POPULATION ECOLOGY OF PACIFIC COMMON EIDERS

ON THE YUKON KUSKOKWIM DELTA, ALASKA

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POPULATION ECOLOGY OF PACIFIC COMMON EIDERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA

A

THESIS

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Abstract

Knowledge of ecological factors that influence birth, death, immigration, and emigration provide insight into natural selection and population dynamics. Populations of Pacific common eiders (*Somateria mollissima v-nigrum*) on the Yukon-Kuskokwim Delta (YKD) in western Alaska declined by 50-90% from 1957 to 1992 and then stabilized at reduced numbers from the early 1990's to the present. This study investigates the primary underlying processes affecting population dynamics of Pacific common eiders, with the goals of understanding factors that may have led to the observed decline and subsequent stabilization, and providing tools from which conservation, management, and recommendations for future research can be drawn.

I examined variation in components of survival and reproduction in order to test hypotheses about the influence of specific ecological factors on life history variables and to investigate their relative contributions to local population dynamics. These analyses include data I collected from 2002 to 2004, in addition to historical data collected from 1991 to 2001. Apparent survival of adult females was high and relatively invariant, while components of reproduction were low and variable, both within and among individuals. Timing of nesting and seasonal declines in clutch size and nest survival indicated that females in the early and mid parts of the breeding season produced the highest numbers of offspring; suggesting directional selection favoring early nesting. Probability of a nest containing ≥ 1 nonviable egg was positively related to blood selenium concentrations in hens, but no other contaminant-related reductions to life history variables were found.

All estimates of population growth (λ) indicated that the YKD population was stable to slightly increasing during the years of the study (range λ: 1.02-1.05 (CI: 0.98-1.11)), and would respond most dramatically to changes in adult female survival. However, historical fluctuations in λ were primarily explained by variation in reproductive parameters, particularly duckling survival. Practical options for increasing adult survival currently may currently be limited. Thus, enhancing productivity, particularly via methods with simultaneous positive effects on adult survival (e.g., predator removal), may offer a more plausible starting point for management aimed at increasing population growth.

Table of Contents

Page

List of Figures

Page

CHAPTER 1.

CHAPTER 2.

CHAPTER 3.

CHAPTER 4.

List of Tables

Page

CHAPTER 1

CHAPTER 2

CHAPTER 3

Page

CHAPTER 4

List of Appendices

Preface

This dissertation is written in four separate chapters that are each formatted for specific journals. The first and second chapters are in press in *The Journal of Wildlife Management* and *Environmental Toxicology and Chemistry*, respectively. Chapters 3 and 4 are formatted for *The Journal of Wildlife Management.* Although this thesis is single authored, coauthors are included for each individual manuscript. The "we" in each chapter therefore refers to the multiple-authors listed, but I, alone take responsibility for any errors.

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General Introduction

Several of the common eider (*Somateria mollissima*) subspecies have been well studied in Europe and eastern North America (Milne 1974, Reed 1975, Baillie and Milne 1982, Coulson 1984, Krementz et al. 1996, Goudie et al. 2000). However, prior to this study, little was known of the ecology of Pacific common eiders (*S. m. v-nigrum*), aside from a few isolated studies of reproduction, duckling survival, and population structure (Schamel 1977, Seguin 1981, Johnson et al. 1987, Flint et al. 1998, Petersen and Flint 2002). Further, no studies examined the annual survival or population dynamics of this subspecies. The Pacific subspecies is considered the most distinct, morphologically and genetically, of the 4 to 7 recognized subspecies (Livezey 1995) and its breeding is primarily isolated to the coastal fringe of Alaska, western Canada, and far eastern Russia (Goudie et al. 2000).

Survey data indicate that Pacific common eiders have declined by approximately 50-90% over the past 25-50 years, leading to their current designation as a "Focal Species" by the U.S. Fish and Wildlife Service (Woodby and Divoky 1982, Stehn et al. 1993, Hodges et al. 1996, Suydam et al. 2000, U.S Fish and Wildlife Service 2005). Historically, the Yukon-Kuskokwim Delta (YKD) in western Alaska supported one of the largest breeding populations of Pacific common eiders in the state, more than 51,000 breeding pairs as of the 1950's (Bellrose 1980). However, present-day surveys (Platte and Stehn 2005), estimate that only 1,800 to 2,300 pairs currently exist, a reduction of greater than 90% (Stehn et al. 1993, Hodges et al. 1996, Platte and Stehn 2005). Two other species of eiders breeding in western Alaska also appear to have also undergone severe declines (particularly on the YKD); spectacled (*S. fischeri*) and Steller's (*Polysticta stelleri*) eiders were listed as "Threatened" under the Endangered Species Act in 1993 and 1997, respectively (Federal Register 1993; 1997). After listing, a large body of research emerged on the ecology, population biology, and potential causes of decline for spectacled eiders (Franson et al. 1995, Flint et al. 1997, Flint and Grand 1997, Grand and Flint 1997, Grand et al. 1998, Flint and Grand 1999, Petersen et al. 1999, Grand et al. 2002, Petersen and Douglas 2004). In contrast, only limited information currently exists on the ecology of sympatrically nesting Pacific common eiders. Given that estimates of demographic rates are necessary to predict future population trends and assess the relative influence of life history parameters on population growth, this study aims to provide comparable vital rates for Pacific common eiders, and develop models which evaluate current population growth and quantify the response of population growth to changes in reproduction and survival.

The specific goals of this research were to:

1. Assess annual and geographic variation in apparent survival of adult females, clutch initiation dates, clutch size, daily nest survival, nest success, and productivity of Pacific common eiders at three study sites across the YKD using current and historical data.
2. Determine concentrations and estimate exposure rates to lead and selenium in common eiders on the YKD, and examine variation in components of reproduction and annual survival in relation to contaminant burdens.

3. Develop population models to examine the relative influence of components of survival and reproduction on population dynamics, in order to facilitate prioritization of management strategies, and identify future research needs.

CHAPTER 1. Survival of breeding Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska[1]

Abstract: Populations of Pacific common eiders (*Somateria mollissima v-nigrum*) breeding in Alaska have declined markedly over the past 40 years. We studied survival of adult female Pacific common eiders using capture-recapture of nesting hens at three sites on the Yukon-Kuskokwim Delta (YKD), Alaska from 1994-2004. We used data consisting of 268 recapture events from 361 uniquely marked individuals to investigate temporal, geographic, and environmental variation in adult female survival. Our results suggest apparent annual survival of adult eiders from the YKD was high (0.892, SE = 0.022), and spatially and temporally invariant ($\sigma^2 = 0.005$); a pattern consistent with other long-lived marine birds. Moreover, our results suggest adult survival may be functionally fixed for Pacific common eiders, and at the present, adult survival may be relatively unresponsive to environmental or management perturbations. Our data did not support hypothesized variation in survival relative to mortality factors such as predation on breeding grounds, physiologic costs of reproduction, and wintering conditions. Although changes in adult survival likely have a large potential effect on prospective population growth, our results suggest viable management actions aimed at increasing survival may be extremely limited.

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[1] Wilson, H.M., P.L. Flint, T.L. Moran, and A.N. Powell. 2007. Survival of breeding Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. *Journal of Wildlife Management* 71(2):in press.

Introduction

For long-lived species, annual survival of adult females is often the most sensitive parameter in population dynamics since it has the largest proportional influence on prospective population growth relative to other vital rates (Schmutz et al. 1997, Tombre et al. 1998). Because species exist in variable environments, incorporation of spatial and temporal variation in survival is also an important component of population modeling, as simple averages can result in overestimation of population performance (Morris and Doak 2002). Estimated variation in survival includes true environmental variation, as well as sampling error, and where estimates of true variability are over-inflated (i.e., sampling error is not removed), negatively biased stochastic population growth rates can result. Increased variance in vital rates leads to wider fluctuations in stochastic growth rates and overestimates uncertainty in predicted population sizes (Ludwig 1999, Morris and Doak 2002). Thus, the accurate estimation of vital rates (such as adult survival) and associated process variation are critical to population analyses and subsequent estimation of population fluctuations and extinction probabilities (Mills and Lindberg 2002).

Common eiders (*Somateria mollissima*) are among the most marine of all waterfowl, with females spending more than 90% of their annual cycle at sea and returning to land only during the brief breeding period (Goudie et al. 2000). Common eiders generally stage and winter at high latitudes and their survival during winter may be negatively influenced by extended periods of extreme sea ice and harsh winter weather conditions (Gilchrist and Robertson 2000, Petersen and Douglas 2004). A myriad of mortality factors may also affect adult female common eider survival on breeding grounds, including predation (e.g., arctic foxes [*Alopex lagopus*]; Schamel 1977, Quinlan and Lehnhausen 1982), diseases (Korschgen et al. 1978), contaminants (Franson et al. 1995), severe weather events, and subsistence hunting (Barry 1968, Wentworth 2004). Successful reproduction also exacts significant physiologic costs on common eiders; females fast during their entire 26-d incubation period and expend roughly 45% of their total body mass from laying through hatch (Milne 1976, Korschgen 1977). Moreover, the physiologic demands associated with brood rearing may further reduce adult body condition, causing subsequent decreases in adult survival (Golet et al. 1998, Hanssen et al. 2003).

The Pacific common eider (*S. m. v-nigrum*) is the most distinct, morphologically and genetically, of the 4 to 7 recognized subspecies, and it has been recommended for separate species status based upon uniqueness of characteristics and relative geographic separation from others in the common eider complex (Livezey 1995). Pacific common eiders breed primarily along the coastal fringe of Alaska, western Canada, and far eastern Russia (Goudie et al. 2000) and they are more dispersed in their nesting than common eiders found elsewhere, lacking the strong colonialism characteristic of the other subspecies (Gabrielson and Lincoln 1959).

Survey data indicate that the Pacific subspecies has declined by more than 50% over the past 25 years (Woodby and Divoky 1982, Suydam et al. 2000) and estimates from the Yukon-Kuskokwim Delta (YKD), Alaska indicate a > 90% local decline in breeding eiders over the last 40 years (Hodges et al. 1996). During the same period, dramatic population reductions in sympatrically nesting spectacled (*S. fischeri*) and

Steller's (*Polysticta stelleri*) eiders resulted in their listing as threatened under the Endangered Species Act (Kertell 1991, Federal Register 1993, Stehn et al. 1993, Federal Register 1997).

At present, it remains unclear whether common, spectacled, and Steller's eiders have declined due to common causes or as a result of independent factors. Also, because early breeding pair surveys on the YKD (Hodges et al. 1996) did not discriminate among eider species, the proportion of common and spectacled eiders in historical counts is unknown, and ambiguity exists with regard to the magnitude of the apparent Pacific common eider decline. Only sparse demographic information exists for Pacific common eiders (Schamel 1977, Seguin 1981, Johnson et al. 1987, Flint et al. 1998, Petersen and Flint 2002) and researchers have not examined their annual survival, variation in survival among geographically discreet breeding groups, or the effect of environmental variation on life history parameters throughout the annual cycle.

From 1994–2004 we collected capture-recapture data from individually-banded female Pacific common eiders nesting on the YKD, Alaska to meet 3 objectives. First, we examined temporal and geographic variation in annual apparent survival of adult females. Second, we addressed specific hypotheses concerning variation in apparent survival in relation to physiologic stress associated with reproduction, predator densities on breeding grounds, and wintering conditions, in an effort to identify potential sources of mortality and critical periods in the annual cycle. Finally, we quantified process variation in apparent survival in order to disentangle sampling error from true environmental (i.e., process) variation, and to minimize potential negative bias in future stochastic population models.

Study area

We studied apparent survival of Pacific common eiders from three sites on the YKD (Figure 1): Kashunuk River (61°20’N, 165°35’W), Tutakoke River (60°51’N, 165°49’W), and Kigigak Island (60°50’N, 165°50’W). The Kashunuk River (KR) study area (27.6 km^2) was located along the lower Kashunuk River, approximately 5 km inland from the central coast of the YKD (see Grand et al. 1997 for a detailed description). KR supported few common eiders (12-34 nests per year), and these females primarily nested in habitats near the river edge. The Tutakoke River (TR) study area was a coastal, mainland site, approximately 52 km north of the Kigigak Island (KI) study area and 10 km southwest of the KR study area. The TR study site covered approximately 12 km^2 and supported a large aggregation (average: 110 nests) of common eiders located primarily within a black brant (*Branta bernicla nigricans*) colony (~5000 pairs; Sedinger et al. 1998). Common eiders at the TR site nested in wet sedge meadows dominated by *Carex ramenskii* several hundred meters inland from coastal mudflats. The third study area, KI, consisted of nearly the entire island (32.5 km^2), and nesting habitat included low coastal tundra and high graminoid and intermediate sedge meadows. KI was approximately 1 km from the mainland and was bordered by the Ninglick River to the northeast, Baird Inlet to the southeast, and the Bering Sea to the west. KI supported a high abundance of nesting common eiders (> 200 total nests annually) that appeared to nest in a greater variety of habitats and social situations relative to birds at other sites. At

KI we found common eiders nesting within medium to large colonies of black brant, within small conspecific colonies (~15-20 eiders around a single lake), and solitarily along the coastal fringe. All study areas on the YKD contained many shallow ponds, lakes, and networks of tidally influenced sloughs. The three areas were also populated by a similar suite of nest predators, including arctic fox, glaucous gulls (*Larus hyperboreus*), mew gulls (*L. canus*), and parasitic jaegers (*Stercorarius parasiticus*). Arctic foxes were the only predator of adult female eiders on breeding grounds, and fox abundance was highly variable across study areas and years.

Methods

Field methods

We searched for Pacific common eider nests on foot, beginning shortly after spring breakup (10-25 May) through the end of the first week of incubation (~10 June) each year. During the search period we covered most of the available (vegetated) nesting habitat within each study area (average = ~9 km^2 each). Once found, we revisited nests at 7-d intervals and candled eggs (Weller 1956) at each visit to determine incubation stages. We used candling data and a 26-d incubation period to calculate hatch dates and determine best capture dates.

We captured nesting Pacific common eiders using mist nets and bow-net traps (Salyer 1962) usually within 1 to 3 days before hatch. We marked all newly captured females with U.S. Geological Survey metal bands and yellow, alpha-numerically inscribed, plastic leg bands. Common eiders generally do not breed until 2 to 3 years of age (Baillie and Milne 1982), and we classified all captured nesting females as after-hatch year (AHY) birds. Although we relied almost entirely on recapturing birds in order to read bands in subsequent years, approximately 4% of our total detections were the result of resightings using spotting scopes (2003 and 2004 only). Because our captures were primarily focused late in the nesting period (usually a few days before hatch), apparent annual survival in our study represented the period between hatch in year *i* and hatch in year *i*+1, and our sample was mostly comprised of successful breeders.

Data analysis

We estimated annual apparent survival (φ) and encounter (p) probabilities using Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in program MARK (White and Burnham 1999). We used a logit link to bound parameter estimates between 0 and 1. Our dataset included 11 total encounter occasions (1994 -2004) and three geographic areas on the YKD; KR, TR, and KI. Sampling efforts were not continuous among the three sites and eleven years of study. We marked and recaptured females at KR from 1994 to 2002, at TR from 1997 to 2004, and at KI in 1997 and 2001-2004. We did not estimate apparent survival or recapture probabilities for years in which we did not collect data. Rather than exclude data, we accounted for the lack of resighting at KI from 1998 to 2000 by treating birds banded in 1997 as part of the year-2000 cohort. We then estimated apparent survival from 2000 to 2001 as a unique parameter, representing 3 years of constant survival. Our most complex model included annual and geographic variation in φ and p. We took a hierarchical approach in our modeling, and considered candidate models of encounter probability which included all combinations of site and year. Because our study focused on nesting hens, and variation in annual nesting success may have influenced encounter probabilities, we also considered nesting success in our models of encounter probability. Where specific common eider nesting data were lacking (i.e., between 1998 and 2001 at the TR site), we used common eider nesting success estimates from the nearby KR study area as a surrogate measure of common eider success at TR.

We developed a limited suite of survival models to test our hypotheses regarding variation in adult female survival. First, we considered models examining temporal and geographic variation in survival. We began with our most complex hypothesis (e.g., site-year specific variability), followed by progressively less complex models. For example, we compared models where apparent survival probability varied among sites and years with models where apparent survival varied only among years, only among sites, or did not vary at all. Second, we hypothesized that survival varied according to broader geographic characteristics, and we developed a geographic model representing similar apparent survival probabilities among the two mainland sites (KR and TR) that differed from the island site (KI).

Third, we examined a suite of hypotheses regarding relationships between hypothesized mortality factors and annual adult female survival. In each analysis of specific mortality factors, we coded annual or site-year specific covariates using a single group-covariate column within our design matrix in program MARK. In our first mortality-specific model, we examined the hypothesis that physiologic stress associated with rearing young reduced subsequent survival. Under this hypothesis, we argued that females who were successful in nesting in year *i* expended significant reserves to achieve successful nesting and likely expended further reserves in brood rearing. Thus, under this scenario we predicted a negative relationship between site-specific annual survival and site-specific annual nest success estimates in the previous year (*i*). Second, we hypothesized that predators such as foxes likely captured and killed hens on nests (Quinlan and Lehnhausen 1982); thus, high mammalian predator densities in year *i*+1 would result in both low nest survival and low adult female survival. Under this scenario, we predicted a positive relationship between site-specific annual survival and site-specific annual nest success in the current year. However, because nest success could also be affected by predators such as gulls, which do not kill adult females, we sought a more direct examination of the relationship between female eider survival and mammalian predators on breeding grounds in the same year. Thus, our third specific-mortality model included an annual index of YKD arctic fox abundance, based on counts of arctic fox hair and scat across random nest plots on the YKD (U.S. Fish and Wildlife Service, unpublished data). This model examined annual fox abundance estimates in relation to annual survival across all study areas (i.e., no site-year specificity). Finally, we examined the relationship between annual survival and annual wintering conditions using an index of Bering Sea winter sea ice. This index was composed of several highly correlated ice coverage and ice extent variables from sites throughout the Bering Sea and it represented general annual sea ice severity across the region (National Oceanic and Atmospheric Administration 2004). Like our fox abundance index, we applied the annual sea ice covariate across all sites. Finally, because we lacked resighting data for

KI during the interval between 1997 and 2000, we accounted for multiple covariate values for the single survival parameter representing 1997-2000 at KI using the average covariate value across the 4-year period.

We used AIC (Akaike's Information Criterion) adjusted for sample sizes and overdispersion (i.e., $QAIC_c$; Burnham and Anderson 1998) to select the best approximating model from our suite of 43 candidate models. We evaluated goodness of fit of the most complex model using Test 2 and 3 results from program RELEASE and estimated overdispersion using the parametric bootstrap procedure in program MARK (White 2002). We estimated an overdispersion parameter ($\hat{c}$) by dividing the observed deviance of our global model by the mean expected deviance from 500 bootstrap replicates of the global model (Efron and Tibshirani 1993, Schmutz and Ely 1999, Breton et al. 2005). Because this type of method may produce positively biased estimates of $\hat{c}$ with ordinary sample sizes (McCullagh and Nelder 1989), we may have over-inflated our sampling error by an unknown amount when applying this inflation factor. However, for lack of a suitable alternative, we adjusted standard errors by our calculated $\hat{c}$ to account for any overdispersion in our data (White 2002). We ranked competing models in our candidate set by their $QAIC_c$ values in ascending order. We used $\Delta QAIC_c$ values to assess relative support for individual models and used differences in $QAIC_c$ weights to assess the relative likelihood of each model, given the data, on a scale of 0 to 1 (Burnham and Anderson 1998).

Our measurements of the variation in apparent survival estimates were a combination of sampling error (variation due to measurement) and process variation

(variation due to true biological change). To quantify each of these components independently, we used the variance components function in Program MARK (White and Burnham 1999), and treated variation in apparent survival as a random effect among site-years with mean μ and variance σ^2.

Results

Our dataset included 361 breeding adult (ASY) female Pacific common eiders (KR: $n = 42$, TR: $n = 161$, KI: $n = 158$) banded between 1994-2003, which resulted in 268 future recaptures and resightings between 1995-2004 (KR: $n = 54$, TR: $n = 124$, KI: $n = 90$). We excluded individuals newly banded in the last year of study at each site from the analysis (KR: $n = 2$, TR: $n = 34$, KI: $n = 61$), as they made no contribution to encounter histories. We had no band recoveries during the course of our study and our estimates reflect apparent, rather than true survival as we could not account for individuals that survived, but permanently emigrated outside study areas. We had sufficient data to estimate apparent survival and encounter rates for 19 site-years; including 8 site-yrs at KR (1994-2002), 7 at TR (1997-2004), and 4 at KI (1997/2000-2004). Our global model included an interaction between sites and years for both apparent survival and encounter probabilities. Results from Tests 2 and 3 indicated good fit between our global model and the data ($\chi^2_{40} = 38.6$, $P = 0.53$), and our bootstrapped estimates of overdispersion ($\hat{c} = 1.19$) confirmed this goodness of fit. Although overdispersion appeared to be minimal in our analysis, we nevertheless inflated sampling errors and adjusted AIC$_c$ values by our estimated $\hat{c}$ of 1.19.

The best approximating model ($\varphi_{.}$, p_{s*t}), from our candidate suite was one in which apparent survival was constant and encounter probabilities varied by site and year (Table 1). Estimated apparent survival using this model was 0.892 (95% CI: 0.842 to 0.928). We estimated spatial and temporal process variation in apparent survival (σ^2) to be 0.005 (95% CI: 0.001 to 0.020). Estimated encounter probabilities averaged 0.352 (95% CI: 0.178 to 0.598) at KR, 0.258 (95% CI: 0.175 to 0.367) at TR, and 0.289 (95% CI: 0.189 to 0.433) at KI.

Overall, we had strong support for several models describing variation in apparent annual survival ($\Delta QAIC_c < 2.0$; Table 1, Models 2-4). However, the addition of covariates in these models did not improve model fit (Δ model deviance < 0.49). In other words, models that included group-specific covariates of survival, such as nest success, winter sea ice severity, and breeding-ground fox abundance, were all within approximately 2 $\Delta QAIC_c$ units of the best approximating model (Table 1, Models 2-6), but failed to improve fit to the data (Burnham and Anderson 1998:131). Moreover, parameters describing variation in survival were poorly estimated (95% confidence intervals included zero on the logit scale). Thus, we interpreted results from these models with caution (Neter et al. 1996), and we did not consider any model-averaged survival estimates in our analysis.

Encounter probabilities were highly variable across sites and years (Range: 0.07–0.53). We found no support for reduced parameter models of encounter probability ($\Delta QAIC_c > 5$), including models in which encounter probability varied with site-specific annual nesting success ($\Delta QAIC_c > 44$) or with years of extremely poor reproduction ($\Delta QAIC_c > 41$).

Discussion

The best approximating model from our analysis suggested apparent survival probability of adult female Pacific common eiders on the YKD was relatively high and demonstrated little environmental variation. Our apparent survival estimate was near the highest reported among other subspecies of adult common eiders at breeding areas across the species' distribution (Table 2). However, our results regarding hypothesized variation in survival associated with discrete breeding areas, time, physiologic stress associated with reproduction, predator densities on breeding grounds, or wintering conditions were equivocal. Effects sizes for the covariates of interest were all small and had confidence intervals that overlapped zero. Furthermore, our estimates of process variation in apparent survival were extremely low, suggesting that most of the variation was due to sampling error, rather than true year to year fluctuations in survival.

Variation in encounter probabilities

Variation in encounter probabilities across study areas and years was likely the result of variation in sampling effort; crew sizes, experience levels, daily work hours, and logistical support all varied considerably across sites and years. Our lack of support for a relationship between nesting success and encounter probabilities may have reflected our inability to capture birds in proportion to their availability. Additionally, periodic non-breeding (Coulson 1984) may have further confounded patterns of encounter probabilities in our study. Finally, we considered birds nesting in our three study areas to be part of separate breeding groups and permanent emigration to be minimal, based on high nest-site fidelity among local females (H. M. Wilson, University of Alaska Fairbanks, unpublished data) and evidence of high breeding-site fidelity in other populations of common eiders (94-100%; Reed 1975, Wakely and Mendall 1976, Coulson 1984, Bustnes and Erikstad 1993). However, we did observe two exchanges between females at the nearby KR and TR study sites (< 2 km) during the 11 years of our study. Though we did not have sufficient data to estimate dispersal probabilities directly (given small sample sizes), we reasoned that with an average encounter probability of 0.31, emigration could have accounted for some unknown portion of the annual mortality we estimated, resulting in estimates of apparent survival which were lower than true survival.

Lack of variation in apparent survival

In general, our results support life history theory, where strong selection pressure is expected to minimize variation in demographic parameters with the greatest proportional effects on fitness, such as adult survival (Meats 1971, Stearns 1992, Pfister 1998, Heppell et al. 2000). Prospective population analyses suggest that altering survival of long-lived adults can often have much greater relative effects on population growth rate than equally proportionate changes in either juvenile survival or reproductive parameters (Schmutz et al. 1997, Tombre et al. 1998, Sæther and Bakke 2000). Our results indicating high, relatively invariant adult survival in Pacific common eiders were consistent with: 1) the expected life history pattern of common eiders (i.e., delayed maturity, low, variable productivity, and long life spans; Goudie et al. 2000), and 2) results found in other long-lived, marine birds, and many large mammal species (Weimerskirch et al. 1987, Spendelow and Nichols 1989, Renken and Smith 1995, Gaillard et al. 1998, Breton et al. 2005).

Survival probabilities for adult common eiders apparently vary only slightly across broad geographic areas and subspecies (Range: 6%, Table 2), and we did not find evidence of geographic variation at the local scale, among discrete breeding aggregations on the YKD. In general, our results suggest discrete breeding aggregations on the YKD share similarly high survival and in terms of this vital rate alone, individuals from separate breeding areas may be viewed as part of one population (Breton et al. 2005). Thus, future population models could potentially incorporate a single YKD-wide estimate to parameterize adult female survival.

