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Population Ecology 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*) 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 1990s to the present. We investigated the underlying processes affecting their population dynamics by collection and analysis of demographic data from Pacific common eiders at 3 sites on the YKD (1991–2004) for 29 site-years. We examined variation in components of reproduction, tested hypotheses about the influence of specific ecological factors on life-history variables, and investigated their relative contributions to local population dynamics. Reproductive output was low and variable, both within and among individuals, whereas apparent survival of adult females was high and relatively invariant (0.89 ± 0.005). 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 an island study site consistently initiated clutches 3–5 days earlier in each year than those on 2 mainland sites. Population variance in nest initiation date was negatively related to the peak, suggesting increased synchrony in years of delayed initiation. On average, total clutch size (laid) ranged from 4.8 to 6.6 eggs, and declined with date of nest initiation. After accounting for partial predation and non-viability 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 likely attributed to sampling error. We found evidence that observer effects may have reduced overall nest survival by 0.0–0.36 across site-years. Study sites with lower sample sizes and more frequent visitations appeared to experience greater observer effects. In general, Pacific common 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 precluded response to this apparent selection pressure. Our results suggest that females breeding early in the season have the greatest reproductive value, as these birds lay the largest clutches and have the highest probability of successfully hatching. 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 and variance decomposition to assess the proportion of variation in λ explained by process variation in each vital rate. 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 ($\geq$4 yr of age), and all calculations of λ indicated that the YKD population was stable to slightly increasing ($\lambda^{\text{matrix}} = 1.02$, CI: 1.00–1.04); $\lambda^{\text{reverse-capture–recapture}} = 1.05$, 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 to changes in adult female survival (relative influence of adult survival was 1.5 times that of fecundity), whereas retrospective variation in λ was primarily explained by fecundity parameters (60%), particularly duckling survival (42%). Among components of fecundity, sensitivities were highest for duckling survival, suggesting this vital rate may be a current restriction to further population growth. Increasing adult survival would have the largest positive effects on population growth, but practical ways to influence this vital rate are currently limited. Given that eider laying dates and nest fates may be closely tied to those of sympatrically nesting species, we 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. If enhancing population growth is the objective and assuming the population is not currently at carrying capacity, we recommend an adaptive management approach. This approach

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would begin with focused efforts towards increasing reproductive output, with particular emphasis on strategies to increase both fecundity and nest survival, such as predator control on breeding grounds, followed by evaluation of population response. However, we conducted our modeling efforts under assumptions of density independence, whereas density-dependent mechanisms may have played an important role in the historic decline and subsequent stabilization of our population at a new, lower equilibrium. In an adaptive-management context, our results can be used to test additional (density-related) models; our predicted response would be compared with actual population response to prescribed management manipulations. Failure of the population to positively respond to increases in vital rates and negative correlations among vital rates would serve as evidence of density-dependent regulation. Rejection of the density-independent model would support management actions focused on habitat improvement.

KEY WORDS Alaska, nest survival, Pacific common eider, population model, process variation, productivity, *Somateria mollissima v-nigrum*, Yukon-Kuskokwim Delta.

Ecología Demográfica de Criar Eiders Común Pacífico en el Delta de Yukón-Kuskokwim, Alaska

RESUMEN La poblacione de *Somateria mollissima v-nigrum* en el Delta Yukon-Kuskokwim de Alaska occidental decayó 50–90% de 1957 a 1992 y luego se estabilizó a un nivel reducido de los 1990s en adelante. Recolectamos y analizamos datos demográficos de *Somateria mollissima v-nigrum* en 3 lugares del Delta Yukon-Kuskokwim durante 1991–2004 para investigar los procesos que afectan las dinámicas de la población. Examinamos la varianza en los componentes de reproducción, evaluamos hipótesis sobre la influencia de factores ecológicos en las características de la historia de vida, e investigamos las contribuciones de estas a la dinámica de la población local. La producción de crías era baja y variable entre años, tanto para un individuo como entre individuos, mientras que la supervivencia de las hembras adultas era alta y poco variable (0.89 ± 0.005). Todos los parámetros de reproducción variaron entre los lugares y años de estudio. Las fechas de anidación tenían un rango de 4 mayo a 28 junio, con una moda de 26 mayo. Las hembras que anidaban en una isla anidaban 3–5 días antes que las hembras en lugares continentales. La varianza poblacional de la fecha de anidación estaba negativamente relacionada con la moda, sugiriendo mayor sincronía en los años cuando se atrasó el inicio de la nidada. El tamaño de la nidada tenía un rango de 4.8 a 6.6 huevos, y disminuyó con el avance de la fecha de inicio de la nidada. Después de considerar la depredación y la inviabilidad de los huevos, el tamaño de la nidada al eclosionar tenía un rango de 2.0 a 5.8 huevos. Dentro de una temporada, la probabilidad de supervivencia diaria de los nidos era menor durante la puesta y para los de fecha de inicio atrasada. La supervivencia de los nidos varió bastante entre lugares y entre años (promedio = 0.55; rango: 0.06–0.92), pero la varianza de proceso de supervivencia de nidos era baja (0.02, interval de confianza: 0.01–0.05), lo cual indica que la mayoría de la varianza era causada por error de muestreo. Encontramos evidencia de qué el efecto del observador redujo la supervivencia de los nidos por 0.0–0.36 dependiendo del lugar-año. Los lugares con muestras más pequeñas y visitas más frecuentes parecieron sufrir un mayor efecto del observador. En general, *Somateria mollissima v-nigrum* tuvo alta varianza espacio-temporal en su biología de reproducción. Nidadas más grandes y alta supervivencia de los nidos que se iniciaron temprano sugiere una selección que favorece anidación temprana. Sin embargo, efectos ambientales estocásticos pudieron impedir la acción de esta presión de selección. Nuestros resultados sugieren que las hembras que anidan temprano tienen el mayor valor reproductivo, porque éstas ponen las nidadas más grandes y con mayor probabilidad de eclosionar. Construimos modelos de población de matriz estocásticas y con etapas que incorporaron la varianza espacio-temporal (de proceso) y covarianza en las tasas vitales, y proyectamos la distribución estable (w) y la tasa de aumento de la población (λ). Usamos análisis de perturbación para examinar las influencias de cambiar las tasas vitales sobre λ y la descomposición de varianza para determinar la proporción de varianza de λ que se explica con la varianza de proceso en cada tasa vital. Además de estimar λ usando la matriz, lo estimamos usando el análisis de captura-recaptura y regresión logarítmica. Encontramos que la distribución de edad estable para *Somateria mollissima v-nigrum* esta ponderada hacia las hembras adultas ($\geq$4 años de edad) y con experiencia en anidación, y todos los cálculos de λ indicaron que la población en el Delta Yukon-Kuskokwim estaba estable o aumentando ($\lambda^{\text{matriz}} = 1.02$, IC: 1.00–1.04; $\lambda^{\text{captura-recaptura}} = 1.05$, IC: 0.99–1.11; $\lambda^{\text{logarítmico}} = 1.04$, IC: 0.98–1.10). El análisis de perturbación sugirió que la población respondería mas dramáticamente a los cambios en la tasa de supervivencia de las hembras adultas (la influencia de la supervivencia de los adultos era 1.5 veces la de fecundidad), mientras que la varianza retrospectiva de λ se explicaba principalmente con los parámetros de fecundidad (60%), sobre todo la supervivencia de los patipollos (42%). Entre los componentes de fecundidad, la sensibilidad era mayor para la supervivencia de los patipollos, lo cual sugiere que esta tasa vital puede ser la que restringe el aumento de la población en el futuro. Aumentar la supervivencia de los adultos tendría el efecto positivo más grande para el aumento de la población, pero hay pocas maneras practicas de influir esta tasa vital. Dado que las fechas de anidación y el éxito de los nidos están relacionados con los de otras especies que anidan cerca, tenemos la hipótesis que las acciones de manejo que facilitan anidación temprana y se enfocan en otras especies (e.g., aumentar las poblaciones para reducir el efecto de depredación) puede también tener un efecto positivo para *Somateria mollissima*. Si el objetivo se trata de aumentar la población y suponiendo que la población no ha llegado a lo máximo que puede soportar el hábitat, sugerimos un enfoque en el manejo adaptiva. Este enfoque empezaría por aumentar la reproducción, con un énfasis en las estrategias que pueden aumentar la fecundidad y la supervivencia de los nidos, por ejemplo controlar a los depredadores en las áreas de anidación, y luego evaluar la reacción de la población. Sin embargo, nuestros modelos tenían la presunción de ser independientes de la densidad, mientras que los mecanismos dependientes de la densidad puede que hayan contribuido a la decaída y subsiguiente estabilización de la población a niveles nuevos y más bajos. En el contexto de manejo adaptivo, nuestros resultados sirven para examinar otros modelos que dependen de densidad. Así, nuestras predicciones se compararían con las poblaciones actuales para hacer recomendaciones de manejo. Si la población no responde positivamente a los aumentos de tasas vitales y hay correlaciones negativas entra las tasas vitales, servirá como evidencia que hay regulación que depende de densidad. El rechazo del modelo que no depende de densidad apoyaría las acciones de manejo que se enfocan en mejorar el hábitat.

Écologie de la Population Reproductrice des Eiders à Duvet du Pacifique sur le Delta du Yukon-Kuskokwim, Alaska

