The Journal of Wildlife Management 76(5):1011–1020; 2012; DOI: 10.1002/jwmg.335

Population Ecology

Population Dynamics of King Eiders Breeding in Northern Alaska

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ABSTRACT The North American population of king eiders (*Somateria spectabilis*) has declined by more than 50% since the late 1970s for unknown reasons. King eiders spend most of their lives in remote areas, forcing managers to make regulatory and conservation decisions based on very little information. We incorporated available published estimates of vital rates with new estimates to build a female, stage-based matrix population model for king eiders and examine the processes underlying population dynamics of king eiders breeding at 2 sites, Teshekpuk and Kuparuk, on the coastal plain of northern Alaska and wintering around the Bering Sea (2001–2010). We predicted a decreasing population ($\lambda = 0.981$, 95% CI: 0.978–0.985), and that population growth was most sensitive to changes in adult female survival (sensitivity = 0.92). Low duckling survival may be a bottleneck to productivity (variation in ducking survival accounted for 66% of retrospective variation in λ). Adult survival was high (0.94) and invariant ($\hat{\sigma}^2 = 0.0002$, 95% CI: 0.0000–0.0007); however, catastrophic events could have a major impact and we need to consider how to mitigate and manage threats to adult survival. A hypothetical oil spill affecting breeding females in a primary spring staging area resulted in a severe population decline; although, transient population dynamics were relatively stable. However, if no catastrophic events occur, the more variable reproductive parameters (duckling and nest survival) may be more responsive to management actions. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS demography, elasticity, king eider, perturbation analyses, population growth, sensitivity, *Somateria spectabilis*, stage-based matrix modeling.

King eiders (*Somateria spectabilis*) are migratory sea ducks that breed in the circumpolar Arctic and winter near the southern edge of the sea ice (Suydam 2000). The North American population of king eiders has declined by more than 50% since the late 1970s (Dickson et al. 1997, Gratto-Trevor et al. 1998, Suydam et al. 2000) for unknown reasons. King eiders from breeding grounds in northern Alaska and western Canada migrate to wintering areas in the Bering Sea (Suydam 2000, Phillips et al. 2006, Oppel et al. 2009) and are therefore subject to changes in both terrestrial and marine ecosystems. Until recently, little was known about king eider life history (e.g., Lamothe 1973, Cotter et al. 1997, Kellett and Alisauskas 1997), partly because they typically nest in remote locations at low densities and winter on the ice in largely inaccessible locations. However, studies from the last decade in northern Alaska and Canada lead to better parameter estimates for various life-history stages (e.g., Kellett et al. 2003, Mehl 2004, Mehl and Alisauskas 2007, Bentzen et al. 2008, Phillips and Powell 2009, Oppel and Powell 2010).

Potential threats to the population include climate change and increased anthropogenic activities in the Arctic and Subarctic, which may affect eiders both directly and indirectly. Both global warming and anthropogenic disturbance are likely to affect king eider survival through changes in the benthic invertebrate community, northern expansion of competitors, parasites, and infectious diseases, increased collisions with infrastructure, and habitat loss (Kerr 2002, Lovvorn et al. 2003, Dunton et al. 2005, Grebmeier et al. 2006, Bluhm and Gradinger 2008) which could have major consequences for the population. Additionally, receding sea ice cover, decreasing sea ice thickness, and technological advances have facilitated exploration of arctic seas (Kerr 2002, Khain and Polyakova 2006, Stroeve et al. 2008) resulting in increased oil and gas development, which may affect eider survival via displacement and potential oil spills.

Information on the population dynamics of king eiders is needed for management purposes given global climate change (King and Derksen 1986, Hinzman et al. 2005) and the ongoing exploration, development, and proposed lease sales for oil and gas development in prime migratory staging areas (Oppel et al. 2009), wintering areas (Schamber et al. 2010), and breeding areas (Bentzen et al. 2009). Although modeling is dependent on the quality of the data used in the model and may be sensitive to missing parameters, it helps to consolidate our understanding of the population dynamics of a species and we may not

Received: 23 February 2011; Accepted: 22 October 2011;
Published: 6 February 2012

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have the luxury of waiting while long-term data sets on all life-history parameters and any dependence between parameters are assembled. Demographic models aid in distinguishing among the intrinsic processes underlying apparent population trends and provide a functional link between life history and population dynamics. This allows managers to identify critical vital rates, develop strategies to mitigate population declines, and direct research towards the most influential vital rates.

