture). Models are ranked in accordance to AICc values and are denoted as additive models (+) or models with interaction (*).

Model Number/Name	ΔAIC_c^a	AIC_c Weight	No. of Parameters	Devianc e
1 T ₀₁ , T ₀₀ R ₀₀₋₀₁	0.00	0.11	2	212.89
2 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +incubation	0.05	0.11	3	210.89
3 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +condition	0.10	0.11	3	210.94
4 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +incubation+condition	0.24	0.10	4	209.02
5 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +incubation+recapture	0.29	0.10	4	209.07
6 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +recapture	0.31	0.10	3	211.15
7 T _{00, 01} , R ₀₀₋₀₁	0.40	0.09	3	211.23
8 T ₀₁ , T ₀₀ R ₀₀₋₀₁ *condition	1.34	0.06	4	210.11
9 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +incubation*condition	1.59	0.05	5	208.28
10 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +female size	1.87	0.04	3	212.71
11 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +clutch size	1.89	0.04	3	212.72
12 T ₀₁ , T ₀₀ R ₀₀₋₀₁ +initiation	2.01	0.04	3	212.84
13 T ₀₁ , T ₀₀ R ₀₀₋₀₁ *recapture	2.36	0.03	4	211.13
14 T ₀₁ , T ₀₀ R ₀₀₋₀₁ *female size	3.94	0.02	4	212.71
15 (T ₀₀₋₀₁ R ₀₀₋₀₁)	5.99	0.01	2	218.88

^alowest AIC_c value = 216.93

did not vary before capture opportunity (i.e., nests were all successful until mid to late in incubation). Model selection was based on parsimony using Akaike's Information Criterion (AIC_c) to correct for small sample size (Akaike 1985, Burnham and Anderson 2002). I reduced the number of attribute groups and used the best group model to investigate further the influence of covariates on nest success. I used the following covariates to examine sources of variation in nest success: year, relative nest initiation date, clutch size, female structural size and condition, incubation stage at capture, bivariate code to designate if the capture was the first recorded capture for that individual, and for 2001 data, I incorporated handling time for capture events. I included recapture history to better understand if captures affect first time captures differently. Lastly, I used AIC_c weighted model averaging within Program MARK to calculate estimates of daily nest survival rates for each group and covariate effects on nest success after capture (Burnham and Anderson 2002).

A.4 RESULTS

I considered nest success for a total of 56 and 89 captured female King Eiders during 2000 and 2001, respectively (Table A.3). Adult female size (PC1) incorporated 66% of the variation in female body measures, with PCA loadings of 0.80, 0.78, 0.84 for head length, tarsus, and wing, respectively. In general, King Eider captures occurred later in incubation in 2000, relative to 2001 (Figure A.1). Capture dates, relative to incubation stage, varied among years. However, capture dates were similar within years for transmitter-marked groups ($\bar{x} = 5.7$ days before hatch in 2000, 95% CI = 4.8-6.6; $\bar{x} = 8.5$ days before hatch in 2001, 95% CI = 7.6-9.3) and control groups ($\bar{x} = 5.0$ days before hatch in 2000, 95% CI = 3.6-6.4; $\bar{x} = 8.1$ days before hatch in 2001, 95% CI = 6.9-9.3).

Model results indicate that nest success of transmitter-marked and propofol controls was similar, with nest success varying from the band/release group (Table A.1). However, models also show some support for variability among all groups ($\Delta AIC_c < 2$; Burnham and Anderson 2002). Models suggest incubation stage at capture, female condition, and nest initiation date influenced nest success ($\Delta AIC_c < 2$;

Table A.3 Sample size (*n*) and nest fate (successful or failed attempt) for nesting female King Eiders marked with (1) subcutaneous anchor-mount transmitters and sedated with propofol, (2) propofol controls, females sedated with propofol but not marked with transmitters, and (3) nesting females banded and released without transmitter attachment or use of propofol. Eggs of transmitter marked and propofol controls were replaced with color- dyed chicken eggs at time of female capture and eider eggs artificially incubated at camp. Release birds were allowed to incubate and naturally hatch their respective clutches.

Attribute Group	2000 (<i>n</i>)			2000 (<i>n</i>)		
	Successfu	Failed	Total	Successful	Failed	Total
	1					
Transmitter-marked	23	7	30	11	18	29
Propofol controls	NA	NA	NA	8	6	14
Band and release	23	3	26	39	7	46

