



Frontispiece. A large flock of spectacled eiders *Somateria fischeri* wintering in nearly continuous pack ice in the central Bering Sea. Photo credit: William Larned, USFWS.

Contents

	Pages
Abstract	1
Introduction	2
Population status	2
Factors potentially causing the decline	4
Study Areas	6
General Field Methodologies	6
Geographic Variation in Levels of Lead Exposure	7
Methods	8
Sampling scheme	8
Model data	8
Model selection	11
Densities of lead	11
Population on the Y-K Delta	11
Integration of lead and bird population data	11
Results	11
Discussion	12
Nest Success	15
Methods	15
Results	17
Discussion	17
Female Offspring Produced	18
Methods	19
Results	19
Discussion	19
Duckling Survival	19
Survival and Breeding Propensity	19
Methods	20
Statistical analyses	20
Results	21
Discussion	22
Effects of Lead Exposure on Annual Survival	24
Calculating the effect of lead exposure	25
Estimating juvenile, 1-y-old, and 2-y-old survival	26
Deterministic Model of Population Dynamics	26
Variance components of the deterministic model	28
Population Growth in Stochastic Environments	29
Elasticities of the stochastic model	30
Constant lead levels	30
Declining lead levels	31
Population Viability Analyses	31
Metapopulation Dynamics of Spectacled Eiders on the Y-K Delta	32
Model structure	33
Regional Y-K Delta metapopulation	34
Global Metapopulation Dynamics of Spectacled Eiders	35
Methods	35

Results 36
Discussion 36
Management Implications 36
Supplemental Material 38
Archived Material 38
Acknowledgments 38
References 39



Monograph

Effects of Lead Exposure, Environmental Conditions, and Metapopulation Processes on Population Dynamics of Spectacled Eiders

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Abstract

Spectacled eider *Somateria fischeri* numbers have declined and they are considered threatened in accordance with the US Endangered Species Act throughout their range. We synthesized the available information for spectacled eiders to construct deterministic, stochastic, and metapopulation models for this species that incorporated current estimates of vital rates such as nest success, adult survival, and the impact of lead poisoning on survival. Elasticities of our deterministic models suggested that the populations would respond most dramatically to changes in adult female survival and that the reductions in adult female survival related to lead poisoning were locally important. We also examined the sensitivity of the population to changes in lead exposure rates. With the knowledge that some vital rates vary with environmental conditions, we cast stochastic models that mimicked observed variation in productivity. We also used the stochastic model to examine the probability that a specific population will persist for periods of up to 50 y. Elasticity analysis of these models was consistent with that for the deterministic models, with perturbations to adult female survival having the greatest effect on population projections. When used in single population models, demographic data for some localities predicted rapid declines that were inconsistent with our observations in the field. Thus, we constructed a metapopulation model and examined the predictions for local subpopulations and the metapopulation over a wide range of dispersal rates. Using the metapopulation model, we were able to simulate the observed stability of local subpopulations as well as that of the metapopulation. Finally, we developed a global metapopulation model that simulates periodic winter habitat limitation, similar to that which might be experienced in years of heavy sea ice in the core wintering area of spectacled eiders in the central Bering Sea. Our metapopulation analyses suggested that no subpopulation is independent and that future management actions may be improved through a metapopulation framework. For example, management actions could include displacement of breeding females from “sink” areas that reduce the growth potential of the population as a whole. However, this action is contingent upon dispersal among local populations, for which there is limited information. Thus, we recommend that researchers examine dispersal behavior among areas on the Yukon-Kuskokwim Delta in western Alaska. The metapopulation framework could also be applied at the rangewide scale to address the density-dependent limitation of available polynya habitat during winter that may limit the recovery of small subpopulations, such as that on the Yukon-Kuskokwim Delta. Reductions in other subpopulations may be necessary to ensure an increase in the Yukon-Kuskokwim Delta population. Thus, we recommend that managers consider the interpopulation dynamics of spectacled eiders at different spatial scales in future management actions.

Keywords: Alaska; endangered species; lead poisoning; *Mergini*; metapopulation; population model; spectacled eider

Received: August 4, 2014; Accepted: February 25, 2016; Published: June 22, 2016

Citation: Flint PL, Grand JB, Petersen MR, Rockwell RF. Effects of lead exposure, environmental conditions, and metapopulation processes on population dynamics of spectacled eiders. *North American Fauna* 81:1–41. doi:10.3996/nafa.81.0001

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Subject Editor: Scott Gilliland



Introduction

The spectacled eider *Somateria fischeri* is a sea duck (tribe Mergini) that spends only a few months on land during the nesting period and the remainder of the year at sea (Petersen et al. 2000). Spectacled eiders nest primarily in three disjunct regions: in Russia between the Chaun and Yana river deltas (hereafter Arctic Russia; Pearce et al. 1998), in northern Alaska along the north and northwestern coasts of the Arctic Coastal Plain (hereafter ACP), and in western Alaska on the Yukon-Kuskokwim (Y-K) Delta (hereafter Y-K Delta; Dau and Kistchinski 1977; Petersen et al. 2000; Figure 1). All spectacled eiders winter in large, single-species flocks in a relatively small area in the Bering Sea (Petersen et al. 1999; frontispiece).