RÉSUMÉ Les populations d'Eiders à duvet du Pacifique (*Somateria mollissima v-nigrum*) ont décliné de 50–90% sur le delta du Yukon-Kuskokwim (DYK) dans l'ouest de l'Alaska entre 1975 et 1992 puis se sont stabilisées avec des faibles effectifs depuis le début des années 1990 jusqu'à aujourd'hui. Nous avons étudié les processus sous-jacents qui affectent la dynamique de ces populations en récoltant et en analysant les données démographiques des Eiders à duvet du Pacifique à 3 sites sur le DYK (1991–2004) pour un total de 29 site-années. Nous avons examiné la variation des paramètres de la reproduction, testé des hypothèses concernant l'influence de certains facteurs écologiques spécifiques sur les traits d'histoire de vie et évalué leur contribution relative à la dynamique de la population locale. Le succès reproducteur était faible et variable, tant pour un même individu qu'entre les individus alors que la survie apparente des femelles adultes était élevée et peu variable (0.89 ± 0.005). Tous les paramètres reproductifs variaient entre les sites d'étude et les années. Les dates d'initiation des nids s'étalaient du 4 mai au 28 juin, avec un pic (mode) d'initiation le 26 mai. Les femelles qui nichaient à un site insulaire initiaient toujours leurs nids 3–5 jours plus tôt que les femelles nichant à 2 autres sites situés sur la terre ferme. La variance de la date d'initiation des nids pour la population était négativement liée au pic suggérant une synchronisation accrue durant les années plus tardives. En moyenne, la taille de ponte totale (pondue) variait entre 4.8 et 6.6 oeufs et déclinait avec la date d'initiation du nid. En tenant compte de la prédation partielle et des oeufs non-viables, le nombre moyen d'oeufs à l'éclosion variait entre 2.0 et 5.8. Pendant la saison de reproduction, la probabilité de survie journalière (PSJ) des nids était plus faible durant la ponte et pour les nids initiés tardivement. L'estimation de la survie des nids variait considérablement entre les sites et les années (moyenne = 0.55, écart: 0.06–0.92), mais la variance du processus de la survie des nids était relativement faible (0.02, IC: 0.01–0.05), indiquant que la majorité de la variance était attribuable à l'erreur d'échantillonnage. Nous avons trouvé que l'effet des observateurs pouvait réduire le succès global des nids de 0.0 à 0.36 à travers les site-années. Les sites d'étude avec de plus faibles nombres d'échantillons et les plus fréquemment visités semblaient subir un plus grand effet des observateurs. En général, les Eiders à duvet du Pacifique démontraient une grande variance dans leurs paramètres de reproduction. Des tailles de ponte plus élevées et une survie des nids élevée pour les pontes initiées tôt suggèrent une sélection directionnelle pour une nidification hâtive. Cependant, les effets environnementaux stochastiques peuvent masquer la réponse à cette force de sélection. Nos résultats démontrent que les femelles qui se reproduisent tôt en saison ont la plus grande valeur reproductive car elles pondent plus d'oeufs et ont la plus grande probabilité de les amener à éclosion. Nous avons développé des modèles matriciels stochastiques structurés en classes de stades qui incluent la variance spatio-temporelle observée (processus) et la co-variation des indices démographiques puis avons projeté la distribution stable des classes de stades (w) et le taux de croissance de la population (λ). Nous avons utilisé une analyse de perturbation pour évaluer l'influence relative des changements des indices démographiques sur λ et avons décomposé la variance afin de déterminer la proportion de la variation de λ expliquée par la variation du processus de chaque paramètre démographique. En plus du λ obtenu par le modèle matriciel, nous avons estimé λ à partir d'une approche de capture-recapture et de régressions log-linéaires. Nous avons trouvé que la structure d'âge des Eiders à duvet du Pacifique était fortement influencée par les femelles adultes expérimentées ($\geq$4 ans). Tous les calculs de λ indiquaient que la population du DYK était stable ou en légère croissance ($\lambda^{\text{matriciel}} = 1.02$, IC: 1.00–1.04;

$\lambda^{\text{capture-recapture-renversé}} = 1.05$, IC: 0.99–1.11; $\lambda^{\text{log-linéaire}} = 1.04$, IC: 0.98–1.10). Les analyses de perturbation suggèrent que la population répondrait davantage à un changement du taux de survie des femelles adultes (l'influence relative de la survie des adultes était 1.5 fois celle de la fécondité), alors que la variation rétrospective de λ était davantage expliquée par les paramètres de fécondité (60%), en particulier la survie des canetons (42%). Parmi les paramètres de fécondité, la survie des canetons démontrait la plus grande sensibilité suggérant que ce paramètre limiterait la croissance éventuelle de la population. Augmenter la survie des adultes aurait l'effet positif le plus important sur la croissance de la population mais les mesures possibles pour atteindre ce but sont actuellement limitées. Étant donné que les dates de ponte et le sort des nids des eiders sont possiblement liés à ceux d'espèces nicheuses sympatriques, nous soumettons l'hypothèse que les mesures de gestion favorisant une nidification hâtive et visant d'autres espèces (e.g. favoriser les conditions susceptibles de confondre les prédateurs) pourraient avoir des effets positifs concomitants sur la nidification des Eiders à duvet. Si l'objectif est de favoriser la croissance de la population et assumant que la population n'a pas encore atteint la capacité de support du milieu, nous recommandons une approche d'aménagement évolutif. Cette approche débuterait en favorisant une augmentation du succès reproducteur avec une emphase sur des stratégies visant à augmenter la fécondité et la survie des nids, comme un contrôle de prédateurs sur les aires de reproduction suivi d'une évaluation de la réponse de la population. Cependant, nos efforts de modélisation ont été réalisés sous le postulat d'indépendance de la densité alors que les facteurs densité dépendants ont pu jouer un rôle important dans le déclin historique puis la stabilisation de notre population à un nouveau niveau d'équilibre faible. Dans un contexte d'aménagement évolutif, nos résultats peuvent être utilisés pour tester d'autres modèles (densité-dépendants). Ce faisant, nos prévisions seraient comparées à la réponse actuelle de la population aux mesures d'aménagement. L'absence de réponse positive de la population suite à des augmentations des paramètres démographiques et des corrélations négatives parmi ces paramètres confirmeraient une régulation par des facteurs densité-dépendants. Le rejet du modèle basé sur une régulation indépendante de la densité supporterait les actions axées sur l'amélioration de l'habitat.

Contents

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 female offspring produced per adult in a given year) represents the product of lower-level reproductive components (e.g., proportion of birds that breed, clutch size at hatch (CSH), 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, Hoekman et al. 2002). Total variation in components of reproduction include 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 when vital rates are positively correlated with one another (van Tienderen 2000, Doak et al. 2005), or overestimated, when sampling variance is not accounted for by the population model (Link and Nichols 1994).

Estimates that consider broad-scale spatio-temporal variation (e.g., among sites, years) 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, Raveling 1989, Larivière and Messier 1998), 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 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.

Heritable genetic variation must be present for individuals to respond to selection pressure. 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 responses to selection pressure. This information may be especially critical for the biota of arctic and sub-arctic 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 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, Woolfenden and Fitzpatrick 1984, Godfray et al. 1991, Rohwer 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 requires an understanding of the mechanisms that drive patterns of selection. This understanding 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.

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 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 often relies heavily on assumptions, and explicit acknowledgement of departures from assumptions is critical for 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 (population growth rate) 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 (prospective) growth of a population (i.e., λ) based on stage or age-specific vital rates and assuming asymptotic convergence on the stable stage or age structure (Caswell 2001), asking how much λ would likely change in response to changes in vital rates. However, λ can also be estimated directly from 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 different assumptions, their agreement can 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 exist in stochastic environments that influence their demographic characteristics (Tuljapurkar 1990). Incorporating such variation is an important component of population modeling, as using simple averages of vital rates (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, Hoekman et al. 2002). In general, λ will be disproportionately influenced by variation in vital rates with the highest sensitivities (absolute change in λ based on absolute change in vital rate) and elasticities (proportional change in λ resulting from proportional changes in vital rate; Caswell 2001). 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 2002). In this sense, methods that evaluate pro- and retrospective influences on λ provide tools 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).

Common eiders (*Somateria mollissima*) are large-bodied, long-lived, sea ducks with a circumpolar distribution (Goudie et al. 2000). Females are considered to be largely capital breeders (Drent and Daan 1980) on the capital-income continuum, relying primarily on body reserves augmented by some early feeding (Sénéchal et al. 2011) to produce eggs and maintain themselves during the incubation period (Korschgen 1977, Parker and Holm 1990, Rigou and Guillemette 2010). They are the most marine of all waterfowl, returning to land only during the brief nesting season (approx. 1 month), and raising broods at sea or in brackish-water habitats, often in large multi-family crèches (Goudie et al. 2000).

Several common eider 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, the ecology of Pacific common eiders is known only from a few isolated studies of reproduction, duckling survival, and population structure (Schamel 1977, Seguin 1981, Johnson et al. 1987, Flint et al. 1998*a*, Petersen and Flint 2002, Wilson et al. 2007). 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 4–7 recognized subspecies (Livezey 1995), with its breeding range primarily isolated to the coastal fringe of Alaska, western Canada, and far eastern Russia (Goudie et al. 2000) and its pattern of nesting typically more dispersed than other subspecies (Gabrielson and Lincoln 1959, Goudie et al. 2000).

Survey data indicate that Pacific common eiders (in combination with spectacled eiders; *Somateria fischeri*) declined by approximately 50–90% over the past 25–50 years, leading to their current designation as a "Focal Species" by the United States 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; Fig. 1). Historically, the Yukon-Kuskokwim Delta (YKD) in western Alaska supported one of the largest breeding populations of Pacific common eiders in the state, with >51,000 breeding pairs in the 1950s (Bellrose 1980). However, more recent surveys (e.g., 2004; Platte and Stehn 2011), estimated that only 1,800–2,300 pairs currently exist, a possible reduction of >90% (Stehn et al. 1993, Hodges et al. 1996, Platte and Stehn 2011; Fig. 1).

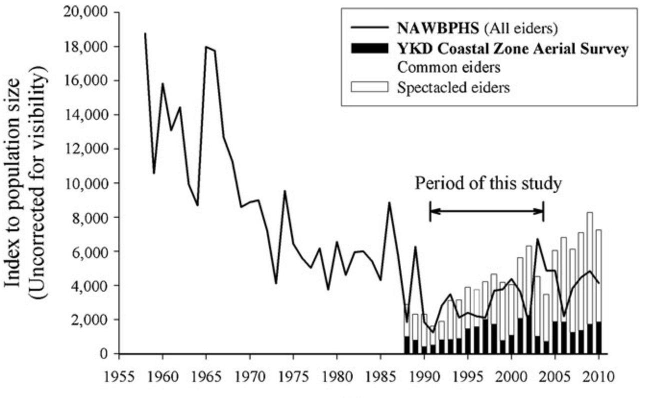


Figure 1. Indices of population size (uncorrected for visibility) for Pacific common eiders on the Yukon-Kuskokwim Delta (YKD), Alaska (1958–2010), as indicated by the North American Waterfowl Breeding Population and Habitat Survey (NAWBPHS 1958–2010; line graph; Migratory Bird Data Center 2012) and more recent intensive surveys along the coastal zone of the YKD (1988–2010; stacked histogram; Platte and Stehn 2011), demonstrating the dramatic population decline and subsequent stabilization. The NAWBPHS data represent a composite of both species of eiders seen on the YKD (spectacled [*Somateria fischeri*] and Pacific common eiders [*S. mollissima. v-nigrum*]), whereas the coastal zone survey accounted for the 2 species individually. The period of our study (1991–2004) is identified for reference.

Two other species of eiders breeding in western Alaska, spectacled and Steller's (*Polysticta stelleri*) eiders, also appear to have undergone concurrent, severe declines (particularly on the YKD). These species 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 (e.g., Flint and Grand 1997, Grand and Flint 1997, Grand et al. 1998, Petersen and Douglas 2004, Flint et al. 2006). In contrast, only limited information currently exists on the ecology of sympatrically nesting Pacific common eiders. To date, no single cause for the historical decline or subsequent stabilization of eiders (Fig. 1) has been identified, but 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). Understanding such changes has been identified as a research priority for Pacific common eiders (U.S. Fish and Wildlife Service 2005).