Our goal was to incorporate available published estimates of vital rates with new estimates to examine the processes underlying population dynamics of king eiders breeding at 2 sites, Teshekpuk and Kuparuk, on the coastal plain of northern Alaska and wintering around the Bering Sea (2001–2010). We had 3 specific objectives. First, we defined and developed a basic population model that represented the age and stage structure, life cycle, and dynamics of king eiders breeding in northern Alaska to estimate the population growth rate (λ) and project it into the future (Caswell 2001). Second, we used analytic perturbation to examine the relative influence of potential changes in vital rates to changes in prospective λ, and variance decomposition to examine the contribution of each vital rate to retrospective variation in λ. Prospective analyses allow the projection of effects of changes in vital rates on λ, allowing research and management to be focused on the most influential vital rates, whereas variance decomposition helps us understand past variability in λ. This dual approach improves understanding of the historical decline and provides management tools for future conservation. Third, we manipulated our model to evaluate the impact of a hypothetical oil spill in a main spring migration staging area.

STUDY AREA

The coastal plain of northern Alaska includes the entire breeding range of king eiders within Alaska (Suydam 2000) and is representative of king eider habitat across a larger scale. We collected demographic data for king eiders nesting at 2 sites on the Arctic coastal plain of Alaska, one near Teshekpuk Lake (153°07′W, 70°25′N), and another within the Kuparuk oilfields (149°41′W, 70°27′N), 2001–2010. King eiders breeding at these sites disperse widely to 3 regions in the north, west, and east of the Bering Sea during the winter (Oppel and Powell 2008), mixing with eiders that breed in the eastern Russian and western Canadian arctic (Suydam et al. 2000, Phillips et al. 2006, Oppel et al. 2009). The Teshekpuk site was approximately 10 km south of the southeast shore of Teshekpuk Lake in the northeast planning area of the National Petroleum Reserve-Alaska (NPR-A), experienced minimal human impact (i.e., no roads, communities, or development for petroleum extraction), and was an area with the highest nest density in Alaska (Larned et al. 2009). The Kuparuk study site was between the Colville and Kuparuk river deltas, within a site developed for petroleum production, and had associated road networks and human activities. These 2 sites and the females sampled should be representative of available nesting habitat, predator communities, and nesting females across the coastal plain.

METHODS

We systematically searched each study area at least twice per breeding season for nests for the reproductive components of this study so as to include early and late initiating females (Bentzen et al. 2008). Adult females were trapped at both sites in early June 2002–2005 and late August 2006–2008 using mist-nets erected in ponds on breeding grounds (Oppel and Powell 2010) for the estimation of survival. Juvenile birds were trapped in late August using funnel traps and mist-net arrays in shallow water approximately 5 days prior to fledging at Kuparuk, and at an unnamed lake south of Teshekpuk Lake (70°26′N; 152°34′W) in 2006–2008 (Oppel and Powell 2010). All aspects of our fieldwork were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29).

Matrix Population Modeling

We developed a female, stage-based matrix population model (Caswell 2001) with the king eider life cycle structured as 3 age-based stages and a birth-pulse fecundity schedule with an annual time-step and pre-breeding census (Fig. 1). The first stage represented progeny that were 1-year-old and reproductively immature. The second stage represented 2-year-old reproductively immature females and the third stage represented breeding adults of age 3 and up (S_{3+}). King eiders do not breed until they are at least 3 years of age (Mehl 2004, Oppel and Powell 2010). These individuals could remain in the S_{3+} stage according to their survival as a self-loop. Matrix element values represented either means drawn directly from specified distributions or were the product of linear equations of lower-level parameters (e.g., fecundity). Each stage graduated to the next at each time step (1 yr), and transition probabilities in our model were the probability of survival to the next stage. We assumed all adult birds (age 3+) experienced a similar adult survival rate, and that pre-breeding females had a similar annual survival rate in their second and

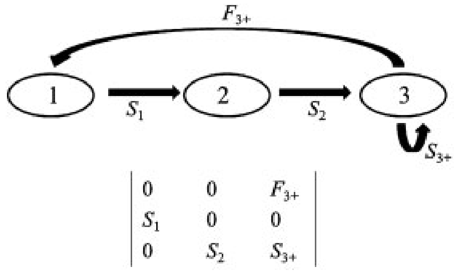

Figure 1. The life-cycle and stage-based matrix for a population model of female king eiders breeding in North America. Stage 1 = reproductively immature 1-yr-old progeny, stage 2 = reproductively immature 2-yr-old females, stage 3 = reproductive adult females age 3 yr and up, fecundity transition (F_{3+}) = reproductive contribution, and survival transitions (S_i) = apparent annual survival probability.

third years (S_1 and S_2). We assessed population change over time using the difference equations

$$\begin{aligned} n_1(t+1) &= n_3(t)F_{3+} \\ n_2(t+1) &= n_1(t)S_1 \\ n_{3+}(t+1) &= n_2(t)S_2 + n_{3+}(t)S_{3+} \end{aligned}$$

where $n_i(t)$ is the number of individuals of age-class i at time t, S_i is the annual survival rate of individuals in age-class i, and F_i is the fecundity of individuals in age-class i.