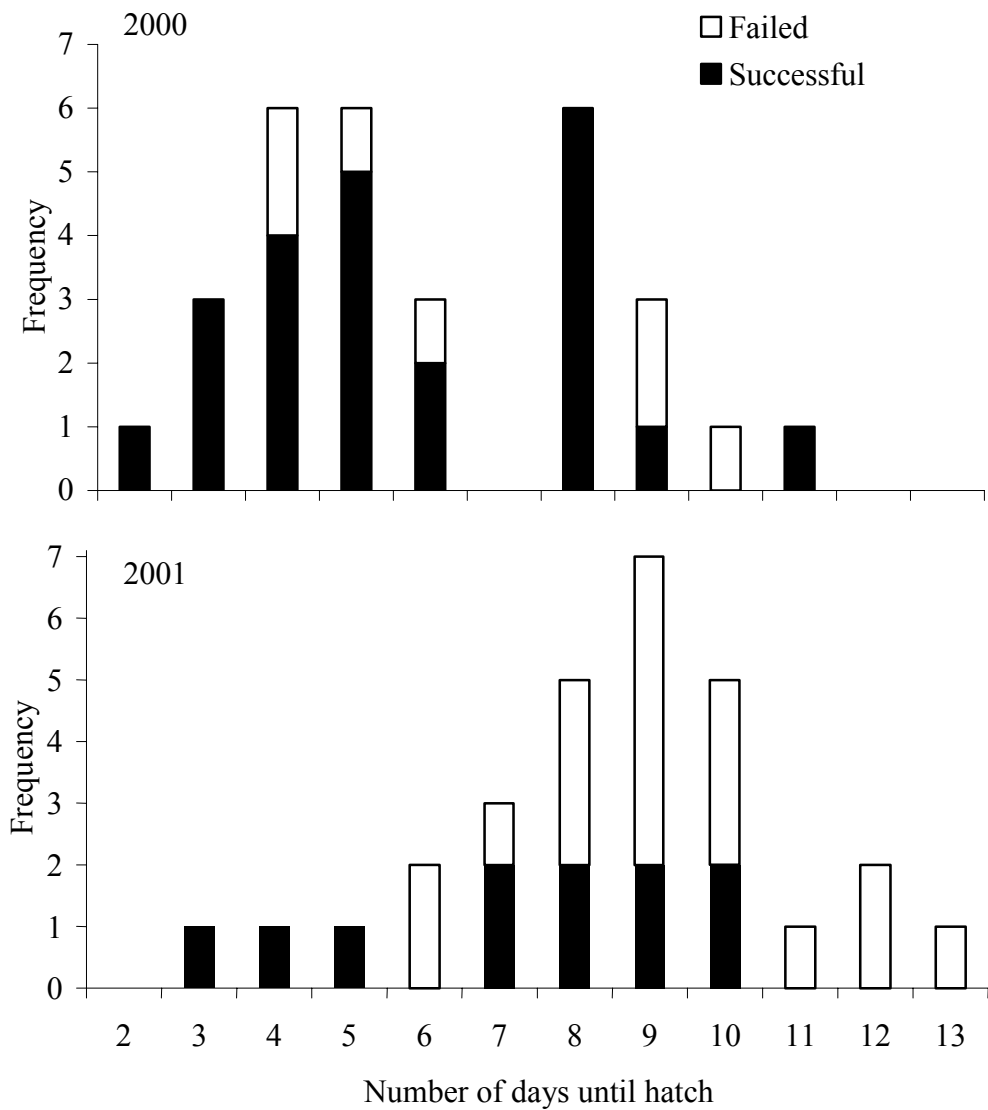


Figure A.1 Frequency of captures, according to the number of days until ducklings hatched from the nest, of transmitter-marked females captured at Karrak and Adventure Lakes, Nunavut during the summers of 2000 and 2001.

however, weighted model averages lacked precision, with all $\hat{SE} > \hat{\beta}$ and all 95% CI encompassing zero. Effects for the top model suggested females captured later in incubation ($\hat{\beta}_{incstage} = 0.40$, 95% CI = -0.08 to 0.88) and females in better condition ($\hat{\beta}_{cond} = 0.30$, 95% CI = -0.09 to 0.69) experienced higher nest success. Weighted model average daily survival rates (DSR) of transmitter-marked females was 0.97 (95% CI = 0.95-0.98), propofol control females was 0.97 (95% CI = 0.95-0.98), while DSR for females banded and released without transmitter attachment or use of propofol was 0.99 (95% CI = 0.98-1.0).

When considering annual effects and the combined effects of transmitters and use of propofol, transmitters and propofol appeared to affect nest success only during 2001 (Table A.2). Model average DSR of nests for both, the transmitter-marked group and the band and release group, was 0.99 (95% CI = 0.99-1.00) in 2000, while DSR in 2001 was 0.97 (95%CI=0.95-0.98) for the transmitter-marked group and 0.99 (95% CI = 0.99-1.00) for the band and release group. My results show some support for influence of covariates on nest success (Table A.3) with model average estimates indicating a general trend for females captured later in incubation, ($\hat{\beta}_{incstage} = 0.11$, 95% CI = -0.23 to 0.45), females in better condition ($\hat{\beta}_{cond} = 0.09$, 95% CI = -0.19 to 0.37), and females with a previous capture history to experience higher nest success ($\hat{\beta}_{recap} = -0.14$, 95% CI = -0.14 to 0.24). No trend occurred with other covariates (i.e., $\hat{SE} > \hat{\beta}$). Lack of precision around slope estimates was likely a consequence of small sample size.

Sutures from two transmitters became detached early in the study: one female was recaptured on the nest (2000) and sutures were retied; a second female was observed with a transmitter hanging to her side during the brood-rearing period (2001). Some transmitters remained attached well after the breeding season had ended. For example, one female marked with a transmitter during 2000 was captured on the nest the following breeding season with the transmitter still attached by the wire prong only (i.e., no sutures remained). Another marked with a transmitter (July 2001) was shot >

200 days later (April 2002) with transmitter still attached. I observed no mortality of transmitter-marked females during the breeding season.

A.5 DISCUSSION

My results suggest that use of propofol and subcutaneous, anchor-mount transmitters may negatively affect nesting behavior of King Eiders. Paquette et al. (1997) found that wild Mallard females fitted with subcutaneous mount transmitters spent fewer, but non-significant, number of days nesting. In King Eiders, the primary nest predators are *Larus* gulls, with eggs from unattended nests being most vulnerable to gull predation (Campbell 1975, Kellett 1999). If transmitter-marked females spent more time engaged in preening activities away from the nest site, as found in Mallards (Pietz et al. 1993), then reduced nest attendance may have contributed to greater nest loss.

Annual variation in the effect of transmitters suggests that female King Eiders may assess mortality risks differently according to prevailing annual conditions. Female King Eiders rely heavily on endogenous reserves (Kellett and Alisauskas 2000) and if spring conditions vary, such that individuals arrive on the breeding grounds in variable condition among years, individuals may chose to abandon nests more readily in years of poorer condition. For instance, female eiders that begin incubation with lower body reserves may exhibit immunosuppression during late incubation, which may lead to increased abandonment when stressed (Hanssen et al. 2003). I suggest that greater nest abandonment or, decreased nest attendance that left eggs vulnerable to gulls, likely contributed to greater nest loss by female King Eiders in lower body condition. I also found some evidence that females captured for their first time experience greater nest loss. Banding at the study site has been continuous since 1995 (Kellett et al. 2003), with about 30-60% of nesting females captured each year (Mehl unpubl. data). Thus, females captured for the first time likely represent young breeders or, at least new recruits into the local breeding population. Assuming that new captures represent a large proportion of young breeders, my results suggest age related effects to King Eider nest success. Age related effects may be, in part, due to younger females having lower incubation constancy (Yerkes 1998). Disturbance to females with lower incubation constancy, may result in greater to nest abandonment when stress of capture

and handling is present. Unfortunately, the marked population at the study area contains only a few birds of known breeding age, which are necessary to determine age-related nest abandonment rates.