Lack of support for any of our hypothesized mortality factors was surprising: 1) given both the high spatial and annual variability of predator abundances and eider reproduction on the YKD (Grand and Flint 1997), 2) the significant expenditure of reserves associated with successful reproduction for common eiders (Korschgen 1977), and 3) evidence of negative effects of winter conditions on sympatrically nesting spectacled eiders (Petersen and Douglas 2004). Overall, our results suggest that the balance between reproduction and future survival in Pacific common eiders weighs heavily in favor of long-term survival. The lack of support for a reproductive-cost hypothesis (physiologic), such as that accepted by Rotella et al. (2003) for lesser scaup (*Aythya affinis*) and Golet et al. (2004) for black-legged kittiwakes (*Rissa tridactyla*), suggests two possible interpretations. Common eiders on the YKD either: 1) do not incur similar survival costs related to reproduction, or 2) the stress of reproduction does not vary markedly enough among years to produce significant variation in survival. Lack of support for a predation-hypothesis similarly suggests that mammalian predation pressure may not be a major source of mortality for nesting Pacific common eiders on the YKD, and we hypothesize that females may benefit from predator swamping by high densities of nearby arctic nesting geese, effectively reducing the eiders' risk of mortality while breeding (Raveling 1989). Finally, we found no support for a relationship between indices of sea ice severity and apparent survival. However, satellite imagery of nearshore areas typically used by wintering common eiders can be of questionable quality due to difficulties in distinguishing land from water (e.g., "spillover" effects), and higher resolution imagery (e.g., Advanced Microwave Scanning Radiometer [AMSR-E]) was not available for the complete range of years and season dates relevant to our study (National Snow and Ice Data Center 2005). Thus, our index may have lacked sufficient specificity to explain annual variation in survival relative to winter conditions. Conversely, YKD common eiders may be relatively unaffected by displacement due to extreme ice fluctuations, if they have access to alternative, high quality winter areas.

A myriad of factors are likely responsible for mortality of adult common eiders. However, because of strong selection pressure on adult survival for long-lived species, very large samples would likely be required to detect significant patterns of variation (Croxall and Rothery 1991). Our indices of specific mortality factors may not have been appropriate, specific, or precise enough to capture subtle variability in survival for our study population. However, several of our top models had covariate effects that were opposite the direction of our predictions, indicating that insufficient power to detect relationships cannot fully explain our results. Further, we estimated process variation in survival to be extremely low, supporting our conclusions regarding the biological invariability of adult female survival and confirming that most variation in our estimates was due to sampling error, rather than true temporal, spatial, or environmental processes.

Finally, although we did not consider the effects of hunting in our study, hunting mortality, via subsistence, sport, and commercial harvest, is an important factor negatively affecting common eider populations in many parts of their distribution (Goudie et al. 2000, Merkel 2004), and it has the potential to similarly affect common eiders in western Alaska. On the YKD, almost all waterfowl hunting occurs through subsistence harvest, mostly during spring migration (Wentworth 2004). However, managing this remote resource has presented unique challenges (King and Derksen 1986) and data regarding YKD subsistence harvests currently do not offer sufficient accuracy or precision to be useful in modeling variation in adult survival. At present, we can only speculate that given the high annual survival rate of common eiders, spring subsistence harvest is likely an additive source of mortality, and as such, has some currently inestimable negative effect on population dynamics.

Differences between sympatrically nesting eiders

Low apparent survival in sympatrically nesting spectacled eiders (partially attributed to high rates of lead poisoning), has been suggested as a potential cause of population declines for that species (U.S. Fish and Wildlife Service 1996, Grand et al.

1998). In contrast, we found apparent survival rates for adult female Pacific common eiders to be relatively high and invariant; 10-20% higher than those estimated for sympatrically nesting spectacled eiders (Grand et al. 1998) and the second highest reported among common eider subspecies (Table 2). Although we cannot reject the hypothesis that common eider survival is reduced compared to historic levels, resulting in the observed population decline; comparison of our estimates with other populations of common eiders makes this hypothesis seem unlikely. Thus, we conclude that entirely different factors may have driven the concurrent declines of common and spectacled eiders.

Management Implications

Our high rate of apparent survival combined with a lack of support for hypothesized sources of variation suggests this vital rate may be near its biological limit, and thus may not respond to management perturbations (Gaillard et al. 1998, Mills et al. 1999, Reed et al. 2002). If the most common management actions to enhance survival are realized through reductions in mortality, our current results suggest that immediate, viable management options to increase adult survival in Pacific common eiders may be extremely limited. We suggest that future work incorporate mark-recapture efforts over broader spatio-temporal scales and strive to enhance the accuracy and precision in measurements of potential mortality factors (particularly subsistence harvest), in an effort to better identify sources of variation in adult survival and to more clearly define potential management actions.

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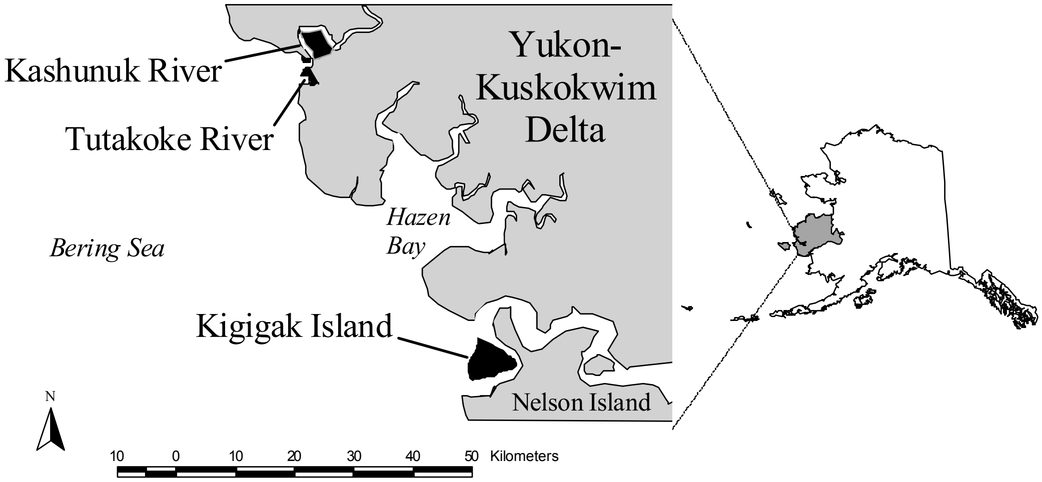

Figure 1. Locations of Kashunuk River (KR), Tutakoke River (TR), and Kigigak Island (KI) study sites of Pacific common eider annual apparent survival (1994-2004) on the Yukon-Kuskowim Delta, Alaska.

Table 1. Candidate set of models used to assess geographic and temporal variation in apparent survival and encounter probabilities of breeding female Pacific common eiders (1994-2004) on the Yukon-Kuskokwim Delta (YKD), Alaska, USA.

Model[a]	Apparent survival hypothesis represented by model	k[b]	$\Delta QAIC_c$[c]	ω	Deviance
1) $\Phi_{.,}\ p_{s*t}$	constant	20	0.00	0.31	172.19
2) $\Phi_{FOX,}\ p_{s*t}$	varies by indices of arctic fox on breeding grounds	21	1.46	0.15	171.50
3) $\Phi_{ICE,}\ p_{s*t}$	varies by indices of Bering Sea ice severity	21	1.98	0.11	172.03
4) $\Phi_{s,}\ p_{s*t}$	broader geographic variation (mainland vs. island)	21	1.99	0.11	172.03
5) $\Phi_{NSphys,}\ p_{s*t}$	varies by nest success in year i (physiologic cost)	21	2.05	0.11	172.10
6) $\Phi_{NSpred,}\ p_{s*t}$	varies by nest success in year i+1 (predation)	21	2.15	0.11	172.19

[a] Notation follows Lebreton et al. (1992) Φ = probability of apparent survival, p = probability of encounter, s = site, t = time

[b] k = number of parameters

[c] The best approximating model has the lowest delta quasi-likelihood Akaike's Information Criterion ($\Delta QAIC_c$) value and the highest model weight (ω) relative to others in the candidate set.

Table 2. Summary of published adult female common eider survival estimates and associated standard errors.

Location	Annual Survival Rate	SE	Subspecies	Source
England	0.895	0.015	*mollissima*	Coulson 1984
W. Alaska, USA	0.892	0.022	*v-nigrum*	This study
Maine, USA	0.886	0.076	*dresseri*	Wakeley and Mendall 1976[a]
E. North America	0.873	0.016	*dresseri*	Krementz et al. 1996
Quebec, Canada	0.826	0.010	*dresseri*	Reed 1975

[a] As reanalyzed and presented in Goudie et al. 2000.

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CHAPTER 2. Coupling contaminants with demography: effects of lead and selenium in Pacific common eiders[2]

Abstract: We coupled intensive population monitoring with collection of blood samples from 383 nesting Pacific common eiders (*Somateria mollisima v-nigrum*), at two locations in Alaska, USA (2002-2004). We investigated annual, geographic, and within-season variation in blood concentrations of lead and selenium, compared exposure patterns with sympatrically nesting spectacled eiders (*Somateria fischeri*), and examined relationships with clutch size, egg viability, probability of hatching, and apparent survival of adult females. Lead concentrations were elevated in 3.6% of females, and all individuals exhibited elevated selenium, most (81%) at concentrations associated with death in captive waterfowl. Blood lead and selenium concentrations varied within and among site-years and were generally lower than those of spectacled eiders. During incubation, blood lead concentrations in females increased significantly (possibly via re-release of stored lead from bone), while selenium concentrations decreased (likely due to natural excretion). Probability of a nest containing ≥ 1 nonviable egg was positively related to blood selenium in hens, but adverse effects related to other life history variables were not detected. Although reproduction appeared sensitive to selenium toxicity, our data suggest high rates of nonviability are unlikely in this population, and selenium-related reductions to clutch size would be inconsequential at the scale of overall

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[2] Wilson, H. M., P. L. Flint, and A. N. Powell. 2007. Coupling contaminants with demography: effects of selenium and lead in Pacific common eiders. *Environmental Toxicology and Chemistry* 26(7):in press.

population dynamics. We conclude that Pacific common eiders and other wild marine birds likely have higher selenium tolerances than freshwater species, and interspecific differences in exposure risks may reflect differences in reproductive strategies.

Introduction

Identification of measurable demographic responses to environmental stressors, such as contaminants, is critical in assessing population-level impacts to wildlife. Linking contaminants with reproduction and survival not only provides a means of estimating specific vital rate effects, but can be used to assess relative influences on overall population dynamics. However, examining demographic effects in wild populations is difficult, as it requires the coupling of nondestructive sampling with detailed, long-term, individual life history information.

Trace elements, such as lead, selenium, mercury, and cadmium, are ubiquitous in the marine environment, and sea birds can serve as sensitive bioindicators of these elements [1, 2]. Among marine birds, sea ducks (tribe Mergini*)* have undergone broad-scale declines across their distribution [3], and exposure to contaminants has been suggested as a potential contributing factor in these declines [3, 4]. Sea ducks have long life spans, occupy high trophic positions, and may be exposed to anthropogenic inputs in both marine and terrestrial environments [4, 5]. They depend on sessile, filter-feeding benthic invertebrates as their primary food source [3, 4] and these organisms are known to bioaccumulate high levels of local contaminants [6]. Further, high prevalence of spent lead shot in areas with historical hunting activity, such as on some sea duck breeding grounds [5, 7], may increase their susceptibility to exposure.

On the Yukon-Kuskokwim Delta (YKD) in western Alaska, Pacific common eiders have declined by > 90% over the past 40 years [8], and this is in accord with similar declines in sympatrically nesting spectacled (*S. fischeri*) and Steller's (*Polysticta stelleri*) eiders [8]. Although no single cause for these population declines has been identified [3], lead poisoning (via ingestion of spent shot) is a known source of mortality for nesting common and spectacled eiders on the YKD [5, 9]. Further, local blood selenium concentrations are within ranges associated with death in experimental mallards (*Anas platyrhynchos*) [5, 10–12].

Lead is considered a nonessential, highly neurotoxic metal, and its effects on adult survival have been well studied [13]. Conversely, selenium is an essential trace element, which can become toxic at high concentrations [14]. Importantly, reproduction (particularly early development; [15, 16]) appears more sensitive to elevated selenium than does adult survival [10, 14]. Laboratory and field studies suggest blood concentrations of both elements can be extremely dynamic [10, 11, 16-18] and offer a better indication of recent exposure than other tissues. Because common eiders fast during their entire incubation period [19], they offer a natural control for examining toxicokinetics and comparing exposure patterns with species that feed on their terrestrial breeding grounds (e.g., the spectacled eider [20]).

Based on high levels of lead and selenium in eiders and other sea ducks [4, 5, 11, 12, 18, 21, 22], combined with the need for estimates of contaminant-related demographic effects, we measured blood concentrations in nesting Pacific common eiders. We evaluated spatial and temporal patterns of lead and selenium occurrence, and quantified differences in blood concentrations among eiders at specific breeding sites and across years. In addition, we examined within-season dynamics of lead and selenium (i.e., changes across the incubation period) both within and among females, and compared exposure patterns between sympatrically nesting common and spectacled eiders. Last, we examined relationships between blood contaminant concentrations and life history traits: clutch size, egg viability, nest survival, and apparent survival of adult females.

Methods

Sample collection

We sampled adult Pacific common eiders during the nesting period at two primary breeding sites on the YKD (Fig. 1), from 2002 to 2004: Tutakoke River (TR: 60°51'N, 165°49'W) and Kigigak Island (KI: 60°50'N, 165°50'W). Each year, we searched for nests and revisited them every 7 d until hatch or failure. We candled all eggs at each visit to assess egg viability and incubation stage. We captured females throughout incubation (where day 0 = clutch initiation and day 26 = hatch) using mist nets, decoys, and bow-net traps. In 2003 and 2004, we collected two samples within each season from a subset of females (*n* = 20) captured early (0-15 d) and late (16-26 d) in incubation. In all captures, we marked birds with U.S. Geological Survey metal, and alpha-numerically-coded-plastic leg bands, weighed individuals to the nearest gram, and collected 5 ml of blood by jugular or brachial venipuncture. All sampling was conducted following protocols approved by the University of Alaska, Fairbanks Institutional Animal Care and

Use Committee. At collection, we immediately transferred 3 ml of whole blood to lithium-hepranized BD Vacutainers® (Becton, Dickinson and Company, Franklin Lakes, NJ, USA) for trace element analyses. All blood samples were frozen within a few hours of collection in liquid nitrogen vapor shippers and were maintained frozen in the laboratory at -80°C until analysis.

Trace element analyses

We analyzed blood lead and selenium concentrations using inductively coupled plasma/mass spectrometry. Mean percent recoveries from standard reference material and spiked samples were 96% and 100% for lead, and 110% and 102% for selenium, respectively. We report all trace element results as µg/g, wet weight, uncorrected for percent recoveries. The lower limit of detection (LDL) for both lead and selenium was 0.01 µg/g wet weight. We assigned a concentration of one-half the LDL to all samples that were below detection limits in calculating group means and standard errors [11], and we report detection rates (% above LDL) for all groups (i.e., by site, year, and sex) where rates were < 100%.

Statistical analyses

The majority (94%) of our sample was composed of adult females, although we captured a small number of males at KI in 2003 ($n = 8$) and TR in 2004 ($n = 15$). Because males were sampled only during the pre-incubation period and only in specific site-years, we analyzed them separately. Most (90%) of the females in our study were sampled only once per year. However, to avoid pseudo-replication for the 20 females sampled twice within seasons (2002-2003), we randomly selected one of the paired samples for inclusion in our overall analysis of spatio-temporal variation in contaminant concentrations. Assumptions of normality within samples were not met (Shapiro-Wilk; lead: $W = 0.10$, $p < 0.01$; selenium: $W = 0.97$, $p < 0.01$), even after log-transformation (Log(lead): $W = 0.98$, $p < 0.01$; Log(selenium): $W = 0.76$, $p = 0.02$). Therefore, we used nonparametric statistics, unless otherwise stated, and report partial coefficients (βs) to indicate direction of relationships. Because we performed analyses on ranked concentrations, estimated βs and their associated variances were in ranked form, and thus were not appropriately scaled for direct interpretation. We report patterns of variation as indicated by our best approximating models, and means and standard errors on the original scale of the data (e.g., Table 1).

Model selection. We tested for multicollinearity among all our explanatory variables before constructing multivariate models. The original data were orthogonal, and estimated variance inflation factors by site-year were low (range: 1.01–1.19), indicating little correlation among explanatory variables. For each of our primary analyses, we created suites of hierarchical models based on biologically meaningful combinations of explanatory variables (≤ 5 variables per analysis). We used Akaike's Information Criterion, adjusted for small sample sizes (AIC_c), model weights (w_i), sums of model weights (Σw_i), and measurements of model fit (-2 log(L) or deviance), to evaluate strength of evidence for competing models and individual explanatory variables [23]. When model-selection uncertainty was high (i.e., when top model w_i was less than 0.9), we calculated model-averaged estimates [23].

Spatio-temporal variation. We hypothesized that lead and selenium concentrations would vary between study sites, among years, and within seasons, as previously observed for spectacled eiders [5, 21]. Because selenium tends to be highly interactive with other elements [14], we also considered the influence of selenium on lead concentrations. We examined these interactions using separate analyses of covariance on ranked trace element concentrations [24].

Temporal dynamics and repeated samples. In previous laboratory and field studies, selenium typically declined nonlinearly after exposure was terminated [10, 17, 21], and in at least one study, blood lead concentrations were positively correlated with stage of incubation [18]. Thus, we considered models in which lead and selenium varied from early to late incubation. We examined within-female temporal variation in blood concentrations using females sampled twice within the same site-year. Herein, we used a method similar to repeated measures analysis, in which we controlled for variation among individuals and then examined variation between early and late incubation. We did so using separate analyses of variance for lead and selenium. To maintain comparable results with previously published studies [17, 21], we also calculated daily change in trace elements using non-linear regression on repeated samples. Herein, we fit our data to the formula [21],

$$\text{Rate of change} = \left(\frac{x_{t_2}}{x_{t_1}} \right)^{\frac{1}{t_2 - t_1}}$$

where x_t is the concentration at a given time t, t_1 is the first sample, and t_2 the second. Finally, we used a general linear model to examine the relationship between ranked blood lead and selenium concentrations and body mass, after controlling for incubation stage.

Selection of life history traits for analysis

In examining demographic effects of contaminants, we chose life history traits based on their direct relation to productivity or survival, their association with lead and/or selenium-effects in laboratory or field studies of waterbirds, and whether or not we had sufficient data to conduct robust demographic analyses. Based on patterns of elevated blood lead and associated negative impacts on the survival of spectacled eiders [21, 25], as well as documented lead poisoning in local common eiders [9], we hypothesized that high blood lead would have a negative effect on life history traits. Similarly, we reasoned that elevated selenium would also result in negative effects on survival and reproduction [10, 14, 26]. However, we did not rule out the possibility that as an essential element, selenium might also have positive effects [27].

Clutch size and nonviable eggs. Given the documented negative effects of elevated selenium on embryo viability [14, 26] and the detrimental properties of lead in relation to adult physiology [13], we hypothesized that clutch size would be negatively related to contaminant burdens. According to the same logic, we reasoned that the probability of a clutch containing ≥ 1 nonviable egg (i.e., an egg which was never fertilized or showed no development) would be positively related to blood concentrations of lead and selenium in the hen. We used general linear models to examine the effect of rank lead and selenium, on clutch size, after controlling for study site, year, initiation date, and incubation stage. Similarly, we used logistic regression [24, 28] to model the probability of at least one nonviable egg in a nest, as a function of blood selenium and lead concentrations in the hen, after controlling for incubation stage at sampling. Using relationships described by our best approximating model(s), we then estimated the probability of a clutch containing ≥ 1 nonviable egg across the range of trace element concentrations observed in our study.

Nest survival. We hypothesized nest survival would be negatively related to lead concentrations, but did not make similar predictions for relationships with selenium, as nest survival has been both negatively [26], and positively [27] related to selenium in previous studies. We used logistic regression to model the probability of at least one egg in a nest hatching (i.e., nest survival) in relation to trace element concentrations in the hen. Because nests of females sampled later in incubation had higher probabilities of hatching than those sampled earlier (due to shorter time until hatch), we controlled for incubation stage at sampling [29]. We calculated expected nest survival using the formula,

$$\text{Nest survival} = \prod_{i=j}^{26} \text{DSR}$$

where nest survival was the product of site-year, incubation-stage-specific (i), daily nest survival rates (DSR) from previous nest survival analysis (H. Wilson, unpublished data), for the interval between incubation stage at time of sampling (j) and hatch (26 d). After controlling for expected nest survival given stage at sampling, we considered only models that allowed probability of hatching to vary according to lead and selenium concentrations, nest survival alone, or not at all (i.e., intercept-only model).

Apparent survival of adult females. Based on reduced apparent survival rates in adult female spectacled eiders exposed to lead (blood lead > 0.02 μg/g) on the YKD [25], we hypothesized that apparent survival of adult female common eiders would be negatively related to their blood lead concentrations. However, we did not make similar directional predictions for selenium. We examined apparent annual survival in relation to blood lead and selenium concentrations, using data from individuals sampled in 2002 and/or 2003, and recaptured in 2003 and/or 2004. Individual lead and selenium concentrations were adjusted for incubation stage by subtracting from predicted values for a given stage of incubation (i.e., residuals from linear regression). As such, concentrations were functionally standardized to a mean of zero. Females unobserved in a particular year, but sampled previously, were assigned the mean standardized contaminant concentration in years they were not encountered. We modeled annual apparent survival (φ), and encounter (*p*) probabilities using a Cormack-Jolly-Seber model in program MARK [30]. We treated adjusted blood concentrations of lead and selenium as annual-time-varying individual covariates (e.g., $t_1 = 2002$, $t_2 = 2003$) of survival [30], and used a logit link to bound parameter estimates between 0 and 1. We developed a limited suite of biologically plausible models in which apparent survival varied with individual trace element concentrations, with lead or selenium differently between study sites, or not at all. Similarly, encounter probabilities could vary across study sites, years, or remain constant. Our most parameterized model included an effect of individual trace element concentrations which varied between study sites, and encounter probabilities which varied across study sites and years. We examined possible overdispersion ($\hat{c}$) of the data and adjusted AIC$_c$ values if $\hat{c} > 1.0$.

Results

We collected a total of 403 blood samples from 360 individual females and 23 males. We detected lead (> 0.01 µg/g) in 84% of birds sampled (Table 1). Although lead was detected in 86% of females and 26% of males, almost all (96%, *n* = 323) were at concentrations below the subclinical toxicity threshold of 0.2 µg/g [13]. No males had lead concentrations above subclinical toxicity. However, we found elevated lead concentrations ranging from 0.2 to 7.0 µg/g in 14 (3.6%) incubating females (Table 1). In contrast, all birds had detectable selenium (Table 1), and most (81%) were at blood concentrations associated with death in experimental mallards (5-14 µg/g; [10]).

Variation in blood concentrations of trace elements

Rank lead and selenium concentrations in females were highly variable between study sites, both within and among years (Table 2). The best approximating model of variation in rank blood lead included study site, year, and incubation stage (Table 2, Model 1, lead), while the top selenium model included each of these variables, in addition to a correlation term between selenium and lead, and an interaction between study sites and years (Table 2, Model 1, selenium). Rank lead concentrations were highest in 2002, while selenium concentrations were highest in 2003 (Table 1). Females at KI were higher generally in lead, but lower in selenium than those at TR; except in 2002 (Table 1). Additionally, the correlation between rank lead and rank selenium was included among the top models for each element (Table 2). This correlation was negative and had reasonably high support ($\Sigma w_{\text{lead}} = 0.42$, $\Sigma w_{\text{selenium}} = 0.75$).

Dynamics of trace elements in blood

After controlling for study site and year, our data supported trends of increasing lead and decreasing selenium concentrations throughout the incubation period ($\Sigma w_{\text{incubation stage}} = 0.99$, Table 2). The linear increase in blood lead was 0.002 ± 0.001 μg/g per day, while selenium concentrations decreased at 0.07 ± 0.02 μg/g per day. We had an insufficient sample size of repeatedly-sampled females with detectable blood lead ($n = 10$) to perform repeated measures analyses. Thus, a nonlinear rate of decline in blood lead could not be calculated. After controlling for individual effects, paired measurements of selenium indicated a decreasing trend with incubation stage ($F_{1,19} = 4.07$, $p = 0.04$) of 0.05 ± 0.02 μg/g per day. Further, we estimated the nonlinear daily rate of decline in blood selenium to be 0.963 ± 0.003% per day. Mass of female common eiders did not vary with blood lead or selenium concentrations after controlling for incubation stage at sampling ($\Delta\text{AIC}_c > 5.23$). On average, females lost 17.09 (± 2.90) grams of body mass per day of incubation.

Clutch size and nonviable eggs

We found no support for relationships between clutch size and female blood concentrations of lead or selenium ($\Delta\text{AIC}_c > 5.19$). However, our best approximating model of the probability of ≥ 1 nonviable egg in the nest (Table 3, Model 1) indicated a positive relationship with blood selenium (Odds ratio: 1.15, 90% Confidence Interval

(CI): 1.01-1.31). These results indicated that the odds of ≥ 1 nonviable egg occurring in a clutch increased 1.15 fold per 1 µg/g increase in blood selenium (Fig. 2). There was some support for an effect of lead in combination with selenium ($\Delta AIC_c = 1.77$), but overall, Σw_{lead} (0.33) was much smaller than $\Sigma w_{selenium}$ (0.66). Moreover, lead-relationships were poorly estimated (Odds ratio: 0.61, 90% CI: 0.05–6.99) and opposite the direction of hypothesized adverse effects. Overall, we detected nonviable eggs in 7.7% of the nests of females that were sampled for lead or selenium and for which data on clutch size were complete (*n* = 284). Blood selenium concentrations in females with ≥ 1 nonviable egg ranged from 4.10 to 14.80 µg/g. Further, using model results, we predicted females at the average blood selenium concentration (6.96 µg/g) would have a 7.2% probability of ≥ 1 nonviable egg in their clutch (Fig. 2), and would approach the 50% effect level at 24.8 ± 0.14 µg/g selenium.