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, according to the equation:

$$F_{3+} = \mathrm{CSH} \times \mathrm{NS} \times \mathrm{SR} \times \mathrm{BI} \times \mathrm{DS} \times \mathrm{JS}$$

where F, fecundity; CSH, clutch sizes at hatch; NS, nest survival; SR, sex ratio of offspring; BI, breeding incidence; DS, duckling survival (hatch to 24 days); and JS, juvenile survival (approx. 30 days to just before 1 yr; Wilson 2007).

Each lower-level vital rate was obtained either from a beta simulation that drew estimates from a beta distribution (calculated from an observed mean and process variance), or a deterministic single point estimate without an estimate of process variance. Incorporating variation, where possible, as a beta distribution mirrors the actual dynamics of the population far better than a simple deterministic point. We used estimates of spatio-temporal process variance in the model as it has been shown that when modeling population dynamics, sampling variation should be removed from total variation so that the focus of a population analysis is on only process variation (Mills and Lindberg 2002). We did not consider covariation between parameters because of data limitations.

Estimates indicate that 10,000–35,000 individuals nest on the arctic coastal plain (Suydam 2000), so we assumed a 50:50 sex ratio and used a starting population of 10,000 females in our model. We projected the population 50 years using 1,000 iterations. We calculated λ from the asymptotic model at stable age distribution from each of our 1,000 simulations according to the Heyde and Cohen (1985) equation. We then calculated mean λ and constructed 95% confidence intervals based on the 2.5 and 97.5 percentiles of the sorted λ. We performed all stochastic modeling with AVESMODELER (www.ag.auburn.edu/aux/alcfwru/avsmdl/, accessed 7 Sep 2010).

Perturbation Analysis

We used prospective analyses (sensitivity and elasticity) to explore the functional dependence of λ on the vital rates (Caswell 2000). Sensitivities measure the absolute change in λ, given an infinitesimal absolute change in a vital rate, while all other vital rates remain constant. Analytical elasticities rescale the sensitivity to account for the magnitude of both λ and the vital rate resulting in a measurement of the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate (Caswell 1989, de Kroon et al. 2000), assuming the population is growing or decreasing at a constant rate and has a stable age distribution. Prospective analyses allow for the identification of future management possibilities as changes in vital rates with high sensitivity or elasticity will produce large changes in λ, but identifying which factors limit population growth is not possible (Beissinger and Westphal 1998).

Using a retrospective approach, we estimated how variability in λ is a function of observed variation in the vital rates (Caswell 2000). We decomposed the variance in λ by weighting a given parameter's elasticity by its coefficient of process variance (Steen and Erikstad 1996, Pfisterer 1998, Wilson 2007). We only investigated parameters for which we had an estimate of process variance, and we only compared these variance components relative to each other.

As this is a long-lived species that does not breed until age 3 and temporal lags may be expected in response to perturbation, we also examined the transient (non-equilibrium) dynamics. We calculated the max reactivity of the population matrix to perturbation of the stable age ratio (R), the speed of convergence to the stable age distribution (the damping ratio, ρ), and the approximate measure of the maximum time to converge to the stable age distribution (T; Ezard et al. 2010).

Parameter Estimation

Transition probabilities.—We reran the analyses described in Oppel and Powell (2010) including data for the year beginning June 2009 and ending June 2010 to update estimates of adult, juvenile (30 days to 1 yr), and sub-adult (1–2 yr) survival with the latest data from satellite transmitters. Additionally we quantified process variation in apparent survival by including an additional model that added trap year × trap site structure to the top model for both the adult ($n = 98$) and juvenile to sub-adult model sets ($n = 61$), used the variance components function (White et al. 2001) in Program MARK (White and Burnham 1999), and treated variation in apparent survival as a random effect among trapping site-years with mean μ and variance σ^2. King eider populations are known to occasionally experience catastrophic events (Suydam 2000); however, none occurred during the study period, which may artificially lower our estimate of variation in adult survival. To evaluate the effect of greater variability in adult survival we re-ran the model with the process variance around adult survival increased to 0.002.

Fecundity.—Because no estimates of breeding incidence are currently available for king eiders, we substituted a mean estimate for adult common eiders (*Somateria mollissima*) breeding between 1958 and 1982 in England (Coulson 1984) as a deterministic point. Additionally, we reran the model as a beta simulation using the above estimate of mean breeding incidence with an arbitrary but relatively large estimate of variance (0.2). Similarly, we assumed a 50:50 sex ratio based on common eider ducklings sexed at hatch in western Alaska (Wilson 2007). Although renesting can potentially increase the probability of reproductive success within a year (Flint et al. 2006), king eiders do not appear to renest (R. L. Bentzen, University of Alaska Fairbanks, unpublished data), and thus renesting was not included in the model.