Our overall goals were to facilitate prioritization of management strategies and identify future research needs for Pacific common eiders. We had 4 specific objectives: 1) to assess annual and geographic variation in fecundity components (i.e., clutch initiation dates, clutch size, daily nest survival, and nest success); 2) to synthesize Pacific common eider demographic data across 3 study sites on the YKD (1991–2004); 3) to use our estimates of vital rates and associated spatio-temporal process variance derived from mark–recapture (Wilson et al. 2007) and productivity analyses (this paper) to parameterize population models (Lebreton et al. 1992, Dinsmore et al. 2002); and 4) to examine the relative influence of components of survival and reproduction on population dynamics.

We began by quantifying the components of productivity for Pacific common eiders nesting on the YKD, Alaska and examining factors influencing variation in reproduction at the population level. Specifically, we summarized 29 site-years of field data that were collected across our 3 study sites (12, 4, and 13 yrs at each site, respectively), described the nesting ecology of Pacific common eiders in western Alaska, evaluated hypotheses related to variation in reproductive components among individuals (i.e., across sites, years, dates within the nesting period, and clutch ages) and within individuals, and finally, provided estimates and associated process variances for clutch initiation date, clutch size, and nest survival to characterize true biological variation across time and space, with sampling variation removed. In our population modeling, we used available estimates of vital rates (and their variances and correlations) for common eiders to examine the primary processes underlying population dynamics of Pacific common eiders on the YKD. We hoped to better understand factors that may have led to the historical decline in eiders and to provide tools from which guidelines for conservation and management could be drawn.

STUDY AREA

We collected demographic data for Pacific common eiders from 1991 to 2004 at 3 primary breeding sites on the YKD (Fig. 2): 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 do not know what proportion of the YKD

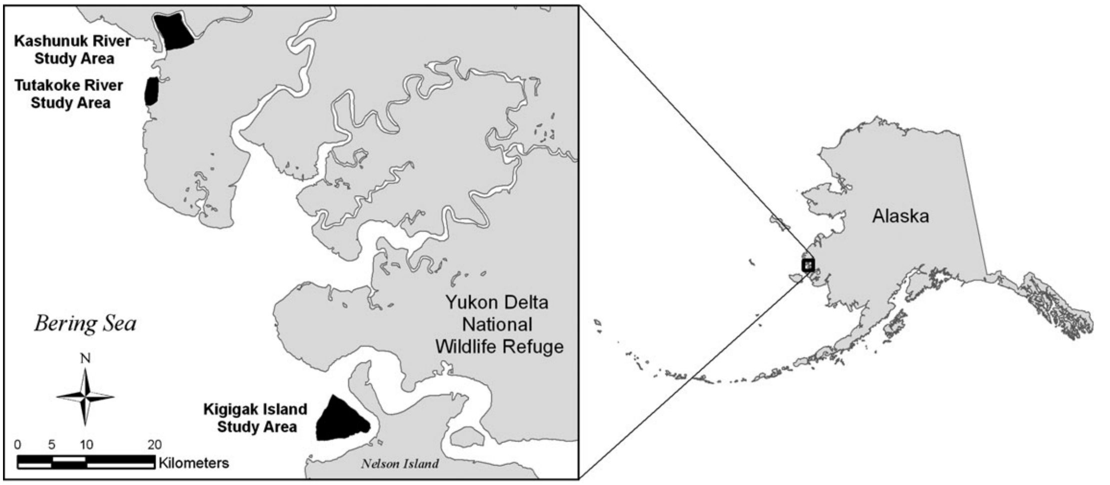


Figure 2. Locations of Kashunuk River (KR), Tutakoke River (TR), and Kigigak Island (KI) study sites for nesting Pacific common eiders (1991–2004) on the Yukon-Kuskokwim Delta, Alaska.

common-eider population was represented by our local demographic studies, our research sites represented 3 of the 4 major nesting aggregations known on the YKD for common eiders. These sites functionally characterized the range of variation in nesting strategies for common eiders across the YKD region, ranging from relatively dispersed mainland aggregations to semi-colonial island nesting. Because we did not give absolute equal search effort to all areas of each study site in all years, we present average abundances rather than attempt to calculate densities.

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). The Kashunuk River (KR) study area (27.6 km^2) was 3 km inland from the coast and common eiders at this site nested in sedge meadows at low abundances (10–15/yr), usually near the banks of the tidally influenced Kashunuk River. The Tutakoke River (TR) study area (12 km^2) was at the mouth of the Kashunuk River, and here common eiders nested in coastal wet sedge meadows several hundred meters inland from coastal mudflats, at medium to high abundances (average: 110 nests/yr), and in association with a black brant (*Branta bernicla nigricans*) colony of approximately 5,000 pairs (Sedinger et al. 1998). The Kigigak Island (KI) study area (32.5 km^2) supported the highest abundance of nesting common eiders (approx. 60–200 nests/yr; U.S. Fish and Wildlife Service and H. M. Wilson, University of Alaska, unpublished data) among a diverse community of other nesting waterfowl. Common eiders at KI tended to use the outer perimeter of the island (i.e., areas $\leq$1 km from the coast) and employed a variety of strategies, including nesting within medium to large colonies of black brant, within small conspecific colonies (e.g., 15–20 eiders around a single lake), or solitarily. All study areas on the YKD were populated by a similar suite of potential nest predators, including 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 and sometimes with the aid of trained dogs, beginning shortly after spring breakup (late May–early Jun) through the end of the first week of incubation (early–mid Jun) each year (1991–2004). During the search period, we covered most of the available (vegetated) nesting habitat within each study site (average area of vegetated habitat = approx. 9 km^2/per study site). We defined a nest as $\geq$1 egg in a bowl with at least some evidence of down. We also included nests discovered incidental to other activities 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.

We mapped each nest on aerial photos and recorded coordinates of the nest location using Global Positioning System units. In addition, we marked each nest with a small flag or wooden lathe placed 5–10 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. We monitored partial predation by numbering all eggs with permanent markers and monitoring their presence or 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 days until hatch or failure. To determine egg fates, we visited all nests either on the day of hatch, or within 5 days 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, Wilson et al. 2007), usually within 1–3 days of hatch. At capture, we collected morphological measurements and hen weights. Between 2002 and 2004, we applied alpha-numerically coded plastic leg bands in addition to United States Geological Survey metal bands (Wilson et al. 2007). We conducted all sampling following University of Alaska, Fairbanks Institutional Animal Care and Use Committee protocols (02-16).

Estimating Fecundity Components

We followed a standard productivity model (Fig. 3) in estimating the primary components of reproduction for Pacific common eiders on the YKD. To reduce the large number of possible parameter permutations, we created suites of hierarchical models. Within this hierarchical approach, we selected the parameters of greatest interest and maintained nuisance parameters, according to their most parsimonious structure (see Doherty et al. 2002). We sought to control for parameters of less explicit interest (e.g., handling and observer effects on daily nest survival), while analyzing effects of parameters we were most interested in. We accomplished this by examining all possible combinations of nuisance parameters and then applying our top nuisance parameterization as a fixed effect in subsequent modeling. We tested for multi-collinearity among explanatory variables before constructing multivariate models and found the original data to be generally orthogonal. Throughout, we used information-theoretic approaches 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_i; Burnham and Anderson 1998). Our model selection criteria followed Burnham and Anderson (1998), where models with $AIC_c \leq 2$ were considered the most parsimonious fit to the data. To quantify the relationship between covariates and parameters of interest, we estimated parameter coefficients (βs) and their standard errors, and, where appropriate, we calculated model-averaged estimates and associated unconditional sampling 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 was defined as the date on which the first egg was laid, incubation period was assumed to be a constant 26 days for common eiders (Goudie et al. 2000), total clutch laid was the maximum number of eggs found in the nest and assumed 1 egg was laid per day (Swennen et al. 1993), and egg age was age at nest discovery. We discovered most nests in our study after the 1-egg stage, and backdated initiation dates based on egg age following the methods of Flint and Grand (1996).

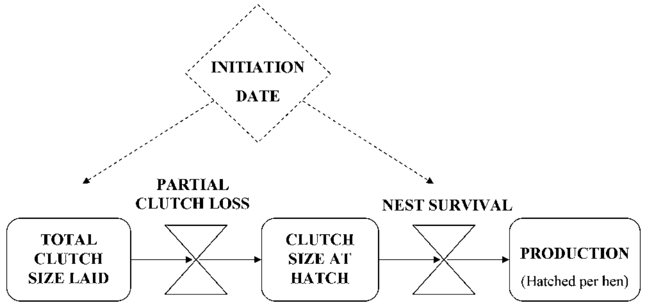


Figure 3. Flow-diagram model of productivity components of Pacific common eider, showing reproductive output from a single nest (through hatch). Boxes denote state variables and bow ties denote transition variables. Dashed-diamonds represent important covariates and dashed-lines denote the reproductive components modified. Note that post-hatch (i.e., duckling and first-year) survival is not included in this model, as they were not estimated directly from productivity data in our study. They are instead included in our models of overall fecundity (i.e., female offspring/hen available to be recruited into the breeding population).

We hypothesized that the primary determinants of initiation date were photoperiod, spring phenology (i.e., availability of open nesting ground), or some combination of the 2 (i.e., females used photoperiod to set target laying dates, but adjusted these dates according to spring phenology or some other local factor; Wikelski et al. 2000). We examined spatial and temporal variation in clutch initiation using analysis of variance (ANOVA) models (PROC GLM; SAS Institute 2002) in which we included all combinations of annual and spatial (study site) variability, interpreting a year effect as support for an annually varying phenomenon, such as spring phenology. We also examined a model in which we replaced annual variation with a linear trend across years. We interpreted support for this linear temporal effect as suggesting eiders may have initiated progressively earlier over time, potentially in response to climate change (Brown et al. 1999, D'Alba et al. 2010). Although some evidence indicates a directional change in spring conditions on the YKD (Fischer et al. 2009), 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. In other words, nesting would take place in a shorter time-window in years of late break-up, with less variance being associated with later initiation dates. 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 used the correlation between site-year residual variances and predicted mean initiation dates to indicate direction of effects.

We were also interested in 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 influential 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 that had bred ≥2 yr; Milne 1974, Spurr and Milne 1976) and calculated r_i for both relative and absolute initiation date. Absolute initiation date represented actual calendar date of initiation (irrespective of others in the population), and relative initiation date 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 laid in each site-year. We assumed that nest parasitism was uncommon, but did exclude 12 nests with >8 eggs (i.e., 2 standard deviations above mean clutch size) for which we suspected intraspecific nest parasitism. We described and quantified spatio-temporal variation in total clutch size of Pacific common eiders, both among and within site-years.

We also tested several hypotheses regarding patterns of variation in clutch size relative to environmental and individual variation. Because we expected clutch size of Pacific common eiders to 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 or relative initiation 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 absolute initiation date 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, support for relative initiation date 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 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 due to partial predation and non-viability. 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 1 egg hatched, and the probability of being successful (i.e., the product of daily nest survival probabilities over the exposure period) as nest survival (Dinsmore et al. 2002). We took a 2-step approach to examining nest survival. First, we used a multi-model, information-theoretic approach (Lebreton et al. 1992, Burnham and Anderson 1998) 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.