King Eiders are long-lived species with small clutch size, relative to most ducks. Short arctic summers, combined with physiological requirements for nutrient reserves in egg-laying, do not likely allow for renesting (Korschegegn 1977). Therefore, each annual nesting attempt contributes relatively little to overall life-time reproductive success. Because greater time spent in incubation, increases the relative time invested in an individual nesting attempt (Götmark 1992, Robin et al. 2001), I suggest that improved nest success for females captured later in incubation was likely because these females were less willing to abandon after having invested a greater amount of time into incubation.

Previous work on wild Mallards (Paquette et al. 1997) and Lesser Scaup (Brook and Clark 2002) found that subcutaneous type transmitters remained attached for only about 40 days. This study required only a short retention period for transmitters (<40 days). I suspect that the 2 transmitters for which sutures became detached was due to improper knots tied in the sutures, as radios were retained on all other individuals throughout the study period. Subcutaneous anchor-mount transmitters did not appear to influence adult survival, as suggested for wild Mallards with subcutaneous anchor-mount transmitters (Paquette et al. 1997).

I acknowledge that exchange of eider eggs for color-dyed chicken eggs, and the artificial incubation of viable eggs, may have influenced nest success for transmitter-marked and propofol control females. However, I suspect that artificial incubation had little to no effect on nest attendance since egg recognition is apparently absent in most avian species (O'Connor 1984) and female King Eiders readily incubate small eggs of Long-tailed Ducks (*Clangula hyemalis*), as well as rocks (pers. obs). Communication of offspring through the shell (Vince 1969, O'Connor 1984) may encourage females that are in relatively poor condition from abandoning. Thus, if lack of communication among unviable eggs lead to increased nest abandonment, I would have expected female condition to be an important covariate to females that incubated chicken eggs; however, these results showed no such support.

Importantly, reduced nest success among eiders that received only propofol and no transmitter, suggest this drug may not be appropriate for use on King Eiders or other species. This association should be taken into account when designing studies that use radio-telemetry. I suggest that future studies address affects of transmitters without use of propofol and simultaneously evaluate time allocation of transmitter-marked individuals to nesting activities in order to help researchers understand potential effects of transmitter use on behavior, and biases in data collected on these individuals.

APPENDIX B. LINKING BREEDING AND WINTERING GROUNDS OF KING EIDERS: MAKING USE OF POLAR ISOTOPIC GRADIENTS

B.1 INTRODUCTION

Linking wintering and breeding areas of migratory wildlife can be important for understanding their population dynamics (Fretwell 1972, Evans and Pienkowski 1984, Webster et al. 2002) because habitat conditions associated with winter or migration areas can directly affect reproduction (Alisauskas 2002) and annual survival (Davidson 1981, Fournier and Hines 1994, Dierscheke 1998). For most waterfowl species, connectivity between breeding and wintering areas can be inferred using band recoveries of hunter-killed birds. However, for sea ducks such as king eiders (*Somateria spectabilis*) that remain in northern latitudes throughout the annual cycle, few birds are marked and available for recovery. For example, from 1940 to 2002, 804 adult king eiders were banded in North America, of which only 24 had been recovered (Bird Banding Office, Laurel, MD). Alternative methods, such as resighting color-marked individuals on breeding and wintering areas (Haig and Plissner 1993), are not easily accomplished because this species winters at sea several kilometers from shore (Mosbech and Johnson 1999, Suydam 2000, Merkel et al. 2002). Satellite telemetry is expensive and so relatively few birds can be marked, thereby compromising ability to draw robust inferences about movements at the population level.

Populations of king eiders appear to have declined in Western North America by about 50% over the last 20 years (Suydam et al. 2000) and numbers of moulting king eiders off the coast of Greenland have declined by about 50% over the last 40 years (Mosbech and Boertmann 1999). King eiders that breed in North America winter along the northwestern and northeastern coasts of the continent, including portions of the Bering Sea near Russia in the west and waters near southwest Greenland in the east (Abraham and Finney 1986, Suydam 2000, L. Dickson, pers. com.). Limited band

recovery data indicate that allopatric winter populations share breeding areas - at least in Canada's central Arctic (Alisauskas unpubl. data). Ability to assign individual breeders reliably to specific winter populations enables avenues of research for understanding the relative influence of ecological effects in different winter areas on recruitment and survival estimated from studies on shared breeding areas.

Naturally-occurring stable isotopes of several elements in animal tissues reflect local food webs (DeNiro and Epstein 1978, Fry and Sherr 1984, Hobson and Welch 1992, Michener and Schell 1994). Different biogeochemical processes produce variation in baseline isotopic signatures of foodwebs and present the opportunity to infer origins of organisms within those foodwebs. Thus, by choosing appropriate tissues for analysis, origins of migratory individuals can be delineated (reviewed by Hobson 1999a). This approach has been used to link breeding and wintering areas of several terrestrial species (Hobson and Wassenaar 1997, Webster et al. 1999, Wassenaar and Hobson 2000, Hobson et al. 2001, Rubenstein et al. 2002). Geographic patterns in stable isotope ratios are less well documented in marine areas. Nevertheless, previous analyses of zooplankton in polar marine environments of North America indicate an east-west gradient in ^{15}N and ^{13}C (Figure B.1), with relative enrichment in portions of the Bering and Chukchi seas, and depletion in arctic waters of eastern North America (Dunton et al. 1989, Saupe et al. 1989, Schell et al. 1998). A portion of this isotopic gradient was used to trace seasonal migration of the western North American population of Bowhead Whales (*Balaena mysticetus*) as they moved between the eastern Beaufort and the Bering/Chukchi region (Schell et al. 1989). The cause of this isotopic gradient is not well understood but is, in part, likely driven by more enriched isotopic values of the Bering Sea, resulting from nutrient-rich upwellings specific to this region. Oceanic currents disperse enriched isotopic waters from the Bering Sea north and eastward and the gradient from the Beaufort Sea eastward is thought to be linked to attenuation of inputs from the Bering Sea (see Schell et al. 1998). Less information is available about isotopic patterns in foodwebs near western Greenland or other eastern wintering areas of king eiders. However, recent work by Hobson et al. (2002a,b) has shown generally depleted values of