Nest survival

We examined 290 nests of hens that were sampled for contaminants over the three years of our study. We found little support for a relationship between trace element concentrations and probability of hatching ≥ 1 egg in the nest, after controlling for predicted nest survival given incubation stage. All models including lead and selenium had ΔAIC_c values ≥ the intercept-only model and Σw_i for all models containing lead and selenium (0.20 and 0.32, respectively), were less than half of those for models containing nest survival (0.73). Overall, probability of hatching did not appear to be related to blood lead concentrations ($\Delta AIC_c = 1.95$, $\Sigma w_{lead} = 0.20$, Odds ratio: 1.13, 90% CI: 0.48-2.69), but there was some support for a model which included selenium ($\Delta AIC_c = 0.45$).

However, selenium effects were weak and poorly estimated (Odds ratio: 1.09, 90% CI: 0.97-1.22).

Of females with elevated blood lead levels (> 0.02 µg/g), for which we had complete nest data (*n* = 12), 25% were unsuccessful in hatching young; 2 due to abandonment (0.5 µg/g and 0.6 µg/g, respectively), and 1 (0.38 µg/g) due to predation. Of females with non-elevated lead (*n* = 92), 18% were unsuccessful in hatching young. Moreover, the female with highest lead blood concentration (7.0 µg/g), successfully hatched all eggs in her clutch during the year of her exposure, but was not encountered again in subsequent years. In contrast, a female with similarly high lead concentrations (6.6 µg/g) in 2002 was encountered again two years later and nested successfully in both years she was observed.

Adult female apparent survival

Our survival dataset included 164 breeding adult females captured and sampled for contaminants in 2002 and/or 2003, resulting in 78 future recaptures and resightings (2003-2004). We had no band recoveries (i.e., bands reported from dead birds) during the course of our study. We examined 25 candidate models of adult female survival and encounter probabilities that incorporated the effects of adjusted selenium and lead concentrations, as well as variation between site-years (Table 4), and found no evidence of overdispersion in our most parameterized model ($\hat{c}$ = 1.0).

In our best approximating model, apparent survival varied with blood selenium concentrations, and encounter probabilities varied across sites and years (Model 1, Table 4). We found no support for reduced parameter structure in encounter probabilities

(Model 5, Table 4, $\Delta AIC_c > 4.83$), and little support for a relationship between apparent survival and blood lead ($\Sigma w_{lead} = 0.18$). Although there was moderate model selection uncertainty (Table 4), overall support for a selenium effect was high ($\Sigma w_{selenium} = 0.74$). Our second best model (Model 2, Table 4) described a selenium effect which varied between study sites. However, this model did not substantially improve fit ($\Delta AIC_c = 1.87$). Thus, it provided little support for additional variation across study sites [23]. Our best model indicated that adjusted blood selenium concentrations were positively related to apparent survival, although precision in this positive effect was low ($\beta_{selenium} = 0.73 \pm 0.37$). Using the odds ratio from this model (Odds ratio = 2.09, 90% CI: 1.12–3.88), we estimated that each 1 µg/g increase in blood selenium, would be related to a 2-fold increase in the odds of surviving. However, interpretation of these effects requires caution, as when rates (herein survival rates) are near the boundaries of 0 and 1, large changes in odds result from small changes in estimated probabilities [28]. For example, a change in blood selenium from 6 to 7 µg/g (i.e., around population means) would result in only a 0.0004 increase in the apparent survival probability.

Discussion

Lead

Elevated lead concentrations within the range we observed were indicative of subclinincal exposure (≥ 0.2 µg/g) to severe clinical poisoning (> 1.0 µg/g), based on laboratory studies of freshwater birds [13]. However, the proportion of common eiders above subclinical toxicity thresholds was low (3.6%), consistent with earlier local studies

(3%; [5]). Moreover, average blood lead concentrations (Table 1) were less than or equal to those reported previously for the YKD (0.14 ± 0.01, *n* = 9; [21]). Overall, common eiders appeared to have markedly reduced exposure to lead in comparison to sympatrically nesting spectacled eiders (36%; [5]), and were rarely at levels associated with toxic effects in waterfowl. We suggest that interspecific differences in lead exposure are likely due to differences in foraging behavior and brood-rearing strategies [5]. During incubation common eiders fast, while spectacled eiders feed. Further, common eiders raise broods at sea, while spectacled eiders raise broods on upland ponds where spent lead shot may remain available more than three years after deposition [7, 20, 31]. In total, nesting common eiders spend approximately half as much time in areas with available shot as do spectacled eiders, significantly reducing their opportunity for exposure. Further, we suspect that previously reported poisoning of common eiders [9] was likely a result of pre-nesting foraging in waters adjacent to the breeding grounds.

Selenium

In contrast to lead, all birds sampled in our study had detectable blood selenium. Average selenium concentrations were consistently above background (< 0.4 µg/g; [18, 32, 33]), and often at levels associated with mortality in captive mallards (5-14 µg/g; [10]). However, we observed no obvious selenium-related health effects, and average detection rates and concentrations were similar to those reported previously for local common eiders [5, 21]. Selenium concentrations in male common eiders were much lower than those observed in male spectacled eiders [21], and we suggest this interspecific variation may be due to differences in selenium elimination times during migration and exposure on wintering and staging areas [21, 22].

Trace element dynamics

Blood lead levels tended to slowly increase through incubation, similar to nesting common eiders in Finland [18]. The low concentrations and slow increase of lead we found supported chronic, low-level metabolic release, rather than point-source exposure (e.g., via ingestion of lead pellets). We agree with others [18], who have suggested that small increases in blood lead are related to reproductive physiology; specifically, the mobilization of stored lead through metabolism of medullary bone. Medullary bone in birds acts as a labile reservoir for calcium used in eggshell formation [34], and because lead is chemically similar to calcium it may be easily assimilated into medullary bone [35]. After egg production, common eiders may continue to utilize medullary stores to meet the nutritional demands of the incubation fast. If so, metabolic release of stored lead could be responsible for the temporal increases in blood lead we observed.

Laboratory studies demonstrate that selenium is metabolically pliable, rapidly accumulates during exposure, and declines once exposure is terminated [17]. Declining blood selenium concentrations during nesting suggest exposure to selenium on breeding grounds was probably negligible in our study. Further, the selenium we measured was likely derived from selenium-rich wintering and staging areas in the Bering Sea [11, 12, 21, 22]. Selenium-elimination rates in common eiders were reduced compared to spectacled eiders (1.9% YKD; [21], 2.3% in northern Alaska; [22]) and YKD emperor geese (± 1%; *Chen canagica*; [11]), and much slower than captive freshwater mallards

(7.1%; [10, 17]). This suggests that the slowed metabolism of common eiders during the incubation fast may decrease their rates of selenium elimination in comparison to non-fasting species.

Life history traits and trace element concentrations

The positive relationship between blood selenium concentrations and egg nonviability is consistent with patterns in wild birds at selenium-contaminated areas (e.g., black-necked stilts (*Heimantopus mexicans*); [36], and eared grebes (*Podiceps nigricollis*); [26], as well as selenium-dosed mallards in laboratory studies [37]). The average rate of nonviability we observed (7.7%) was more than triple the average egg infertility rate for other diving ducks (~2.2%; [38]). This suggests that YKD common eiders may be experiencing much higher frequencies of nonviability than other diving species. However, spectacled eiders nesting on the YKD appear to have even higher nonviability rates (24% of spectacled eider nests had ≥ 1 nonviable egg; [29]), corresponding with their higher blood selenium levels [21]. We suspect that both species are exposed to elevated selenium on their Bering Sea wintering grounds, but hypothesize that spectacled eiders likely winter in areas with higher natural concentrations of selenium [12, 20, 21].

Diminished productivity resulting from reduced egg survival could have major implications for population dynamics [38]. However, reductions in clutch size due to selenium-related nonviability represent only a small portion of overall fecundity [38]. For long-lived species such as the common eider [31], fecundity is expected to have a much lower proportional influence (i.e., elasticity) on prospective population growth than would adult survival [38]. Therefore, although elevated selenium may have acute reproductive costs, we suggest that population-level consequences at the concentrations we observed are expected to be relatively minor.

We found limited evidence for a positive relationship between blood concentrations of selenium and apparent survival of adult females, but effects were estimated with poor precision. Overall, our results suggest that selenium is not detrimental to survival of adult females within the range of concentrations we observed. This supports the hypothesis that sea birds living in high-selenium environments may have evolved higher selenium tolerances based on their chronic exposure [1, 11, 14, 21, 22]. However, we stress that further interpretation of our apparent survival results requires caution, and emphasize that our correlative approach cannot infer causal mechanisms. For example, given the brief period of our study, periodic nonbreeding could have been confounded with emigration or mortality. Moreover, positive correlations between selenium and body condition [9, 39] could have further confounded results. However, we found no evidence of a relationship between blood selenium concentrations and body mass (after controlling for incubation stage) [18]. Thus, selenium-body condition relationships could not fully explain our results. Finally, the thresholds between selenium essentiality and toxicity are generally unknown for marine species. Measures of oxidative stress have been positively related to selenium in at least one study of emperor geese [40]. While a study of common eiders nesting in Canada showed an inverse relationship between corticosterone (stress response) and selenium in nesting hens, suggesting that selenium may acutally help modulate adverse effects of chronic stress in adult birds [39]. We believe that selenium may have both positive and negative effects on the life history variables of marine birds at the concentrations we measured. Further, we suggest that tolerance and effect-levels appropriate for these birds deserve further investigation.

Conclusions

This study links contaminant levels in wild birds to life history traits through integration of demography and non-lethal blood sampling. Our results suggest that elevated selenium may be related to reduced egg fertility and hatchability, resulting in a potential reproductive cost to nesting eiders. However, selenium was not detrimental to probability of apparent survival, suggesting adult marine birds may have higher selenium-tolerances than freshwater species. Reproduction appeared more sensitive to selenium toxicity than did adult survival, but based on average selenium concentrations, we suggest high rates of nonviability are not likely to occur. Further, selenium-related reductions to clutch size are expected to be inconsequential at the scale of overall population dynamics.

Overall, we saw no obvious signs of compromised health in adults, ducklings, or limited samples of embryos during the course of our study, and we conclude that for Pacific common eiders the adverse effects of lead and selenium are minimal. We also suggest that eiders that do not forage in areas with accessible lead shot, are unlikely to show significant effects of lead contamination. While management actions focused on education and enforcement of nontoxic shot regulations are encouraged for species such as the spectacled eider, our results suggest these actions may not have large effects on common eider populations. We encourage continued field and laboratory research to expand upon relationships between selenium and life history traits established in this study. Specifically, future studies should examine selenium tolerances appropriate for marine birds, redistribution and toxicity of blood lead and selenium in species which undergo periodic fasting, and sources of selenium in the marine and terrestrial environment. Finally, we advocate increased integration of non-lethal sampling in long-term demographic studies, in order to better examine contaminant-related fitness consequences and impacts of contaminants on overall population dynamics.

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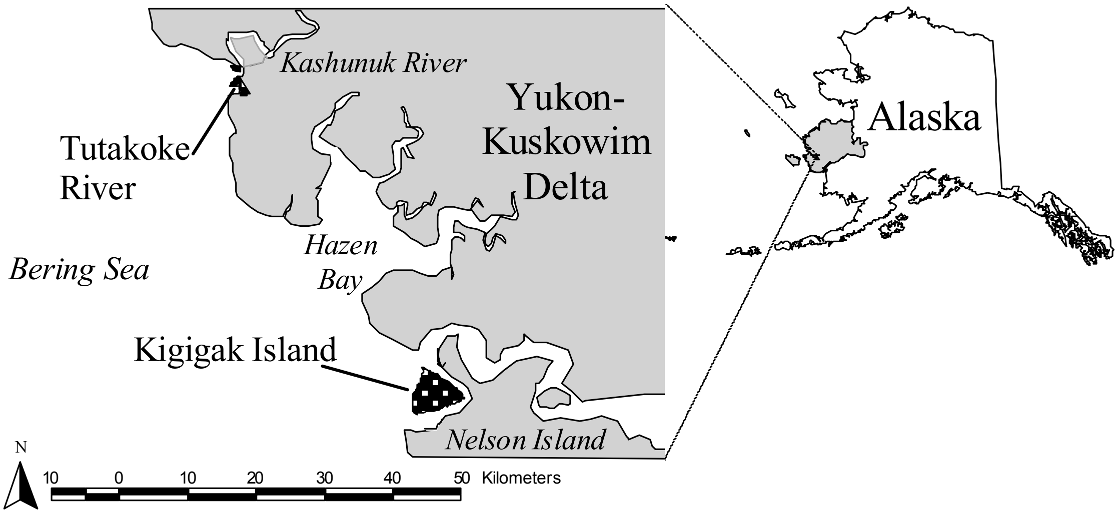

Figure 1. Study sites (Tutakoke River and Kigigak Island) on the Yukon-Kuskowim Delta, Alaska, USA where blood samples were collected from nesting Pacific common eiders (2002-2004).

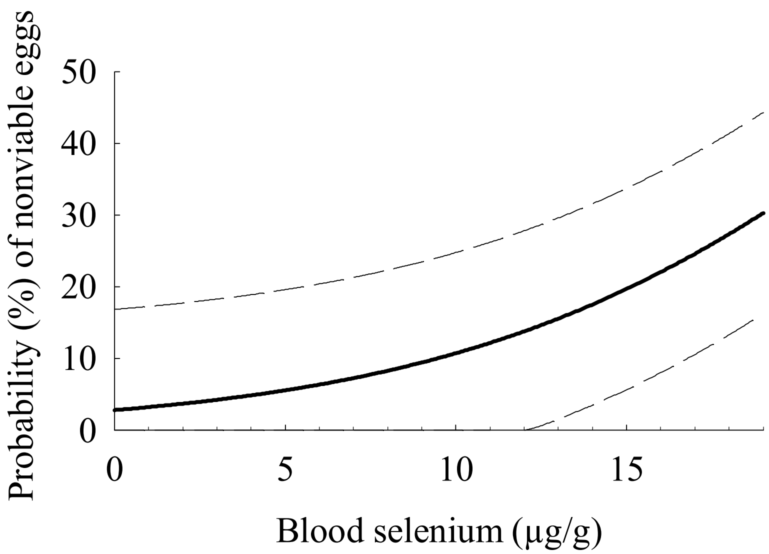

Figure 2. Predicted probabilities (%) of at least one nonviable egg occurring in a nest, as a function of blood selenium concentrations for female Pacific common eiders on the Yukon-Kuskowim Delta, Alaska, USA (2002-2004). Range of selenium values represent concentrations observed in the field. Dashed lines represent 90% confidence intervals.

Table 1. Blood lead and selenium concentrations (µg/g wet wt) in adult Pacific common eiders (2002-2004) at two breeding sites; Kigigak Island (KI) and Tutakoke River (TR), on the Yukon-Kuskokwim Delta, Alaska, USA.

			Lead				Selenium			
Site	Year	Sex	*n*	$\bar{x}$	SE[a]	Range	*n*	$\bar{x}$	SE	Range
KI	2002	F	45	0.27	0.16	0.02-7.00	45	5.77	0.25	2.10-10.50
	2003	F[b]	67	0.04	0.01	0.01-0.28	67	7.11	0.25	3.20-13.00
		M	8	ND[c]	ND	ND	8	9.88	0.58	7.50-13.00
	2004	F[b]	135	0.05	0.01	0.02-0.50	135	6.74	0.21	1.50-15.00
		M	7	0.01	0.01	0.01-0.03	7	9.53	1.26	4.60-12.70
TR	2002	F	61	0.15	0.11	0.01-6.60	61	6.62	0.24	2.20-11.20
	2003	F	2	ND	ND	ND	2	10.00	1.00	9.00-11.00
		M	3	0.01	0.01	0.01-0.03	3	9.47	0.82	8.20-11.00
	2004	F	44	0.05	0.01	0.02-0.60	50	8.71	3.51	4.00-15.70
		M	5	0.01	0.01	0.01-0.03	5	11.40	3.79	5.80-18.80

[a] SE = standard error.

[b] Percentages of samples in which trace elements were detected; lead (KI females: 2003 = 48%, 2004 = 94%). All other groups = 100% detection, unless otherwise noted.

[c] Not detected.

Table 2. Top models used to assess spatial (study site) and temporal variation (year and INC = incubation stage), and contaminant interactions, in blood lead and selenium concentrations of female Pacific common eiders (2002-2004) nesting on the Yukon-Kuskokwim Delta, Alaska, USA.

	Model	k^a	$AIC_c{}^b$	Deviance	ΔAIC_c	w_i
Lead						
1	Site, Year, INC	5	6167.09	6156.91	0.00	0.58
2	Site, Year, INC, Selenium	6	6168.33	6156.08	1.24	0.31
3	Site, Year, INC, Selenium, Site*Year	7	6170.33	6156.00	3.24	0.11
Selenium						
1	Site, Year, INC, Lead, Site*Year	7	6239.37	6225.04	0.00	0.61
2	Year, Site, INC	5	6241.19	6231.01	1.81	0.24
3	Year, Site, INC, Lead	6	6242.42	6230.17	3.05	0.13

[a] k = number of parameters in model.

[b] The best approximating model has the lowest Akaike's Information Criterion adjusted for small sample size (AIC_c) value and the highest model likelihood (w_i), relative to others in the model set.

Table 3. Top models of the probability of ≥ 1 nonviable egg in the nest as a function of blood lead and selenium concentrations (µg/g wet wt), after controlling for incubation stage at the time of sampling, in female Pacific common eiders (2002-2004) nesting on the Yukon-Kuskokwim Delta, Alaska, USA.

	Model	k[a]	AIC_c[b]	$-2\log(L)$	ΔAIC_c	w_i
1	Selenium	2	185.18	181.18	0	0.34
2	Intercept-only	1	186.28	184.28	1.10	0.20
3	Selenium, Lead	3	186.95	180.95	1.77	0.14
4	Lead	2	187.98	183.98	2.80	0.08

[a] k = number of parameters in model

[b] The best approximating model has the lowest Akaike's Information Criterion (AIC_c) value, adjusted for small sample size, and the highest model likelihood (w_i), relative to others in the model set.

Table 4. Models of apparent survival for adult female Pacific common eiders (2002-2004) at Kigigak Island and Tutakoke River study areas, Yukon-Kuskokwim Delta, Alaska, USA, in relation to blood selenium (Se) and lead (Pb) concentrations adjusted by incubation stage.

Apparent survival hypothesis[a]	k[b]	AIC_c[c]	Deviance	ΔAIC_c	w_i[c]
1) varies with selenium exposure	6	267.88	255.39	0.00	0.49
2) varies with selenium differently between study sites	7	269.76	255.09	1.87	0.19
3) varies with lead exposure	6	270.49	258.00	2.61	0.13
4) intercept-only	5	271.60	261.25	3.72	0.07
5) varies with selenium, encounter probability varies with study site + year	5	272.71	262.36	4.83	0.04

[a] Encounter probabilities (*p*) were similar for all top models: *p*(site*year), unless otherwise noted.

[b] *k* = number of parameters in model.

[c] The best approximating model has the lowest Akaike's Information Criterion (AIC_c) value, adjusted for small sample size, and the highest model weight (w_i), relative to others in the model set.

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CHAPTER 3. Productivity components of Pacific common eiders in western Alaska[3]

Abstract: We examined components of productivity in Pacific common eiders (*Somateria mollisima v-nigrum*) at three sites on the Yukon-Kuskokwim Delta (YKD), Alaska from 1991-2004; representing a total of 29 site-years. All reproductive parameters varied across study sites and years. Clutch initiation dates ranged from 4 May to 28 June, with peak (modal) initiation occurring on 26 May. Females at our island study site consistently initiated clutches three to five days earlier in each year than those on the 2 mainland sites. Population variance in initiation date was negatively related to the peak; suggesting increased synchrony in years of delayed initiation. Total clutch size ranged from 4.8 to 6.6 eggs, and declined with date of initiation. After accounting for partial predation and nonviability of eggs, average clutch size at hatch ranged from 2.0 to 5.8 eggs. Within seasons, daily survival probability (DSP) of nests was lowest during egg laying and late initiation dates. Estimated nest survival varied considerably across sites and years (mean = 0.55, range: 0.06–0.92), but process variance in nest survival was relatively low (0.02, CI: 0.01-0.05), indicating that most variance was attributable to sampling. We found evidence that observer effects reduced overall nest survival from 0 to -0.36 across site-years. Study sites with lower sample sizes and more frequent visitations appeared to experience greater observer effects. In general, Pacific common

[3] Wilson, H.M., P.L. Flint, T.L. Moran, and A.N. Powell. Productivity components of Pacific common eiders in western, Alaska. Prepared for submission to *The Journal of Wildlife Management*.

eiders exhibited high spatio-temporal variance in reproductive components. Larger clutch sizes and high nest survival at early initiation dates suggested directional selection favoring early nesting. However, stochastic environmental effects may have masked responses to this selection. Special protection should be afforded to birds early in the breeding season, as these birds lay the largest clutches and have the highest probability of successfully hatching. Finally, we suggest that eider laying dates and nest fates may be closely tied to those of sympatrically-nesting species, and hypothesize that management actions facilitating early nesting and targeting other species (e.g., increasing overall potential for predator-swamping) may have positive, concurrent effects on nesting common eiders.

Introduction

Life-history theory focuses on how patterns of variation in demographic vital rates change in response to particular forms of environmental heterogeneity (Stearns 1992). Fecundity (the number of offspring per adult) represents the product of lower-level reproductive components (e.g., proportion of birds that breed, clutch size at hatch, nest success, and offspring survival; Johnson et al. 1992), and in long-lived species, these components often contribute relatively little to prospective population growth (Pfister 1998, Sæther and Bakke 2000). However, variation in fecundity components has been identified as the primary source of historical population fluctuations in some species (Cooch et al. 2001). Total variation in lower-level reproductive components includes a mix of true environmental (i.e., spatio-temporal process) variation and sampling variation (Burnham et al. 1987, Mills and Lindberg 2002), and where sampling variation is not removed, negatively-biased estimates of population growth can result (Pfister 1998, Morris and Doak 2002). Further, the effects of variation can be compounded where vital rates are positively correlated with one another (van Tienderen 2000, Doak et al. 2005), or overestimated, where sampling variance is not accounted for (Link and Nichols 1994).

Estimates which consider broad-scale spatio-temporal variation (i.e., among sites, years, etc.) provide the primary units of population modeling, but these estimates must first account for finer-scale variation within sites, years, and individuals. In addition to reducing bias in broad-scale estimates, understanding patterns of finer-scale variation may offer insights into life history theory and the response of individuals to environmental variation. For nesting birds, among-individual variation in reproduction across clutch ages or dates, may be driven by a number of ecological variables (Dinsmore et al. 2002, Grand et al. 2006). Factors such as the density and species composition of neighboring nests (Bourget 1973, Larivière and Messier 1998, Raveling 1989), fluctuating predation pressure (Quinlan and Lehnhausen 1982, Bêty et al. 2001), changes in breeding ground conditions (Laurila 1989, Petersen 1990), severe weather events (Dinsmore et al. 2002), or body condition of females (Blums et al. 1997, Bêty et al. 2003) have all been related to variation in components of fecundity. By describing these patterns of variation and assessing their potential causes and consequences, management options and possible selection pressures acting on individuals can be identified.

For individuals to respond to selection pressure there must be heritable genetic variation, and at the finest scale of variation estimates of individual repeatability can be interpreted as “upper-limits” to heritability (Falconer and Mackay 1996). As such, these upper limits can help to define potential response to selection pressure. This information may be especially critical for the biota of arctic and subarctic regions, where global climate change has been marked (Chapin and Körner 1994), and has modified selection pressures on reproductive traits (Brown et al. 1999, Both and Visser 2001, Winkler et al. 2002, Lehikoinen et al. 2006). For example, many of the important measures of reproductive success in birds are strongly influenced by timing of nesting (e.g., seasonal declines in clutch size and nesting success; Lack 1968, Godfray et al. 1991, Woolfenden and Fitzpatrick 1984, Rowher 1992). However, some long-term studies show no directional trend in reproductive timing across years (Brooke 1978, Newton and Marquiss 1984). Resolving these apparently conflicting responses will require an understanding of the mechanisms that drive patterns of selection. This in turn may allow better prediction of the effects of environmental changes on life-history variation and aid in assessing the impacts on associated population dynamics.

Common eiders (*Somateria mollissima*) are large-bodied, long-lived, sea ducks with a circumpolar distribution (Goudie et al. 2000). Females are considered capital breeders (Drent and Daan 1980), relying almost entirely on body reserves acquired during pre-breeding to produce eggs and maintain themselves during the incubation period (Korschgen 1977, Parker and Holm 1990). They are the most marine of all waterfowl, returning to land only during the brief nesting season (~1 month), and raising broods at sea or in brackish-water habitats, often in large multi-family crèches (Goudie et al. 2000). Pacific common eiders (*S.m. v-nigrum*) breed only along selected coastlines and islands of western and northern Alaska, eastern Russia, and eastern Canada, and appear more dispersed in their nesting than other subspecies (Gabrielson and Lincoln 1959, Goudie et al. 2000). In western North America, Pacific common eiders declined by greater than 50% between 1976 and 1996 (Suydam et al. 2000), and local surveys on the western Alaska nesting grounds indicate a > 90% decline in combined counts of common and spectacled (*S. fischeri*) eiders between 1957 and 1992 (Stehn et al. 1993, Hodges et al. 1996). However, more recent trends suggest both species have been stable to slightly increasing since 1993 (Platte and Stehn 2005). Although no single cause for the historical decline or subsequent stabilization has been identified, changes in rates of local reproduction have been suggested as a potential contributing factor to the historic eider declines (U.S. Fish and Wildlife Service 1996), and understanding such changes has been identified as an important research priority for Pacific common eiders (U.S. Fish and Wildlife Service 2005).

