

# Survival of Breeding Pacific Common Eiders on the Yukon-Kuskokwim Delta, Alaska

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**ABSTRACT** Populations of Pacific common eiders (*Somateria mollissima v-nigrum*) breeding in Alaska, USA, have declined markedly over the past 40 years. We studied survival of adult female Pacific common eiders using capture–recapture of nesting hens at 3 sites on the Yukon-Kuskokwim Delta (YKD), Alaska from 1994 to 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. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):403–410; 2007)

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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 overinflated (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 ad 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-day 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).

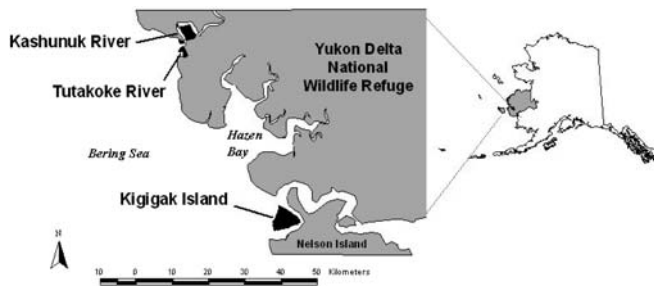
The Pacific common eider (*S. mollissima v-nigrum*) is the most distinct, morphologically and genetically, of the 4–7 recognized subspecies, and it has been recommended for separate species status based upon uniqueness of characteristics and relative geographic separation from others in the common eider complex (Livezey 1995). Pacific common eiders breed primarily along the coastal fringe of Alaska, USA; 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

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**Figure 1.** Locations of Kashunuk River, Tutakoke River, and Kigigak Island study areas of Pacific common eider annual apparent survival (1994–2004) on the Yukon-Kuskowim Delta, Alaska, USA.

declined by >50% over the past 25 years (Woodby and Divoky 1982, Suydam et al. 2000) and estimates from the Yukon-Kuskowim 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, 1997; Stehn et al. 1993).

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 discrete breeding groups, or the effect of environmental variation on life history parameters throughout the annual cycle.

From 1994 to 2004 we collected capture–recapture data from individually banded female Pacific common eiders nesting on the YKD 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 (Fig. 1): Kashunuk River (KR; 61°20'N, 165°35'W), Tutakoke River (TR; 60°51'N,

165°49'W), and Kigigak Island (KI; 60°50'N, 165°50'W). The KR study area (27.6 km<sup>2</sup>) 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). The KR supported few (12–34 nests/yr) common eiders, and these females primarily nested in habitats near the river edge. The TR study area was a coastal, mainland site, approximately 52 km north of the KI study area and 10 km southwest of the KR study area. The TR study site covered approximately 12 km<sup>2</sup> and supported a large aggregation ( $\bar{x}$  = 110 nests) of common eiders located primarily within a black brant (*Branta bernicla nigricans*) colony (approx. 5,000 pairs; Sedinger et al. 1998). Common eiders at the TR site nested in wet sedge meadows dominated by Ramensk's sedge (*Carex ramenskii*) several hundred meters inland from coastal mudflats. The third study area, KI, consisted of nearly the entire island (32.5 km<sup>2</sup>), and nesting habitat included low coastal tundra and high graminoid and intermediate sedge meadows. Kigigak Island 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. Kigigak Island 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 (approx. 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 3 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 (approx. 10 Jun) each year. During the search period we covered most of the available (vegetated) nesting habitat within each study area ( $\bar{x}$  = approx. 9 km<sup>2</sup> each). Once found, we revisited nests at 7-day intervals and candled eggs (Weller 1956) at each visit to determine incubation stages. We used candling data and a 26-day incubation period to calculate hatch dates and determine best capture dates.

We captured nesting Pacific common eiders using mist nets and bow-net traps (Salter 1962) usually within 1–3 days before hatch. We marked all newly captured females with United States Geological Survey metal bands and yellow, alphanumerically inscribed, plastic leg bands. Common eiders generally do not breed until 2–3 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 ( $\phi$ ) and encounter ( $p$ ) probabilities using Cormack–Jolly–Seber models (Lebreton et al. 1992) in program MARK (White and Burnham 1999). We used a logit link to bound parameter estimates between zero and one. Our dataset included 11 total encounter occasions (1994–2004) and 3 geographic areas on the YKD; KR, TR, and KI. Sampling efforts were not continuous among the 3 sites and 11 years of study. We marked and recaptured females at KR from 1994–2002, at TR from 1997–2004, 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 1998–2000 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  $\phi$  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-yr 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 2 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 (United States 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-yr 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 Akaike's Information Criterion (AIC) adjusted for sample sizes and overdispersion (i.e., QAIC<sub>c</sub>; 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 overinflated our sampling