Mate selection occurs at sea, and spectacled eiders arrive on the breeding grounds as pairs in spring (May in western Alaska (Y-K Delta), June in northern Alaska (ACP), and Arctic Russia). Pairs remain together for approximately 1 mo during nest site selection, nest initiation, and early incubation. Males then leave the nesting grounds and remain at sea until the next spring, thus spending approximately 11 mo each year at sea (Petersen et al. 1999). Unsuccessful females return to sea soon after nest or brood loss and by approximately 2 wk after hatch, females with young are the only spectacled eiders remaining on the nesting grounds. Successful females migrate to sea with their broods by late August or early September (Flint et al. 2000). Thus, the longest any females are on the nesting grounds is 3.5 mo; nearly all subadults are believed to remain at sea until they reach sexual maturity at 2–3 y of age (Petersen et al. 2000).

Winter in the northern Bering Sea is characterized by short day lengths, cold temperatures, variable ice cover, frequent storms with strong winds, and severe icing conditions (Brower et al. 1988). Extreme winter weather conditions could influence survival in some years. After extreme winters, some females may not nest as a result of poor body condition (Coulson 1984). Furthermore, annual variation in clutch size (Dau 1976a; Stehn et al. 1993; Grand and Flint 1997; Moran 2000) may result from variation in foraging conditions in winter (Coulson 1999). The relationship of winter conditions to survival and reproduction of spectacled eiders is largely unknown.

Population status

Dau and Kistchinski (1977) estimated the number of spectacled eiders breeding in Arctic Russia and on the Y-K Delta at approximately 50,000 pairs in each location. Their estimate for the ACP was 3,000 pairs, based on subjective estimates of biologists who worked in the general area. Stehn et al. (1993) analyzed data from aerial and ground-based surveys of the Y-K Delta and showed a substantial decline

(96%) in numbers from 1970 to 1992. Taylor et al. (1996) and Ryding et al. (2007) analyzed additional data (1957–1995) and substantiated the severe decline. Ely et al. (1994) reported a 79% decrease in numbers of nesting birds between 1969 and 1992 on two study plots on the Y-K Delta. Based on the reduction in the historic breeding range, the documented declines on the Y-K Delta, localized declines on the ACP, and the unknown status and trends of birds nesting in Arctic Russia (Pearce et al. 1998), the worldwide population of spectacled eiders was listed as threatened under the Endangered Species Act (ESA 1973, as amended) in 1993 (U.S. Fish and Wildlife Service [USFWS] 1993).

There have been varying levels of survey effort conducted at each of the three nesting regions. In some cases, spectacled eider observations were recorded in conjunction with surveys designed for other species. Although survey design was not optimal for spectacled eiders, these data can be used to infer general population sizes and trends. The most current (1993–1995) estimate of breeding birds in Arctic Russia is based on a single survey, and although the total population (both sexes combined) exceeded 146,245 individuals (Hodges and Eldridge 2001), it is unknown whether this population has changed, as there are no historic or more recent estimates for comparison. Relatively consistent aerial surveys have been conducted on the ACP since 1993 (Larned et al. 2008). The average ACP population size estimated during our study (i.e., 1993–2004) was 6,759 total birds, with a population growth rate of 0.987 (although this rate was not significantly different from 1.0; Larned et al. 2008). Assuming that only paired-breeding birds are present during the survey (Dau and Kistchinski 1977), the ACP breeding population represents approximately 3,380 nesting pairs. It cannot be determined whether spectacled eiders were ever more abundant in that region, because no similar surveys were conducted before 1993.

The Y-K Delta nesting population was estimated to have declined from 47,700 nesting pairs in 1971 to approximately 2,876 nesting pairs by 1992 (Dau and Kistchinski 1977; Stehn et al. 1993; USFWS 1996). The population on the Y-K Delta is currently monitored with a combination of aerial surveys and ground plots searched on foot. During our study (1992–2004), the mean population size was 3,664 nests and the population growth rate was 1.016 (not significantly different from 1.0; Fischer et al. 2010). Thus, the breeding population on the Y-K Delta seems to have declined dramatically from historic levels, but currently it is stable or perhaps increasing. In fact, estimates during 2000–2009 indicate a significantly increasing population (Fischer et al. 2010).