We used published estimates for king eider duckling survival from hatch to 24 days at Karrak Lake in northern Canada (Mehl and Alisauskas 2007) as a deterministic point in the matrix model (Table 1). Phillips and Powell (2009) estimated brood survival for king eiders at Kuparuk, Alaska, but were unable to estimate the duckling survival estimates needed for this model and their sample sizes were small. Their estimates of brood survival (0.1, 95% CI: 0.02–0.49) were lower, but overlapped brood survival estimates from Karrak Lake (0.31, 95% CI: 0.13–0.5; Mehl and Alisauskas 2007) and we are possibly biasing our estimate of λ high by using the Canadian estimates. Additionally, we re-ran the model with duckling survival as a beta distribution using the above mean estimate of survival with an estimate of process variance calculated from a 13-year study of common eiders in Scotland (Wilson 2007).

We used published estimates of nest survival and process variance for king eiders at Teshekpuk and Kuparuk (2002–2005) that controlled for observer effects via model structure (Bentzen et al. 2008; Table 1). We used the estimates controlling for observer effects because even small observer effects can strongly decrease estimates of nesting success and population trajectory (Rotella et al. 2000).

We calculated mean clutch size from 340 king eider nests from Teshekpuk and Kuparuk, 2001–2006 (Bentzen et al. 2008). The model called for clutch size at hatch and we substituted clutch size at initiation of incubation. We felt this was appropriate as partial clutch loss is very rare (Bentzen et al. 2008) and we did not have a large enough sample size of clutch size at hatch to estimate process variance. We produced 1,000 bootstrapped-resamples of the original data set (i.e., resampling clutches with replacement, up to the original sample size within each site-year; PROC SURVEYSELECT; SAS Institute, Cary, NC) and calculated clutch size for each. We used the standard deviation among the 1,000 bootstrapped estimates (for each site-year) as the standard error for overall clutch size in each site-year (Efron and Tibshirani 1993), allowing us to estimate spatio-temporal process variation in clutch size using variance-components approaches outlined by Burnham et al. (1987).

Hypothetical Oil Spill

Lastly, we manipulated our model to simulate the impacts of an oil spill in the eastern Chukchi Sea during spring migration. The eastern Chukchi Sea is a primary staging area for king eiders during fall and spring migrations (Oppel et al. 2009) and it is being proposed for oil and gas development and production. The eastern Chukchi Sea is also a primary staging area for the other eider species (common, spectacled [*S. fischeri*], and Steller's [*Polysticta stelleri*] eiders). If the proposed development takes place, the probability of a major spill (>1,000 barrels) in the Chukchi Sea is predicted to be 27–54% (Minerals Management Service 2007). Oppel et al. (2009) found that all king eiders migrating to breeding grounds in western North America used the eastern Chukchi Sea for at least 1 week during spring migration. Given that a small oil spill in the Pribilof Islands, Alaska on 17 February 1996, killed an estimated 1,609 king eiders during the winter period (Suydam 2000), a major oil spill in a primary staging area during migration could kill many more individuals.

To evaluate the impact of an oil spill in a primary staging area during spring migration we used our basic model with deterministic values for all vital rates and ran 3 additional models each with a catastrophic event in the 10th year. First, we modeled a small oil spill that kills 1,000 breeding-stage females (approx. 10% of the breeding age population). We did not include any additional mortality for the non-breeding sub-adult age classes as their timing and use of the Chukchi may differ from breeding adults (Oppel et al. 2009). Second, we increased mortality to 3,000 breeding females. Third, we modeled the possibility that 4,600 adult females (approx. 50% of population) would be killed. We used deterministic simulations to allow the calculation of transient sensitivities and population momentum in AVESMODELER. Population momentum is the relative change in the long-term population size caused by a change

Table 1. Parameters used in a stochastic population model of female king eiders on Alaska's arctic coastal plain, 2001–2010. Simulation types, mean values, and process variance (σ^2) are presented. Beta simulations draw simulated estimates from a beta distribution built from the observed mean and σ^2 for the parameter of interest. Deterministic values represent average parameter estimates with no associated variances or ranges.

Parameter	Mean	Process variance	Simulation type	Years
Breeding incidence[a]	0.78		Deterministic	1958–1981
Clutch size	4.41	0.074	Stretched Beta[b]	2001–2006
Nest survival[c]	0.36	0.007	Beta	2002–2005
Duckling survival	0.10[d]	0.02[e]	Deterministic/Beta	2000–2001
Juvenile survival[f]	0.65	0.003	Beta	2006–2010
Sub-adult survival[g]	1.00		Deterministic	2006–2010
Adult survival[h]	0.94	0.0002	Beta	2002–2010

[a] Estimates from Coulson (1984) for common eiders.
[b] Distribution rescaled to lie between biologically realistic end points (Morris and Doak 2002).
[c] Estimates from Bentzen et al. (2008).
[d] Estimate from Mehl and Alisauskas (2007).
[e] Estimate of process variance for common eider duckings (Wilson 2007).
[f] Survival from 30 days to 1 yr.
[g] Annual survival from 1 yr to 3 yr.
[h] Annual survival of reproductively mature females age 3+ yr.

in the stable age distribution (Ezard et al. 2010). Transient sensitivity is the change in the transient population growth rate caused by a small absolute change in a vital rate (Yearsley 2004, Koons et al. 2006).