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of zooplankton from there compared to those from the Bering Sea.

As with other waterfowl species, female king eiders undergo two body molts, of which basic plumage present during breeding is acquired on previous wintering areas (Weller 1976, Heitmeyer 1986, Suydam 2000). Wing moult occurs once annually, during summer or fall (Weller 1976, Suydam 2000). King eider contour feathers should, thus, reflect isotopic signatures of foodwebs associated with winter regions where feather growth occurs (Mizutani et al. 1990, Hobson and Clark 1992, Hobson et al. 2001). In a preliminary investigation based only on flight feathers, Hobson (1999b) found evidence for isotopic segregation between eastern and western populations of king and common (*Somateria mollissima*) eiders that reflected the expected isotopic gradient in foodwebs across the Canadian Arctic. This encouraged us to investigate this more extensively for king eiders. The objectives of this study were to investigate variations in isotopic signatures of king eider feathers of known winter location to determine if this technique would be useful in determining North American wintering area of breeding king eiders of unknown winter origin. Based on an expected east-west isotopic gradient in polar waters used by wintering king eiders, (e.g. Figure B.1), I predicted that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for feathers from western king eiders would be more enriched, relative to those of feathers from king eiders wintering off western Greenland.

B.2 METHODS

During 2000-2001, contour feathers (back intra-scapular, center chest, top of head, and an outer primary flight feather) were collected from hunter-killed king eiders of both eastern and western populations. King eiders were shot near Holman Island, NWT ($70^{\circ}43' \text{ N } 117^{\circ}45' \text{ W}$) during spring ($n=94$; 23 males and 71 females; 6-15 Jun 2001) and near the coast of Greenland ($60^{\circ}47' \text{ N } 47^{\circ}31' \text{ W}$ to $67^{\circ}30' \text{ N } 54^{\circ}00' \text{ W}$) during winter ($n=22$; 12 males and 10 females 13 Nov 2000 – 26 Feb 2001) and spring ($n=28$; 18 males and 10 females; 16 Mar – 4 Apr 2001; Figure B.1). Feathers collected in