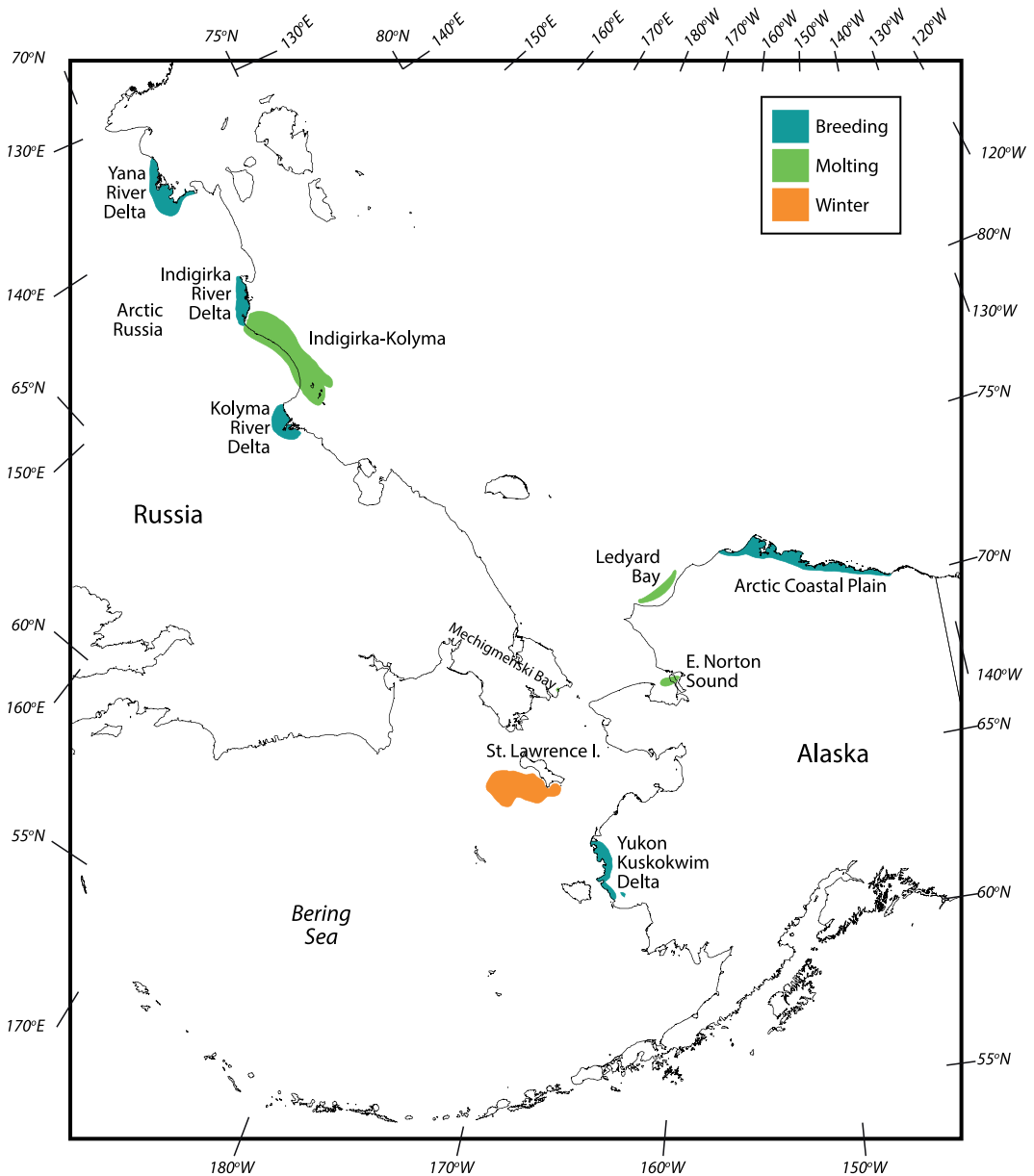


Figure 1. Range map of spectacled eiders *Somateria fischeri* illustrating the three primary breeding areas (Yukon-Kuskokwim Delta, Arctic Coastal Plain, and Arctic Russia), molting, and wintering areas. Adapted from Petersen et al. 2000.