Our goals were to quantify the components of productivity in Pacific common eiders nesting on the Yukon-Kuskokwim Delta (YKD), Alaska and to examine factors influencing variation in reproduction at the population level. We summarize 29 site-years of field data, collected across three study sites (12, 4, and 14 years of data at each site, respectively) with three primary objectives. First, we described the nesting ecology of Pacific common eiders in western Alaska. Second, we examined hypotheses related to variation in reproductive components among individuals (i.e., across sites, years, dates within the nesting period, and clutch ages), as well as within individuals. Third, we provided estimates and associated process variances for clutch initiation date, clutch size, and nest survival in an attempt to characterize true biologic variation across time and space, with sampling variation removed.

Study area

We studied productivity of Pacific common eiders at three primary breeding sites on the YKD; from 1991 to 2002 at Kashunuk River (61°20’N, 165°35’W), in 1997 and 2002 to 2004 at Tutakoke River (TR: 60°51’N, 165°49’W), and from 1992 to 2004 at Kigigak Island (KI: 60°50’N, 165°50’W). Habitat characteristics of the three sites have been described in detail elsewhere (Grand et al. 1997, Sedinger et al. 1998, and Wilson et al. 2007). The Kashunuk River (KR) study site was a mainland nesting area, approximately 27.6 km^2 in size and ~5 km inland from the coast. This site supported low numbers (12-31 nests found per year) of common eiders, and females primarily nested in habitat near the river edge. The Tutakoke River (TR) study site was a coastal, mainland site, approximately 10 km southwest of the KR study area, and 52 km north of the Kigigak Island (KI) study area. The TR study site covered approximately 12 km^2 and supported a substantial aggregation (average: 110 nests) of common eiders nesting within a large black brant (*Branta bernicla nigricans*) colony (~5000 pairs; Sedinger et al. 1998). Common eiders at the TR site nested in wet sedge meadows, several hundred meters inland from coastal mudflats. The Kigigak Island study area (KI; 32.5 km^2), supported the highest numbers of nesting common eiders (~60-200+ total nests annually, between 1991-2004) and primary nesting habitat at KI included low coastal tundra and high graminoid and intermediate sedge meadows. Common eiders at KI tended to utilize the outer perimeter of the island (i.e., areas ≤ 1 km from the coast) and were primarily found nesting: 1) within medium to large colonies of black brant, 2) within small conspecific colonies (e.g., ~15-20 eiders around a single lake), or 3) solitarily. All study areas on the YKD were populated by a similar suite of nest predators, which included glaucous gulls (*Larus hyperboreus*), mew gulls (*L. canus*), parasitic jaegers (*Stercorarius parasiticus*), and arctic foxes (*Alopex lagopus*).

Methods

Field methods

We searched for Pacific common eider nests on foot or with the aid of a trained dog, beginning shortly after spring breakup (late May – early June) through the end of the first week of incubation (early - mid June) each year (1991-2004). During the search period we covered most of the available (vegetated) nesting habitat within each study site (average = ~9 km^2 each). We defined a nest as ≥ 1 egg in a bowl with at least some evidence of down. Nests discovered incidental to other activities were also included in our sample. We did not include nests found destroyed, abandoned, or hatched at first encounter in our analyses of clutch initiation dates, clutch sizes, or daily nest survival. Upon discovery, we mapped each nest on aerial photos and recorded UTM coordinates of the nest location using GPS receivers. In addition, each nest was marked with a small flag or wooden-lathe placed 10 m north of the nest. We recorded clutch size, incubation stage, female status (flushed, present, near nest, or absent), abundance of down, and condition of nest (laying, incubating, flooded, or depredated) at each visit. We used egg candling (Weller 1956) and floating (Westerkov 1950) to determine incubation stage, predict hatch date, and assess egg viability, and we monitored partial predation by numbering all eggs with permanent markers and monitoring their presence/absence at each nest visit. After each visit, we covered the nest with down to conceal eggs from avian predators (Götmark and Åhlund 1984). We revisited nests every 5-7 d until hatch or failure. In order to determine egg fates, we visited all nests either on the day of hatch, or within 5 d post-hatch, and used the remaining nest contents (membranes, depredated egg shells) or presence of ducklings in the bowl to assess final fates.

We captured female Pacific common eiders on or near their nests using mist nets and bow-net traps (Salyer 1962), usually within 1 to 3 d of hatch. At capture, we collected morphological measurements and hen weights. Between 2002-2004, we applied alpha-numerically coded plastic leg bands in addition to U.S. Geological Survey metal bands.

Data analyses

We followed a general productivity model (Fig. 1), in estimating the primary components of reproduction for Pacific common eiders on the YKD. In an effort to reduce the large number of possible parameter permutations, we created suites of hierarchical models. Herein, we selected the parameters we were most interested in and maintained less important parameters according to their most parsimonious structure (e.g., Doherty et al. 2002). We tested for multicollinearity among explanatory variables before constructing multivariate models and found the original data to be generally orthogonal. Throughout, we used information theoretic approaches (Burnham and

Anderson 1998) to evaluate relative strength of support for competing models (representing our biological hypotheses) using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and model weights (*w*; Burnham and Anderson 1998). To quantify the relationship between covariates and parameters of interest, we estimated coefficients (βs), and their standard errors, and, where appropriate, we calculated model-averaged estimates and associated unconditional variances (Burnham and Anderson 1998:150,162).

Phenology. To summarize information on nesting phenology, we followed definitions and formulas outlined by Cooke et al. (1985); where clutch initiation (INIT) was defined as the date on which the first egg was laid, (IP) was the incubation period (assumed to be a constant 26 d for common eiders; Goudie et al. 2000), (TCL) was the total clutch laid (i.e., the maximum number of eggs found in the nest and assuming 1 egg-laid/d; Swennen et al. 1993), and (EA) was egg age at nest discovery. We discovered most nests in our study after the one-egg stage, and backdated INIT dates based on EA following the methods of Flint and Grand (1996).

We examined spatial and temporal variation in clutch initiation using ANOVA models (PROC GLM; SAS Institute 2002) in which we included all combinations of annual (YEAR) and spatial (study SITE) variability. Although clutch initiation distributions tend to be positively skewed, ANOVAs are relatively robust to departures from normality. In addition to examining general spatio-temporal variation, we also examined a model in which we replaced annual variation (YEAR) with a linear trend (TREND) across years. We hypothesized that the primary determinants of initiation date were: 1) photoperiod, 2) spring phenology (i.e., ice/snow break-up), or 3) some combination of the two (i.e., females used photoperiod to ‘set target’ laying dates, but subsequently adjusted these dates according to spring phenology or some other local factor; Wikelski et al. 2000). We interpreted a YEAR effect as support for an annually varying phenomenon, such as spring phenology, and we interpreted support for a TREND effect as suggesting eiders may have initiated progressively earlier over time, potentially in response to climate change (Brown et al. 1999). Although there is some evidence of a directional change in spring conditions on the YKD (C. Ely unpublished data), precise data on site-specific snow and ice conditions were not available for our study sites. Thus, we examined distributional patterns in timing of nesting, following Lindberg et al. (1997), as an indirect means of assessing the effects of spring phenology. Specifically, we reasoned that if spring phenology was driving initiation of egg laying, we would observe a negative relationship between mean initiation dates and their variances. That is, nesting would take place in a shorter time-window, with less variance being associated with later initiation dates, in years of late break-up. To test this hypothesis, we examined equality of variances in clutch initiation dates among site-years using Levene’s test (Brown and Forsythe 1974) and then used the correlation between site-year residual variances and predicted mean initiation dates to indicate direction of effects.

Beyond large, among-individual spatio-temporal patterns, we were also interested in hypotheses related to individual variation. Specifically, we wondered how variation in initiation date might be influenced by individual phenotypic quality. We hypothesized that high individual consistency in timing of nesting, measured as repeatability (r_i), would suggest individual quality as an important factor explaining variation in timing of nesting (Sydeman and Eddy 1995). Although we could not control for the effects of age or experience, we examined repeatability using marked individuals measured across 2-6 seasons (i.e., females who had already bred one or more years; Milne 1974, Spurr and Milne 1976) and calculated r_i for both relative and absolute initiation date. Herein, absolute initiation date (AINIT) represented actual calendar date of initiation (irrespective of others in the population), and relative initiation date (RINIT) represented the difference between each individual female's clutch initiation date and the site-year population mean (Sydeman and Eddy 1995, Winkler et al. 2002). We calculated repeatabilities using the intra-class correlation coefficient following Lessells and Boag (1987) and associated standard error following Becker (1984).

Clutch size. We used only 'complete' nests (i.e., clutches in which all eggs apparently survived from laying into incubation) in our analyses of total clutch size laid (TCL) in each site-year. We excluded nests with > 8 eggs (i.e., ~2 standard deviations above mean clutch size; $n = 12$), for which intraspecific nest parasitism was suspected. We sought to describe and quantify spatio-temporal variation in total clutch size of Pacific common eiders, both among and within site-years. We also sought to test several hypotheses regarding patterns of variation in clutch size relative to environmental and individual variation. Because we expected clutch size of Pacific common eiders would decline with later initiation date (Lack 1968, Rohwer 1992, Emery et al. 2005), we treated initiation date as a continuous covariate and used analysis of covariance

(ANCOVA; PROC GLM; SAS Institute 2002) to examine patterns of variation. In general, we wondered whether absolute (AINIT) or relative initiation (RINIT) date (Sydeman and Eddy 1995, Winkler et al. 2002) explained a greater proportion of the seasonal variation in clutch size. We hypothesized that greater support for AINIT would indicate clutch size was more heavily influenced by the calendar date on which females nested each year; suggesting that females used photoperiod as their primary initiation cue, then made adjustments based on local conditions. In contrast, we reasoned that support for RINIT would indicate clutch size to be more heavily influenced by spring phenology, (i.e., the timing of nesting relative to others in the same site-year). Based on evidence of a directional trend in annual clutch size found in other common eider populations (Hario and Selin 1988, Coulson 1999), we also conducted a *post hoc* analysis testing for directional effects (TREND) in annual clutch size. To assess the magnitude of individual heterogeneity in clutch size, we calculated repeatability (r) using the same methods outlined for $r_{\text{clutch initiation}}$. Finally, in calculating clutch size at hatch (CSH), we considered a nest to be partially depredated if it had missing eggs, but remained active, and we pooled egg loss (EL) due to partial predation and nonviability. We calculated CSH for all nests that were ultimately successful, according to the formula:

$$\text{CSH} = \text{TCL} - \text{EL}$$

where egg loss (EL) during the incubation period was subtracted from the total clutch size laid (TCL) for each nest.

Nest survival. We defined successful nests as those in which at least one egg hatched, and the probability of being successful (i.e., the product of daily nest survival probabilites over the exposure period) as nest survival (Dinsmore et al. 2002). We took a two-step approach to examining nest survival. First, we used a multi-model, information theoretic approach (Burnham and Anderson 1998, Lebreton et al. 1992) to examine factors that influenced variation in daily nest survival probability (DSP). Second, we used maximum-likelihood methods to estimate model-averaged DSPs, overall nest survival, and associated sampling variances for each site-year.

Sources of variation in daily nest survival. We developed a suite of generalized nonlinear mixed models (PROC NLMIXED; SAS Institute 2002, Rotella et al. 2004) to test hypotheses regarding variation in DSP. Given sensitivity of common eider nesting success to human disturbance (Bolduc and Guillemette 2003*a*), and the potential for observer-induced negative bias in nest survival estimates, we also included observer-effects models (Rotella et al. 2000). Our observer effects models encompassed two primary hypotheses: 1) an effect on DSP on the day following a nest visit, after flushing the female (hereafter referred to as "observer effect" (OBS; Rotella et al. 2000), and 2) an effect of a female being captured at any time during nesting (i.e., trapping effect; TRAP). We examined all possible combinations of observer and trapping effects across study sites and years, then applied our top 'observer-effects' parameterization as a fixed effect in all subsequent modeling.

Within our larger spatio-temporal model set, we constructed models that included all possible combinations of our primary covariates of interest: study site, year, clutch age, date, quadratic clutch age and date terms, and interactions among these covariates. However, quadratic models do not always perform well at the tails of independent variable distributions (i.e., where data tend to be sparse), and we tested two additional non-linear age and date models, representing shape-variations on the quadratic theme. First, given females tend to initially increase and then stabilize their incubation constancy (Bolduc and Guillemette 2003*b*), we hypothesized that DSP would change according to an exponential rise to a maximum ($y = a * (1-(\exp^{(-b*x)}))$, gradually reaching an asymptote over time (Gunnarsson et al. 2006). Alternatively, we hypothesized that decreased incubation investment due to loss of body reserves through the nesting season (Criscuolo et al. 2002, Hanssen et al. 2003), might result in an exponential decay in DSP ($y = a * \exp^{(-bx)}$). To examine these hypotheses, we created a series of models which replaced quadratic age and date functions with those describing exponential rise and decay. Therein, a was the asymptote, b was the slope of the curve, and x signified the specific age or date value (i.e., $x(0) = \text{age}(0)$).

In addition, we sought to better understand potential sources of annual variation and we hypothesized that arctic fox predation may have been responsible for year to year variation in nest survival. To examine this hypothesis, we created a series of models in which we replaced YEAR with an annual index of YKD-wide arctic fox abundance. This index was based on counts of arctic fox hair and scat across random nest plots searched annually on the YKD (U.S. Fish and Wildlife Service, unpublished data). Importantly, this index did not track site-specific variation in fox abundance. However, it did represent an initial assessment of annual changes in predator abundances across the YKD, and in this sense, was useful in evaluating one potential source of annual variation in nest survival.

Nest survival estimates and variance. After describing patterns of variation in daily nest survival, our second objective was to produce the most accurate site-year estimates of overall nest survival (i.e., nest success) and its associated process variance. To do so, we obtained β estimates according to each of our top models of DSP (those with $\omega \geq 0.01$), including βs for observer effects (Rotella et al. 2000), using PROC NLMIXED (SAS Institute 2002, Rotella et al. 2004). We then backtransformed the logit equations and calculated DSP for each clutch age and initiation date within each site-year, using a program we created in R (R Development Core Team 2003). However, we did not include the observer effect βs (Rotella et al. 2000) in our back-transformations, reasoning that with the exception of our study sites, the remainder of the YKD common eider population was not affected by observers, and to include these effects would have resulted in negatively-biased population-level estimates. Instead, we calculated observer effects separately, as the difference between overall nest survival estimates from models with and without the OBS and TRAP terms; reasoning that observer effects were only applicable to those days on which we visited nests during the 31 d laying and incubation period (rather than all days in that period).

In summary, we calculated nest survival estimates within each site-year, across the 31 clutch ages (5 d for laying + 26 d incubation), within each of the 51 possible initiation dates for which we had data. In order to account for unequal numbers of nests initiated on each date, we considered the frequency distribution of initiation dates within each site-year and calculated the weighted average of nest survival estimates ($\hat{\theta}$) across this distribution (Grand et al. 2006). We then estimated overall nest survival for each site-year using estimates from each of our top models ($i = 1, 2, \ldots, R$) and we accounted for under-inflated sampling variance related to model-selection uncertainty by model-averaging nest survival estimates ($\hat{\bar{\theta}}$),

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_o \hat{\theta}_i$$

where w_0 was the model weight and $\hat{\theta}_i$ was the nest survival estimate for model i (Burnham and Anderson 1998). Variance of overall nest survival can be approximated using the Delta Method or bootstrapping simulation and we chose bootstrapping approaches (Efron and Tibshirani 1993) because of computational difficulties of the Delta Method when many covariates are included. We produced model-averaged nest survival estimates for the original data set and 500 bootstrap-resamples (i.e., resampling with replacement, up to the original sample size within each site-year; PROC SURVEYSELECT; SAS Institute 2002). We used the standard deviation among the 500 bootstrapped estimates (for each site-year) as the standard error for overall nest survival in each site-year (Efron and Tibshirani 1993). Further, we used the 0.025 and 0.975 quantiles of this distribution as our 95% confidence limits (CL) on overall nest survival estimates for each site-year (Grand et al. 2006). Finally, we calculated average annual productivity (P) as the expected number of ducklings hatched per hen:

$$P_i = CSH_i * NS_i$$

where P_i was the product of our site-year estimates of annual nest survival (NS_i) and corresponding site-year clutch sizes at hatch (CSH_i).

Process variation

We estimated spatio-temporal process variation in each of our reproductive parameters using variance-components approaches outlined by Burnham et al. (1987), Gould and Nichols (1998), and White et al. (2001)

$$\sigma^2_{total} = \sigma^2_{process} + \sigma^2_{error}$$

where total variability (σ^2_{total}) was decomposed into true biological variation ($\sigma^2_{process}$) and sampling variation (i.e., σ^2_{error}). In calculating process variance in survival estimates, we assumed that all individuals had the same inherent probability of survival and site-year survival estimates represented random fluctuations around grand site-year means (Burnham et al. 1987, White et al. 2001). However, with parameters such as clutch initiation date and clutch size, there is no biological expectation that all individuals will be the same (Kendall and Fox 2003). Further, if individual heterogeneity (i.e., acutal variation among individuals) is included in estimates of sampling variance, those estimates may be artificially inflated. Moreover, because overall variance represents the combination of sampling and process variance, positively biased sampling variance can result in negatively biased estimates of process variance, and can ultimately result in positively biased predictions of stochastic population growth (Robert et al. 2003). In an effort to lessen such biases, we attempted to decompose process variance in initiation date and clutch size by estimating the sampling variance, separate from individual heterogeneity. We did so by calculating bootstrapped mean estimates for each site-year from 1000 resampled iterations of the original site-year data (with replacement; Efron and Tibshirani 1993). We then used the variance among the 1000 means as our estimate of sampling variance for each site-year. Further, in the case of clutch size, we applied the initiation date adjustment (β_{INIT}) from our best approximating model using least squares methodology, prior to resampling (Neter et al. 1996), and then calculated sampling variances at mean site-year initiation dates.

Results

Phenology and clutch size

We used clutch initiation dates from 1805 nests (1991-2004). Our best approximating model for timing of nesting indicated that initiation date varied among sites and years (Table 1). No other models of initiation date were supported by our data ($\Delta AIC_c > 6.54$, $\sum w < 0.05$; Table 1). Initiation dates ranged from 4 May to 28 June across all years of study; 90% of nests were initiated between 8 May and 5 June, and 50% of all nests were initiated between 19-30 May. The mean initiation date across sites and years was 25 May (SE: ± 0.20 d), and peak (modal) initiation was 26 May. Process variance in initiation date was $\sigma^2 = 26.0$ d (95% CI: 22.54 – 49.12). Average initiation dates were consistently earlier (by 2–5 d) at the island site (KI), than at the mainland sites (TR and KR; Fig. 2), as reflected by differences in grand means; KI: 24 May (± 0.28), TR: 26 May (± 0.56), KR: 29 May (± 0.55). Variances around mean site-year initiation dates were unequal ($F_{13,\,1791} = 7.48$, $p < 0.001$), and negatively correlated with predicted means ($r = -0.127$, $p < 0.001$); indicating nesting was less variable in years of later clutch initiation.

We had repeated measurements of clutch initiation date and clutch size laid for 95 individuals (number captured in 2-6 subsequent yrs.: 2-yrs. = 70, 3-yrs. = 18, 4-yrs. = 4, 5-yrs. = 2, and 6-yrs. = 1), from which we estimated $r_{\text{absolute initiation date}}$ to be 0.49 (± 0.01) and $r_{\text{relative initiation date}}$ to be 0.33 (± 0.01).

We included data from 1778 complete clutches to examine variation in clutch size. Our best approximating model included year and absolute initiation date (Table 2, Model 1), but there was also support ($\Delta \text{AIC}_c > 0.76$) for an effect of site (Table 2, Model 2). There was little support for other models of total clutch size ($\Delta \text{AIC}_c > 4.07$). Among models, YEAR appeared to be the most influential parameter ($\sum \omega_{YEAR} = 0.94$), followed by absolute initiation date ($\sum w_{AINIT} = 0.85$), and site ($\sum w_{SITE} = 0.34$). We found little support for models which included "relative" initiation date ($\sum \omega_{RINIT} = <0.01$) or linear trends in clutch size across years ($\sum \omega_{NYEAR} = <0.01$). The estimated seasonal decline in clutch size was 0.05 (± 0.01) eggs/d. After adjusting for mean initiation date at each site-year (i.e., least squares means, Fig. 3), model-averaged clutch sizes (total clutch laid) ranged from 4.8 to 6.6 eggs across site-years, and on average clutches at the island site (KI) had 0.1 to 0.3 more eggs than clutches at either of the mainland sites (KR and TR, Fig. 3). We calculated the grand mean clutch size (laid) to be 5.2 (± 0.19) and estimated its process variance (σ^2) to be 0.07 (CI: 0.06–0.19). Repeatability of total clutch size laid was 0.33 (± 0.01).

The overall proportion of successful nests in which at least one egg was lost was 0.24 (303 of 1281 nests). Annual egg loss for nests in which at least one egg hatched ranged from 0 to 2.3 eggs/nest (average = 0.7 ± 0.2) across sites and was negatively correlated with site-year nest survival ($r^2 = -0.41$, $p = 0.02$). Thus, in site-years of high partial loss of eggs, complete loss of eggs also was high. We calculated average clutch size at hatch to be 4.7 (± 0.2), ranging from 2 to 5.8 eggs/nest across site-years (Table 3), and clutch size at hatch was positively correlated with site-year nest survival ($r^2 = 0.67$, $p < 0.01$). However, clutch size-nest survival correlations were not completely independent, as both were influenced by timing of clutch initiation.

Nest survival

We monitored 2136 common eider nests during the 29 site-years of our study, comprising 29,272 total exposure days. This sample included 221 nests at the KR study area, 1511 at KI, and 404 at TR. In each year, we found an average of 18.4 ± 0.52 (range: 10-34) nests at KR, 116.2 ± 1.36 (range: 67-224) at KI, and 101.0 ± 1.83 (range: 56-138) at TR. Of all nest failures, 73% were due to predation, 26% to abandonment, and 1% due to other factors (Appendix 1).

Patterns of variation in daily nest survival. After examining all possible combinations of observer and trapping effects across study sites and years (Table 4), we used our top 'observer-effects' model (OB*site + TRAP*site; Table 4, Model 1) as a fixed effect in all subsequent modeling. That is, all models in the remainder of our analysis contained the OB*site + TRAP*site term. Among models we examined, there was overwhelming support for variation in DSP among sites and years, across clutch ages, and across dates within years (Tables 4 and 5). All top models ($w_i > 0$) included a site*year interaction, quadratic effects of both clutch age (aa^2) and date (dd^2) on DSP, and an interaction between non-linear date and year (dd^2*year; Table 5). There was also limited support ($w_{model\ 2}$ = 0.11; Table 5) for a quadratic effect of clutch age that varied among years (aa^2*y). Less parameterized models were not supported by our data (Table 5; $\Delta AIC_c > 39.19$), and we found no model support for *a priori* predictions regarding the influence of fox abundance on annual variation in DSP (Table 5; $\Delta AIC_c > 95$), or asymptotic clutch age and date functions ($\Delta AIC_c > 101$).

In general, daily survival probabilities of nests decreased with (absolute) date, dropping sharply late in the season (after 25 June; Fig. 4). Although the early and late season reductions were much more pronounced in some years (e.g., 1998 and 2003), all followed a similar quadratic form. Thus, we illustrated age/date-DSP patterns with a single composite graph of all site-years (Fig. 4). DSP was lowest during the earliest clutch ages (i.e., 0 to 8 days; during egg laying), increased during early incubation, and then stabilized after approximately 8 days of age (Fig. 4). This was followed by a small decline at the latest clutch ages, which appeared much smaller for clutches initiated earlier in the season than those initiated later (Fig. 4). Overall, DSP was highest for middle-aged clutches at early season dates and lowest for young nests (in the laying stage) during the latest dates of the season (Fig. 4).

Overall nest survival and productivity. Overall nest survival estimates ranged from 0.06 at Kigigak in 2001 to 0.92 at Kashunuk River in 1995 (Fig. 5 and Table 3), and bootstrap confidence intervals for nest survival across all site-years ranged from 0 to 1 (Fig. 5 and Table 3). Grand mean nest survival among site-years was 0.55 (± 0.17, CI: 0.22–0.88), with an estimated process variance (σ^2) of 0.02 (CI: 0.01-0.05). Although overall nest survival (i.e., success) consistently increased with clutch age and generally decreased with later initiation date, relationships between nest survival and initiation date varied considerably across sites and years (Fig. 6); declining in most site-years (KR and TR sites; Fig. 6) and increasing in others (KI; Fig. 6). Overall, observer effects (measured as a percentage point reduction in nest survival) had a negative impact on nest survival (Table 3; OBS_{NS}) which varied consistently among sites. Observer effects were higher at sites with lower samples sizes (KR: $\overline{N} = 18$, $\overline{OBS}_{NS} = -0.28 \pm 0.02$, TR: $\overline{N} = 101$, $\overline{OBS}_{NS} = -0.18 \pm 0.03$), and vice versa (KI: $\overline{N} = 116$, $\overline{OBS}_{NS} = -0.06 \pm 0.01$; Table 3; OBS_{NS}). Finally, using site-year estimates of clutch size at hatch and nest survival, we calculated average productivity across site-years to be 2.7 ducklings hatched/hen (range: 0.2-4.7; Table 3).