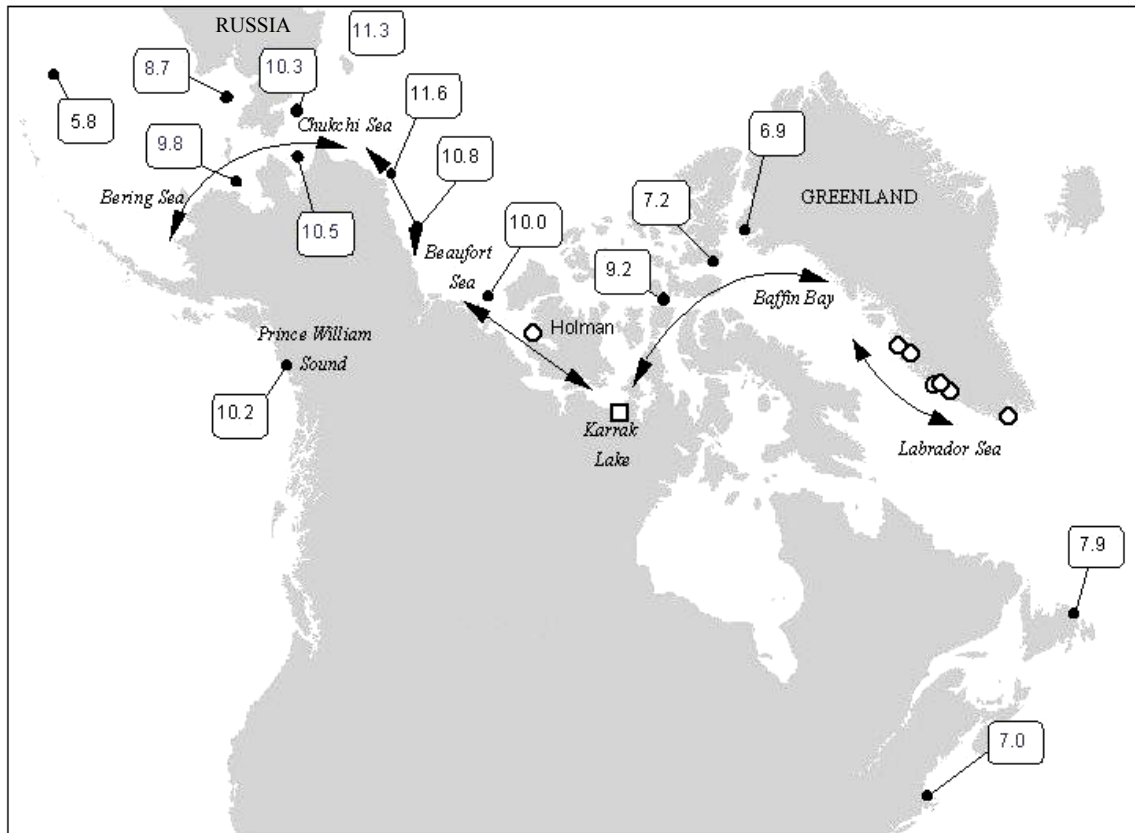


Figure B.1 Spatial distribution of summer $\delta^{15}\text{N}$ values estimated for copepods from marine waters of northern North America (Hobson and Welch 1992, Schell et al. 1998, Hobson et al. 2001, Hobson et al. 2002a,b). Values for the Chukchi and Bering Seas are means for samples collected off the coast of Alaska and Russia (Shell et al. 1998). Isotope value given for the north coast of Newfoundland is from northern shrimp (*Pandalus borealis*; Lawson and Hobson 2000) corrected for trophic level (-3.4‰; Fry 1988, Hobson and Welch 1992), and the mid-Atlantic isotopic value is for copepods collected on the Georges Bank (Fry 1988). Also shown are locations (open circles) where king eiders were shot near Holman, NWT, and southwestern Greenland. Arrows indicate likely and known migration routes of king eiders. Isotope values for $\delta^{13}\text{C}$ are not shown, as these values contributed only 4% more precision in delineating between eastern and western wintering eiders.

Greenland were taken from 11 hunter-killed king eiders, 2 mistnet captures, and 37 king eiders that collided with navy ship lanterns. Samples taken in Greenland are centrally located and likely representative of isotopic values from the eastern arctic and mid-Atlantic. Samples from Holman were taken from only one geographic location, but represent individuals that wintered over a larger western geographic region because 1) Sea ice prevents eiders from overwintering near Holman and king eider migration is highly synchronous and occurs over a short period of time (Woodby and Divoky 1982, Suydam 2000) for which dates of hunter-killed birds coincide with arrival of king eiders to the eastern Beaufort Sea (Suydam 2000); 2) The most important spring staging areas are located within polynyas west of Holman, near the Amundsen Gulf (southwest Banks Island and Balillie Islands; Alexander et al. 1997). It is expected that 90% of the western wintering king eiders stage in this area during spring (Barry 1986) with about 20% of all western wintering king eiders passing near Holman Island en route to more easterly breeding areas (see Byers and Dickson 2001, Suydam et al. 2000).

Feathers collected for stable isotope analyses were rinsed in a 2:1 chloroform:methanol solution and allowed to air dry. Samples (1 mg) were then weighed in tin cups and combusted in a Robo Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS, Hobson and Schell 1998). Stable isotope values are expressed in δ notation relative to the Pee Dee Belemnite (PDB) and atmospheric air standards for ^{13}C and ^{15}N measurements, respectively. Based on thousands of measurements of albumen lab standard, I estimate measurement precision to be $\pm 0.1\%$ for $\delta^{13}\text{C}$ measurements and $\pm 0.3\%$ for $\delta^{15}\text{N}$ measurements.

B.3 STATISTICAL ANALYSES

I plotted values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from each feather tract to interpret amount of overlap between western and eastern populations. I assessed my ability to discriminate between western and eastern populations based on isotopic ratios from one or more feather tract(s), using discriminate function analysis (DFA; SAS Institute 1996). I tested for homogeneity of within-covariance matrices using a chi-square test of

homogeneity (POOL=TEST option with SAS) and used quadratic discriminate function analysis (QDFA) when heterogeneous variances were present. I set prior probabilities equal to sample sizes for each group and performed separate DFAs using values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from all four feather tracts combined and all possible combinations of feather tracts, including each tract independently. To find the most informative feather tract(s) to best discriminate king eider populations, the performance of each DFA was evaluated based on the error rate from cross-validation. I performed a separate DFA using isotope data from all feather samples (male and female), and on data from females only. Lastly, graphical representation of the data revealed that most variation between populations occurred with $\delta^{15}\text{N}$ values. Thus, using the most informative feather tract(s), I tested my ability to delineate populations using only $\delta^{15}\text{N}$ values. All statistical analyses were performed using SAS (SAS Institute 1996).

B.4 RESULTS

Degree of segregation in isotopic values between eastern and western populations varied with respect to feather tract with differences of as much as 10‰ for all feather tracts of both populations (Figure B.2). I found that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were enriched for king eiders that wintered in seas of western North America relative to those of king eiders that wintered in seas of eastern North America (Table B.1). Within-class covariance matrices were unequal for all feather tracts ($P < 0.01$), motivating use of quadratic discriminate function analysis (QDFA). All QDFAs resulted in greater misclassification of eastern birds than western birds (Table B.2). Head feathers provided the best discrimination between king eiders from different winter areas (Table B.2). When both males and females were included in the QDFA, three of 50 eastern individuals were misclassified (6% error). Two of three misclassified individuals were females, resulting in slightly higher error rates when only female data were considered (2/21; 10% error). Use of only female data resulted in 100% correct classification of western king eiders (Table B.2). Use of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values led to slightly greater classification success (99% west, 94% east),

compared to use of $\delta^{15}\text{N}$ alone (94% west, 92% east). Classification equations from QDFA for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of king eider head feathers are in Appendix C.