Petersen et al. (1999) identified previously unknown staging, molting, and wintering areas by using satellite telemetry and offshore aerial surveys. Their data demonstrate that all three breeding populations are sympatric on wintering areas in the central Bering Sea. Larned and Tiplady (1997) estimated that at least 363,930 birds wintered in large, single-species flocks in the Bering Sea pack ice. This count was not corrected for detection probability of flocks, so we consider this count to be a minimum estimate.

Reconciling the breeding ground survey estimates with the winter count suggests that detection probabilities on the breeding ground surveys must be less than perfect (i.e., <1.0). We used a simplistic age-structured model that assumed a stable population, an adult survival rate of 0.85, and age of first breeding at 3 y. In addition, this model estimated that only 70% of the total population is of breeding age and hence would be present for the breeding ground surveys. Summing the three breeding ground estimates (i.e., 160,332) and accounting for subadult

and nonbreeding birds that are not present on the breeding ground (i.e., $160,332/0.7 = 229,046$) demonstrate that the breeding populations must be larger than estimated to yield the observed winter count. The Y-K Delta count is based on nest plots with real-time ground truthing; therefore, it is not biased by aerial survey detection probability. We assumed that the estimates for the ACP and Arctic Russia were biased by detection probabilities less than 1.0. Under the assumption that detection probability was the same for the ACP and Arctic Russian surveys, we calculated the detection probability and associated subpopulation sizes that would yield the observed winter count. Under this scenario, the estimated detection probability was 0.62 and the population size for the ACP was 10,930 (i.e., 5,465 nests) and for Arctic Russia was 236,493 (i.e., 118,247 nests). We consider these population sizes to be minimum estimates because the winter count may also be subject to imperfect detection probabilities. We used these adjusted estimates of population size in our modeling efforts.

Factors potentially causing the decline

The causes of the decline of spectacled eiders and obstacles to recovery were unknown when the species was listed as threatened (ESA 1973; USFWS 1996). As a result, studies began on the breeding grounds and on the wintering area. Beyond evaluating vital rates and factors influencing them, initial priority actions focused on spring subsistence harvest, contaminants, and the potential effects of research activities on survival and productivity. Management actions that were recommended and implemented included efforts to reduce the use of lead shot by hunters on the breeding areas, enforcement of the Migratory Bird Treaty Act, dissemination of information to local residents regarding the status of spectacled eiders, and involvement of native people and organizations in eider management (USFWS 1996). Additional surveys and inventories on breeding areas (see above), studies on reproduction and survival (Flint et al. 2000; Moran 2000; Bart and Earnst 2005; Flint et al. 2006b), and research focused on availability and toxicity of lead (Flint et al. 1997; Flint 1998) began or were expanded.

Spectacled eiders were found dead and dying on the Y-K Delta, and a relatively large proportion of birds were found with elevated blood lead levels resulting from ingesting lead shotgun pellets (Franson et al. 1995; Flint et al. 1997; Figure 2). The proportion of spectacled eiders exposed to lead increased with the amount of time birds remained on the breeding grounds, with the proportion of females with elevated blood lead levels being lowest in spring soon after their arrival on the breeding grounds, increasing by the end of incubation, and being highest near the end of brood rearing (Flint

et al. 1997). Grand et al. (1998) subsequently found that the annual survival of adult female spectacled eiders with elevated blood lead levels was reduced compared to that of unexposed birds. This association creates the potential for lead poisoning to be influencing population dynamics of spectacled eiders on the Y-K Delta. Spectacled eiders with elevated blood lead levels have also been reported in Arctic Russia (2 of 15; Indigirka River Delta; M.R.P., unpublished data) and the ACP (3 of 94; Wilson et al. 2004). Although the scope of sampling was limited, the frequency of birds with elevated blood lead levels was low and likely had little effect on annual survival rates at those two breeding areas.

Stehn et al. (1993) speculated that the effects of contaminants may have contributed to the decline of spectacled eiders. Studies of trace elements in spectacled eiders were conducted on the ACP and Y-K Delta breeding grounds. On the ACP, Wilson et al. (2004) found variability in trace element exposure (Ba, Cd, Hg, Pb, and Se) among two species of eiders (spectacled and king *Somateria spectabilis*) and sexes. Except for lead in three individuals, they concluded that these trace elements did not significantly impact the health of these eiders. On the Y-K Delta, Grand et al. (2002) found no effects of five trace elements (As, Cd, Se, Pb, and Hg) on nest success or egg viability. Wang et al. (2005) found polychlorinated biphenyls below harmful levels in addled spectacled eider eggs from the Y-K Delta. Trust et al. (2000) examined birds collected near their wintering grounds, and Stout et al. (2002) evaluated birds from near the wintering grounds and all three breeding areas. Although neither group could find direct health effects, both suggested that contaminants could not be ruled out as contributing to the decline of nesting birds on the Y-K Delta.