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 2 primary hypotheses: 1) an effect on DSP on the day following a nest visit, after flushing the female (hereafter referred to as observer effect; Rotella et al. 2000), and 2) an effect of a female being captured at any time during nesting (i.e., trapping effect). We examined all possible combinations of observer and trapping effects across study sites and years and then applied our top observer-effects parameterization as a fixed effect in all subsequent modeling.

Within our larger spatio-temporal model set, we constructed 48 models, including all possible 3-way 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 2 additional nonlinear age and date models, representing shape variations on the quadratic theme. First, given that 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 ($\text{DSP} = a \times (1 - (\exp^{(-bx)}))$, gradually reaching an asymptote over time (Gunnarsson et al. 2006). Herein, a was the asymptote, b was the slope of the curve, and x signified the specific age or date value (i.e., $x(0) = \text{age}(0)$). Alternatively, we hypothesized that decreased incubation investment because of loss of body reserves through the nesting season (Criscuolo et al. 2002, Hanssen et al. 2003), might result in an exponential decay in DSP ($\text{DSP} = a \times \exp^{(-bx)}$). To examine these hypotheses, we created a series of models that replaced quadratic age and date functions with those describing exponential rise and decay.

We estimated overall nest survival and its associated process variance. To do so, we obtained β estimates according to each of our top models of DSP (those with $w_i \geq 0.01$), including βs for observer effects (Rotella et al. 2000), using PROC NLMIXED (SAS Institute 2002, Rotella et al. 2004). We then back-transformed 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, http://www.R-project.org, accessed 10 Jun 2006). 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. Including these effects would have resulted in negatively biased population-level estimates. Instead, we calculated observer effects as the difference between overall nest survival estimates from models with and without the observer effect and trapping effect terms, reasoning that observer effects were only applicable to those days on which we visited nests during the 31-day 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 days for laying + 26 days incubation), within each of the 51 possible initiation dates for which we had data. 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

(R) top models ($i = 1, 2, \ldots, R$) and we accounted for underinflated sampling variance related to model-selection uncertainty by model-averaging nest survival estimates ($\hat{\hat{\theta}}$),

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

where w_i 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, Bentzen et al. 2008). 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 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:

$$P_i = \mathrm{CSH}_i \times \mathrm{NS}_i$$

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):

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

where total variability (σ^2_{total}) was decomposed into true biological variation ($\sigma^2_{\text{process}}$) and sampling variation (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).

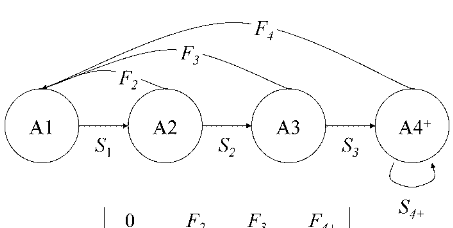
Parameters such as clutch initiation date and clutch size are expected to vary among individuals (Kendall and Fox 2002). Further, if individual heterogeneity (i.e., actual variation among individuals) is included in estimates of sampling variance, those estimates may be artificially inflated. Moreover, because overall variance represents the combination of sampling and process variances, 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). To lessen such biases, we attempted to decompose process variance in initiation date and clutch size by estimating sampling variance separate from individual heterogeneity. We did so by calculating bootstrapped mean estimates for each site-year from 1,000 resampled iterations of the original site-year data (with replacement; Efron and Tibshirani 1993). We then used the variance among the 1,000 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.

Population Modeling

We examined λ using multiple methods to maximize our understanding of Pacific common eider population dynamics. The 3 methods had different assumptions and provided varying levels of management application. Further, comparison among methods provided cross-validation and assessment of violation of assumptions. First, we developed a female, stage-based matrix population model in which we structured the common eider life cycle according to 4 age-based stages and a birth-pulse fecundity schedule, beginning with the annual prebreeding census (Fig. 4). Typical age of first reproduction in common eiders is 3–4 years old, but some may breed as early as 2 years old (Baillie and Milne 1982, Kats et al. 2007), whereas 1-year-olds have not been documented to breed (Goudie et al. 2000, Hario and Rintala 2009). Thus, we set the first stage (A_1) in our common eider life cycle to represent progeny that were <1 year old and reproductively immature. The second through fourth stages (A_2–A_{4+}) represented 2-, 3-, and ≥4-year-olds, and all could contribute to the progeny class (A_1) through reproduction. The fourth stage (A_{4+}) was a composite of experienced breeding adults ≥4 years of age. These individuals could remain in the (A_{4+}) stage according to their survival, forming a self-loop.

Matrix models.—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).

We parameterized our matrix model based on life-history characteristics (elements of fecundity and survival) defined within



$$\begin{vmatrix} 0 & F_2 & F_3 & F_{4+} \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & S_{4+} \end{vmatrix}$$

Figure 4. The life-cycle and corresponding stage-classified matrix for a population model of female Pacific common eiders (1991–2004) on the Yukon-Kuskokwim Delta, Alaska, USA, where stage A_1 = reproductively immature progeny, stages A_2–A_{4+} = reproductive adults, fecundity transitions (F_i) = stage-specific reproductive contribution, and survival transitions (S_i) = apparent annual survival probability for adult females.

a management context. 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 (Fig. 4). Because we lacked data on age-specific survival rates (i.e., our mark–recapture efforts did not involve known-age birds; Wilson et al. 2007), we assumed all birds in adult plumage (A_1–A_{4+}) experienced a similar adult survival rate. Thus, we used the estimate of adult female apparent survival and associated process variance from our previous mark–recapture analysis of Pacific common eiders across the 3 YKD study areas (1994–2004; Wilson et al. 2007) as annual 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). Finally, we calculated the stable age distribution based on methods described in Caswell (2001; e.g., using the eigenvector correspondent with the dominant eigenvalue in our matrix models).

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:

$$F_i = \mathrm{CSH}_i \times \mathrm{NS} \times \mathrm{SR} \times \mathrm{BI}_i \times \mathrm{DS} \times \mathrm{JS}$$

where F_i = stage-specific fecundity, CSH_i = stage-specific clutch sizes at hatch, NS = nest survival, SR = sex ratio of offspring (i.e., proportion of female ducklings hatched), BI_i = stage-specific breeding incidence (i.e., breeding propensity), DS = duckling survival (hatch to 30 days), and JS = juvenile survival (30 days to just before 1 yr). We used reproductive estimates from Pacific common eiders at our 3 study locations on the YKD (1991–2004; Appendix 1) to populate these parameters, unless otherwise stated.

We assumed that variation in site-year point estimates of ≥4-year-old breeding probabilities (Coulson 1984), CSH, and nest survival (this study) 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 used 29 site-year estimates of CSH from the YKD population (accounting for initiation date and partial predation) to create a string of observed clutch sizes (Appendix 1) from which we drew stochastic inputs. We adjusted estimates proportional to their sampling variance as described above (White et al. 2001). 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-year-old breeders, and ≥4-year-old breeders, respectively (Baillie and Milne 1982). Using this method, we calculated CSH for 2-year-old breeders as observed CSH × 0.77, for 3-year-old breeders as CSH × 0.96, and for ≥4-year-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, adjusted proportionally to their sampling variance, to populate the nest-survival parameter of our fecundity equation (Appendix 1). Because no data currently exist on age-specific hatching rates, we drew nest survival rates for all stage classes from the same data-string.

We determined sex ratios based on a subset of nests observed at hatch in which all ducklings could be sexed ($n = 20$ nests, 49:51 male:female). Given a near 50:50 sex ratio, we assumed a 0.5 probability of being female in our model. We based breeding incidences for 2- and 3-year-olds on age-specific common eider breeding propensities reported in Kats et al. (2007): $\mathrm{BI}_2 = 0.19$, $\mathrm{BI}_3 = 0.70$. For breeding incidences of ≥4-year-olds we randomly drew from a distribution of 24 annual point estimates for similarly aged common eiders in England (1958–1982, mean $\mathrm{BI}_{4+} = 0.78$, range: 0.35–1.0; Coulson 1984), adjusting for sampling variance, which incorporated years of non-breeding.

We defined duckling survival as survival from hatch to 30 days of age. We generated a beta distribution of duckling survival centered around 0.19, the mean estimate for duckling survival of common eiders from a single-year study (1997) on the YKD (Flint et al. 1998*a*). 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 average for the period of our study (Platte and Stehn 2011, this study), suggesting it was not an unusual year for the YKD population. However, annual survival of common eider ducklings varies dramatically elsewhere (Mendenhall and Milne 1985, Mawhinney 1999), and we sought to incorporate a measure of temporal variance in our estimate of this vital rate for the YKD. To do so, we bounded our beta distribution using our best estimate of naïve process variance in duckling survival calculated from a 13-year study of common eiders in Scotland (0.02; Mendenhall and Milne 1985) following the methods of Burnham et al. (1987) and White et al. (2001). We calculated this estimate of variance assuming 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 range of variance in YKD duckling survival rates.

We defined juvenile survival as the period from 31 days to 364 days of age. Because we did not have direct estimates of juvenile survival from the YKD, we calculated it based on the ratio of adult to juvenile survival from known-age common eiders in the Baltic Sea (Kats et al. 2007). Kats et al. (2007) estimated local juvenile survival (defined as "immature survival" from 7 weeks to 364 days of age) and reported that it was not appreciably lower than adult survival using mark–recapture–recovery of known-age birds. Thus, we estimated juvenile survival for an 11-month period (i.e., from 30 days to 1 yr) according to the equation

$$\mathrm{JS} = ((S_{1+})^{1/12})^{11} = 0.905$$

and we assumed process variance in juvenile survival was the same as that of adult survival (0.005), given adults and juveniles in our study were presumably exposed to similar environments. Although juvenile survival for many waterfowl species tends to be lower and more variable than adult survival, this pattern has not been established in the limited data available for common eiders. Further, under the assumptions we made, our calculated mean and process variance for juvenile survival were similar to those from Kats et al. (2007; mean: 0.926, $\sigma^2_{\text{process}}$: 0.004).

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 (Appendix 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 1,000 stochastic simulations. For example, at each annual step of a simulation, we randomly drew 1 nest-survival estimate from the set, incorporated it into the stage-specific fecundity equation, and created a new matrix using the updated fecundity estimate. We then multiplied new matrices by the stage-specific population size vector at each time-step of the model.

For each vital rate in our population model, we drew from 1 of 3 distributions types: 1) deterministic, 2) beta, or 3) observed and discontinuous. 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, because of 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 and maximum parameter values (Morris and Doak 2002). Observed and discontinuous distributions comprised sets of observed vital-rate estimates for each of our site-years (Appendix 1). We randomly drew an observed value from these observed pools of estimates with equal probability at each time step (Kaye and Pyke 2003; Appendix 1).