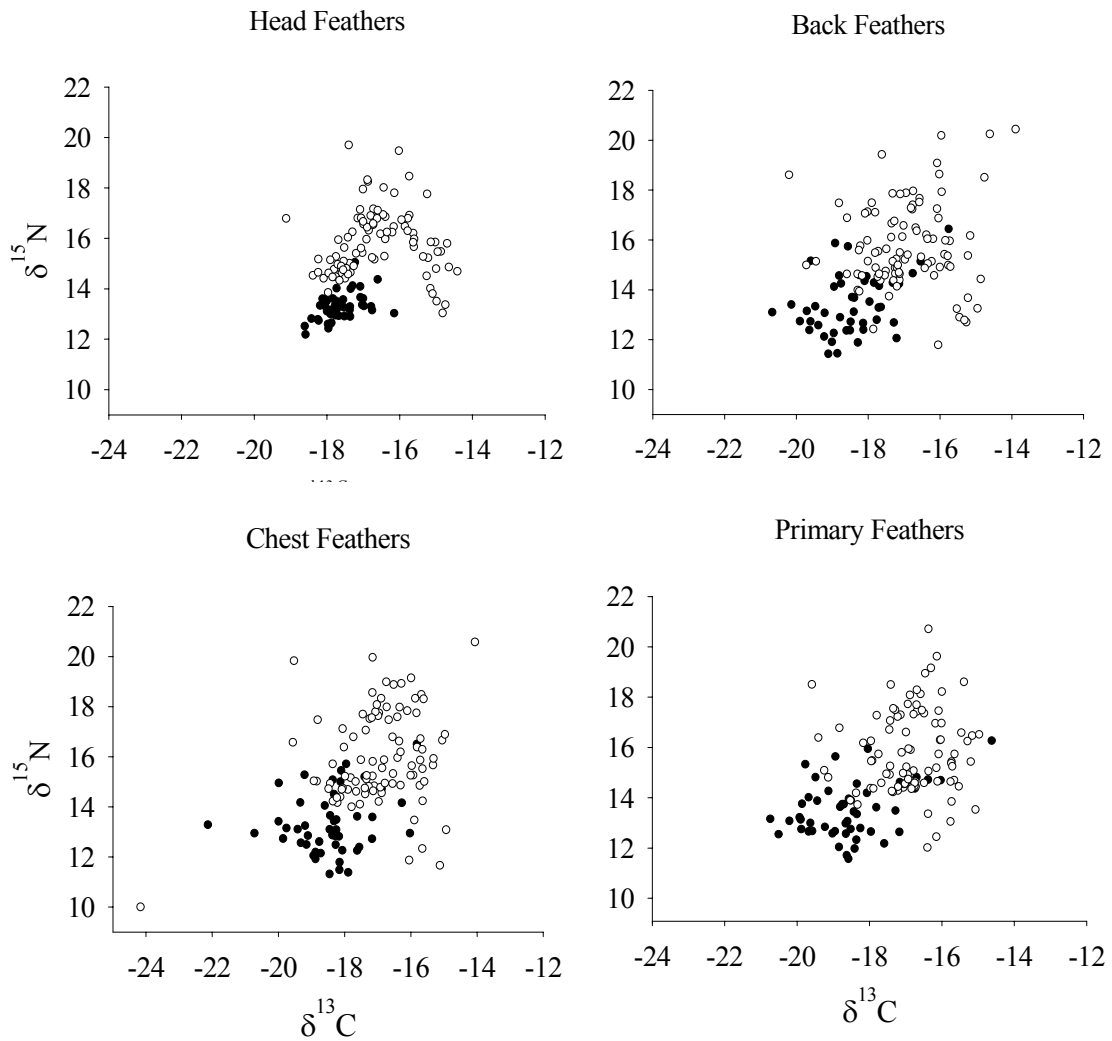


Figure B.2 Isotopic values from head, back, chest, and primary wing feathers of hunter-killed king eiders that wintered in eastern (n=49) or western seas (n=94) of northern North America. Open circles are values from western populations, closed circles are values from eastern populations.

Table B.1 Mean isotopic values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of feathers collected from hunter-killed King Eiders that were shot near the coast of Greenland (east) and Holman Island, Nunavut (west).

Feather tract	Population	<i>n</i>	Feather $\delta^{15}\text{N}$		Feather $\delta^{13}\text{C}$	
			Mean	\pm SD	Mean	\pm SD
Back	East	47	13.44	1.18	-18.45	0.99
	West	94	15.79	1.15	-16.91	1.15
Chest	East	48	13.31	1.22	-18.46	1.13
	West	94	15.96	1.31	-16.95	1.31
Head	East	48	13.27	1.05	-17.65	0.51
	West	94	15.80	0.98	-16.64	1.05
Wing	East	50	13.49	1.08	-18.58	1.19
	West	94	15.80	0.98	-16.84	0.98

[†] Sample sizes varied, as I was missing feathers from some tracts for a few individuals.

Table B.2 Classification success (%) of quadratic discriminate function analysis for isotopic values of $\delta^{13}\text{C}$ $\delta^{15}\text{N}$ from King Eider feathers of eastern and western populations. Feather tract(s) are listed in order of classification success for eastern populations. Bias represents $\% \text{Success}_{\text{west}} - \% \text{Success}_{\text{east}}$ where bias represents favor toward the western population.

Feather Tract(s)	Male and Female					Female Only				
	East		West		Bias ^a	East		West		Bias
	<i>n</i>	%	<i>n</i>	%		<i>n</i>	%	<i>n</i>	%	
Head	48	94	94	99	5	21	90	71	100	10
Head, Wing	48	94	94	99	5	21	86	71	99	13
Chest, Head	47	94	94	100	6	21	81	71	100	19
Back, Chest, Head, Wing	47	91	94	98	6	21	62	71	99	37
Back, Head	47	89	94	98	9	21	86	71	100	14
Chest, Head, Wing	47	89	94	98	9	21	81	71	97	16
Back, Head, Wing.	47	89	94	99	10	21	76	71	99	22
Back, Head, Chest	47	87	94	98	11	21	86	71	99	13
Wing	50	80	94	93	13	21	67	71	96	29
Chest	48	79	94	94	14	21	71	71	96	24
Back	47	79	94	90	12	21	62	71	96	34
Back, Wing	47	79	94	90	12	21	67	71	94	28
Back, Chest	47	74	94	87	13	21	71	71	93	22