Because of the lack of knowledge of the nonbreeding distribution of spectacled eiders (Dau and Kistchinski 1977), factors influencing survival when at sea were speculative (Stehn et al. 1993). Studies focused first on identifying the at-sea distribution of spectacled eiders and surveying these areas (Petersen et al. 1999); then, the studies were expanded to determine winter food and body condition (Petersen et al. 1998; Lovvorn et al. 2003; Richman and Lovvorn 2003) as well as weather and ice effects (Bump and Lovvorn 2004; Petersen and Douglas 2004). Ice and weather conditions in the Bering Sea are known to vary greatly from year to year (Brower et al. 1988; Wyllie-Echeverria and Wooster 1998; Parkinson 2000; Petersen and Douglas 2004), and changes in weather regimes in the Bering Sea have been associated with changes in benthic invertebrates (Sirenko and Koltun 1992; National Research Council 1996; Grebmeier and Dunton 2000) and other fauna (Hare and Mantua 2000). The decline of spectacled eider populations could

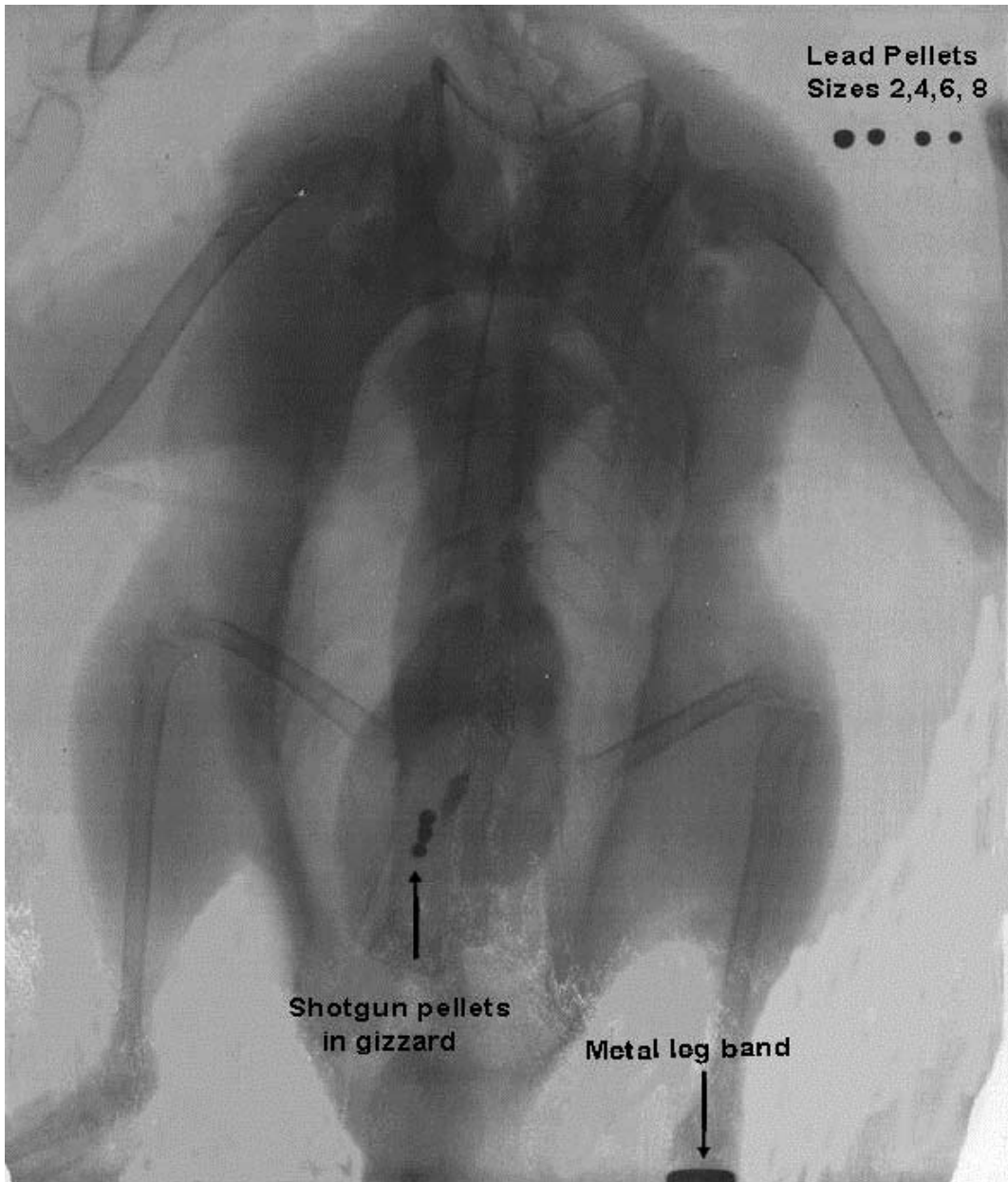


Figure 2. X-ray of a live spectacled eider *Somateria fischeri* female from the Kashunuk River on the Yukon-Kuskokwim Delta, Alaska, in 1995 with three lead shotgun pellets in its gizzard. Lead pellets were removed by lavage, and the bird was released at its capture site. A size standard of lead pellets is attached to the top right side of the X-ray plate.

be a result of long-term changes in weather, particularly ice, and resulting changes in fauna (Stehn et al. 1993; Lovvorn et al. 2003). Petersen and Douglas (2004) analyzed extreme weather and ice data in the wintering area in the Bering Sea in relationship to the long-term aerial survey data of the Y-K Delta breeding population. They concluded that dense sea ice concentrations and inclement weather during winter can negatively impact the

survey index the following summer. Bump and Lovvorn (2004) suggest that only during extreme weather would ice conditions change enough to have an appreciable impact on spectacled eiders energetics. Examination of long-term (50-y) survey and weather data suggests that the population decline began before the regime shift (from warm to cold) in the Bering Sea occurred in the late 1970s (Petersen and Douglas 2004; Flint 2013).

Stehn et al. (1993) speculated that changes in forage used by spectacled eiders in the Bering Sea may have contributed to the decline or are impeding recovery of the species. Birds collected near St. Lawrence Island in May (Petersen et al. 1998) were found to have eaten different foods than those collected on the primary wintering area in March and April (Lovvorn et al. 2003). There are no data during the previous decades that can be used for comparisons of forage species and their relative values to spectacled eiders in the years before or during the declines of the Y-K Delta population (Richman and Lovvorn 2003).