We did not have measures of all vital rates within the same site-years. We incorporated correlated clutch size and nest survival into our stochastic simulations by randomly selecting clutch size and nest survival estimates grouped by the same site-year (Appendix 1). Thus, these vital rate estimates were paired within our random sampling, preserving any site-year covariance structure. We did not sample any other sub-vital rates as a unit. We did not examine correlations between matrix elements (e.g., survival and fecundity; Yoccoz et al. 2002), or between adult survival and any underlying components of fecundity (i.e., lower-level vital rates), as previous analyses of our population revealed no support for spatial or temporal variation in adult survival (Wilson et al. 2007).

We set our initial population size (*N*) to 1,880 individuals, based on the population indices near the start of our study of Pacific common eiders on the YKD (Platte and Stehn 2011) and conducted 1,000 stochastic simulations projecting 100 years into the future. We calculated $\hat{\lambda}_i^{\text{matrix}}$ from each of our 1,000 simulations according to the Heyde and Cohen (1985) equation,

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

We then calculated $\overline{\hat{\lambda}}_i^{\text{matrix}}$ and constructed 95% confidence intervals based on the 2.5 and 97.5 quantiles of the sorted $\hat{\lambda}_i^{\text{matrix}}$. We performed all stochastic modeling with AVESMODELER (AvesModeler, Version 0.9, http://www.ag.auburn.edu/aux/alcfwru/avsmdl/, accessed 25 Feb 2012), using runtime components in MATLAB (MathWorks, Natick, MA).

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., CSH, NS). Although 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 for specific stage-classes), and calculated elasticities for stochastic models using a modification of the Heyde and Cohen (1985) equation:

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

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; Brault and Caswell 1993, Horvitz et al. 1997, Caswell 2000, Cooch et al. 2001) addresses how variability in λ may have been attributed to environmental variability in each of the vital rates. This distinction is important, as vital rates with high sensitivity or elasticity may be very different from those that make the largest contributions to variability in population growth (Gaillard et al. 1998, Pfister 1998, Cooch et al. 2001, Hoekman et al. 2002). 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 used the equation:

$$\text{Variance component}_i = \mathrm{CV}_i \times e_i$$

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. 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 or assumption of process variance (i.e., clutch size and nest, duckling, juvenile, and adult survival; Wilson et al. 2007), and we compared these variance components only relative to one another.

Reverse capture–recapture model.—Our second estimate of λ used reverse capture–recapture (RCR) techniques (Pradel 1996, Nichols et al. 2000, Nichols and Hines 2002, Mehl 2004) in Program MARK (White and Burnham 1999). This approach provided estimates of λ without the asymptotic assumptions that accompany some matrix analysis methods, and instead relied on observed mark–recapture encounter histories. In our case, RCR used Cormack–Jolly–Seber models (i.e., the probability that an individual present at time *t* will survive and be captured 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) and seniority (γ) probabilities can be used to directly estimate population growth rates,

$$\lambda_i^{\mathrm{RCR}} = \frac{\phi_t}{\gamma_{t+1}}$$

as well as recruitment (*f*) (Pradel 1996)

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

We estimated γ, λ^{RCR}, and *f*, with ϕ and p fixed to the best approximating model structure from earlier Cormack–Jolly–Seber analysis ({$\phi.$ and $p_{g\times t}$}; Wilson et al. 2007).

Our primary goal was to compare and contrast different modeling approaches, but because our sample size was limited; we only considered RCR model structure that did not allow lambda to vary, thus allowing us to compare estimates of λ among techniques with parallel structures. Because seniority models use 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; Hines and Nichols 2002). 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 goodness-of-fit TEST2.C in Program RELEASE (Burnham et al. 1987) implemented in Program MARK. We calculated the variance inflation factor ($\hat{c}$) by dividing the overall χ^2 (TESTS 2 + 3) by the overall degrees of freedom (Dodd et al. 2006) and corrected for overdispersion where $\hat{c}$ was >1.

Log-linear **λ** *model.*—Estimates of λ based on measuring vital rates in the field can be vulnerable to a variety of biases. Therefore, 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 2011). We compared count-based estimates with those from models based on vital rates 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 1 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 used 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 2011), and estimated average λ using log-linear regression (Eberhardt and Simmons 1992):

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

where $\log \lambda = e^r$, and *r* is the intrinsic rate of increase. 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 errors in population counts are multiplicative and log-normally distributed (Eberhardt and Simmons 1992).

RESULTS

Fecundity Components

Phenology and clutch size.—We used clutch initiation dates from 1,804 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, including a linear trend across years, were supported by our data ($\Delta\mathrm{AIC}_c > 7.27$, $\sum w_i < 0.03$; 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 during 19–30 May. The mean initiation date across sites and years was 25 May (SE: ±0.20 days), and peak (modal) initiation was 26 May. Process variance in initiation date was $\sigma^2 = 26.0$ days (95% CI: 22.54–49.12). Average initiation dates were 2–5 days earlier at the island site (KI) than at the mainland sites (TR and KR; Fig. 5), 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 (at least weakly) that timing of nesting was less variable in years of later clutch initiation. Further, 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 averaging 17 days. Repeated measurements of clutch initiation date and clutch size laid for 95 individuals (number captured in 2–6 subsequent yr: 2 yr = 70, 3 yr = 18, 4 yr = 4, 5 yr = 2, and 6 yr = 1) led to estimates of $r_{\text{absolute initiation date}}$ to be 0.49 (±0.01) and $r_{\text{relative initiation date}}$ to be 0.33 (±0.01).

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

Model	K^a	AIC_c^b	ΔAIC_c	w_i^b	r^2
1. Year, site	17	7,214.26	0.00	0.96	0.30
2. Year, site, year × site	30	7,221.52	7.27	0.03	0.30
3. Year	15	7,281.67	67.4	<0.01	0.27
4. Year (linear), site, year (linear) × site	7	7,703.70	489	<0.01	0.07
5. Year (linear), site	5	7,731.58	517	<0.01	0.05
6. Site	4	7,735.98	522	<0.01	0.05
7. Year (linear)	3	7,795.49	581	<0.01	0.01

[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 (w_i), relative to others in the model set.

We included data from 1,778 complete clutches to examine variation in clutch size. Our best approximating model included year and absolute initiation date (Table 2, model 1), but we also found limited support for a site effect (Table 2, model 2). We found little support for other models of total clutch size ($\Delta AIC_c \geq 4.90$). Among models, year and absolute initiation date (AINIT) were the most influential parameters ($\sum w_{\text{year}} = 0.99$, $\sum w_{\text{AINIT}} = 0.99$), followed by site ($\sum w_{\text{site}} = 0.28$). We found little support for models that included relative initiation date (RINIT; $\sum w_{\text{RINIT}} < 0.01$) or a linear trend in clutch size across years ($\sum w_{\text{NYEAR}} < 0.01$). The estimated seasonal decline in clutch size was 0.05 (±0.01) eggs/day. After adjusting for mean initiation date at each site-year (i.e., least squares means, Fig. 5), model-averaged clutch sizes (total clutch laid) ranged from 4.8 to 6.6 eggs across site-years. 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. 6). We calculated the grand mean (laid) to be 5.2 (±0.19) eggs/clutch 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 1 egg was lost was 0.24 (303 of 1281 nests). Annual egg loss for nests in which at least 1 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 CSH to be 4.7 (±0.2), ranging from 2 to 5.8 eggs/nest across site-years, and CSH 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.

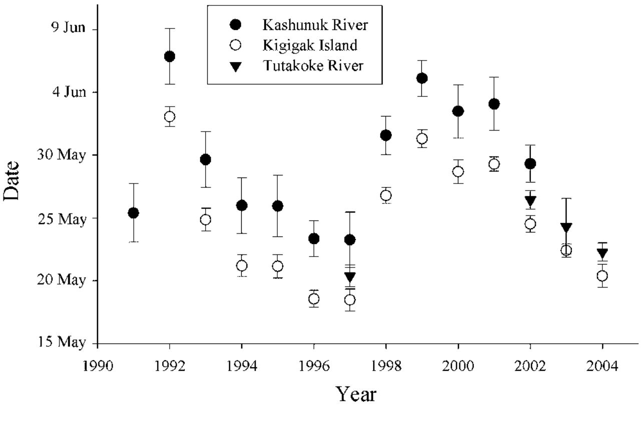


Figure 5. Least-squares estimates of mean clutch initiation dates (±SE) by study site and year for Pacific common eiders nesting on the Yukon-Kuskowim Delta, Alaska (1991–2004).

Nest survival.—We monitored 2,136 common eider nests during the 29 site-years of our study, comprising 29,272 total nest exposure days. This sample included 221 nests at the KR study area, 1,511 at KI, and 404 at TR. We found an average of 18 ± 1 (range: 10–34) nests/year at KR, 116 ± 1 (range: 67–224) at KI, and 101.0 ± 2 (range: 56–138) at TR. Of all nest failures (n = 1,029), 73% were due to predation, 26% to abandonment, and 1% due to other factors (Appendix 2).

After examining all possible combinations of observer (OBS) and trapping effects (TRAP) across study sites and years (Table 3), we used our top observer-effects model (OBS × site + TRAP × site; Table 4, model 1) as a fixed effect in all subsequent modeling. All models in the remainder of our analysis contained the OBS × site + TRAP × site term. Among models we examined, we found overwhelming support for variation in DSP among sites and years, across clutch ages, and across dates within years (Table 4). The 2 top models ($w_i > 0$) included a site × year interaction, quadratic effects of both clutch age (age^2) and date (date^2) on DSP, and an interaction between nonlinear date and year (date^2 × year; Table 4). We also found limited support ($w_{\text{model 2}} = 0.11$; Table 4) for a quadratic effect of clutch age that varied among years (age^2 × year). Less parameterized models were not supported by our data (Table 4; $\Delta AIC_c > 39.19$), and we found no model support for a priori predictions regarding asymptotic clutch age and date functions ($w = 0$).

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

Models	K^a	AIC_c^b	ΔAIC_c	w_i^b	r^2
1. Year, AINIT[c]	16	382.63	0.00	0.67	0.13
2. Year, AINIT, site	18	385.50	2.84	0.16	0.13
3. Year, AINIT, site, site × year	31	387.53	4.90	0.06	0.14
4. Year, AINIT, year × AINIT	29	387.88	5.25	0.05	0.14
5. Year, AINIT, site, year × AINIT	30	388.57	5.93	0.03	0.14
6. Year, ANIT, site, site × AINIT	20	389.01	6.38	0.03	0.14

[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 (w_i), relative to others in the model set.

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

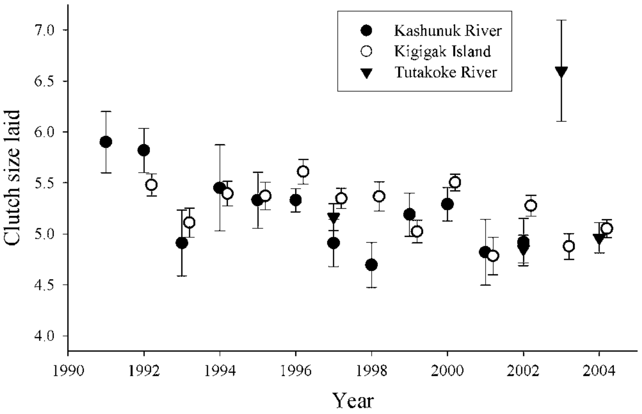


Figure 6. Least-squares estimates of mean clutch size laid (±SE) by study site and year at mean site-year initiation dates for Pacific common eiders nesting on the Yukon-Kuskowim Delta, Alaska (1991–2004).