B.5 DISCUSSION

I have determined that naturally-occurring stable isotope ratios in feathers can be used with considerable success to assign king eiders to western and eastern North American wintering populations. My results clearly indicate that the greatest distinction between isotopic values of feathers from eastern and western king eiders was due to differences in $\delta^{15}\text{N}$ values, as only 4% of the bias for eastern and western classifications was corrected by inclusion of $\delta^{13}\text{C}$ measurements. These results are consistent with available information about geographic patterns in isotopic signatures of lower trophic levels (i.e., copepods) in marine foodwebs between western (Bering) and eastern (Greenland) seas (Figure 1). However, complete information about stable isotope ratios of eider winter diet from western and, in particular, eastern foodwebs is not yet available. Hence, it is unclear to what extent signatures from king eider feathers are due to differences in predominant trophic levels of winter diet. Nevertheless, these findings offer an opportunity for assigning arctic-breeding king eiders to the broad winter areas in question. These results could have wider applicability to other marine-associated species with similar dichotomous wintering distributions. For example, ongoing research on white-winged scoters (*Melanitta fusca deglandi*) shows this same western vs. east trend in feather isotope values (Swoboda et al., unpubl. data) at lower latitudes than investigated in the current study. I found that $\delta^{15}\text{N}$ values varied by as much as 8‰ for feathers grown within the same winter area (i.e., eastern or western seas). Several factors may have influenced stable isotope composition of these feathers within and between wintering areas. In addition to potential differences in trophic level of king eider prey between winter areas noted above, variation within winter areas may have resulted from individual birds foraging on foods of different trophic levels. Feathers grown during consumption of foods from higher trophic levels would have more enriched $\delta^{15}\text{N}$ values relative to feathers grown during the consumption of foods from lower trophic levels (DeNiro and Epstein 1978, Hobson and Welch 1992). King eiders forage on a number of prey items including algae, polychaetes (*Pectinaria* spp), gastropods, (*Oenopota* spp) bivalves, and fish eggs (Suydam 2000, Frimer 1997); however, the extent and timing of factors that influence winter/spring dietary composition are unknown. King eiders also winter over a broad geographical range

and variation in molt location might involve isotopic changes in foodweb signatures at local or regional scales (Dunton et al. 1989, Schell et al. 1998). Finally, use of endogenous reserves can cause isotope signatures to drift from their geographic specific signatures (Hobson 1995), but I expect that this had little impact on my results, as feather synthesis occurs primarily from exogenous sources (Ankney 1979, Murphy 1996).

Discrimination of ^{13}C between trophic levels is conservative, so variations in observed $\delta^{13}\text{C}$ values (about 6 ‰ for western and eastern king eider feathers) are likely due to spatial differences rather than diet *per se*. Enrichment in ^{13}C generally is greater in benthic vs. pelagic foodwebs (Hobson and Welch 1992, France 1995) and so feeding in the water column or epontic foraging around sea ice might result in considerably depleted eider $\delta^{13}\text{C}$ values compared to those feeding exclusively on benthic foods. My data suggest that some contour feathers are occasionally grown from nutrients acquired on freshwater habitats. One female western king eider had chest feather isotope profiles that strongly suggest freshwater input during feather growth (e.g., Mizutani et al. 1990). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the chest feather of this individual ($\delta^{13}\text{C} = -24.17\text{‰}$, $\delta^{15}\text{N} = 10.00\text{‰}$; Figure 2) were lower than those expected from marine habitats. Alternatively, growth of this feather may have occurred near a river delta where fresh water inputs are greater than marine inputs (see Schell et al. 1998). Head feathers provided the best discrimination between populations likely because these feathers are small relative to feathers from other tracts. Nutrient requirements for growth of small feathers are more easily met through daily diet than for larger feathers (see Thompson and Drobney 1996), thereby more likely reflecting local diet signatures. Moreover, completion of growth for the lightest feathers should be most rapid, thereby reducing the influence of variation in diet from (1) changes in trophic level of principal king eider prey, and (2) movement of King Eiders during the time of feather growth. Spring migration begins in late April to early May, depending on sea ice conditions, with growth of head feathers often complete by mid-May (Suydam 2000). Nutrients for head feathers worn in the spring may be acquired in more geographically confined areas such as nutrient-rich polynyas with correspondingly narrower ranges in isotopic signature associated with local foodwebs. In contrast, flight feathers provided less

accuracy in discriminating between eastern and western populations, as also determined by Hobson (1999b). This is likely because flight feathers are grown during fall when most king eiders undergo a molt migration to marine habitats which may not necessarily coincide with wintering areas.

In addition to further research on isotopic patterns in winter foodwebs of eiders, I recommend future research to include collection of head feathers from king eiders captured on breeding areas in conjunction with local banding efforts. My classification equation derived from head feathers of king eiders from known winter location (Appendix A), used with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values obtained from head feathers of breeding king eiders, allows assignment of breeding birds to either western or eastern winter location. Such an approach using birds from several breeding areas would allow estimation of degree of breeding overlap between eastern and western winter populations. Furthermore, use of isotopic measurements in conjunction with multistate models based on capture-recapture of breeding birds could be used for direct estimation of probabilities of survival for each winter area, and philopatry to winter areas as defined herein (e.g., Hestbeck et al. 1995). For example, encounter histories of a marked individual could be coded as one of two wintering states, west or east. Such multistate models permit estimation of (1) survival, (2) recapture probability, and (3) the transition probability of moving among wintering areas (Lebreton et al. 1999). If both young and adults are marked, the extent to which adults and their offspring winter in the same areas can also be investigated. Because pair formation occurs on staging areas away from breeding areas (Barry 1986), dispersal between winter areas would result in gene flow between western and eastern populations. Knowledge of philopatry to wintering area is especially important for king eider management, given their declining population trends. Population trends of king eiders are based on count surveys at key migrational areas (Suydam et al. 2000), so regular movement between western and eastern wintering areas would bias interpretations of true population trajectory. In conjunction with use of stable isotopes, information on dispersal and migration would increase understanding of King Eider population structure, and of the effects of mortality in multiple winter areas on dynamics of breeding populations.