RESULTS

Parameter Estimation

Clutch size ranged from 2 to 8 eggs and averaged 4.4 eggs/nest at Teshekpuk and Kuparuk, Alaska, between 2001 and 2006. Estimated site year-specific process variation in clutch size was 0.07 (95% CI = 0.06–0.23).

An additional year of data did not change the ranking of the models describing adult survival reported by Oppel and Powell (2010). The top model, constant survival, still received the most support (second-order Akaike's Information Criterion [AIC_c] weight = 0.55) and estimates of adult annual survival rate did not change (0.94, 95% CI: 0.90–0.96, $n = 98$; Table 1), although confidence intervals were slightly narrower. The model we included for estimation of process variance, where survival varied by trap year and site, was 9.62 AIC_c units from the top model and carried 0.4% of the AIC_c weight. Our results suggest that apparent annual survival of adult eiders is spatially and temporally invariant ($\hat{\sigma}^2 = 0.0002$, 95% CI: 0.0000–0.0007).

Similarly, including an additional year of data for first and second year survival did not change the ranking of the top models reported by Oppel and Powell (2010), although it increased our confidence in model ranking. The top model, of seasonal variation in first year survival and constant survival the second year (AIC_c weight = 0.84), was 3.3 AIC_c units from the next best model which included variation by sex in the first year. Survival estimates for the first year were very similar with the larger data set; we estimated survival for the first year as 0.65 (95% CI: 0.53–0.76; Table 1) and Oppel and Powell (2010) reported a survival rate of (0.67, 95% CI: 0.48–0.80). We estimated second-year survival as 1.00 (95% CI: 0.94–1.00), using profile likelihood confidence intervals as we recorded no mortalities in the second year. The model we included for estimation of process variance, where we added trap year × trap site structure to the top model, was 19.73 AIC_c units from the top model and carried <0.01% of the AIC_c weight. Our results suggest that apparent annual survival of juvenile eiders was more variable ($\hat{\sigma}^2 = 0.0034$, 95% CI: 0.0020–0.0063) than that of adults.

Population Model

If 2001–2010 demographic rates are maintained and duckling survival is simulated as a deterministic point, estimates of λ from the asymptotic model at stable age distribution indicated a 1.9% population decline per year ($\lambda = 0.981$, 95% CI: 0.985–0.978) for king eiders breeding in northern Alaska. However, the population decline is not significant when duckling survival is included as a beta distribution with the estimated process variance ($\lambda = 0.980$, 95% CI: 0.960–1.010). If breeding incidence is modeled as a beta distribution with a wide range, while keeping duckling survival as a deterministic point, the population decline decreases slightly to 1.8% per year ($\lambda = 0.982$, 95% CI: 0.978–0.985) but is still significant. If variability around adult survival was increased, the population decline decreased and confidence intervals around that estimate increased ($\lambda = 0.982$, 95% CI: 0.976–0.987). Prospective analysis suggested that λ was more sensitive to adult survival than to sub-adult survival and lower-level reproductive parameters (breeding incidence, clutch size, nest survival, duckling survival, and juvenile survival; Fig. 2). With a sensitivity of 0.93, a small change in adult survival will produce a large change in λ. However, λ was relatively sensitive (0.35) to duckling survival (Fig. 2).

The max reactivity of the population matrix to perturbation of the stable age ratio (R) was 0.317, the damping ratio (ρ) was 4.85, and the approximate measure of the maximum time to converge to the stable age distribution (T) was 4.37.

The retrospective analysis demonstrated a somewhat different emphasis than did the prospective analysis. Of the parameters considered, where estimates of spatio-temporal process variance for Alaska's north slope are available, variation in lower-level reproductive parameters accounted for 53% of retrospective variation in λ (clutch 9%, nest survival 32%, juvenile survival 12%). Adult survival accounted for 47% of retrospective fluctuations in λ despite its high elasticity because of its very low process variance. However, if duckling survival is included using a naïve estimate of process variance estimated for common eider ducklings, the picture changes significantly. In the latter case, retrospective variation in λ was largely due to variation in the lower-level reproductive parameters (84%; clutch 3%, nest survival 11%, duckling survival 66%, juvenile survival 4%), and adult survival accounted for only 16% of retrospective fluctuations in λ. If variation in adult survival is increased, adult survival accounts 74% of retrospective fluctuations in λ while the contributions from lower-level reproductive parameters decrease to 26% (clutch 4%, nest survival 16%, juvenile survival 6%).