We illustrated age-date DSP patterns with a single composite graph of all site-years (Fig. 7). 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 (Fig. 7). In general, DSP decreased with initiation date, dropping sharply after mid-June (Fig. 7). We also found 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. 7). This pattern 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. 7). 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. 7).

Overall nest-survival estimates ranged from 0.06 at Kigigak in 2001 to 0.92 at Kashunuk River in 1995 (Fig. 8, Table 5), and bootstrap confidence intervals for nest survival across all site-years ranged from 0 to 1 (Fig. 8, Table 5). The grand mean of 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). Overall, nest survival (i.e., success) consistently increased with clutch age and generally decreased with later initiation date (Fig. 7). Overall, observer effects (measured as a reduction in the probability of nest survival because of nest visitation) had a negative impact on nest survival (Table 5; $\mathrm{OBS}_{\mathrm{NS}}$) and varied consistently among sites. Observer effects were greater at sites with lower sample sizes (KR: $\overline{N} = 18$, $\overline{\mathrm{OBS}}_{\mathrm{NS}} = -0.28 \pm 0.02$, TR: $\overline{N} = 101$, $\overline{\mathrm{OBS}}_{\mathrm{NS}} = -0.18 \pm 0.03$), and vice versa (KI: $\overline{N} = 116$, $\overline{\mathrm{OBS}}_{\mathrm{NS}} = -0.06 \pm 0.01$; Table 3). Finally, using site-year estimates of CSH and nest survival, we calculated average productivity across site-years to be 2.7 ducklings hatched/hen (range: 0.2–4.7; Table 5).

Population Modeling

Matrix approaches.—Using mean values, process variance, and ranges for parameters in our stochastic population model (Table 6), we estimated summary matrix element values for YKD common eiders to be $F_1 = 0$, $F_2 = 0.03$, $F_3 = 0.15$, $F_{4+} = 0.17$, and all transition probabilities (S_{1+}) were 0.892, with $\lambda = 1.02$ (CI: 1.00–1.04). Under this scenario, the vectors for the proportional stable age-stage distribution (w) and relative reproductive values (i.e., the proportional reproductive

Table 3. Models of observer visits (obs) and trapping effects (trap) on daily survival probability for nests of adult female Pacific common eiders on Yukon-Kuskokwim Delta, Alaska, USA, 1991–2004.

Models	K^a	$\mathrm{AIC}_c{}^b$	$\Delta\mathrm{AIC}_c$	$w_i{}^b$
Trap × site, obs × site, year × site, age^2, date^2, year × date^2	52	3,708.39	0.00	0.47
Obs, trap, year × site, age^2, date^2, year × date^2	48	3,709.64	1.25	0.25
Trap × site, year × site, age^2, date^2, year × date^2	50	3,710.50	2.29	0.15
Obs × site, year × site, age^2, date^2, year × date^2	50	3,711.46	3.08	0.10
Obs, year × site, age^2, date^2, year × date^2	47	3,713.77	5.38	0.03
Trap × site, obs × year, year × site, age^2, date^2, year × date^2	63	3,719.30	10.91	0.00
Year × site, age^2, date^2, year × date^2	46	3,745.44	37.06	0.00
Constant	1	4,495.61	793.89	0.00

[a] K = number of parameters in model.

[b] 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 4. Selected models of daily survival probability for nests of adult female Pacific common eiders on Yukon-Kuskokwim Delta, Alaska, USA, 1991–2004.

Models[a]	K^b	$\mathrm{AIC}_c{}^c$	$\Delta\mathrm{AIC}_c$	$w_i{}^c$
Year × site, age^2, date^2, year × date^2, obs × site, trap × site	52	3,708.39	0.00	0.89
Year × site, age^2, date^2, year × date^2, year × age^2, obs × site, trap × site	65	3,712.46	4.08	0.11
Year × site, age^2, date^2, year × age^2, obs × site, trap × site	52	3,747.57	39.19	0.00
Age^2, obs × site, trap × site	10	4,016.26	307.88	0.00
Year, site, obs × site, trap × site	22	4,108.48	400.09	0.00
Constant	1	4,495.61	787.23	0.00

[a] Abbreviations: obs, observer effect; trap, trapping effect.

[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.

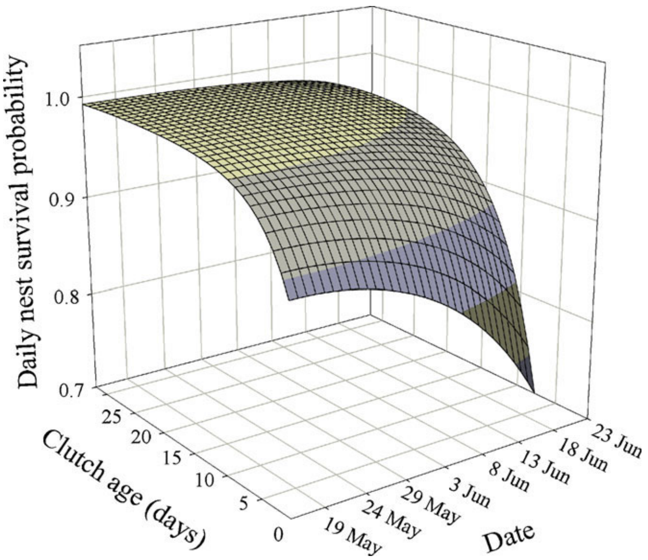


Figure 7. Daily nest survival probability of Pacific common eider nests on the Yukon-Kuskowim Delta, Alaska (1991–2004) as modeled by clutch age (laying through hatch) and by date within season. Daily survival rates were lowest during late season dates and early incubation and laying.

contribution of a given age-class female to the ancestry of future generations) among classes (v) were

$$w = \begin{bmatrix} 0.13 \\ 0.11 \\ 0.10 \\ 0.66 \end{bmatrix} \qquad v = \begin{bmatrix} 0.21 \\ 0.24 \\ 0.27 \\ 0.27 \end{bmatrix}$$

Our rankings of vital-rate analytic sensitivities and elasticities demonstrated that λ was always most sensitive to adult survival in the 4^+ (experienced breeder) stage-class (Fig. 9). In a prospective sense, λ was much less sensitive to age-specific lower-level reproductive parameters, particularly clutch size, juvenile survival, and breeding incidence (Fig. 9), than to adult survival. However, sensitivity to duckling survival appeared relatively high among fecundity parameters (Fig. 9). From a sensitivity perspective, adult survival had 1.5 times the relative influence on prospective population growth rate than did fecundity, and 9 times the relative influence from an elasticity standpoint. Further, despite its very low process variance, adult survival also contributed to a relatively large portion of retrospective fluctuations in λ (38%), primarily because of its high elasticity. Although these results are somewhat intuitive, given 66% of the individuals are in the 4^+ 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 fecundity components we included, duckling survival accounted for 42% of the variation in λ, nest survival accounted for 15%, juvenile survival for 4%, and CSH for 3%.

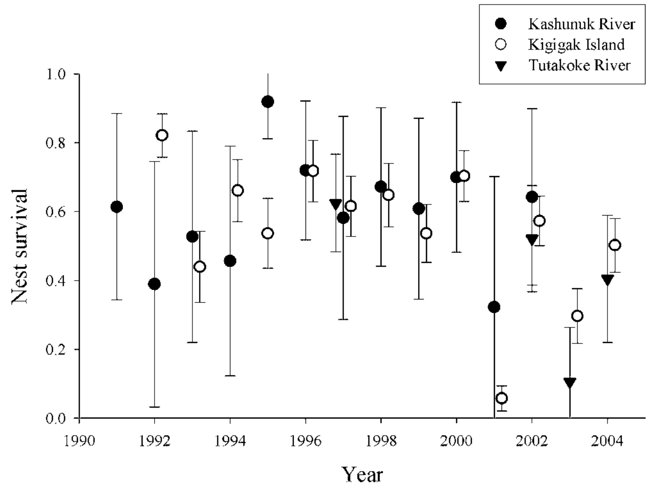


Figure 8. Estimated nest survival (±bootstrapped SE) of Pacific common eiders by study site and year on the Yukon-Kuskowim Delta, Alaska (1991–2004).

Table 5. 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, Alaska, USA, 1991–2004. Standard errors (SE) represent standard deviations for 500–1,000 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	[b]	[b]	0.11	0.16	−0.09	[b]
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.

[b] Years in which no nests survived to calculate clutch size at hatch.

Reverse-capture–recapture and log-linear regression.—Using reverse-capture–recapture techniques, we assessed encounter probabilities to be equal between previously marked and unmarked animals captured in $t + 1$ ($\chi^2_{15} = 11.19$, $P = 0.74$), suggesting no trap-dependent behavior among female Pacific common eiders. Our calculation of $\hat{c}$ (0.96) was $\leq$1. Thus, we did not adjust for overdispersion. 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). Our estimate of annual population growth based on log-linear regression of indices from aerial population surveys (1991–2004; Platte and Stehn 2011; Fig. 1) was 1.04 (CI: 0.98–1.10).

Table 6. Simulation types, mean values, process variance (σ^2), and ranges for parameters used in a stochastic population model of female Pacific common eiders (1991–2004) on the Yukon-Kuskokwim Delta, Alaska, USA.

Parameter	Simulation type[a]	Stage[b]	Mean	σ^2	Range
Clutch size at hatch	Stochastic	2 yr[c]	3.61	0.07	(2.85–4.09)
		3 yr[c]	4.50	0.07	(3.55–5.10)
		4^+ yr	4.85	0.07	(3.82–5.49)
Nest survival	Stochastic	2–4^+ yr	0.55	0.02	(0.06–0.92)
Duckling survival[d]	Beta	2–4^+ yr	0.19	0.02	(0.01–0.55)
Breeding incidence[c,e]	Deterministic[c]	2 yr	0.19	0.03	(0.35–1.00)
	Deterministic[c]	3 yr	0.70		
	Stochastic[e]	4^+ yr	0.78		
Juvenile survival	Beta	2–4^+ yr	0.90	0.005	
Adult survival	Beta	2–4^+ yr	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. Raw annual 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. 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 2–4^+-year-old class represents where a similar estimate was used for all classes of breeding adults.

[c] Estimates from Kats et al. (2007).

[d] Estimate of the mean from Flint et al. (1998*a*). Variance and range from Mendenhall and Milne (1985), 1961–1973.

[e] Estimates from Coulson (1984).