Discussion

Phenology

Initiation dates of common eiders on the YKD ranged widely over the period of our study (total interval = 56 d), similar to common eiders studied elsewhere (58 d; Finland; Laurila and Hario 1988), and we found process variance in initiation dates to be high. Each year, initiation dates were earliest at our most marine site (KI: an island ~1 km from the mainland), intermediate at our coastal site (TR), and latest at our inland site (KR; ~1-2 km from the coast), suggesting a consistent gradient in spring-breakup patterns related to distance from the coast. Although spatial variation in timing of nesting appeared high, within years, we found 80% of all clutches to be initiated within a relatively small laying-window (on average 17 d). Further, 80% of nests were initiated prior to 6 June each year, suggesting eiders undergo strict time constraints related to the short subarctic breeding season. As with black brant (Lindberg et al. 1997) and emperor geese (*Chen canagicus*; Petersen 1992) on the YKD, as well as common eiders in Finland (Laurila and Hario 1988), we found nesting to be more synchronized (i.e., less variance around the mean) in years of later initiation dates. This may have been the result of the delayed availability of nest sites in late break-up years (Findlay and Cooke 1982*b*, Lindberg et al. 1997), but it is possible that differences in age-related breeding propensities in early and late years could have led to the results we observed. For example, in late years, young females may have been more likely to skip breeding (Barry 1962, Murphy et al. 1991, Lindberg et al. 1997).

Our estimates of repeatability in clutch initiation dates indicated that much of the variation in timing of nesting may have also been attributed to differences within, rather than among-individuals. Initiation date repeatabilities similar to ours (0.33-0.49) were observed in other common eider populations ($r = 0.42$; Laurila and Hario 1988, Finland; $r = 0.38$; Erikstad et al. 1993, Norway), as well as in lesser snow geese (*Chen caerulescens caerulescens*) in Canada ($r_{\text{hatching date}} = 0.49$; Findlay and Cooke 1982*a*). When interpreted in combination, these results suggest that > 50% of the variation in absolute initiation date is due to variability within-females among years. Further, we found $r_{\text{absolute initiation date}}$ (0.49) to be higher than $r_{\text{relative initiation date}}$ (0.33), implying calendar date (i.e., photoperiod) is the dominant overall initiation cue used by nesting Pacific common eiders on the YKD, with local phenologies serving as secondary proximate cues. Although, it is important to note that age and/or experience may be confounding factors (which we were unable to control for in our study), in general, considerable within-individual variation in nesting date would imply a lack of strong selection pressure for timing of nesting in this population. However, we suggest that response to this selection may be masked by strong environmental variability in our system (Larsson et al. 1998, Kruuk et al. 2002). That is, selection for early nesting may appear strong, but not every individual female may have been able to match the optimum date that she should lay (in every year), due to high environmental stochasticity.

Clutch size

Because common eiders are capital breeders (Korschgen 1977, Drent and Daan 1980), determination of their clutch size depends on pre-breeding nutrient reserves (Parker and Holm 1990, Erikstad et al. 1993, Coulson 1999), as well as seasonal phenology at breeding grounds (Laurila and Hario 1988). The seasonal decline in clutch size we observed (about one egg fewer per 20 d delay in initiation) was similar to that observed in other eider studies (Coulson 1999, Grand and Flint 1997). In our study, this decline was best explained by absolute, rather than relative initiation date. This suggests two possible explanations. First, broader climatic cues may have been a better indicator of clutch size than local conditions. Second, females may have used some of their reserves in late years, or reabsorbed follicles (similar to arctic-nesting geese; Ankney and MacInnes 1978), resulting in the seasonal declines in clutch size we observed. However, Pacific common eiders on the YKD (although largely capital breeders) appear to be short-distance migrants or possibly residents, based on the results of satellite telemetry (Petersen and Flint 2002). Thus, they may have more flexibility in responding to local environmental conditions than other YKD nesters which undergo substantial migrations (Both and Visser 2001).

Initiation dates in our study were consistently earlier at some sites versus others (Fig. 2), and model-averaged clutch sizes, adjusted for site-specific initiation dates, generally followed the same pattern (Fig. 3); clutch size tended to be largest at the site with the earliest initiation dates (KI; Fig. 3). However, study site effects on clutch size were generally weak and differences were largely explained by variation in absolute laying dates among years (i.e., the seasonal decline was similar among years). In this sense, clutch size emerged as a relatively static component of overall reproduction in Pacific common eiders. For example, coefficient of variation (CV) in process variance of actual clutch size laid (0.01) was much lower than that for timing of nesting (0.18). Further, the primary source of variation in clutch size in our study was year, but we found no consistent trend in clutch size across years (Laurila and Hario 1988). This is in contrast to longer-term studies of common eiders (30-40 yrs; Hario and Selin 1988, Coulson 1999), which noted significant temporal trends in clutch size. For example, Hario and Selin (1988) observed a marked increase in clutch size through time, concurrent with steep population growth, while Coulson (1999) found a pattern of steady decline, which he attributed to locally declining resources. Based on published data, we suspect that most variation in clutch size of common eiders reflects variation in body reserves at the time of clutch initiation (Ankney and MacInnes 1978, Arnold and Rohwer 1991, Erikstad et al. 1993, Bêty et al. 2003, Hanssen et al. 2003). If so, the annual variation in clutch size we observed may have represented common effects of winter (sea-ice) and spring conditions at all three breeding sites (Petersen and Flint 2002, Petersen and Douglas 2004). Further, the subtle differences among our study areas may have represented small localized differences in the habitat quality where birds forage immediately prior to clutch initiation (e.g., Coulson 1984).

Though our best approximating models indicated that most of the variation in clutch size was driven by annual variation in timing of nesting, coefficients of correlation in these models were low ($r^2 = 0.13$), and we suggest that some proportion of the unexplained variation could have been attributed to individual differences, such as hen age and nesting experience (Baillie and Milne 1982, Laurila and Hario 1988). For example, if young birds lay smaller clutches and initiate those clutches later in the season, some proportion of the variation in clutch size across sites and years may reflect variation in recruitment. Further, if timing of nesting is correlated with age and experience, then these factors may partially explain the seasonal decline in clutch size. The degree to which clutch size variation was due to individual differences in our study (i.e., 0.67), appeared similar to that reported for common eiders elsewhere (0.69; Laurila and Hario 1988). These results indicate that clutch size varied less among individuals in a given site-year (0.33), than within individuals across years (in our case; ~67%). Although our study only partitions the variance for a small subset of individuals and site-year samples, higher within-individual variability suggests extrinsic, rather than intrinsic factors, may ultimately play a larger role in determination of clutch size laid.

Nest Survival

Patterns of daily survival across sites and years. As with other high latitude breeders (e.g., Murphy et al. 1991), point estimates of nest survival in YKD Pacific common eiders varied across sites and years of our study (Fig. 6), ranging from < 0.1 (2001 at KI; Fig 6), to > 0.9 (1995 at KR; Fig 6). Although factors such as climate and breeding ground conditions, likely contributed to, or exacerbated annual fluctuations, we suspect that functional and numeric changes in predation pressure were largely responsible for the wide range of nest survival estimates we observed (Milne 1974, Anthony et al. 1991, Flint and Grand 1996, Grand and Flint 1997, Bêty et al. 2001, Sovada et al. 2001, Miller et al. 2006). That said, we were surprised to find a lack of support for DSP models in which fox abundance replaced general YEAR variation; especially given substantial annual variation in arctic fox abundance observed across the three study areas (H. Wilson personal observation). Moreover, visual inspection of site-year daily nest survival plots suggested quadratic date-effects were strongest (i.e., early and late-season nest survival was lowest) in the years of highest fox abundance.

Arctic fox removal has been shown to improve success of sympatrically-nesting black brant on the YKD (Anthony et al. 1991), and we speculate that our failue to find fox effects was either due to: 1) our YKD-wide index of arctic fox abundance not tracking site-specific predation pressure within years, or 2) additional broad-scale or site-specific sources of nest failure which we did not model. For example, we did not account for avian predation pressure in our index. However, avian predation may have been equally important to mammalian influences (Flint and Grand 1996, Grand and Flint

1997). Frequently, we could not assign nest predators (or other factors) to failed nests, and, thus, we can only speculate as to the proportion of eider nests destroyed by avian versus mammalian predators. However, we found clutch sizes at hatch to be positively related to nest survival within a given site-year, suggesting factors which contribute to partial loss (primarily avian predators) also contribute to total nest failure. Further, local nest success for northern pintails (*Anas acuta*) and spectacled eiders on the YKD was higher in years of mew gull population control (Flint and Grand 1996, Grand and Flint 1997). Studies specific to common eiders have found similar reduced nest success in areas of high gull density (Bolduc and Guillemette 2003*a*); although others have concluded that territorial gulls benefit neighboring eiders by providing indirect nest protection (Bourget 1973, Schamel 1977, Götmark and Ǻhlund 1988). We speculate that the beneficial or harmful relationship between gulls and eiders depends on timing of nesting, hatching, and associated behavioral changes in gulls relative to the phenology and density of nesting eiders. Further, whether elevated nest success is related to presence of gulls, or is simply shared selection for optimal breeding sites (Laurila 1989), is still unknown, and deserves further study. Although avian predators are likely responsible for most of the partial predation we observed, mammalian predators can cause complete nesting failure across broad geographic regions (Quinlan and Lehnhausen 1982, Goudie et al. 2000, our data; TR 2003). Thus, we contend that although avian predators play a substantial role, their influence is not likely to fluctuate to the same magnitude as mammalian predation (Quinlan and Lehnhausen 1982, Bêty et al. 2001, Sovada et al. 2001, Roth 2003), and will not contribute to increased oscillations in overall productivity to the same degree as will mammalian predators.

Patterns of daily nest survival across dates and clutch ages. Our data exhibited strong temporal variation in nest survival within seasons. DSP varied according to quadratic trends in clutch ages and dates, indicating that nests initiated early and late in the season (particularly those in the laying stage) were less likely to survive than those initiated at early to intermediate dates. Daily survival of nests may change with calendar date for a variety of reasons, including greater nest concealment with increased vegetative growth (Laurila 1989, Petersen 1990), functional and numeric changes in predator populations (Bêty et al. 2001, Miller et al. 2006), or changes in the abundance of nesting neighbors (i.e., increased predator swamping; Raveling 1989). For example, on the YKD early-initiating common eiders begin egg-laying approximately one week after peak initiation for black brant (U.S. Fish and Wildlife Service, unpublished data); likely a period of maximimal predator swamping. Our results for DSP suggested strong directional selection for nesting at early dates (Fig. 4) and this pattern may be reinforced by positive correlations between early nesting and other life-history parameters (e.g., higher hen survival; Blums et al. 2005). Similar to other studies (Klett and Johnson 1982, Grand and Flint 1997, Traylor et al. 2004, Grand et al. 2006), we found DSP to be lowest during the earliest clutch ages (i.e., laying); a period when the female's investment (Hanssen et al. 2003, Andersson and Waldeck 2006) and consequent nest attendance tend to be lower (Swennen 1983, Goudie et al. 2000). Several studies of nesting common eiders have noted that most egg loss occurs when hens are off their nests (Swennen 1983), and researchers have hypothesized that eiders likely begin incubating during the laying stage to protect eggs against avian predators (Milne 1974, Schamel 1977, Hanssen et al. 2003, Andersson and Waldeck 2006). In addition to reduced DSPs at early clutch ages, our quadratic results also indicated that DSP dropped near hatch, albeit to a much smaller degree. We suggest this reduction could have been caused by a depletion of energy reserves of hens late in incubation (Korshegen 1977), resulting in decreased incubation constancy or nest abandonment as hens left the nest to feed shortly before hatching (Criscuolo et al. 2002).

Observer effects. We found support for negative effects of our nest visitations and trapping on daily nest survival (Tables 3 and 6). However, these effects were only applicable to those days on which we visited nests during the 31-d laying and incubation period. When scaled to the level of overall nest survival, we found observer effects to be extremely variable (range: a 0 to -0.36 reduction in nest survival; Table 3; OBS_{NS}) and their magnitude negatively related to sample sizes of nests (Table 3). Estimated effects were greatest at sites with small sample sizes (i.e., KR; $\beta = -3.21$, TR; $\beta = -1.73$), and vice versa (i.e., KI; $\beta = -0.96$).

We speculate that the greater effects of individual visits at the KR site may have reflected lower nesting densities at that location, and potentially greater predator effects (Raveling et al. 1989, Bêty et al. 2001). In addition, average visitation intervals varied by ~1 d among sites (KR = 5.71 d, TR = 5.14 d, and KI = 6.45 d). Thus, overall observer effects on nesting success appeared to be a combination of disturbance caused by each individual visit and the frequency of nest visitation. We contend that nest visitation and trapping undoubtedly disturb the natural incubation constancy of common eiders (which is ~99.7% in the absence of these activities; Criscuolo et al. 2002, Bolduc and Guillemette 2003*b*), and likely leave the nest more vulnerable to avian predators (Swennen 1983, Bolduc and Guillemette 2003*a*). However, higher hetereogenity at sites with smaller sample sizes may also influence the magnitude of observer effects. For example, we found average observer effects to be smallest at our study site with the largest samples sizes, and vice versa. Overall, increased visitation intervals will lead to increased precision in nest survival estimates because the period between the final two visits will be shorter, thus reducing uncertainty in the true number of 'exposure' days (Klett and Johnson 1982). However, increased frequency of visitation may lead to greater potential for observer effects. Thus, observers must balance the need for increased precision with the potentially negative consequences related to their activity. In conclusion, we encourage use of observer effects models (to evaluate potential bias), but caution that direct interpretation of results (especially for small sample size situations) may be misleading.

Nest survival, overall productivity, and selection for timing of nesting

The wide range of our nest survival estimates was similar to that of published apparent nest success estimates (0.33-0.86; Sargent and Raveling 1992) and summary nest survival estimates for common eiders across their distribution (9.8-93%; Goudie et al. 2000). Our site-year average nest survival (0.55; 95% CI: 0.12 – 0.95) was higher than that calculated for sympatrically-nesting spectacled eiders (0.48, 95% CI: 0.24 - 0.71; Grand and Flint 1997), and that for Pacific common eiders in northern Alaska (average: 0.33; Schamel 1977, apparent nest success: 0.51; Seguin 1981). Average productivity for Pacific common eiders on the YKD (2.7 ducklings/hen) was almost double that of Pacific common eiders nesting on barrier islands in the Beaufort Sea (1.5 ducklings/hen; Schamel 1977); suggesting broad regional differences in reproductive rates may exist between northern and western breeding common eiders in Alaska.

Overall, high nest survival at early initiation dates (found at two of our three sites), combined with larger clutch sizes, would suggest directional selection favoring early nesting. However, the bulk of clutch initiation at the KR and TR sites began later than would have been predicted for optimal nest survival (Fig. 6), and, in general, we found no evidence for a long-term shift towards earlier nesting. This suggests that individuals are either not responding to the apparent selection gradient for timing of nesting, or their response is masked by strong environmental variation (Larsson et al. 1998, Kruuk et al. 2002). Our relatively low (0.33) estimate of repeatability in timing of nesting would suggest a lack of heritable variation on which selection can act (Price et al. 1988), but variation in the selection gradient as a result of stochastic environmental conditions may preclude, or mask, an overall population response, as seen in other long-lived waterfowl (e.g., barnacle geese (*Branta leucopsis*); Larsson et al. 1998). Finally, there may be corresponding counter selection against very early breeding in other fitness components. For example, Blums et al. (2005) found that females nesting somewhat earlier than the norm exhibited the highest adult survival rates, but the very earliest and latest nesters experienced reduced adult survival. Further, Coulson (1984) suggested that breeding propensity of common eiders may fluctuate in response to environmental conditions; similar to patterns observed in other long-lived marine birds (Barry 1962, Murphy et al. 1991). Under this scenario, it may be that early breeding phenotypes are forced to skip reproduction in relatively late years of spring phenology, resulting in a form of counter selection. We suggest that further detailed studies examining a broader suite of fecundity components and exploring the fitness consequences of various reproductive strategies will be required to distinguish among these potential explanations.

Management Implications

Our results indicate that there is considerable variability in the productivity components of Pacific common eiders in western Alaska. We found high levels of within- and among-year variation in each of the reproductive rates we measured. Timing of nesting and seasonal declines in clutch size and nest survival indicated that early breeding females make the largest contribution to productivity. Additionally, early-hatched offspring tend to have higher growth rates, breeding propensities, and future probability of recruitment than late-hatched individuals (e.g., lesser snow geese; Cooke et al. 1984, black brant; Sedinger and Flint 1991, canvasbacks (*Aythya valisineria*); Anderson et al. 2001). Thus, enhanced protection during the early nesting period may be an effective management strategy for increasing current reproductive output and future recruitment, as well as increasing directional selection for early breeding. Finally, we hypothesize that the fate of common eiders may be closely tied to the fate of sympatrically nesting species (e.g., black brant; Raveling 1989), and we predict that management actions targeted at other species (i.e., those which facilitate predator swamping) will have positive, concurrent effects on nesting common eiders.

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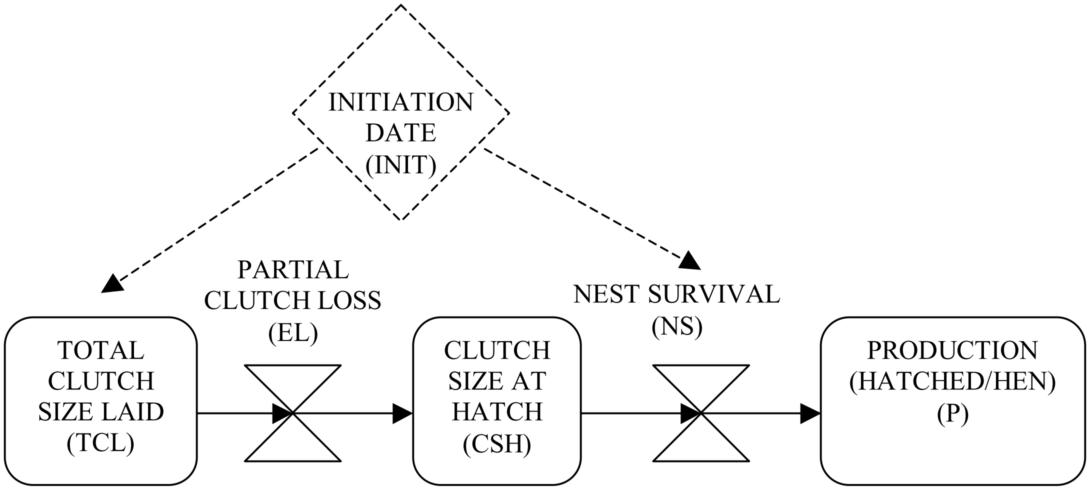

Figure 1. Flow diagram model of Pacific common eider productivity components, showing reproductive output from a single nest. Boxes denote state variables and bow ties denote transition variables. Dashed-diamonds represent important covariates and dashed-lines denote the reproductive components modified.

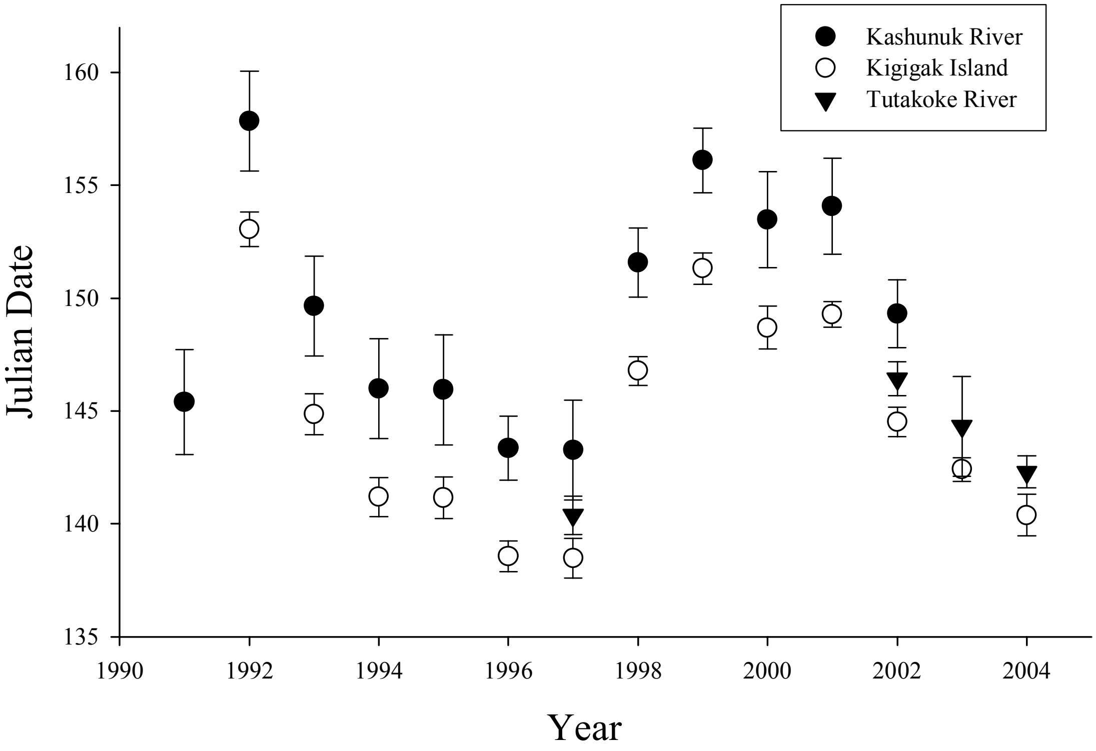

Figure 2. Least-squares estimates of mean clutch initiation dates (± SE) by study site and year for Pacific common eiders nesting on the Yukon-Kuskowim Delta, Alaska (1991-2004).

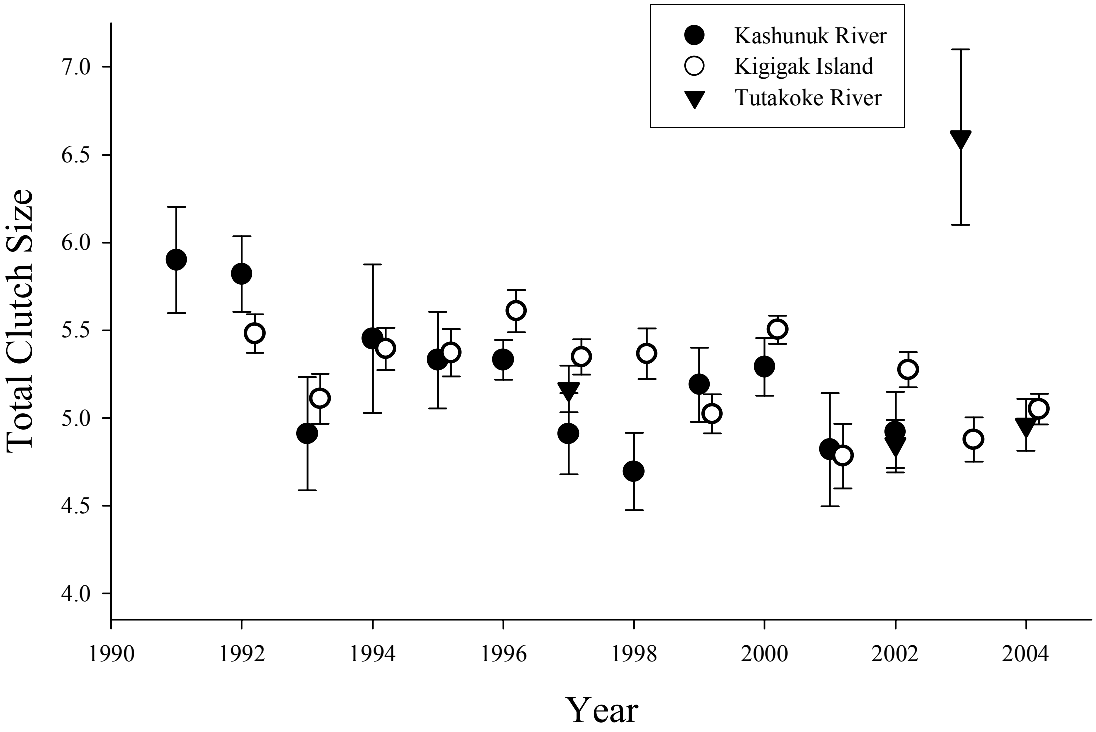

Figure 3. Least-squares estimates of mean clutch size laid (± SE) by study site and year at mean site-year initiation dates for Pacific common eiders nesting on the Yukon-Kuskowim Delta, Alaska (1991-2004).