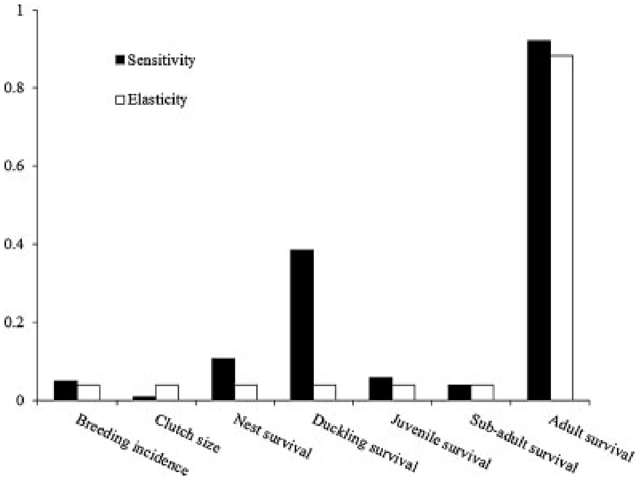

Figure 2. Sensitivities and elasticities calculated from a demographic model of king eiders breeding on the coastal plain in northern Alaska, 2002–2009. Sensitivities measure the absolute change in population growth rate (λ), given an infinitesimal absolute change in a vital rate, while all other vital rates remain constant. Elasticities rescale the sensitivity to account for the magnitude of both λ and the vital rate resulting in a measurement of the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate.

Hypothetical Oil Spill

Estimates of λ from the model simulating an oil spill killing 1,000 breeding age females in the 10th year showed a 2.1% population decline per year ($\lambda = 0.979$) with the population decreasing to just 3,494 individuals in 50 years. The population momentum (M) was 1.0. Increasing the adult female mortality in the 10th year to 3,000 individuals resulted in a 2.7% mean population decline per year ($\lambda = 0.973$) with the population decreasing to just 2,540 individuals in 50 years ($M = 1.0$). Further increasing the adult female mortality to 5,000 individuals resulted in a 3.4% population decline per year ($\lambda = 0.964$) with the population decreasing to just 1,587 individuals in 50 years ($M = 1.0$). The transient sensitivities were similar to asymptotic sensitivities in the first 10 years following perturbation for all 3 scenarios. Average change from asymptotic sensitivities was 0.03 (all 3 scenarios); adult survival had the largest relative effect (0.14) followed by duckling survival (0.06).

DISCUSSION

Matrix population models are particularly useful for identification of parameters lacking good estimates, identification of sensitive life-history stages, and in aiding in management decisions. Sensitivity, elasticity, and variance decomposition analyses are based on relative differences in λ rather than precise estimation of λ, and thus are relatively robust to minor inaccuracies in model structure or parameter estimates. Prospectively, the population growth rate for king eiders breeding in northern Alaska was most sensitive to changes in adult survival. Retrospectively, adult survival was also influential, although less so. This is alarming given that the 2 major threats facing king eiders, global warming and anthropogenic disturbance, are likely to affect adult survival, which could have major consequences for the population. Hunting pressure can also affect adult survival and thus the population trajectory. The population nesting on the Alaskan coastal plain may be affected by subsistence harvest at Barrow, or possibly in Russia where the harvest is unknown but where a substantial proportion of North American breeding eiders molt and winter (Phillips et al. 2006, Oppel et al. 2008). However, given our very high estimates of adult and sub-adult survival and only a single reported hunting mortality out of 159 king eiders implanted with satellite transmitters, hunting pressure is unlikely an influential factor in the dynamics of this population. Of larger concern is how global change and anthropogenic disturbance may change the balance between more frequent but lower impact events and infrequent but potentially catastrophic events.

Adult survival was high and invariant resulting in the high sensitivity estimate but lower estimate of influence on past fluctuations of λ. However, we are possibly underestimating the variability in adult survival because no catastrophic events occurred during our study. Catastrophic events affecting a large proportion of the population have been documented; an estimated 100,000 king eiders (possibly 10% of the population) starved while on spring migration in 1964, about 50,000 flightless females and young perished during a sudden freeze, or epidemic, on Banks Island, Northwest Territories, and the small oil spill in the Pribilof Islands in the late 1990s killed an estimated 1,609 (Suydam 2000). Evaluating the effect of a possible underestimation of the variance around adult survival resulted in an increase in the influence of adult survival in past population fluctuations indicating that adult survival may be more influential retrospectively than we initially predicted.

Population growth rate was relatively sensitive to duckling survival, prospectively. Duckling survival was also included in a retrospective analysis, and explained 65% of retrospective fluctuations in λ. Although our estimates of duckling survival and associated process variance are sub-optimal, in general, whether we included duckling survival in the variance decomposition analysis or not, measures of fecundity were influential in retrospective fluctuations of population size. However, caution must be used when interpreting the relative influence of parameters when some parameters are not included (e.g., breeding incidence). Duckling survival is a case in point: variation in lower-level reproductive parameters accounted for 50% of retrospective variation in λ when duckling survival was not included, but accounted for 83% of retrospective fluctuations when duckling survival was included.