Finally, I suggest that much remains to be learned despite my success at discrimination of king eiders from two important winter areas. Isotopic ratios of food webs that include king eiders are poorly known for marine wintering sites in general and these may vary through time. As well, in years of heavy sea ice, king eiders may be forced south of areas which my data represent. I suggest that future studies investigate molt chronology more thoroughly in order to better understand age and sex specific feather growth periods. Furthermore, investigation of isotopic ratios in feathers of eiders that winter south of my samples would help to understand isotopic variability and the applicability of this method to king eiders during heavy ice years. The success in delineating populations of northern wintering king eiders, and support of the western vs. eastern trend in feather isotope values at lower latitudes (Swoboda et al., unpubl. data), indicate that stable isotopic analysis is a viable method that may be useful to other marine species.

APPENDIX C. PREDICTIVE EQUATIONS FOR DELINEATING BETWEEN EASTERN AND WESTERN POPULATIONS OF KING EIDERS.

Quadratic discriminate function equation was based on isotopic values from King eiders killed near the coasts of Holman Island, NWT (n=94) and Greenland (n=50).

The quadratic classification equation using isotopic ratios was

$$D_{east} = -1722.51 + [103.02 \quad -1722.51] * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix} + \begin{bmatrix} {}^{15}N_i & {}^{13}C_i \end{bmatrix} * \begin{bmatrix} -2.35 & 1.15 \\ 1.15 & -2.47 \end{bmatrix} * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix}$$

(C.1)

$$D_{west} = -210.37 + [10.08 \quad -15.64] * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix} + \begin{bmatrix} {}^{15}N_i & {}^{13}C_i \end{bmatrix} * \begin{bmatrix} -0.30 & 0.02 \\ 0.02 & -0.45 \end{bmatrix} * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix}$$

(C.2)

Where ${}^{15}N_i$ and ${}^{13}C_i = \delta {}^{15}N$ and $\delta {}^{13}C$ values for observation i , respectively. If $D_{east} > D_{west}$, the individual is then classified as wintering in the east

The equation used to calculate the probability of belonging to each population was

$$\text{Denominator} = \exp(D_{east}) + \exp(D_{west})$$

$$\text{Probability}_{east} = \exp(D_{east}) / \text{denominator}$$

$$\text{Probability}_{west} = \exp(D_{west}) / \text{denominator}$$

APPENDIX D. BODY SIZE: PARENT OFFSPRING ESTIMATES OF HERITABILITY

B.1 RATIONAL AND METHODS

I estimated parent-offspring heritability of body size among King Eiders to assess the degree at which this trait is passed from one generation to the next and thus, the ability for natural selection to occur. I estimated heritability of body size by first regressing the PC1 scores of breeding adults that were marked as ducklings on PC1 scores of their putative mothers. Heritability analysis includes data from 1995-2003. When >1 offspring for the same female was present ($n = 3$), I used the mean PC1 score of the offspring for the analysis (Falconer and Mackay 1989). I then multiplied the slope of the regression by two and used this as an estimate of heritability (Falconer and Mackay 1989). I also regressed PC1 scores from an equal number of randomly chosen breeding females on the PC1 scores of maternal females to assess if body size co-varied among the Karrak Lake nesting population. Such heritability estimates assume additive genetic effects and lack of covariance between parents and offspring (Falconer and Mackay 1989).

B.1 ESTIMATES OF HERITABILITY

Results from offspring size regressed on maternal size suggest that body size is heritable with strong maternal influence (Falconer and Mackay 1989; >100% heritable, Figure 3.1; $\hat{\beta}_{size} = 0.60 \pm 0.22$ SE, $r^2 = 0.31$, $F_{1,17} = 7.19$, $P = 0.02$). Heritability estimates >100% suggest the presence of strong maternal effects. Factors such as covariances between the use of productive brooding habitat and final adult size (Cox 1998) would lead to greater measurement error, resulting in positive biases of heritability estimates (Falconer and Mackay 1989).

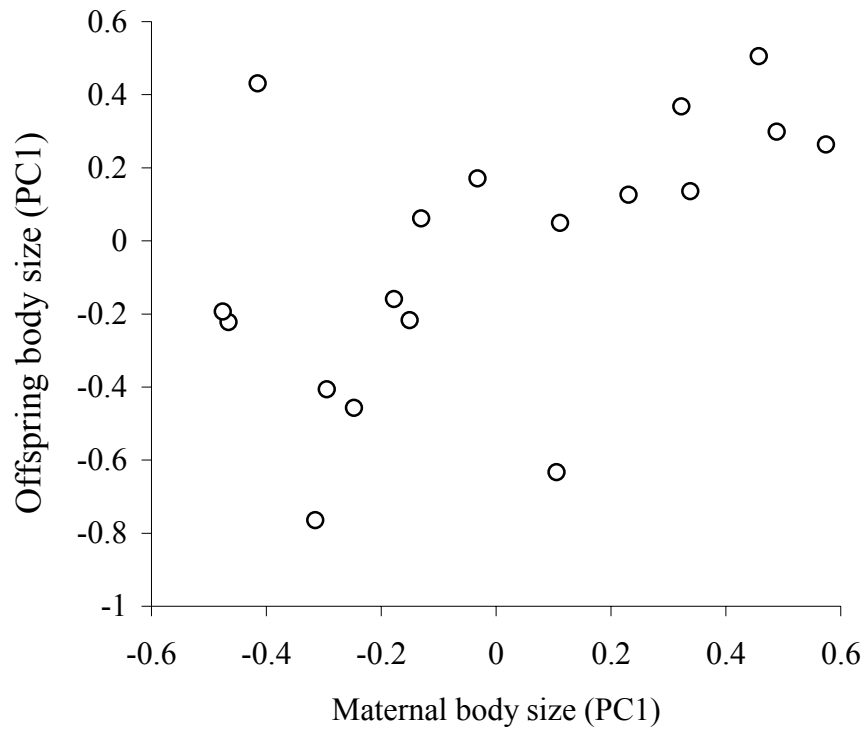


Figure D.1 Relationship between body size of known age breeding adults and body size of maternal females. Body sizes are derived from principal components analysis based on the correlation matrix of mean metric measurements of each individual.