DISCUSSION

Fecundity Components

Phenology.—Nest initiation dates of common eiders on the YKD ranged over 56 days, similar to common eiders studied elsewhere (58 days; 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. Eighty percent of nests were initiated before 6 June each year, suggesting eiders undergo strict time constraints related to the short sub-arctic breeding season. As with black brant (Lindberg et al. 1997) and emperor geese (*Chen canagica*; Petersen 1992) on the YKD, as well as common eiders in Finland (Laurila and Hario 1988), we found some evidence that mean dates of nest initiation were less variable (i.e., tended to be more synchronized) in years of later initiation dates. However, the relationship was relatively weak in our case. Nonetheless, this may result from delayed availability of nest sites in late break-up years (Findlay and Cooke 1982*a*, Lindberg et al. 1997), but differences in age-related breeding propensities in early and late years also could contribute to this result. For example, in late years, young females may be more likely to skip breeding (Barry 1962, Murphy et al. 1991, Lindberg et al. 1997).

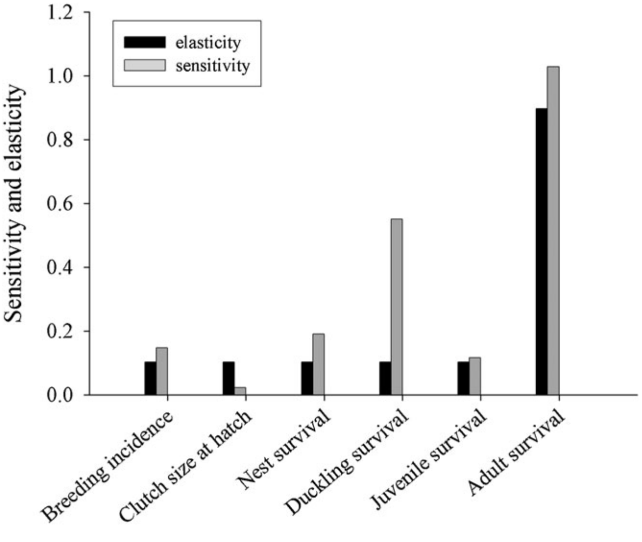


Figure 9. Sensitivity and elasticity of annual population growth rate associated with stage-specific vital rates for Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska (1991–2004).

Our estimates of repeatability in clutch initiation dates indicate that much of the variation in timing of nesting may be 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*b*). 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 age, experience, and/or body condition may be confounding factors (which we were unable to control for in our study), in general, considerable within-individual variation in nesting date implies a lack of strong selection pressure for timing of nesting in this population or perhaps, selection for flexibility to respond to environmental variability. 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, Lehikoinen et al. 2006, Jónsson et al. 2009). That is, selection for early nesting may appear strong, but not every individual female can match the optimum date that she should lay (in every year) because of high local environmental stochasticity (Lehikoinen et al. 2006, Jónsson et al. 2009, D'Alba et al. 2010).

Clutch size.—Because common eiders tend towards the capital breeding end of the capital-income continuum (Korschgen 1977, Drent and Daan 1980, Sénéchal et al. 2011), determination of their clutch size depends largely on endogenous reserves (Parker and Holm 1990, Erikstad et al. 1993, Coulson 1999) and seasonal phenology at breeding grounds (Laurila and Hario 1988, Sénéchal et al. 2011). The seasonal decline in clutch size we observed (about 1 egg fewer per 20-day delay in initiation) was similar to that observed in other eider studies (Grand and Flint 1997, Coulson 1999). In our study, this decline was best explained by absolute, rather than relative initiation date. We suggest 2 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 observed seasonal declines in clutch size. Although largely capital breeders, Pacific common eiders on the YKD 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 that undergo substantial migrations (Both and Visser 2001, D'Alba et al. 2010, Rigou and Guillemette 2010).

Clutch size emerged as a relatively static component of overall reproduction in Pacific common eiders. Initiation dates were consistently earlier at some sites versus others (Fig. 5), and model-averaged clutch sizes, adjusted for site-specific initiation dates, generally followed the same pattern (Fig. 6). Coefficient of variation 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 (see Laurila and Hario 1988). Conversely, longer-term (30–40 yr) studies of common eiders elsewhere (Hario and Selin 1988, Coulson 1999) 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, whereas Coulson (1999) found a pattern of steady decline, which he attributed to locally declining resources. 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 3 breeding sites (Petersen and Flint 2002, Petersen and Douglas 2004, Lehikoinen et al. 2006, Jónsson et al. 2009, D'Alba et al. 2010). Further, the subtle differences among our study sites may represent small localized differences in the habitat quality where birds forage immediately before clutch initiation (e.g., Coulson 1984, Rigou and Guillemette 2010).

Our best approximating models indicated that annual variation in timing of nesting was the primary driver of variation in clutch size. However, coefficients of determination in these models were low ($r^2 = 0.13$), and we suggest that some proportion of the unexplained variation could be 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; 0.67). 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, ultimately play a larger role in determination of clutch size.

Nest survival.—As with other high-latitude breeders (e.g., Murphy et al. 1991), point estimates of nest survival in YKD Pacific common eiders varied markedly across sites and years of our study (Fig. 8), ranging from <0.1 (2001 at KI; Fig. 8), to >0.9 (1995 at KR; Fig. 8). We suspect that factors such as climate and breeding ground conditions, variation in depletion rates of stored energy (Jónsson et al. 2009), and functional and numerical changes in predation pressure likely contributed to annual fluctuations in nest-survival estimates (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). However, the data available to us were either inadequate to test these hypotheses or did not track site-specific variation in nest survival within years. For example, we did not have adequate information to model the effects of fox abundance on DSP. Avian predators also are known to be responsible for most of the partial predation observed for other nesting waterfowl species on the YKD (Flint and Grand 1996, Grand and Flint 1997). Further, clutch sizes at hatch in our study were positively related to nest survival, suggesting factors that contributed to partial loss, such as avian predators, also contributed to total nest failure. However, the overall influence of avian predators is not likely to fluctuate to the same magnitude as that of mammalian predation (Quinlan and Lehnhausen 1982, Bêty et al. 2001, Sovada et al. 2001, Roth 2003), and would not be expected to contribute to increased oscillations in overall productivity to the same degree as mammalian predators. In summary, although 73% of all nest failures were ultimately attributed to predation, the role of specific predators and other factors influencing annual variation in nest survival for the YKD population of common eiders remain poorly understood.

Nest survival exhibited strong temporal variation within seasons. Daily survival probability varied according to quadratic trends in clutch age and date, the shape of which indicated that nests initiated early in some years and late in the season in most years (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 numerical 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). On the YKD, early-initiating common eiders begin egg-laying approximately 1 week after peak initiation for black brant (Fischer et al. 2009); likely a period of maximum predator swamping. Our results for DSP suggested strong directional selection for nesting at early dates (Fig. 7) 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 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). Several researchers (Milne 1974, Schamel 1977, Hanssen et al. 2003, Andersson and Waldeck 2006) have hypothesized that eiders likely begin incubating during the laying stage to protect eggs against avian predators. 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 (Korschgen 1977), resulting in decreased incubation constancy or nest abandonment as hens left the nest to feed shortly before hatching (Criscuolo et al. 2002).

We found support for negative effects of nest visitations and trapping (i.e., observer effects) on daily nest survival (Table 3). 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*). Disturbances likely leave the nest more vulnerable to avian predators (Swennen 1983, Bolduc and Guillemette 2003*a*). When scaled to the level of overall nest survival, we found observer effects to be extremely variable (range: 0.0 to −0.36 reduction in nest survival; Table 5; OBS_{NS}) and their magnitude negatively related to sample sizes of nests. 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 1989, Bêty et al. 2001). In addition, average visitation intervals varied by about 1 day among sites (KR = 5.71 days, TR = 5.14 days, and KI = 6.45 days). 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.

Increased visitation intervals will lead to increased precision in nest-survival estimates because the period between the final 2 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 somewhat misleading.

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 (0.10–0.93; Goudie et al. 2000). Our estimate of site-year average nest survival (0.55; 95% CI: 0.12–0.95) was higher than that calculated for sympatric-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 2 of our 3 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, and, in general, we found no evidence for a long-term shift towards earlier nesting. This result 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).

Conversely, other fitness components may demonstrate corresponding counter selection against very early breeding. 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, early breeding phenotypes may be 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.

Population Modeling

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 Bakke 2000, Eberhardt 2002). Pacific common eiders on the YKD were characterized by high, relatively invariant adult survival (Wilson et al. 2007) and low, variable fecundity (this study). Perturbation analysis revealed that the YKD population would respond most dramatically to changes in adult female survival, although 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. Finally, our finding of high sensitivity of λ to nest and duckling survival (relative to other fecundity parameters) suggested these vital rates may be influential in altering λ (Hoekman et al. 2002, 2006; Hario and Rintala 2006), and could be key factors in limiting population growth (Hoekman et al. 2006).

Demographic parameters ideally would be derived from long-term, multi-location studies of the population of interest, but management decisions and other conservation efforts are often forced to proceed despite incomplete demographic 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 common eider data sets collected by other researchers (Baillie and Milne 1982, Coulson 1984, Mendenhall and Milne 1985). A similar strategy has been used by other researchers, where not all parameters were locally available (e.g., Schmutz et al. 1997, Flint et al. 1998*b*, Gilliland et al. 2009). For some demographic measures, broad regional differences existed between our population and others, even within Alaska (e.g., overall reproductive rates between northern Alaska and our study). In other instances, our estimates and relationships between parameters matched closely with those from other populations (e.g., repeatability estimates, adult survival rates).

We have attempted to incorporate estimates and variability bounded by empirical data in parameters for which we did not have local estimates. 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, Schmutz et al. (1997) demonstrated that elasticity estimates for lower-level parameters were relatively robust to changes in mean parameter input values. Further, all substituted parameters in our study had inherently low elasticities and thus, likely had little effect on the conclusions of perturbation and variance decomposition analyses. Also, in our case, estimates of λ from stage-structured models (which used substituted data) were not appreciably different from λ 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 influential enough to dramatically alter estimated rates of growth (Schmutz et al. 1997, Flint et al. 1998*b*, Eberhardt 2002).

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). Traits closely linked to fitness should demonstrate little heritable variation (Falconer and Mackay 1996), and 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 could not 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 circumventing issues of inequality and inappropriate comparisons among matrix elements (e.g., bounded vs. unbounded elements; Doherty et al. 2004, Morris and Doak 2004). Under the hypothesis of selective buffering of vital rates that most influence fitness (Morris and Doak 2004), we suggest that adult survival is likely the most influential fitness component for Pacific common eiders.

Our multi-faceted 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 researchers should consider estimates from 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, mean estimates of λ^{matrix} predicted an average increase of 2% per year, whereas λ^{RCR} and $\lambda^{\text{log-linear}}$ predicted growth rates 2–3 percentage points higher than λ^{matrix}. Although our levels of precision in these estimates implies that the difference could be related to sampling error, the pattern of higher $\lambda^{\text{log-linear}}$ than λ^{matrix} appears consistent with previous studies (Schmutz et al. 1997, Doherty et al. 2004, Peery et al. 2006). Following the logic of Hines and Nichols (2002), λ^{matrix} (built upon capture–recapture estimates of apparent survival) is predicted to be consistently lower than λ^{RCR} or $\lambda^{\text{log-linear}}$ because movement is asymmetrical and apparent survival incorporates permanent emigration (loss), but not immigration (Nichols et al. 2000, Peery et al. 2006). Although common eiders tend to show high fidelity to breeding locations, genetic evidence indicates low levels of dispersal at multiple scales (Sonsthagan et al. 2007, 2011). Thus, differences among estimates could represent the relative contribution of immigration to population growth (Nichols et al. 2000, Peery et al. 2006).