The relative influence of duckling survival to λ may indicate that it is a bottleneck to population growth (Hoekman et al. 2006). High sensitivities of λ to duckling survival have been found in other studies of waterfowl (Hoekman et al. 2006, Wilson 2007, Schamber et al. 2009) suggesting that it is a particularly critical stage of life regardless of the ecosystem. If duckling survival is actually lower in Alaska than the model assumes, it may create an even more severe reproductive bottleneck and further increase the sensitivity of λ to duckling survival and the contribution of duckling survival to past variation in λ. The highest densities of king eiders breeding in Alaska are within the National Petroleum Reserve-Alaska (Larned et al. 2009) of which >87% is designated for oil and gas leasing (Bureau of Land Management 1998, 2004). The impacts of oil and gas development in the breeding areas include habitat loss, increased predation by foxes and gulls, and potential spills. In addition, climate change in the terrestrial environment is predicted to affect shrub cover, timing of snow and ice melt, and wetland hydrology (Traylor and Alisauskas 2006). Although the relationship between anthropogenic disturbance, changing wetland structure, and predator communities has not been specifically investigated for king eider ducklings, these variables affect other species of waterfowl (Quinlan and Lehnhausen 1982, Pamplin 1986, Sargeant and Raveling 1992, Stickney and Ritchie 1996, Suydam et al. 2000, Traylor and Alisauskas 2006).

We projected that the population of king eiders breeding in northern Alaska is declining by approximately 1.9% per year, although confidence intervals overlapped 1 when duckling survival was included with associated variance. This decline is similar to that estimated by migration counts in northern Alaska between 1953 and 1996 (3.6%; Suydam et al. 2000). However, aerial survey data showed a significant increase of about 2.8% per year in king eiders breeding on the coastal plan between 1992 and 2009 (1.028, 90% CI: 1.016–1.039; Larned et al. 2009). A similar pattern of λ being greater when estimated by aerial surveys than when estimated via a Leslie style population matrix was found in a number of studies (Nichols et al. 2000, Doherty et al. 2004, Peery et al. 2006, Wilson 2007) and was attributed to asymmetry in movement; matrix approaches generally incorporate emigration into their apparent survival rates but not immigration (Sæther and Bakke 2000). Additionally, aerial surveys have a number of assumptions including no bias in detection or timing of the survey. Trends in either can be misidentified as trends in bird numbers. It is also possible that the proportion of females present on the breeding grounds but not participating in breeding has changed over time. Alternatively, our estimates of adult, juvenile, and/or duckling survival could be biased low as all are based on birds that have been subjected to capture, handling, and in some cases implanted with satellite transmitters. However, mortality after transmitter implantation was extremely low and our survival estimates were quite high. The different results from our modeling and aerial surveys highlight the potential problems with estimating a population trajectory, the importance of defining what question is being asked, delineation of the population, and the assumptions inherent in each technique. Reliable estimation of λ using a matrix population model requires that the correct model structure has been specified (i.e., correct parameters, structural relationships, consistent spatial scale, selection of representative sample of individuals for parameter estimates) and that parameter estimates are unbiased and suitably precise. Of the 3 approaches, matrix modeling can best aid in the identification of sensitive life-history stages and in directing future research needs. Our model highlights the need for better estimates of duckling survival and breeding incidence and that any decrease in adult survival may seriously affect the population.

Our model is density-independent and we have assumed no compensatory relations between parameters. If the king eider population is below historical numbers then an additive model is justified; however, this, although likely, is unknown. As the population is predicted to be stable to declining, we feel it is unlikely to be regulated in a density-dependent fashion. However, if sources of adult mortality shift it, managers must determine if they act in an additive or compensatory fashion. For example, king eiders have very low natural adult mortality rates and above a certain level, hunting mortality must be additive. Although we do not have the long-term data needed to assess relationships between density and life-history parameters, lack of data does not eliminate the need to consider these factors and may guide data collection efforts for the future. Additionally, we are ignoring temporal correlations between vital rates (e.g., trade-offs between life-cycle components), which can strongly influence the values of elasticities and estimates of lambda (Sæther and Bakke 2000).

We were forced to substitute estimates of breeding incidence from common eiders nesting in Northumberland for king eiders in North America. The model would be much improved if we had estimates of the proportion of the king eider population that go to the breeding grounds on the coastal plain and the proportion of those that actually attempt breeding. Unfortunately, these rates are difficult to estimate. Periodic non-breeding has been reported for king eiders possibly due to bad weather, extensive spring ice, or low densities of lemmings and high densities of foxes (Suydam 2000), as has the presence of non-breeding females on the breeding grounds (Lamothe 1973), and habitat conditions experienced by this population of king eiders are much more severe than those experienced by common eiders breeding in Northumberland. This suggests that breeding incidence may be lower and more variable for king eiders, possibly leading to a positive bias in our estimate of λ. However, our evaluation of the impact of increasing the variability around breeding incidence suggests that even a very large variance only resulted in a slight decrease in the predicted population decline. Although the common eider values for breeding incidence had inherently low elasticities, and, thus, little effect on the estimation of λ, king eider breeding incidence may actually have greater variability than reflected in our model and thus have had an impact on past population fluctuations.