This monograph presents a synthesis of new data with existing published data. Accordingly, the presentation is separated into sections. We present the new data on field and analytical methods, results, and discussion in a manner directly comparable to previously published reports. We then combine these new results with the previously published results and develop an overall demographic model. We start with a deterministic model and then expand into a stochastic model based on process variance. We modeled dynamics across a hierarchical suite of metapopulations by using a range of definitions for subpopulations. At the global scale, we considered the entire species as the metapopulation and each of the three breeding regions (i.e., Arctic Russia, ACP, and Y-K Delta) as the subpopulations. At the regional scale, we treated the Y-K Delta breeding birds as the metapopulation and defined specific study locations as the subpopulations. Our goals were to 1) summarize and synthesize existing demographic data, 2) define and describe a deterministic model that simulates the dynamics of spectacled eider populations, 3) illustrate the behavior of the model by using the best demographic data available, 4) examine the potential effects of stochastic variation on spectacled eider populations, 5) examine the behavior of a metapopulation model that may explain the dynamics of the Y-K Delta population, and 6) develop a global metapopulation model to describe the relationships among the three nesting regional subpopulations.

Study Areas

Detailed studies of spectacled eider survival and productivity were conducted at two sites on the Y-K Delta (Figure 3) with reasonably high densities of nests (≥ 4 nests/km²): the Kashunuk River (61°20'N, 165°35'W) and Kigigak Island (60°50'N, 165°50'W). The Kashunuk River study area was described by Grand et al. (1997). The Kigigak Island study area consisted of nearly the entire island; it closely resembled the high graminoid and intermediate sedge meadows characterized in Grand et al. (1997). Both study sites lie along the coastal fringe of the Y-K Delta in tidally influenced habitats,

and both areas have high densities of other species of breeding birds, including cackling goose *Branta hutchinsii*, white-fronted goose *Anser albifrons*, emperor goose *Chen canagica*, black brant *Brant bernicla nigricans*, northern pintail *Anas acuta*, tundra swan *Cygnus columbianus*, and sandhill crane *Grus canadensis*. There were also numerous species of shorebirds, several species of gulls and terns, a few species of passerines, and willow ptarmigan *Lagopus lagopus*. Kigigak Island has one of the highest overall nesting densities of waterfowl on the Y-K Delta, whereas Kashunuk River is perhaps more typical or average. Kigigak Island study site is on a nearshore island, with the closest village (Newtok, population ~350) more than 30 km by boat, and access is difficult because the island is surrounded by extensive mudflats. The Kashunuk River site is along a major river and is more than 40 km by boat from two villages (Chevak, population ~765 and Hooper Bay, population ~1,014); this area is traditionally used for subsistence hunting or fishing by people from these villages.