Our 3 measures of population change not only allowed us to use all available data in creating a multi-faceted view of the population, but converged on a similar conclusion: the YKD Pacific common eider population appeared to be stable to slightly increasing from 1991 to 2004. We believe that no 1 measure alone would have provided as complete a picture as the complement of the 3 measures together. Each of the approaches has different levels of management application. The general agreement between the approaches functionally serves as a test of assumptions inherent in each technique. For example, population surveys are direct indices to status and trends and are commonly used to establish population goals and objectives, but survey data provide little information on inherent processes driving population change. Retrospective mark–recapture analyses are an efficient means to assess recruitment versus survival processes, but such analyses cannot identify specific management options or predict population response to perturbations. Finally, matrix models rely on difficult-to-collect data, but can identify the potential efficacy of viable management options (e.g., raising nest or duckling survival).

We do not know what precipitated the population decline of eiders from the 1950s to the early 1990s, but based on a log-linear model, the 85–96% eider population decline on the YKD (observed from 1955 to 1992; Stehn et al. 1993) would have resulted from an average annual reduction of 5–7% per year (i.e., $\lambda = 0.93$–0.95). Thus, using matrix approaches, 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, (e.g., fecundity was never less than 72% of the average during our 14-yr study), 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, not many animals would have to die (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 1950s to the 1990s. Therefore, very small increases in adult survival, combined with increases in fecundity (within the range of variation in our data), could lead to substantial rates of population increase for YKD Pacific common eiders. However, we caution that such a recovery may not be possible if the ultimate cause of the historic decline was something outside the scope of our research, such as a reduction in marine habitat conditions (e.g., benthic food shifts), as has been suggested for common eider populations elsewhere (Coulson 1984, Kats et al. 2007, Hario et al. 2009).

We provide several hypotheses for future study based on our results. First, given the strong influence of adult survival on prospective population growth, 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. Estimates of subsistence harvest of common eiders on the YKD during our study were relatively low (Wentworth 2004). In addition, little industrial development occurred in marine wintering areas used by these birds (Petersen and Flint 2002). However, changes in sea ice (Petersen and Douglas 2004, Petersen et al. 2012), general wintering conditions (Lehikoinen et al. 2006, Flint 2013), and marine benthic communities (Grebmeier et al. 2006, Lovvorn et al. 2009) may have greatly influenced adult survival.

Habitat changes on wintering grounds (Grebmeier et al. 2006, Lovvorn et al. 2009, Flint 2013) or brood rearing areas (e.g., near-shore benthic invertebrate food availability) could have possibly led to the reductions in populations to their current levels. If so, only a functional change in the carrying capacity of the environment would release the population to achieve recovery to historical levels. Initially, we assumed such density-dependent factors were not responsible for the historic decline in eiders on the YKD and likely played little role in the dynamics of our breeding population. This assumption was primarily based on observation of concurrent sharp declines in several sympatric nesting goose species on the YKD (King and Derksen 1986). These declines were largely attributed to excessive harvest and populations began to increase when harvest was restricted (Raveling 1984, King and Derksen 1986, Fischer et al. 2009).

Recent long-term studies of common eiders elsewhere have found evidence of density-dependent mechanisms, such as possible reductions in food resources resulting in combinations of reductions in reproductive parameters (e.g., fledging rate) and adult survival at high population levels (Coulson 1984, Hario and Rintala 2006, Kats et al. 2007, Hario et al. 2009). If similar mechanisms operate on our population (e.g., a reduction in carrying-capacity on wintering or brood-rearing grounds), they could explain both the long-term historic decline and more recent trends toward stabilization at lower levels. In fact, under this scenario, many of the management recommendations we suggest based on the elasticity analyses (assumed for a population with some possibility of increase) would be misleading (Grant and Benton 2000), because vital rates for a population at carrying capacity are predicted to be negatively correlated under the regulating ceiling of functional carrying capacity (Grant and Benton 2000). In other words, increasing any 1 vital rate would result in a decrease in another, as the population continually tries to right itself towards stability through counteracting mechanisms. We did not focus on density-dependent mechanisms in our study and have no data to address such factors given our current data, but suggest density processes as a plausible hypothesis for further investigation under an adaptive management framework.

The high prospective sensitivity and retrospective influence of duckling survival in our study suggests its potential as an important factor in the dynamics of Pacific common eiders. High duckling mortality is a common occurrence in eiders (Mendenhall and Milne 1985, Mawhinney 1999), and could potentially regulate population numbers through low annual recruitment over a series of years, as has been found for common eiders in the Baltic Sea (Desholm et al. 2002, Hario and Rintala 2006, Hario et al. 2009). Our results suggest depressed duckling survival may be a viable mechanism by which density-dependence could operate in this population; particularly given the sensitivity of this parameter to environmental fluctuations. Several studies have suggested that annual variation in duckling survival of eiders may be driven by environmental conditions (Swennen 1989, Flint et al. 2006) and that subsequent recruitment may be influenced by body condition obtained during brood rearing (Christensen 1999). Thus, more data will be necessary to better quantify and characterize factors influencing process variance in this vital rate for the YKD population.

Changes in emigration and immigration also may have 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 to have a 3.24 times greater effect on 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, Alisauskas et al. 2004, Mehl 2004, Peery et al. 2006, Sonsthagan et al. 2011). However, future work will be required to quantify the respective contributions of in situ recruitment and immigration to λ, and identify potential source populations from which emigration could be occurring (see Sonsthagan et al. 2011 for 1 approach).

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 and efforts to increase the already high adult survival rate on the YKD may be impractical.

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 2 components when developing conservation strategies. Our modeling demonstrated that potential population growth of YKD Pacific common eiders is most sensitive to changes in adult survival. Therefore, mortality pressures on adults, such as hunting and marine pollution, would be expected to have larger relative impacts on population dynamics than similar changes in reproductive parameters. Population models for other subspecies of common eiders have found analogous results (Coulson 1984, Gilliland et al. 2009), predicting dramatic shifts in population growth with changes in adult survival. In 1 example (western Greenland), where overharvest was hypothesized to be responsible for the 81% decline in breeding populations (1960–2000; Merkel 2004), a subsequent population model (Gilliland et al. 2009) predicted annual increases of 11% if recommended harvest restrictions were adopted. After just 6 years under the recommended restrictions, the population realized a >12.6% increase in growth (Merkel 2010), demonstrating the utility of the model with regards to the importance of adult survival and its accuracy in predicting the scope and scale of management actions and population response.

Reported hunting pressure on YKD Pacific common eiders during the period of our study was minimal (Wentworth 2004), and managing for at-sea mortality factors (i.e., near-shore Bering Sea wintering conditions) is likely unfeasible. Although we hypothesize that restricting harvest at any level 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. Alternatively, we suggest that immediate management strategies take an adaptive approach and begin by focusing on traits that may have lower elasticities, but higher inherent variation and management potential, such as components of fecundity (particularly duckling survival). Specifically, we advocate management actions such as periodic predator control at common eider breeding aggregations, which we hypothesize would simultaneously influence means and variances of both fecundity and adult survival, in addition to potentially benefiting other sympatric nesting species. Our results indicate considerable variability in the productivity components of Pacific common eiders in western Alaska. However, 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 speculate that the fate of common eiders may be closely tied to the fate of sympatric-nesting species (e.g., black brant; Raveling 1989), and we predict that management actions targeted at other species (i.e., those that facilitate predator swamping) will have positive, concurrent effects on nesting common eiders.

In summary, we suggest the best way forward may be an adaptive management approach starting under the assumption of density independence. Under this framework, we envision our modeling results being used as part of an iterative process, beginning with prediction of population response to management action, implementation of a management action, followed by assessment of actual response. We suggest that the only way to assess if density dependence is acting on our population is to manipulate life-history parameters and assess population response. If the population's response is contrary to model predictions, the assumption of density independence may be rejected and new models, including density-dependent models, should be explored. Rejection of the density-independent model would support management actions focused on habitat improvement.

SUMMARY

1. Components of reproduction of Pacific common eiders on the YKD Delta, Alaska, were low and variable across study sites and years, and within and among individuals.
2. Clutch initiation dates ranged from 4 May to 28 June, with peak (modal) initiation occurring on 26 May. We found limited evidence that population variance in initiation date was negatively related to the peak, suggesting increased synchrony in years of delayed initiation.
3. Total clutch size ranged from 4.8 to 6.6 eggs, and declined with date of initiation. After accounting for partial predation and non-viability of eggs, average CSH ranged from 2.0 to 5.8 eggs across years.
4. Within seasons, daily survival probability 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 likely attributed to sampling error. Slight observer effects reduced overall nest survival from 0.0 to −0.36 across site-years.
5. Larger clutch sizes and high nest survival at early initiation dates suggested a general pattern that favored early nesting.
6. The stable age distribution for Pacific common eiders was weighted heavily towards experienced adult females (≥4 yr). All calculations of λ indicated that the YKD population was stable to slightly increasing ($\lambda^{\text{matrix}} = 1.02$, CI: 1.00–1.054; $\lambda^{\text{reverse-capture–recapture}} = 1.05$, CI: 0.99–1.11; $\lambda^{\text{log-linear}} = 1.04$, CI: 0.98–1.10).
7. Perturbation analyses suggested the population would respond most dramatically to changes in adult female survival, whereas retrospective variation in λ was primarily explained by fecundity parameters (60%), particularly duckling survival (42%).
8. Increasing adult survival would have large positive effects on population growth, but practical ways to influence this vital rate are currently limited. We suggest that facilitating early nesting and targeting other sympatric-nesting species (e.g., increasing overall potential for predator-swamping through periodic predator control) may be the best means of producing positive, concurrent effects on populations of nesting common eiders.
9. We conducted our modeling efforts under assumptions of density independence, but density-dependent mechanisms may be responsible for the historic decline and subsequent stabilization of our population at a new, lower equilibrium. We recommend an adaptive-management approach using

our modeling results in comparison with actual population response to a management manipulation. Failure of the population to positively respond to increases in vital rates and negative correlations among vital rates may be seen as evidence of density-dependent regulation. Rejection of the density-independent model would support management actions focused on habitat improvement.

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Appendix 1. Adjusted[a] 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$_{4+}$	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	[b]	[b]	[b]	0.36
2004	KI	3.6	4.5	4.9	0.51
	TR	3.2	4.0	4.4	0.49

[a] 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.

[b] No nests survived to calculate clutch size hatched.

Appendix 2. Proportion 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.