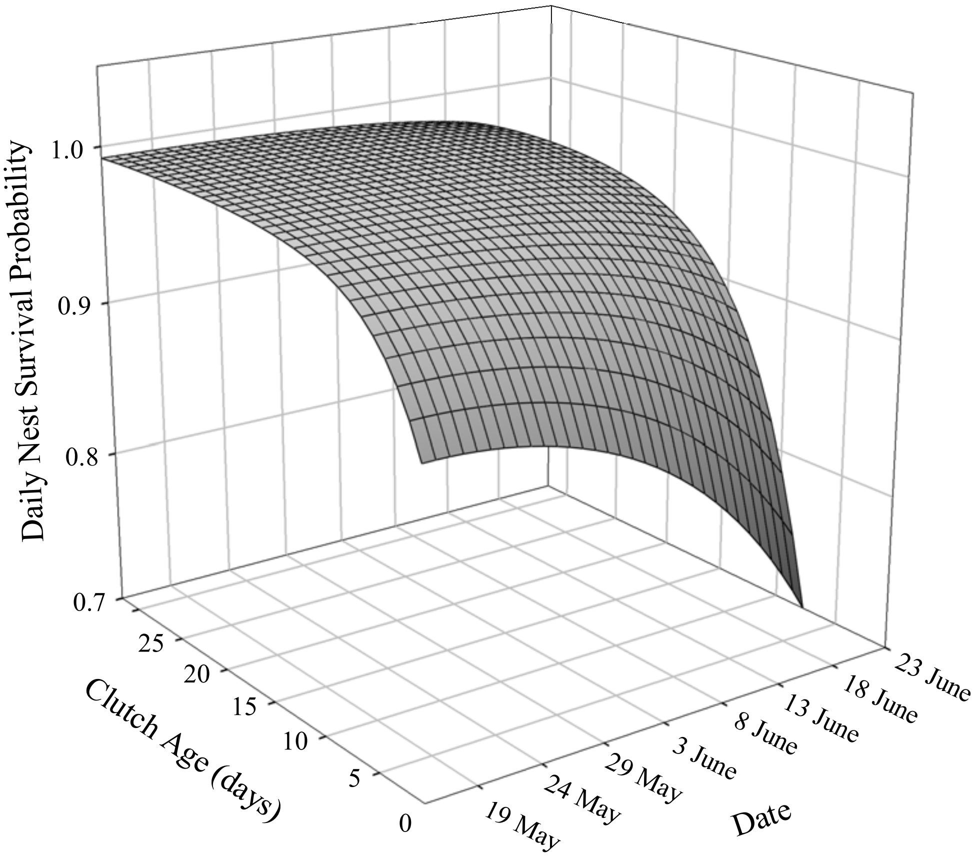

Figure 4. Daily nest survival probability (DSP) by clutch age (laying through hatch) for each season date of Pacific common eider nests on the Yukon-Kuskowim Delta, Alaska (1991-2004). Daily survival rates were lowest during late season dates and early incubation and laying.

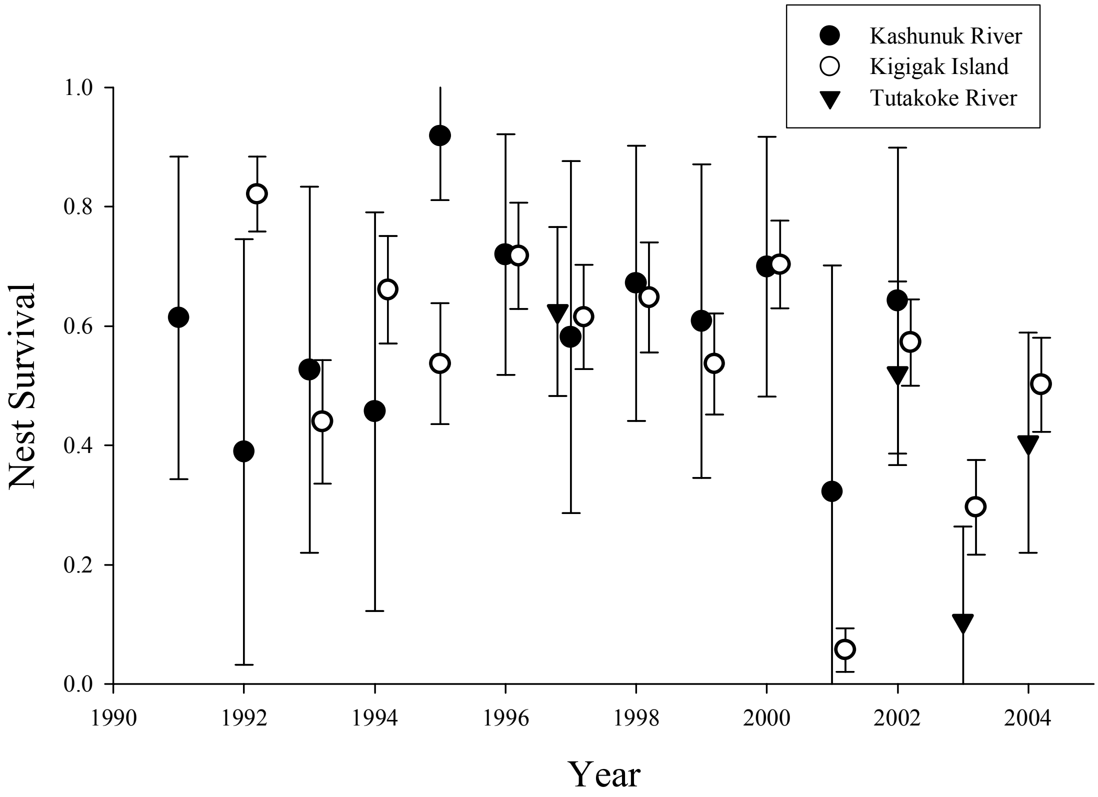

Figure 5. Estimated nest survival (± bootstrapped SE) by study site and year on the Yukon-Kuskowim Delta, Alaska (1991-2004).

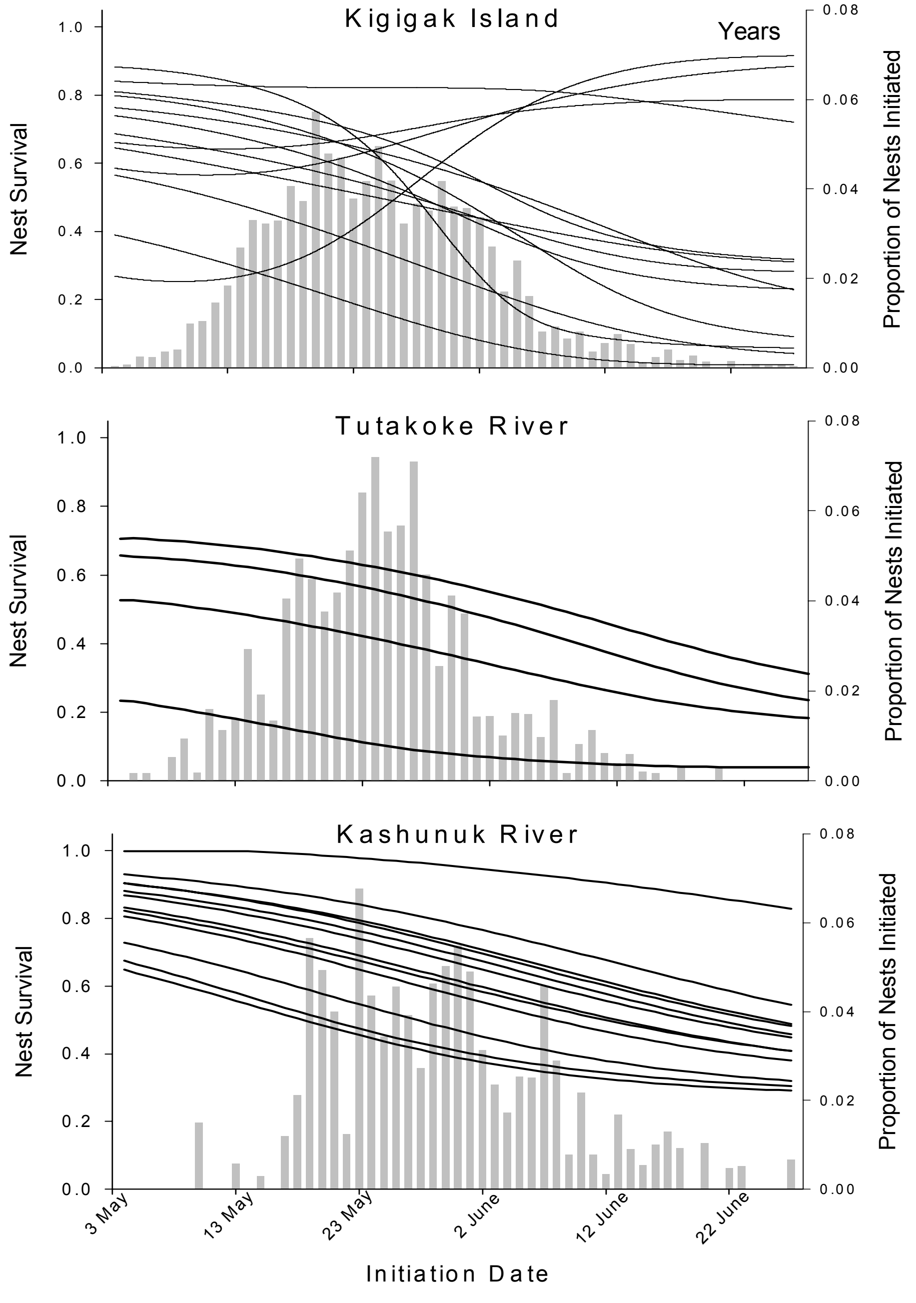

Figure 6. Patterns of nest survival across initiation dates during each year of study for Pacific common eiders at the Kashunuk River, Tutakoke River, and Kigigak Island study sites, on the Yukon-Kuskowim Delta, Alaska (1991-2004). Each line represents an individual year. The mean proportional frequency of nests initiated on each date within each study area is included for reference.

Table 1. Models used to assess spatial (study site) and temporal (year) variation in initiation dates for Pacific common eiders (1991-2004) nesting on the Yukon-Kuskokwim Delta (YKD), Alaska, USA.

Model	k^a	$AIC_c{}^b$	ΔAIC_c	ω^b	r^2
1) Year, Site	16	0.00	0.00	0.95	0.30
2) Year, Site, Year*Site	29	6.54	6.54	0.04	0.30
3) Year	14	67.5	67.5	<0.01	0.27
4) Site	3	522	522	<0.01	0.04

[a] k = number of parameters in model

[b] The best approximating model has the lowest Akaike's Information Criterion (AIC_c) value and the highest model weight (ω), relative to others in the model set.

Table 2. Top models used to assess variation in clutch size of Pacific common eiders nesting on the Yukon-Kuskokwim Delta (YKD), Alaska, USA (1991-2004).

Models	k^b	AIC_c^c	ΔAIC_c	ω	r^2
1) Year, AINIT[a]	15	380.32	0.00	0.50	0.13
2) Year, AINIT, Site	16	381.08	0.76	0.34	0.13
3) Year, AINIT, Site, Site*Year	30	384.40	4.07	0.07	0.14
4) Year, AINIT, Year*AINIT	28	384.89	4.56	0.05	0.14
5) Year, Site, AINIT, Site*AINIT	19	386.54	6.21	0.02	0.13

[a] AINIT = absolute initiation date (i.e., calendar date)

[b] k = number of parameters in model

[c] The best approximating model has the lowest Akaike's Information Criterion (AIC_c) value and the highest model weight (ω), relative to others in the model set

Table 3. Mean clutch size at hatch (CSH), overall nest survival (NS), reduction in nest survival due to observer effects (OBS_{NS}), and calculated productivity (P; ducklings hatched/female) for Pacific common eiders on Yukon-Kuskokwim Delta (YKD), Alaska, USA, 1991-2004. Standard errors (SE) represent standard deviations for 500-1000 bootstrap samples of the original data.

		CSH		NS		OBS_{NS}	P
Site[a]	Year	Mean	SE	Mean	SE	Mean	Mean
KR	1991	5.83	0.37	0.61	0.27	-0.22	3.58
KR	1992	3.67	0.27	0.39	0.36	-0.30	1.43
KR	1993	4.29	0.52	0.53	0.31	-0.27	2.26
KR	1994	4.50	0.55	0.46	0.33	-0.33	2.06
KR	1995	5.11	0.40	0.92	0.11	-0.07	4.69
KR	1996	5.12	0.25	0.72	0.20	-0.25	3.68
KR	1997	4.00	0.29	0.58	0.29	-0.33	2.33
KR	1998	4.67	0.30	0.67	0.23	-0.29	3.14
KR	1999	4.86	0.32	0.61	0.26	-0.34	2.96
KR	2000	4.76	0.29	0.70	0.22	-0.26	3.33
KR	2001	2.00	0.35	0.32	0.38	-0.30	0.64
KR	2002	5.00	0.80	0.64	0.26	-0.36	3.21
KI	1992	5.44	0.12	0.82	0.06	-0.03	4.47
KI	1993	4.53	0.26	0.44	0.10	-0.08	1.99
KI	1994	5.27	0.15	0.66	0.09	-0.09	3.48
KI	1995	5.27	0.19	0.54	0.10	-0.07	2.83
KI	1996	5.36	0.19	0.72	0.09	-0.01	3.85
KI	1997	5.13	0.13	0.62	0.09	-0.11	3.16
KI	1998	5.37	0.14	0.65	0.09	-0.05	3.48
KI	1999	4.82	0.14	0.54	0.08	-0.09	2.59
KI	2000	5.37	0.10	0.70	0.07	-0.05	3.78
KI	2001	4.35	0.29	0.06	0.04	-0.00	0.25
KI	2002	5.01	0.12	0.57	0.07	-0.09	2.87
KI	2003	3.76	0.20	0.30	0.08	-0.07	1.11
KI	2004	4.75	0.12	0.50	0.08	-0.11	2.38
TR	1997	4.85	0.16	0.62	0.14	-0.18	3.03
TR	2002	3.61	0.23	0.52	0.15	-0.21	1.88
TR	2003	*	*	0.11	0.16	-0.09	*
TR	2004	3.92	0.21	0.40	0.18	-0.22	1.59

[a] Study sites: KR=Kashunuk River, KI=Kigigak Island, TR=Tutatkoke River.

*Indicates years in which no nests survived to calculate clutch size at hatch.

Table 4. Models of observer visits and trapping effects on daily survival probability (DSP) for nests of adult female Pacific common eiders on Yukon-Kuskokwim Delta (YKD), Alaska, USA, 1991-2004.

Models[a]	*k*[b]	AIC_c[c]	ΔAIC_c	w_i
(TRAP*s) (OB*s) (y*s) aa^2 dd^2 (y*dd^2)	52	3708.39	0.00	0.47
OB TRAP (y*s) aa^2 dd^2 (y*dd^2)	48	3709.64	1.25	0.25
(TRAP*s) (y*s) aa^2 dd^2 (y*dd^2)	50	3710.50	2.29	0.15
(OB*s) (y*s) aa^2 dd^2 (y*dd^2)	50	3711.46	3.08	0.10
OB (y*s) aa^2 dd^2 (y*dd^2)	47	3713.77	5.38	0.03
(TRAP*s) (OB*y) (y*s) aa^2 dd^2 (y*dd^2)	63	3719.30	10.91	0.00
(y*s) aa^2 dd^2 (y*dd^2)	46	3745.44	37.06	0.00
constant	1	4495.61	793.89	0.00

[a] Abbreviations: y = year, d = date, a = clutch age, dd^2 = quadratic season date, aa^2 = quadratic clutch age, OB = observer, TRAP = trapping. Asterisk (*) indicates effect interactions; otherwise effects are additive.

[b] *k* = number of parameters in model

[c] The best approximating model has the lowest Akaike's Information Criterion value, adjusted for small sample size (AIC_c), and the highest model weight (w_i), relative to others in the model set.

Table 5. Selected models of daily survival probability (DSP) for nests of adult female Pacific common eiders on Yukon-Kuskokwim Delta (YKD), Alaska, USA, 1991-2004.

Models[a]	k[b]	AIC_c[c]	ΔAIC_c	w_i
(y*s) aa^2 dd^2 (y*dd^2) (ob*s) (trap*s)	52	3708.39	0.00	0.89
(y*s) aa^2 dd^2 (y*dd^2) (y*aa^2) (ob*s) (trap*s)	65	3712.46	4.08	0.11
(y*s) aa^2 dd^2 (y*aa^2) (ob*s) (trap*s)	52	3747.57	39.19	0.00
(FOX*s) aa^2 dd^2 (ob*s) (trap*s)	16	3804.37	95.98	0.00
aa^2 (ob*s) (trap*s)	10	4016.26	307.88	0.00
y s (ob*s) (trap*s)	22	4108.48	400.09	0.00
constant	1	4495.61	787.23	0.00

[a] Abbreviations: y = year, d = date, a = clutch age, dd^2 = quadratic season date, aa^2 = quadratic clutch age, ob = observer, trap = trapping. Asterisk (*) indicates effect interactions; otherwise effects are additive.

[b] k = number of parameters in model

[c] The best approximating model has the lowest Akaike's Information Criterion value, adjusted for small sample size (AIC_c), and the highest model weight (w_i), relative to others in the model set.

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Appendix 1. Percent of Pacific common eider nests in each fate category for each site year (1991-2004) on the Yukon-Kuskokwim Delta, Alaska.

Site[a]	Year	*N*[b]	Abandoned	Depredated	Hatched	Non-viable	Flooded	Still Inc.[c]	Abandoned (Human)	Unkn.[d]
KR	1991	12	0.42	0.08	0.50	0	0	0	0	0
KR	1992	17	0.06	0.76	0.18	0	0	0	0	0
KR	1993	13	0.00	0.38	0.54	0	0	0	0.08	0
KR	1994	13	0.23	0.46	0.31	0	0	0	0.00	0
KR	1995	12	0.08	0.08	0.75	0	0	0	0.08	0
KR	1996	29	0.07	0.34	0.59	0	0	0	0	0
KR	1997	17	0.12	0.47	0.41	0	0	0	0	0
KR	1998	31	0.13	0.19	0.58	0	0.06	0.03	0	0
KR	1999	34	0.12	0.41	0.41	0	0.03	0	0.03	0
KR	2000	27	0.19	0.11	0.67	0	0	0	0.04	0
KR	2001	28	0.11	0.82	0.07	0	0	0	0	0
KR	2002	15	0.33	0.13	0.20	0	0	0.33	0	0
KI	1992	94	0.03	0.11	0.83	0	0	0.03	0	0
KI	1993	73	0.04	0.29	0.62	0.01	0	0.04	0	0
KI	1994	82	0.07	0.11	0.78	0.01	0	0.02	0	0
KI	1995	67	0.03	0.21	0.72	0	0	0.01	0.03	0
KI	1996	70	0.07	0.07	0.79	0	0	0.04	0.01	0.01
KI	1997	125	0.13	0.07	0.73	0	0	0.02	0.06	0
KI	1998	77	0.09	0.13	0.70	0	0	0.06	0	0.01
KI	1999	149	0.07	0.23	0.60	0	0	0.08	0.01	0
KI	2000	120	0.08	0.11	0.79	0	0	0.01	0.02	0
KI	2001	108	0.03	0.78	0.16	0	0	0.03	0.01	0
KI	2002	205	0.09	0.22	0.63	0	0	0.01	0.03	0.01
KI	2003	188	0.10	0.51	0.35	0	0	0.02	0.02	0.01
KI	2004	245	0.04	0.22	0.55	0.03	0	0.06	0.07	0.03
TR	1997	92	0.03	0.25	0.67	0	0	0.03	0	0.01
TR	2002	131	0.08	0.37	0.41	0	0	0.12	0.01	0
TR	2003	66	0.02	0.74	0.00	0	0	0.24	0.00	0
TR	2004	145	0.09	0.46	0.35	0	0	0.08	0.02	0

[a] Study sites: KR=Kashunuk River, KI=Kigigak Island, TR=Tutatkoke River.

[b] *N* = number of nests

[c] Still incubating at final visit.

[d] Final fate unknown.

CHAPTER 4. Population dynamics of Pacific common eiders on the Yukon-Kuksokwim Delta, Alaska[4]

Abstract: We synthesized demographic data from Pacific common eiders (*Somateria mollissima v-nigrum*) at three sites on the Yukon-Kuskokwim Delta (YKD) in western Alaska (1991-2004). Our goals were to investigate the primary underlying processes affecting population dynamics, identify critical life-history data gaps, and provide modeling tools for use in developing future eider management strategies. We developed stochastic stage-based matrix population models that incorporated observed spatio-temporal (process) variance and co-variation in vital rates, and projected the stable stage distribution (w) and population growth rate (λ). We used perturbation analyses to examine the relative influence of changes in vital rates on λ, variance decomposition to assess the proportion of variation in λ explained by process variation in each vital rate, and examined transient dynamics to assess the short-term stability of the population. In addition to matrix-based λ, we estimated λ using capture-recapture approaches, and log-linear regression. We found the stable age distribution for Pacific common eiders was weighted heavily towards experienced adult females (5^+ yrs of age), and all calculations of λ indicated that the YKD population was stable to slightly increasing ($\lambda_{\text{matrix}} = 1.02$ (CI: 0.99-1.05), $\lambda_{\text{reverse-capture-recapture}} = 1.05$ (CI: 0.99-1.11), $\lambda_{\text{log-linear}} = 1.04$ (CI: 0.98-1.10)). Perturbation analyses suggested the population would respond most dramatically

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[4] Wilson, H.M., P.L. Flint, J.B. Grand, and A.N. Powell. Population dynamics of Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. Prepared for submission to *The Journal of Wildlife Management.*

to changes in adult female survival (relative influence of adult survival was 2.07 times that of fecundity), while retrospective variation in λ was primarily explained by fecundity parameters (60%); particularly duckling survival (44%). Among components of fecundity, both short and long-term sensitivities were highest for duckling survival, suggesting this vital rate may be important to both immediate and long-term population growth. Short-term (transient) population dynamics appeared relatively stable for Pacific common eiders. Increasing adult survival would have large positive effects on population growth, but practical ways to influence this vital rate are currently limited. Thus, we recommend focusing efforts towards increasing reproduction, with particular emphasis on strategies which could increase both fecundity and survival, such as predator control on breeding grounds.

Introduction

Pacific common eiders breed primarily along the coastal fringe of Alaska and western Canada (Goudie et al. 2000), where surveys have estimated a decline of more than 50% from 1976 to 1996 (Woodby and Divoky 1982, Suydam et al. 2000). Additionally, the local breeding population on the Yukon-Kuskokwim Delta (YKD) in western Alaska appears to have undergone declines estimated at greater than 90% between 1957 and 1992 (Stehn et al. 1993, Hodges et al. 1996). This populations then stabilized at reduced numbers from the early 1990's to the present (Platte and Stehn 2005). During the same period, dramatic population reductions in sympatrically nesting spectacled (*S. fischeri*) and Steller's (*Polysticta stelleri*) eiders on the YKD resulted in their listing as threatened under the Endangered Species Act (Kertell 1991, Federal Register 1993, Stehn et al. 1993, Federal Register 1997). At present, it remains unclear whether common, spectacled, and Steller's eiders have declined due to shared causes or as a result of independent factors, and ambiguity still exists with regard to the magnitude of actual declines.

Information for species of conservation concern is often lacking, yet managers are increasingly asked to make decisions based on minimal demographic data (Heppell et al. 2000). In this context, population models can serve as important tools for prioritizing management actions, learning about the uncertainties and inaccuracies of predictions, and helping to identify information needs (Nichols et al. 1995). However, modeling relies heavily on assumptions, and explicit acknowledgement of departures from assumptions is critical to correctly interpreting results. Because estimates of population growth can be vulnerable to a variety of biases (e.g., all vital rates may not be available for the population of interest, or count-based indices may not consider detection probabilities), management decisions based on inference from multiple models may be more robust than those from a single model alone (Eberhardt 2002, Sandercock and Beissinger 2002). Further, where independent estimates of λ exist, their differences may allow evaluation of previously unknown parameters (Nichols et al. 2000, Peery et al. 2006) or aid in identifying critical areas of future study (Eberhardt 2002). For example, matrix approaches have traditionally been used to characterize the long-term, projected growth of a population based on stage or age-specific vital rates and assuming asymptotic convergence on the stable-stage/age structure (Caswell 2001). However, λ can also be estimated directly, based on observed changes in abundance (i.e., changes in successive population counts; Eberhardt and Simmons 1992) or mark-recapture encounter histories (Pradel 1996, Nichols et al. 2000).

Although these estimates are not expected to be equal, as they encompass very different assumptions, their agreement can serve to validate independent measures of population change (Sandercock and Beissinger 2002). Moreover, contrasting results may provide a better understanding of how components considered in the various models affect overall dynamics of the population in question (Nichols et al. 2000, Doherty et al. 2004, Peery et al. 2006).

Populations are rarely stationary, but instead exist in variable (stochastic) environments (Tuljapurkar 1990). Incorporating such variation is an important component of population modeling, as using simple averages (i.e., deterministic models) can result in overestimation of population performance (Tuljapurkar 1990, Morris and Doak 2002). Moreover, because stochastic population models explicitly include such variation, they also allow examination of relationships between variation in vital rates and variation in λ (i.e, retrospective analyses; Pfister 1998, Caswell 2000, Cooch et al. 2001). In general, λ will be disproportionately influenced by variation in vital rates with the highest sensitivities/elasticities (i.e., prospectively). However, λ also tends to be negatively related to the variance in underlying vital rates (i.e., retrospectively; Pfister 1998, Doak et al. 2005), and thus, increased variance in λ can lead to increased probabilities of extinction (Kendall and Fox 2003). In this sense, methods which evaluate both pro- and retrospective influences on λ provide an important tool for population management, helping to assess how both sensitivities and variation in vital rates might influence population change and/or be shaped by natural selection (Pfister 1998).

The goal of this study was to incorporate the best available estimates of vital rates (and their variances and covariances) of common eiders to examine the primary processes underlying population dynamics of Pacific common eiders on the YKD. In doing so, we hoped to better understand factors that may have led to their historical decline and to provide tools from which guidelines for conservation and management could be drawn. We synthesized 14 years of Pacific common eider demographic data across three study sites on the YKD (1991-2004), and utilized estimates of vital rates and associated spatio-temporal process variance (Wilson et al. 2007*a*; *b*) derived from mark-recapture and nest survival analyses to parameterize our models (Lebreton et al. 1992, Dinsmore et al. 2002). We explicitly incorporated all temporal and geographic variation in vital rate estimates, with sampling error removed and covariance structure retained wherever possible.