General Field Methodologies

Following the protocols established by Grand and Flint (1997), we searched for spectacled eider nests during late May through mid-June 1993–2002 at Kashunuk River and 1993–2004 at Kigigak Island. Nests discovered at both sites incidental to other activities were also included in these analyses. We trapped adult females on their nests 0–5 d before hatch by using string-activated or remote-controlled bow-nets (Sayler 1962). Females were weighed (± 10 g) at capture by using handheld spring scales. We marked adult female spectacled eiders with uniquely coded metal leg bands, numbered plastic leg bands (20 mm in height \times 15 mm in diameter), and plastic nasal disks (16 mm in diameter). Plastic leg bands and nasal disks were bright yellow with black alphanumeric codes. We attached nasal disks using 1-mm-diameter stainless steel pins passed through the nares. We placed a disk and a 3-mm washer over the protruding ends of the pin and secured the assembly by crimping each end of the pin (Lokemoen and Sharp 1985). In 1993, we used plastic washers, which quickly wore through, resulting in frequent loss of nasal disks. After 1993, we used stainless steel washers, which improved disk retention. A sample of females were marked at hatch with radio transmitters and monitored regularly to assess duckling survival (Flint and Grand 1997). We captured broods (i.e., females with ducklings) at approximately 30 d posthatching. Ducklings were sexed by cloacal exam and marked with stainless steel and plastic bands. Ducklings were not marked with nasal disks because their bills were not fully grown. Detailed methods relative to specific parameter estimates are provided below.