Immigration, emigration, survival, and recruitment ultimately determine the dynamics of a population. The influence of immigration and emigration are dependent on the scale of the study in question. If the entire population of a species is under consideration then immigration and emigration are non-existent. However, in reality, studies typically investigate population dynamics of a subset of the entire population, often based on arbitrary limits such as international borders. Although we too, are using somewhat arbitrary population delineations, king eiders exhibit high female natal site fidelity (Oppel and Powell 2010), and breeding area fidelity (Phillips and Powell 2006, Bentzen 2009) which should limit the influence of emigration and immigration on population dynamics. The results of this study apply only to the population of king eiders which breed in northern Alaska and winter around the Bering Sea.

These data represent a first attempt to build a population model for king eiders breeding in northern Alaska. We predicted a 2% annual population decline and that population growth was most sensitive to changes in adult female survival but that low duckling survival may be a bottleneck to productivity. Our estimate of population momentum for king eiders was not substantially different from 1, indicating that the long-term abundance will not be greatly affected by historical population structure (Ezard et al. 2010). Additionally, the transient sensitivities were similar to the asymptotic sensitivities. This suggests that king eiders should be resilient to perturbations to the stable age distribution and indicates that asymptotic analysis is applicable. Although we were limited in some aspects by sample size (sub-adult survival) and missing parameters (breeding incidence, duckling survival), our model contributes toward managing the population and mitigating future impacts. Future research should investigate duckling survival, breeding incidence, and stage- and age-specific vital rates. Duckling survival appeared to have the potential to control annual fluctuations in λ, underlining the need to understand the environmental determinants of variation in duckling survival. Although we were unable to incorporate age- or stage-specific reproductive rates, older, more experienced, or more fit females may have higher reproductive rates (Mehl 2004, Mehl and Alisauskas 2007, Bentzen et al. 2010). Lastly, we need to better understand the influence of winter diet and environmental factors on adult survival.

MANAGEMENT IMPLICATIONS

Minerals Management Service (2007) predicts a 27–54% chance of a major oil spill if proposed development occurs in the eastern Chukchi Sea, an area where all western North American king eider females stage during spring migration. We show that if an oil spill during spring migration kills 1,000–5,000 breeding age king eider females that the population will decline to just 1,500–3,500 females in 50 years. An oil spill of this size would also affect juveniles, males, and non-breeding females, which were not included in the model, and would likely result in the overall impacts of the spill being greater than our prediction. Such a serious event did not appear to change the population's sensitivity to the different vital rates and evaluating impacts to the population can likely be based on asymptotic analysis. Catastrophic events, such as an oil spill or mass starvation, that affect otherwise high and invariant vital rates, are rare and infrequent, leading to the variability of these vital rates being underestimated in many studies. Catastrophic events differ from less variable impacts, such as hunting mortality, and only in the absence of catastrophes will the more variable, but less sensitive, vital rates respond adequately to management. Preventing such impacts may involve protecting primary staging, wintering, and molting areas in the Chukchi (Ledyard Bay, Kasegaluk Lagoon, Icy Cape, and Peard Bay), eastern Beaufort (Harrison Bay, upper Smith Bay, and the Colville River Delta), and Bristol Bay (Phillips et al. 2007, Oppel et al. 2008, 2009, Schamber et al. 2010) from disturbance from off-shore oil and gas development, including transport of oil and gas across these areas.

ACKNOWLEDGMENTS

This study would not be possible without the financial and logistical support of the U.S. Geological Survey Outer Continental Shelf Program, Minerals Management Service, Coastal Marine Institute, Bureau of Land Management, ConocoPhillips Alaska Inc., U.S. Geological Survey Alaska Cooperative Fish and Wildlife Research Unit, North Slope Borough's Department of Wildlife Management and Grants Office, and the North Slope Borough Search and Rescue. The North Slope Borough provided funding through the National Petroleum Reserve-Alaska Impact Mitigation Program from the State of Alaska Department of Commerce, Community and Economic Development. We thank R. Suydam, L. Phillips, and S. Oppel for much of the initial work and publication that made this model possible. Office space made available by the Tetlin Wildlife Refuge was greatly appreciated. Comments by P. Flint, S. Hoekman, S. Oppel, G. White, and 2 anonymous reviewers were greatly appreciated and improved previous versions of the manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government.

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Associate Editor: Gary C. White.