**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, Alaska, USA.

Model <sup>a</sup>	Apparent survival hypothesis represented by model	$k^b$	$\Delta\text{QAIC}_c$	$w_i$	Deviance
1) $\Phi, p_{s \times t}$	Constant	20	0.00	0.31	172.19
2) $\Phi_{\text{FOX}}, p_{s \times t}$	Varies by indices of arctic fox on breeding grounds	21	1.46	0.15	171.50
3) $\Phi_{\text{ICE}}, p_{s \times t}$	Varies by indices of Bering Sea ice severity	21	1.98	0.11	172.03
4) $\Phi_s, p_{s \times t}$	Broader geographic variation (mainland vs. island)	21	1.99	0.11	172.03
5) $\Phi_{\text{NSphys}}, p_{s \times t}$	Varies by nest success in yr $i$ (physiologic cost)	21	2.05	0.11	172.10
6) $\Phi_{\text{NSpred}}, p_{s \times t}$	Varies by nest success in yr $i+1$ (predation)	21	2.15	0.11	172.19

<sup>a</sup> Notation follows Lebreton et al. (1992)  $\Phi$  = probability of apparent survival,  $p$  = probability of encounter,  $s$  = site,  $t$  = time

<sup>b</sup>  $k$  = no. of parameters

<sup>c</sup> The best approximating model has the lowest delta quasi-likelihood Akaike's Information Criterion ( $\Delta\text{QAIC}_c$ ) value and the highest model wt ( $w_i$ ) relative to others in the candidate set.

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  $\text{QAIC}_c$  values in ascending order. We used  $\Delta\text{QAIC}_c$  values to assess relative support for individual models and used differences in  $\text{QAIC}_c$  weights to assess the relative likelihood of each model, given the data, on a scale of zero to one (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  $\mu$  and variance  $\sigma^2$ .

## RESULTS

Our dataset included 361 breeding adult (AHY) female Pacific common eiders (KR:  $n = 42$ , TR:  $n = 161$ , KI:  $n = 158$ ) banded between 1994 and 2003, which resulted in 268 future recaptures and resightings between 1995 and 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-years 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  $\text{AIC}_c$  values by our estimated  $\hat{c}$  of 1.19.

The best approximating model ( $\phi, p_{s \times t}$ ), 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: 0.842–0.928). We estimated spatial and temporal process variation in apparent survival ( $\sigma^2$ ) to be 0.005 (95% CI: 0.001 to 0.020). Estimated encounter probabilities averaged 0.352 (95% CI: 0.178–0.598) at KR, 0.258 (95% CI: 0.175–0.367) at TR, and 0.289 (95% CI: 0.189–0.433) at KI.

Overall, we had strong support for several models describing variation in apparent annual survival ( $\Delta\text{QAIC}_c < 2.0$ ; Table 1, Models 2–4). However, the addition of covariates in these models did not improve model fit ( $\Delta$  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  $\Delta\text{QAIC}_c$  units of the best approximating model (Table 1, Models 2–6), but failed to improve fit to the data (Burnham and Anderson 1998). Moreover, parameters describing variation in survival were poorly estimated (95% CIs 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 ( $\Delta\text{QAIC}_c > 5$ ), including models in which encounter probability varied with site-specific annual nesting success ( $\Delta\text{QAIC}_c > 44$ ) or with years of extremely poor reproduction ( $\Delta\text{QAIC}_c > 41$ ).

## 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 had 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

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

Location	Annual survival rate	SE	Subspecies	Source
PQ, Canada	0.826	0.010	<i>dresseri</i>	Reed (1975)
ME, USA	0.886	0.076	<i>dresseri</i>	Wakeley and Mendall (1976) <sup>a</sup>
England	0.895	0.015	<i>mollissima</i>	Coulson (1984)
Western AK, USA	0.892	0.022	<i>v-nigrum</i>	This study
Eastern North America	0.873	0.016	<i>dresseri</i>	Krementz et al. (1996)

<sup>a</sup> As reanalyzed and presented in Goudie et al. (2000).

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, as 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 nonbreeding (Coulson 1984) may have further confounded patterns of encounter probabilities in our study. Finally, we considered birds nesting in our 3 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, Wakeley and Mendall 1976, Coulson 1984, Bustnes and Erikstad 1993). However, we did observe 2 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 that 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, Spende-low 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 sympatric 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 2 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 spatiotemporal 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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## LITERATURE CITED

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