The specific objectives of our study were four-fold. First, we defined and developed a basic population model that represented the age/stage structure, life-cycle, and dynamics of Pacific common eiders on the YKD, using the best data available. Second, we used our model to calculate a stable age distribution and examined both the long and short-term population dynamics for YKD Pacific common eiders. Third, we used analytic perturbation to examine the relative influence of potential changes in vital rates to changes in prospective λ, and variance decomposition to examine the contribution of each vital rate to retrospective variation in λ. Fourth, we used mark-recapture and aerial survey data to derive direct estimates of λ, and we compared and contrasted these estimates with those from matrix approaches.

Study area

From 1991-2004, we collected demographic data for Pacific common eiders at three primary breeding sites on the YKD; Kashunuk River (61°20'N, 165°35'W); Tutakoke River (60°51'N, 165°49'W), and Kigigak Island (60°50'N, 165°50'W). Although we cannot say with certainty what proportion of the YKD common eider population was represented by our local demographic studies, we know our research sites represented 3 of the 4 major common eider nesting aggregations known on the YKD (U.S. Fish and Wildlife Service, unpublished data). Importantly, these sites functionally characterized the range of variation in nesting strategies for common eiders across the YKD region. The geographic and floristic characteristics of our study sites have been described in detail by Grand et al. (1997), Sedinger et al. (1998), and Wilson et al. (2007*a*). Because equal attention was not given to all areas of each study site in all years, we present average abundances rather than attempt to calculate densities. The Kashunuk River (KR) study site was several miles inland from the coast and common eiders at this site nested at low abundances (10-15/yr), usually near the banks of the tidally influenced Kashunuk River. The Tutakoke River (TR) study area was at the mouth of the Kashunuk River, and here common eiders nested along the coastal fringe, at medium to high abundances (average: 110 nests), in association with a large dynamic black brant (*Branta bernicla nigricans*) colony (~5000 pairs; Sedinger et al. 1998). The Kigigak Island (KI) study area supported the highest abundance of nesting common eiders (~60-200 nests/yr; U.S. Fish and Wildlife Service and H.M. Wilson 1991-2004, unpublished data). Common eiders at the KI site employed a variety of nesting strategies, including nesting within black brant colonies, small conspecific colonies (e.g., ~15-20 nests on a single lake), as well as solitarily.

Methods

Matrix population modeling

Life-cycle and age/stage structure. We developed a female, stage-based matrix population model in which we structured the common eider life cycle according to 5 age-based stages and a birth-pulse fecundity schedule, beginning with the annual prebreeding census (Fig. 1). The first stage (S_1) in our common eider life cycle represented progeny who were 1^+ yrs-old, but reproductively immature. The second through fifth stages (S_2 - S_{5+}) represented 2, 3, 4, and 5^+ yr-olds, and all had the potential to contribute to the progeny class (S_1) through reproduction. The fifth stage (S_{5+}) was a composite of experienced breeding adults $\geq$ 5 yrs of age. These individuals could remain in the (S_{5+}) stage according to their survival, forming a self-loop. We used a Leslie-style matrix to summarize the demographic data according to stage-specific survival (S_i) and fecundity rates (F_i; Caswell 2001). Matrix element values represented either means drawn directly from specified distributions (as was the case for S_i) or were the product of linear equations of lower-level parameters (as with F_i).

Model parameters. We parameterized our matrix model based on important life history characteristics, defined within a management context (Fig. 1, Table 1). In our matrix models, each age-based stage graduated to the next at each time step (1 yr), and transition probabilities in our model simply represented the probability of survival to the next stage. Because we lacked data on age-specific survival rates, we assumed all birds in adult plumage (S_1 - S_{5+}) experienced a similar adult survival rate. Thus, we used the estimate of adult female apparent survival and associated process variance from previous mark-recapture analysis of Pacific common eiders across the three YKD study areas (1994-2004; Wilson et al. 2007*a*), as our single survival probability for all adult age-stages. We used a stretched beta distribution (Morris and Doak 2002; 2004, Ramula and Lehtilä 2005) to simulate a random distribution of apparent survival rates based on the mean and associated process variance from Wilson et al. (2007*a*).

Fecundity. We defined fecundity as the number of female offspring produced per female that survived to just before their first birthday and calculated this as the linear product of reproductive components for each stage, according to the equation:

$$F_i = CSH_i * NS * SR * BI_i * DS * JS$$

where F_i = stage-specific fecundity, CSH_i = stage specific-clutch sizes at hatch, NS = nest survival, SR = sex ratio of offspring, BI_i = stage-specific breeding incidence (i.e., breeding propensity), DS = duckling survival (hatch to 30 d), and JS = juvenile survival (30 d to just before 1 yr). We used reproductive estimates from Pacific common eiders at our three study locations on the YKD (1991-2004) to populate these parameters (Wilson et al. 2007*b*, Table 1), unless otherwise stated.

We based breeding incidences for 2 and 3 yr-olds on age-specific common eider breeding propensities reported in Baillie and Milne (1982); $BI_2 = 0.26$, $BI_3 = 0.46$, and we considered the probability of breeding as a 4 yr-old to be 0.8, based on annual estimates of non-breeding for common eiders between 2 - 4 yr of age from Coulson (1984). For the 5^+ yr class, we randomly drew from a distribution of 24 annual point estimates of breeding probabilities for 5^+ yr-old common eiders in England (1958-1982; Coulson 1984).

We used 29 site-year estimates of clutch size at hatch (CSH) from the YKD population (accounting for initiation date and partial predation; Wilson et al. 2007*b*: Table 1) to create a string of observed clutch sizes (Appendix 1) from which stochastic inputs were drawn. Annual estimates of the average CSH represented a composite of age-specific clutch sizes. Therefore, we back-calculated age-specific CSHs using the stable stage distribution and the ratio of stage-specific clutch sizes between 2 and 3 yr-old breeders, and 4^+ yr-old breeders, respectively (Baillie and Milne 1982). Using this method, CSH for 2 yr-old breeders was calculated as observed CSH* 0.77, for 3 yr-old breeders as CSH*0.96, and for 4^+ yr-old breeders as observed CSH*1.034 (Appendix 1) Similar to methods for clutch size, we drew from a string of nest survival point estimates derived from 29 site-years of local data to populate the nest survival parameter of our fecundity equation (Wilson et al. 2007*b,* Table 1, Appendix 1). Because no data currently exist on age-specific hatching rates, nest survival rates for all stage classes were drawn from the same data-string. Finally, we assumed that variation in site-year point estimates of clutch size and nest survival followed a random effects model, where some portion of the observed variation among site-years (i.e., fluctuation around the grand site-year mean), was the result of sampling error (White et al. 2001)**.** Operating under this assumption, we applied the methods of White et al. (2001) to shrink individual estimates proportional to their sampling variance, such that the overall mean of the data points had the appropriate process variation (Appendix 1).

We determined sex ratios (SR) based on a subset of nests observed at hatch in which all ducklings could be sexed (*n* = 20 nests, 49:51 male:female; Wilson et al. 2007*b*). Given a near 50:50 sex ratio, we assumed a 0.5 probability of being female in our model. We defined duckling survival as survival from hatch to 30 d of age. In order to use the best local data available to us, we generated a beta distribution of duckling survival centered around 0.19; the mean common eider duckling survival estimate from a single-year study (1997) on the YKD (Flint et al. 1998). We acknowledge that using a single-year's estimate may not have adequately characterized annual fluctuations, and that the 1997 estimate may have been higher or lower than the long-term mean. However, in 1997, population counts and productivity estimates were near the average for the period of our study (Platte and Stehn 2005, Wilson et al. unpublished data), suggesting it was not an unusual year (at least by other metrics) for the YKD population. That said, annual common eider duckling survival has been shown to vary dramatically elsewhere (Mendenhall and Milne 1985, Mawhinney 1999), and we sought to incorporate a measure of such temporal variance in our estimates of common eider duckling survival on the YKD. Thus, we bounded our beta distribution using our best estimate of naïve process variance in duckling survival calculated from a 13-yr study of common eiders in Scotland (0.02; Mendenhall and Milne 1985) following the methods of Burhnam et al. (1987) and White et al. (2001). We calculated this estimate of variance assuming there was no sampling variance, as no estimates of sampling error were provided in the literature (Mendenhall and Milne 1985). Further, we assumed that the naïve estimate of process variance calculated from this study adequately characterized the variance in YKD duckling survival rates.

We defined juvenile survival (JS) as the period from 30 d post hatch to just before the 1st birthday (31-364 d). Because we did not have estimates of juvenile survival from the YKD, we took two distinct approaches to calculating this parameter. Under scenario 1, we set λ equal 1 and iteratively solved for JS (see Flint et al. 2006). Herein, we made the assumption of population stability, based on lack of a significant trend in λ from aerial surveys over the period of our study (1991-2004; Platte and Stehn 2005). Under scenario 2, we calculated JS as equal to adult survival over an 11 m period (i.e., from 30 d to 1 yr) according to the equation

$$JS = ((S_A)^{1/12})^{11}.$$

We assumed this value was constant (for lack of juvenile survival estimates from any population) and used it as a deterministic value in our matrix modeling.

Modeling environmental stochasticity. Vital rates vary across time and space, and λ is intrinsically linked to this variance (Tuljapurkar 1990). Thus, we drew each lower-level vital rate, which was not considered deterministic, from distributions based on our own data (Table 1), or in the case of duckling survival, the distribution bound by estimates of variability from Mendenhall and Milne (1985). We then created new matrix element values for each of our 1000 stochastic simulations. For example, at each simulation, we randomly drew one nest survival estimate from the set, incorporated it into the stage-specific fecundity equation, and created a new matrix using the updated fecundity estimate.

New matrices were then multiplied by the stage-specific population size vector at each time-step of the model. We employed one of three distributions for each vital rate: 1) deterministic, 2) beta, or 3) observed/discontinuous (Table 1). Deterministic values represented average parameter estimates with no associated variances or ranges. Beta distributions were composed of a probability density function for the vital rate of interest, built upon the observed or specified mean and variance (Morris and Doak 2002). In general, the beta distribution is useful for binomial variables, such as survival, due to its flexibility in possible shapes and bounding between 0 and 1 (Burnham et al. 1987, Kaye and Pyke 2003). We used the 'stretched beta' in our model (Morris and Doak 2002, Ramula and Lehtilä 2005), which allowed us to rescale the distribution to lie between biologically realistic minimum-maximum parameter values (Morris and Doak 2002). Observed/discontinuous distributions were comprised of sets of observed vital rate estimates for each of our site-years (Stochastic; Table 1, Appendix 1). We randomly drew an observed value from these observed/discontinuous pool of estimates with equal probability at each time step (Kaye and Pyke 2003, Appendix 1) and maintained covariance structure by drawing estimates from within the same site-year (where such estimates existed; Appendix 1). We set our initial population size (*N*) to 1880 individuals, (based on the most recent population indices of Pacific common eiders on the YKD; Platte and Stehn 2005) and conducted 1000 stochastic simulations, projecting for 100 years into the future. We calculated $\hat{\lambda}_i$ from each of our 1000 simulations according to the Heyde and Cohen (1985) equation,

$$\hat{\lambda}_i = e^{\left(\frac{\ln N_{ti} - \ln N_{1i}}{t-1}\right)}.$$

We then calculated $\bar{\hat{\lambda}}_i$ and constructed 95% confidence intervals based on the 2.5 and 97.5 quantiles of the sorted $\hat{\lambda}_i$. We performed all stochastic modeling with AVESMODELER (AvesModeler, Version 0.9, 2005, <http://www.ag.auburn.edu/aux/alcfwru/avsmdl/>), utilizing runtime components in MATLAB (Matlab 2001).

Covariation among vital rates. We did not have measures of all vital rates within the same site-years; where we did have such measures, we incorporated correlated vital rates into our stochastic simulations by randomly selecting vital rate estimates grouped by the same site-year. For example, clutch size and nest survival estimates from the same site-year were paired within our random sampling, thus preserving site-year covariance structure. We did not examine correlations between matrix elements (e.g., survival and fecundity), or between adult survival and any underlying components of fecundity (i.e., lower-level vital rates), as there was no support for spatial or temporal variation in adult survival based on previous analyses (Wilson et al. 2007*a*).

Perturbation analysis. We conducted analytic sensitivity and elasticity analyses to examine the relative influence of changes in vital rates to potential changes in population growth (Caswell 2001). Sensitivities and elasticities provide decomposition of the population growth rate into contributions made by matrix elements, such as fecundity and survival, as well as the lower-level vital rates (i.e., clutch size at hatch, nesting success, etc.). While sensitivities provide quantification of absolute change in λ based on absolute change in matrix elements, elasticities quantify the proportional change in λ resulting from proportional changes in matrix elements (Caswell 2001). We calculated analytical sensitivities

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

according to Caswell (2001), where a_{ij} represented matrix elements (i.e., survival and fecundity), and calculated elasticities for stochastic models using a modification of the Heyde and Cohen (1985) equation,

$$e_{ij} = \sum_{k=1}^{n} \frac{\left(\frac{\lambda_k - \lambda_k^*}{\lambda}\right)\left(\frac{1}{p}\right)}{n}$$

where λ_k is the average growth rate, λ^*_k is the average growth rate with the a_{ij} multiplied by p (a small proportionate change in the a_{ij}), and n is the number of model iterations.

Variance decomposition. Where prospective perturbation analysis examines the potential effects of changes in vital rates to changes in λ, variance decomposition (or retrospective analysis; Caswell 2000, Cooch et al. 2001) addresses how variability in λ may have been attributed to variability in each of the vital rates. This is an important distinction, as vital rates with high sensitivity may be very different from those that make the largest contributions to variability in population growth (Pfister 1998, Gaillard et al. 1998, Cooch et al. 2001). We decomposed the variation in λ according to contributions by each vital rate by weighting the elasticities of each lower level parameter by its corresponding coefficient of process variance. We did so, following the equation:

$$\text{Variance component}_i = \text{CV}_i * e_i$$

(Steen and Erikstad 1996, Pfister 1998, Tombre et al. 1998), where CV_i was the coefficient of process variation for parameter i and e_i was the elasticity of parameter i with respect to λ. Herein, we calculated the CV for each demographic parameter by dividing the square-root of its process variance by the corresponding mean parameter value

$$\mathrm{CV}_i = \frac{\sqrt{\sigma_i^{\ 2}}}{\bar{x}_i}.$$

We did this only for those parameters for which we had some measure of process variance (i.e., clutch size, nest survival, duckling survival, and adult survival; Wilson et al. 2007*a*;*b*), and we compared these variance components only relative to one another.

Transient dynamics. Because asymptotic assumptions may not be appropriate for describing the short-term dynamics of a population strongly subject to perturbation (Fox and Gurevitch 2000), we examined the transient dynamics (the dynamics of populations with unstable age/stage distributions en route to asymptotic dynamics; Caswell 2001, Koons et al. 2005) in addition to long-term projections. Herein, we calculated the rate of convergence to the stable population structure (i.e., the damping ratio; ρ), the maximum time to convergence towards the stable-stage distribution (τ), and the maximum reactivity of the population matrix to perturbations of the stable stage distribution (R). We created an artificial perturbation of the system by removing 10 individuals from each of the stage classes for one year, and then examined the changes in short-term vital rate sensitivities following this perturbation (Yearsley 2004).

Reverse capture-recapture approaches

In order to maximize our understanding of Pacific common eider population dynamics, we examined λ using multiple methods. In addition to matrix modeling (which calculates a convergent, long-term λ, assuming a stable stage/age distribution), we estimated λ using reverse capture-recapture techniques (Pradel 1996, Nichols et al. 2000; 2002) in Program MARK (White and Burnham 1999). This approach provided estimates of λ without the asymptotic assumptions that generally plague matrix methods, and instead relied on observed mark-recapture encounter histories. In our case, reverse capture-recapture (CR) utilized Cormack-Jolly-Seber models (i.e., the probability that an individual present at time *t* will survival and be caught at time *t* + 1), but interpreted the encounter histories in reverse (Pradel 1996). Thus, it estimated the probability that an individual caught at time *t* + 1 was present in the population at time t. Pradel (1996) termed these probabilities 'seniorities' (γ) and described them as representing the resident fraction of the population. Because of their inherent relationships, apparent survival (φ), encounter (p), and seniority (γ) probabilities can be used to directly estimate population growth rates,

$$\lambda_{reverse-CR} = \frac{\phi_t}{\gamma_{t+1}}$$

as well as recruitment (*f*),

$$f_t = \phi_t \left(\frac{1-\gamma_{t+1}}{\gamma_{t+1}} \right)$$

(Pradel 1996). We estimated γ, $\lambda_{\text{reverse-CR}}$, and *f,* with φ and p fixed to the best approximating model structure from earlier CJS analysis ($\{\varphi.$ and $p_{g*t}\}$; Wilson et al.

2007*a*). Because seniority models utilize the encounter probability of marked animals, but make inference to the population of marked and unmarked animals, their robustness is conditional on equal encounter probabilities among marked and unmarked individuals (e.g., no trap response). Thus, we tested for differences in encounter probabilities between animals captured in $t + 1$ that were encountered or not encountered on the previous occasion (t), conditional on presence at both occasions, using the two-tailed goodness of fit (GOF) test2.CT in U-CARE (Pradel 2003, Mehl 2004, Choquet et al. 2005). Finally, the variance inflation factor ($\hat{c}$) for the CJS analysis in Wilson et al. (2007*a*) was 1.19, but we assumed $\hat{c} = 1$ in our Pradel Seniority model, as CJS estimates of $\hat{c}$ have been considered inappropriate for this method (White and Burnham 1999, Franklin 2001).

Log-linear λ

Because estimates of λ based on measuring vital rates in the field can be vulnerable to a variety of biases, we were interested in obtaining an independent estimate of λ based solely on observed changes in successive population indices (in our case, from aerial surveys; Platte and Stehn 2005). Here we sought to compare count-based estimates with those from models based on vital rates, in an effort to better assess population dynamics (Eberhardt 2002). In its simplest form, λ can be estimated directly from count-based indices, as the ratio of population sizes (N) from one time step (t) to the next (t+1):

$$\lambda = \frac{N_{t+1}}{N_t}.$$

assuming that detection probabilities and other observer effects remained constant through time. Thus, we utilized data from a sequence of population indices for Pacific common eiders on the YKD over the years of our field study (1991-2004: Platte and Stehn 2005), and estimated average λ using log-linear regression (Eberhardt and Simmons 1992)

$$\log N_t = \log N_0 + t \log \lambda$$

where log λ = e^r, and r is the intrinsic rate of increase. Here the dependent variable was the natural logarithm of the trend index and the independent variable was time (yr). This method assumes that measurements of population size are taken at the same time each year and that errors in population counts are multiplicative and log-normally distributed (Eberhardt and Simmons 1992).

Results

Matrix approaches

Under the assumption that there was no overall trend in population size (i.e., λ fixed at 1.0), we estimated juvenile survival (30 d to 1 yr) to be 0.71. Under this scenario, summary matrix fecundity values for YKD common eiders were $F_1 = 0$, $F_2 = 0.035$, $F_3 = 0.078$, $F_4 = 0.137$, and $F_{5+} = 0.137$, and all transition probabilities (S_A) were 0.892. Vectors (i.e., proportion of birds in each class) for the stable age-stage distribution (w), and relative reproductive values among classes (v) under this scenario were

$$w = \begin{bmatrix} 0.11 \\ 0.10 \\ 0.08 \\ 0.08 \\ 0.63 \end{bmatrix} \qquad v = \begin{bmatrix} 0.17 \\ 0.19 \\ 0.21 \\ 0.22 \\ 0.22 \end{bmatrix}.$$

Second, under the assumption that juvenile survival was equal to adult survival over an 11-m period $(((S_A)^{1/12})^{11}) = 0.90$, we estimated summary matrix element values for YKD common eiders to be $F_1 = 0$, $F_2 = 0.044$, $F_3 = 0.096$, $F_4 = 0.169$, and $F_5+ = 0.169$, and all transition probabilities (S_A) were 0.892, with $\lambda = 1.0194$ (CI: 0.99-1.05). Under this scenario, the vectors for the stable age-stage distribution (w) and relative reproductive values among classes (v) were

$$w = \begin{bmatrix} 0.13 \\ 0.11 \\ 0.09 \\ 0.08 \\ 0.59 \end{bmatrix} \qquad v = \begin{bmatrix} 0.17 \\ 0.19 \\ 0.21 \\ 0.22 \\ 0.22 \end{bmatrix}.$$

Overall, scenario 2 resulted in a 4% increase in the proportion of individuals in the 1 to 4 year-old age-stage classes, while the proportion in the 5^+yr-old class decreased by the same quantity. There were no differences between the distribution of reproductive values between the two scenarios. In general, we found that differences between the two scenarios of juvenile survival resulted in only a small (0.02) change in estimated λ and parameter rankings based on analytic sensitivities and elasticities were similar between the two methods (Fig. 2).

Our rankings of vital rate analytic sensitivities and elasticities demonstrated an overwhelmingly similar pattern; λ was always most sensitive to adult survival in the 5^+ (experienced breeder) stage-class (Fig. 2), regardless of the scenario for juvenile survival. In a prospective sense, λ was much less sensitive to age-specific lower-level reproductive parameters, particularly clutch size, juvenile survival, and breeding incidence of younger age classes (2-4 yr-olds; Fig. 2), than to adult survival. However, sensitivity to duckling survival appeared relatively high (Fig. 2). On average, adult survival had more than double 2.07 times) the relative influence on prospective population growth rate that did fecundity. Further, despite its very low process variance, adult survival contributed to a relatively large portion of retrospective fluctuations in λ (40%), primarily due to its high elasticity. Although these results are somewhat intuitive, given > 60% of the individuals are in the 5^+ stage-class and only about 10% are in any younger stage, retrospective analyses demonstrated contrasting points of emphasis. Retrospective variation in λ was primarily explained by variation in components of fecundity (60%). Of the lower level components of fecundity we included, duckling survival accounted for 44% of the variation in λ, nest survival accounted for 13%, and clutch size at hatch accounted for 3%.

Transient dynamics

We found the maximum reactivity to perturbations of the stable stage distribution (R) was 0.25, the damping ratio (ρ) 2.58, and the approximate time until convergence on the stable stage distribution (τ) 7.28 yrs. The predicted period of oscillation before reaching stable structure was short (2 to 4.78 yrs) and predicted time to convergence (10.69 yrs) was similar to estimated generation time (11.37 yrs). Short-term (transient) sensitivities and elasticities were similar to those estimated under long-term dynamics and did not appear to undergo substantial change in the first 10 years following perturbation (average change from asymptotic sensitivites was 0.01); adult survival had the largest relative effect (1.01), followed by duckling survival (0.59) and nest survival (0.20), with very low sensitivities for all other fecundity components (< 0.17).

Reverse-capture recapture

Using reverse-capture-recapture techniques, encounter probabilities were assessed to be equal between previously marked and unmarked animals captured in t+1 (X^2 = -1.34, P = 0.18), suggesting no trap-dependent behavior among female Pacific common eiders. Our estimate of realized λ from reverse capture-recapture methods was 1.05 (CI: 0.99-1.11), γ was 0.84 (CI: 0.79-0.89), and f was 0.16 (CI: 0.12-0.23).

Log-linear regression

Our estimate of annual population growth based on log-linear regression of indices from aerial population surveys (1991-2004; Platte and Stehn 2005) was 1.039 (CI: 0.98-1.10).

Discussion

Our data and subsequent population model for YKD Pacific common eiders were consistent with the predictions of life history theory for long-lived species (Sæther and Baake 2000, Eberhardt 2002); Pacific common eiders on the YKD were characterized by high, relatively invariant adult survival (Wilson et al. 2007*a*), and low, variable fecundity (Wilson et al. 2007*b*). Perturbation analysis revealed that the YKD population would respond most dramatically to changes in adult female survival, while the greatest proportion of historical variation in λ was due to variability in components of fecundity (e.g., Cooch et al. 2001), primarily duckling survival. However, we likely underestimated the variance in λ associated with variation in fecundity, as not all fecundity components were included in our retrospective analysis. Further, our finding of high sensitivity of λ to duckling survival (relative to other fecundity parameters), suggested this vital rate may be important in altering λ (Hoekman et al. 2006, Hario and Rintala 2006), and at current rates, could be serving as a bottleneck to population growth (Hoekman et al. 2006).

Overall, the potential effect of changes in vital rates on short-term (transient) population dynamics appeared to be minimal for Pacific common eiders. Our population had a single, dominant eigenvalue (1.02) relative to other values (i.e., $\text{eigenvalue}_2 = 0.10$ and $\text{eigenvalue}_3 = -0.33$), and this, in addition to the short predicted period of oscillation before reaching stable stage structure (2-5 yrs), indicated the general insensitivity of the YKD population to perturbations of the stage-structure (i.e., lack of imprimitivity; Caswell 2001). In general, short-term (transient) sensitivities were similar to those indicated for long-term population dynamics, where λ was most sensitive to adult survival. However, the short-term sensitivity to duckling survival was much higher than for other fecundity components, suggesting immediate management actions aimed at increasing this vital rate may be useful in enhancing short-term population growth.

Although, demographic parameters should ideally be derived directly from long-term, multi-location studies of the population of interest, management decisions and other conservation efforts are often forced to proceed without such data (Heppell et al. 2000). Most parameter estimates in our study were derived from local data and incorporated spatial and temporal variability, but some were based on long-term data sets of common eiders elsewhere (Baillie and Milne 1982, Coulson 1984, Mendenhall and Milne 1985). We acknowledge that by using substituted estimates we may not have accurately characterized the YKD population, and thus, inference at the local scale may have been compromised. However, all substituted parameters in our study had inherently low elasticities, and, thus, little effect on the conclusions of perturbation and variance decomposition analyses. For example, resulting differences in analytic sensitivites and elasticities between our two scenarios of juvenile survival were small, suggesting that our overall model was robust to potential violations of assumptions relative to this vital rate. Further, our estimates of λ from stage-structured models (which utilized substituted data) were not appreciably different from λs estimated from trend data (see also Sandercock and Beissinger 2002), indicating that substituted parameters either did a relatively good job of characterizing the population of interest, or were not important enough to overall dynamics to dramatically alter estimated rates of growth (Eberhardt 2002).

In general, our results agree with the predictions of stochastic population dynamics, in that the variable to which λ was most sensitive (i.e. adult survival) also had the least process variance (Pfister 1998, Heppell et al. 2000, Doherty et al. 2004, Morris and Doak 2004). Theory predicts that traits closely linked to fitness will demonstrate little heritable variation (Falconer and Mackay 1996), and some have suggested that the inverse relationship between the sensitivity or elasticity of a given vital rate and its natural variation may be a form of 'buffering' against environmental stochasticity (i.e. canalization; Stearns and Kawecki 1994, Pfister 1998, Morris and Doak 2004). Although we were unable to directly test such hypotheses with our data, we did make comparisons based on lower-level vital rates, corrected for sampling variation (Morris and Doak 2004). Thus, we were able to circumvent issues of inequality and inappropriate comparisons among matrix elements (e.g., bounded vs. unbounded elements; Doherty et al. 2004, Morris and Doak 2004), and overall, our results suggest that adult survival is likely the most important fitness component for Pacific common eiders.

Our multifaceted approach to examining population growth in Pacific common eiders allowed us to compare and contrast several measures of λ, rather than rely on inference from a single estimate alone. Others have suggested that it is important to consider estimates from both reproductive and survival information, as well as direct measures of population change, given potential biases and error in collection of both types of data (Eberhardt 2002, Sandercock and Beissinger 2002). In our case, the mean estimate of λ_{matrix} predicted an average increase of 2% per year, while $\lambda_{\text{reverse-CR}}$ and $\lambda_{\text{log-linear}}$ predicted growth rates 2 to 3 percentage points higher than λ_{matrix}. Although our levels of precision in these estimates precluded in-depth interpretation, the pattern of higher $\lambda_{\text{realized}}$ than λ_{matrix} appears consistent with several recent studies (Schmutz et al. 1997, Doherty et al. 2004, Peery et al. 2006). Following the logic of Hines and Nichols (2002), λ_{matrix} is predicted to be consistently lower than $\lambda_{\text{reverse-CR}}$ or $\lambda_{\text{log-linear}}$ due to asymmetry in movement; matrix approaches consider emigration, incorporated in apparent survival rates, but not immigration (Nichols et al. 2000, Peery et al. 2006). Thus, differences among estimates (~3% in our case) could represent the relative contribution of immigration to population growth (Nichols et al. 2000, Peery et al. 2006).

At the broader level, our disparate measures of population change converged on a similar conclusion: the YKD Pacific common eider population appeared to be stable to slightly increasing from 1991 to 2004. However, we do not know what precipitated the population decline from the 1950's to the early 1990's. Based on a log-linear model, the

85-96% population decline (observed from 1955 to 1992; Stehn et al. 1993) would have resulted from an annual reduction of 5 to 7% per year (i.e., $\lambda = 0.93$-0.95). Thus, relative to a model where $\lambda = 1$, the observed long-term decline could have been produced by either a 60-65% reduction in fecundity (in each age class) or a 4-6% reduction in adult survival (based on our model). However, we suggest that a consistent 60-65% reduction in fecundity is unrealistic (particularly if one considers data from recent years), and we conclude that the observed decline was at least partially attributable to reductions in adult survival. Although current estimates indicate very little variation exists in adult survival, it would not require many animals dying (from anthropogenic or other causes) to reduce annual survival by several percent. Further, we estimate that even a 1-2 % increase in adult mortality, combined with a 10-20% decrease in fecundity, could have led to a decline similar to that observed from the 1950's to the 1990's. This suggests that very small increases in adult survival, combined with increases in fecundity (within the range of variation in our data), could lead to recovery of YKD Pacific common eiders to historical levels.

At present, we can only speculate as to what factors (or combination of factors) may have led to the historical decline. Nevertheless, we provide several hypotheses for future study based on our results. First, given the strong influence of adult survival on prospective population growth (the elasticity of adult survival was 2.07 times that of fecundity), factors having the potential to act as additive sources of mortality, such as spring subsistence harvest, marine pollution, or disease, would be predicted to have large negative effects on λ. That said, current estimates of common eider subsistence harvest on the YKD appear relatively low (Wentworth 2004), and there is little industrial development of marine wintering areas used by these birds (Petersen and Flint 2002); although factors such as changes in sea ice (Petersen and Douglas 2004) and marine benthic communities (Grebmeier et al. 2006) may be important.

Changes in emigration and immigration may have also affected historical counts of eiders on the YKD, although this type of change would not be expected to be large, given generally high breeding-site fidelity documented for female common eiders elsewhere (Bustnes and Erikstad 1993, Goudie et al. 2000). Our reverse-capture analysis indicated that the contribution of survivors to the Yukon Delta population of breeding females (γ) was high (84%) and could be considered ~3.24 times more important to λ than the addition of new recruits, further supporting the importance of adult survival. However, the estimated contribution of recruits (16%; including *in situ* recruits and immigrants) from this analysis was much larger than we previously considered. Thus, in combination with potential movement-related differences between projected and realized estimates of λ, these results suggest that immigration (both from movement and recruitment of young) may play an important, and perhaps previously underrepresented, role in the population dynamics of YKD Pacific common eiders (Lindberg et al. 1998, Nichols et al. 2000, Alisauskus et al. 2004, Mehl 2004, Peery et al. 2006). However, future work will be required to quantify the respective contributions of *in situ* recruitment and immigration to λ, and identify putative "source" populations from which emigration could be occuring.

Our results demonstrate that variation in duckling survival may be important to both short and long-term population growth. High duckling mortality is a common occurrence in eiders (Mendenhall and Milne 1985, Mawhinney 1999), and could potentially limit population numbers through low annual recruitment over a series of years, as has been found for common eiders in the Baltic Sea (Hario and Rintala 2006). The high prospective sensitivity and retrospective importance of duckling survival in our study indicated its potential as an important factor in the dynamics of Pacific common eiders. However, more data will be necessary to better characterize process variance in this vital rate for the YKD population.

Finally, we caution that managing a population based on model-generated priorities alone does not address the practical ability to change parameters (Mills et al. 1999), and managers must balance these two components when developing conservation strategies. Our modeling demonstrated that population growth of YKD Pacific common eiders is most sensitive to changes in adult survival, and, thus, mortality pressures on adults, such as hunting and marine pollution, are expected to have larger relative impacts on population dynamics than similar changes in reproductive parameters. However, current reported hunting pressure for YKD Pacific common eiders is minimal (Wentworth 2004), and managing for at-sea mortality factors (i.e., Bering Sea wintering conditions), is likely unfeasible. Although we hypothesize that restricting harvest would likely increase adult survival, such a strategy would be difficult to implement, and perhaps unnecessary, particularly if stability, rather than growth is the management goal. This study suggests that long-term management should consider ways to increase adult survival. However, we hope to emphasize that immediate actions may be better focused on traits with lower elasticities and greater management potential, such as components of fecundity.

Management Implications

The importance of adult survival to λ emphasizes the need for long-term management efforts that carefully monitor and attempt to reduce adult mortality for Pacific common eiders throughout the annual cycle. We hypothesize that spring harvest is likely an additive source of mortality for YKD Pacific common eiders. However, precise measures of local harvest and estimates of how harvest and other hypothesized mortality factors relate to the local breeding population are currently missing. Thus, options to affect adult mortality may be limited. Alternatively, we suggest that immediate management strategies focus on traits that may have lower elasticities, but higher management potential, such as components of fecundity (particularly duckling survival), while striving to increase adult survival wherever possible. Specifically, we advocate management actions such as periodic predator control on breeding grounds, which we hypothesize would simultaneously influence means and variances of both fecundity and adult survival, in addition to potentially benefiting other sympatrically nesting species.

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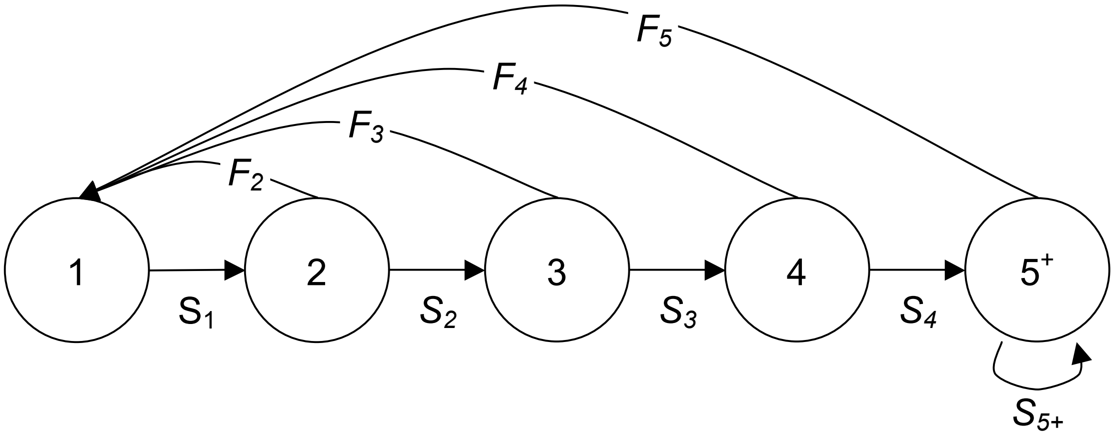

$$\begin{vmatrix} 0 & F_2 & F_3 & F_4 & F_{5+} \\ S_1 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & S_4 & S_{5+} \end{vmatrix}$$

Figure 1. The life-cycle and corresponding stage-classified matrix for a population model of female Pacific common eiders (1991-2004) on the Yukon-Kuskokwim Delta (YKD), Alaska, USA, where stage 1 = reproductively immature progeny, stages 2-5 = reproductive adults, fecundity transitions (F_i) = stage-specific reproductive contribution, and survival transitions (S_i) = apparent annual survival probability for adult females.

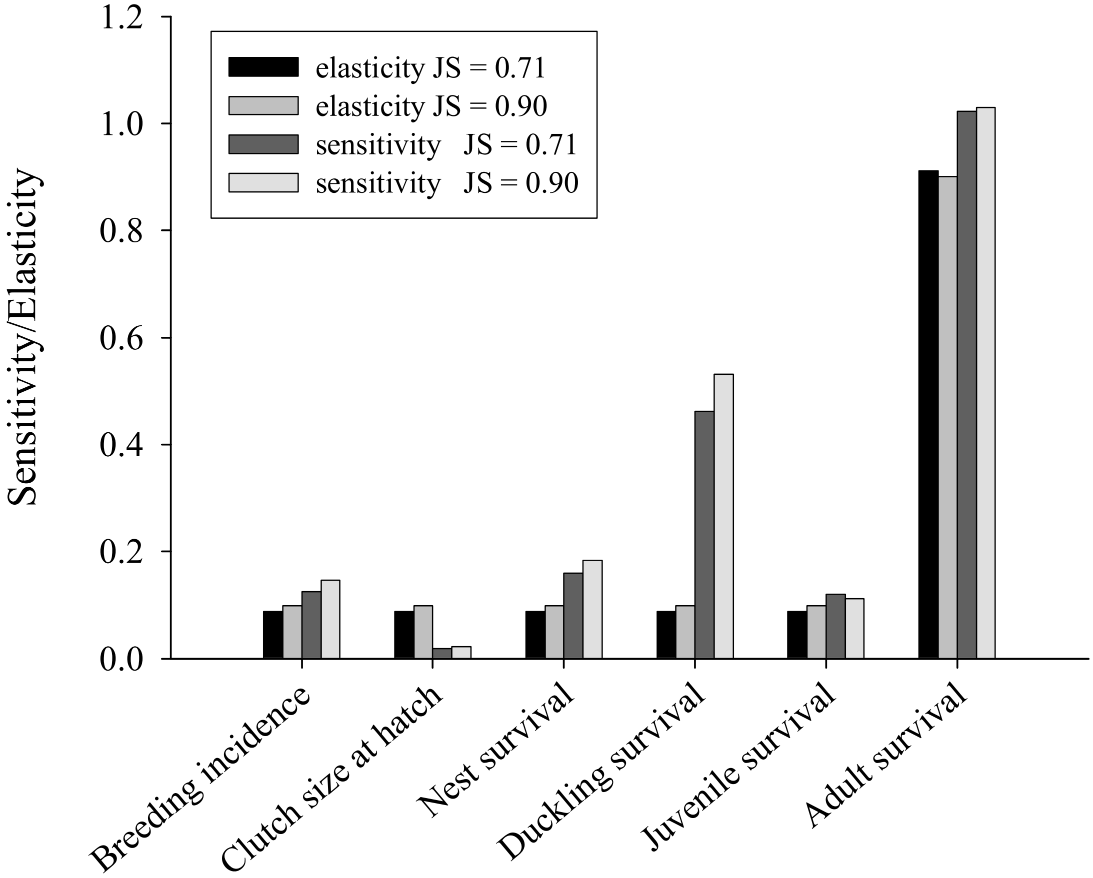

Figure 2. Sensitivity and elasticity of annual population growth rate, associated with stage-specific vital rates for Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska (1991-2004), under two scenarios for juvenile survival (JS). Scenario #1: JS solved to be 0.71 under the assumption that $\lambda = 1$, and scenario #2: JS = $((\text{Adult survival})^{1/12})^{11} = 0.90$.

Table 1. Simulation types, mean values, process variance (σ^2), and ranges for and sample size for parameters used in a stochastic population model of female Pacific common eiders (1991-2004) on the Yukon-Kuskokwim Delta (YKD), Alaska, USA.

Parameter	Simulation type[a]	Stage[b]	Mean	σ^2	Range
Clutch size at hatch	Stochastic	2 y[c]	3.61	0.07	(2.85–4.09)
		3 y[c]	4.50	0.07	(3.55–5.10)
		4–5^+ y	4.85	0.07	(3.82–5.49)
Nest survival	Stochastic	2-4 y	0.55	0.02	(0.06–0.92)
Duckling survival[d]	Beta	2-4 y	0.19	0.02	(0.01–0.55)
Breeding incidence[c,e]	Deterministic[c]	2 y	0.26	-	-
	Deterministic[c]	3 y	0.46	-	-
	Stochastic[e]	4,5^+ y	0.78	0.03	(0.35–1.00)
Juvenile survival	Deterministic	2-5^+ y	0.90	-	-
Adult survival	Beta	2-5^+ y	0.89	0.005	(0.77–1.00)

[a] Stochastic simulations draw randomly from pools of annual point estimates across site-years of demographic data. Beta simulations draw simulated estimates from a beta distribution built from the observed mean, σ^2, and range for the parameter of interest. Deterministic simulations draw only from observed means and incorporate no variability.

[b] Stages represent age-based classes. The 2–5^+ year-old class represents where a similar estimate was used for all classes of breeding adults.

[c] Estimates from Baillie and Milne (1982).

[d] Estimate of the mean from Flint et al. (1998). Variance and range from Mendenhall & Milne (1985); 1961-1973.

[e] Estimates from Coulson (1984).

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Appendix 1. Adjusted[1] mean input values for each site-year of a stochastic population model of female Pacific common eiders at Kashunuk River (KR), Kigigak Island (KI), and Tutakoke River (TR) study sites on the Yukon-Kuskokwim Delta (YKD), Alaska, USA. (CSH_i) = Age-specific clutch size at hatch.

Year	Site	CSH_2	CSH_3	$CSH_{4,5}$	Nest survival
1991	KR	3.9	4.9	5.2	0.56
1992	KR	3.2	4.0	4.3	0.53
	KI	4.1	5.1	5.5	0.78
1993	KR	3.5	4.4	4.7	0.55
	KI	3.5	4.4	4.8	0.48
1994	KR	3.6	4.4	4.8	0.54
	KI	3.9	4.9	5.3	0.63
1995	KR	3.7	4.6	5.0	0.78
	KI	3.9	4.9	5.2	0.54
1996	KR	3.8	4.7	5.1	0.61
	KI	3.9	4.9	5.3	0.67
1997	KR	3.4	4.2	4.5	0.55
	KI	3.9	4.8	5.2	0.60
	TR	3.7	4.6	5.0	0.58
1998	KR	3.6	4.5	4.8	0.58
	KI	4.0	5.0	5.4	0.62
1999	KR	3.7	4.6	4.9	0.56
	KI	3.7	4.6	4.9	0.54
2000	KR	3.6	4.5	4.9	0.59
	KI	4.1	5.1	5.5	0.67
2001	KR	2.8	3.5	3.8	0.52
	KI	3.5	4.3	4.7	0.10
2002	KR	3.6	4.5	4.9	0.57
	KI	3.8	4.8	5.1	0.57
	TR	3.1	3.9	4.2	0.53
2003	KI	3.1	3.9	4.2	0.36
	TR	*	*	*	0.36
2004	KI	3.6	4.5	4.9	0.51
	TR	3.2	4.0	4.4	0.49

[1] Raw estimates were adjusted according to the methods of White et al. (2001), assuming variation in site-year point estimates followed a random effects model. Herein, individual estimates were 'shrunk'proportional to their sampling variance, such that the overall mean of the data points had the appropriate process variation.

General Conclusions

Although it is impossible to know what precipitated the dramatic decline of eiders from the 1950's to the early 1990's, understanding factors currently influencing population growth (and its component vital rates) can aid in predicting future population response to ecological change (Berryman 2002) and help guide management actions. In agreement with life-history predictions for long-lived species, I found Pacific common eiders to have high, relatively invariant adult survival, and low, variable productivity. Further, adult survival appeared to be the most influential parameter in terms of prospective population growth, while variation in fecundity parameters tended to drive variation in retrospective growth. Throughout the dissertation, my results reinforce the utility of life-history predictions for long-lived species, but also consider the feasibility and efficacy of management actions prioritized by models, relative to the population in question.

Chapter 1 highlighted the paradox between one parameter's (survival of adult females) expected importance in terms of prospective population growth (i.e., high sensitivity) and limited options for practical management (Gaillard et al. 1998). Further, in Chapter 1 and throughout the dissertation, I provided estimates of process variance in vital rates (i.e., accounting for sampling variance). This constitutes an important contribution towards correctly quantifying spatio-temporal variability in parameters, and is critical to reducing potential negative bias in stochastic population models (Gould and Nichols 1998, White et al. 2002).

In Chapter 2, I highlighted the high degree of spatio-temporal variability in blood lead and selenium concentrations in nesting common eiders and compared differences in exposure patterns between sympatrically nesting eider species on the YKD (spectacled and common). In general, common eiders tended to have low lead exposure rates, but very high exposure to selenium. Typical concentrations of selenium in nesting common eiders were equivalent to those associated with death in captive waterfowl, yet no outward signs of selenium toxicity were observed. I found evidence that blood selenium was positively related to the probability of non-viable eggs occurring in a clutch, indicating a potential demographic cost. However, selenium-related reductions to clutch size were predicted to be small at the concentrations observed, and overall exposure to lead and selenium did not appear to be a threat to population growth. I concluded that interspecific differences in contaminant burdens and exposure risks were likely the result of distinct reproductive strategies (e.g., spectacled eiders feed on breeding grounds and spend more time in areas with available lead), emphasizing the importance of understanding individual species' ecology when assessing population-level toxicological effects and developing management strategies.

In Chapter 3, I examined within and among-individual variation in components of productivity and related findings to life history theory and implications for management. Pacific common eiders on the YKD exhibited considerable variability in all components of productivity, including high levels of within- and among-year variation in timing of nesting, clutch size, and nest survival. Overall, strong seasonal declines in clutch size and nest survival demonstrated that females breeding in the early and mid parts of the season had larger clutch sizes and a higher probability of hatching success than late nesters. Although these results suggest directional selection for early nesting, I found no evidence for a long-term shift towards earlier nesting in the population. I hypothesize that strong environmental variation could be masking such a response (Larsson et al. 1998, Kruuk et al. 2002), or that corresponding counter-selection may be acting against very early breeding via reductions in other fitness components (e.g., lower annual survival in the earliest breeders; Blums et al. 2005). Finally, I hypothesize that nest fates of common eiders are closely tied to those of sympatrically nesting species (Raveling 1989), and management actions targeted at other species (e.g., those which facilitate predator swamping), are likely to have positive, concurrent effects on nesting common eiders.

Lastly, in Chapter 4, I incorporated the best available information on vital rates for common eiders and their variances and covariances to examine the primary processes underlying population dynamics of Pacific common eiders on the YKD. Here I viewed population modeling as a tool for: 1) providing critical information for management, 2) learning from the uncertainties and inaccuracies of predictions, and 3) identifying future information needs (Nichols et al. 1995). Because modeling relies on many assumptions, I tried to explicitly acknowledge all assumptions and associated departures throughout the chapter. For example, most parameter estimates in my study were derived from local data, but a few were based on comparable, long-term data sets from breeding common eiders elsewhere (Baillie and Milne 1982, Coulson 1984, Mendenhall and Milne 1985). Because substituted estimates may not have accurately characterized the YKD population, inference at the local scale may have been compromised. However, I point out that all substituted parameters had inherently low elasticities, and, thus, little effect on conclusions of perturbation and variance decomposition analyses.

Overall, the results in Chapter 4 were consistent with life history predictions for common eiders and other long-lived species (Pfister 1998, Sæther and Bakke 2000). They suggested that prospective population growth would respond most dramatically to changes in adult survival (relative influence of adult survival on λ was 2.07 times that of productivity), while retrospective variation was primarily driven by fluctuations in productivity. In particular, my results indicated that duckling survival explained a large proportion of retrospective variance in λ (44%) and tended to have a high short-term sensitivity. This suggests that immediate management actions aimed at increasing duckling survival may be useful in enhancing short-term population growth on the YKD. Overall, mean estimates of λ from matrix models appeared somewhat lower that those from reverse-capture recapture or log-linear approaches (~3%), and these differences may represent the influence of immigration (Nichols et al. 2000, Peery et al. 2006). Further, reverse-capture recapture methods suggested that ~16% of the YKD population could be attributed to recruits, suggesting that immigration may play a larger role in the population dynamics of YKD Pacific common eiders than previously considered. At a larger scale, I interpreted the three measures of λ to be in general agreement: all indicating that the YKD Pacific common eider population was stable to slightly increasing over the period of study (range λ: 1.02-1.05 (CI: 0.98-1.11)).

In conclusion, my study emphasized the complexities of population dynamics and provided insight into ecological pressures that have helped to shape the ecology of YKD Pacific common eiders. I found that early breeding females make the largest contribution to productivity, and other work suggests that early-hatched offspring have higher growth rates, breeding propensities, and probabilities of survival than late-hatched individuals (black brant (*Branta bernicla nigricans*); Sedinger and Flint 1991, canvasbacks (*Aythya valisineria*); Anderson et al. 2001). Thus, enhanced protection during the early nesting period may be an effective management strategy for increasing current reproductive output and future recruitment (Cooke et al. 1984), as well as increasing directional selection for early breeding. Additionally, my modeling results emphasized the importance of adult survival to λ, highlighting the need for long-term management efforts that carefully monitor and attempt to reduce adult mortality throughout the annual cycle. However, managing a population based on model-generated priorities alone does not address the practical ability to change parameters (Mills et al. 1999), and managers must balance these two components when developing conservation strategies. The results of my modeling demonstrated that population growth of YKD Pacific common eiders is most sensitive to changes in adult survival, and, thus, mortality pressures on adults, such as hunting and marine pollution, are expected to have larger relative impacts on population dynamics than similar changes in reproductive parameters. Yet, current reported hunting pressure for YKD Pacific common eiders is minimal (Wentworth 2004), and managing for at-sea mortality factors (i.e., Bering Sea wintering conditions), is likely unfeasible. Therefore, although restricting harvest would likely increase adult survival, such a strategy would be difficult to implement, and perhaps unnecessary, particularly if stability, rather than growth is the management goal.

This study suggests that long-term management should consider ways to increase adult survival, while emphasizing that immediate actions may be better focused on traits with lower elasticities and greater management potential, such as components of fecundity. For example, my population analyses indicate that only a small change in adult survival (1-2%), coupled with larger (10-20%) changes in productivity, would be necessary to restore the population to historical levels within a 50-yr period (assuming current environmental conditions). Thus, management strategies aimed at influencing productivity, but which may also simultaneously benefit adult survival (e.g., predator control on breeding grounds), may be a more feasible immediate strategy for increasing numbers of Pacific common eiders on the YKD. Additionally, such efforts might also improve nesting conditions for other sympatric nesters on the YKD, thereby having community-wide impacts.

As a final note, my study has helped to identify several important future information needs. Investigation of the deficiency/toxicity threshold for selenium in wild marine birds would aid in quantifying concentrations at which this element may negatively or positively effect survival and reproduction. Additionally, examination of factors limiting adult and duckling survival, would greatly improve our understanding of Pacific common eider population dynamics. I believe much of this work will require multiple years of radio tracking of broods, as well as investigation of predator-prey dynamics and experimental manipulation of predator populations. Moreover, improved harvest information (e.g., age, sex, and harvest location data, as well as band-returns) could help in quantifying the effect of local hunting on adult survival and aid in understanding the relationship between harvested birds and the resident breeding population. Lastly, establishment of a known-age population (likely via large-scale marking of ducklings at the nest), in combination with continued mark-recapture efforts at multiple breeding aggregations, would aid in quantifying the respective contributions of *in situ* recruitment and immigration to λ (Nichols et al. 2000); thus improving our understanding of the factors that ultimately contribute to population growth.

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