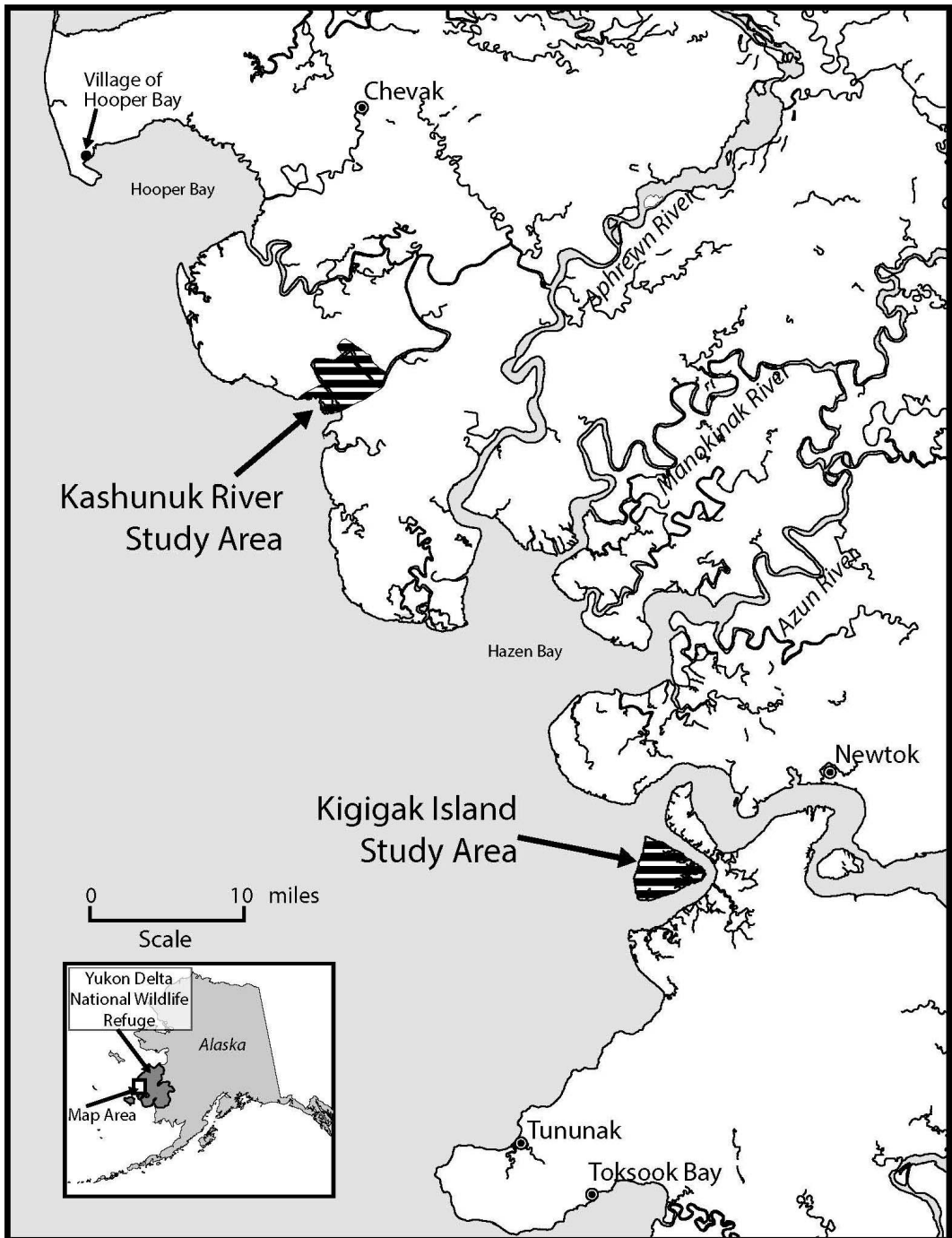


Figure 3. Location of Kashunuk River and Kigigak Island study sites on the Yukon-Kuskokwim Delta, Alaska, where intensive studies of spectacled eider *Somateria fischeri* ecology were conducted from 1992 to 2004.

Geographic Variation in Levels of Lead Exposure

Correct inference of the effects of lead poisoning at the regional scale requires estimating the exposure

rate for the entire Y-K Delta. Data on lead exposure rates were only available from the two intensive study areas, and there was no basis to extrapolate these rates to the remainder of the Y-K Delta. Estimation of the Y-K Delta lead exposure rate

requires estimation of the overall spatial distribution of lead exposure rates integrated with the overall density distribution of nesting spectacled eiders. Thus, we sought to functionally develop a weighted average where lead exposure rates for specific areas were weighted by the proportion of the Y-K Delta population that occurred within each area. We hypothesized that the highest exposure rates in birds would be associated with areas most used by hunters. Thus, we considered variables associated with access such as distance to nearest village and distance from rivers and sloughs. Furthermore, spectacled eiders are not likely a species targeted by hunters on the Y-K Delta, as they occur at relatively low densities. Accordingly, most hunting efforts are focused on geese, and lead deposition where spectacled eiders occur is likely a result of goose hunting. Therefore, we considered variables associated with goose densities in our analysis. We collected data from a suite of sampling locations and developed a spatial model of predicted lead exposure rates. We then combined this model with spectacled eider nesting density to estimate the overall Y-K Delta lead exposure level.

Methods

Sampling scheme. A random sample of plots on the Y-K Delta (Figure 4) was searched for broods in 1995. The sampling area was bounded by the Askinuk Mountains and Nelson Island, at variable distances from the coast, but within spectacled eider habitat. A grid consisting of 2.56-km² blocks was then placed over the area, and a random sample of 200 plots was selected. Searching began when most young spectacled eiders were at least 30 d old, and plots were searched from a helicopter in the order they were randomly selected. In total, 107 plots were examined before young fledged and adult females could no longer be captured. Blood samples were taken from each adult female and all ducklings captured in plots.

In addition to the two long-term study sites (i.e., Kashunuk River and Kigigak Island), seven areas were selected for sampling in 1995–1998 based on the relative density derived from USFWS aerial survey data (Figure 5). Study areas were placed throughout the high-density nesting area. We believed that these additional sites would contain high enough densities of nesting birds to provide a good probability of two people capturing 50 or more adult females per site over a 3-wk period. Although lead poisoning may occur in lower density nesting areas, an insufficient sample of these low-density nesting birds could be captured to provide for meaningful statistical analysis. The higher density nesting regions outlined in Figure 5 included approximately 63% of the total breeding population of spectacled eiders and 6% of the

total eider nesting area on the Y-K Delta in 1993–2000 (Fischer et al. 2010).

Birds within the study sites were not randomly sampled. Because we had only a short time before eggs hatched to find and capture adult females, we attempted to capture every bird we could find. There were no preset sizes or shapes of the areas. The area searched generally reflected the availability of appropriate nesting habitat, physiographic structures (abrupt break from one habitat to another), or small (nonnavigable) sloughs. All study plots included areas with high, medium, and low densities of nesting spectacled eiders. Because of the potential disturbance to nontarget species, no searching for nests occurred on the Tutakoke River black brant colony study site or the emperor goose study site on the Manokinak River (Figure 5). Overall, we searched 25% of the 716-km² area that was identified as the high-density nesting area (Figure 5). No area was searched on the south side of the Naskonat Peninsula, 71% of Kigigak Island was searched, and 14–36% of the remaining areas were searched.

Data presented here are from nesting birds, except for females with broods that were captured during the helicopter searches and at the Manokinak River study site. The lead exposure probability of adult females differs between hatch and 30 d after hatch (Flint et al. 1997). The proportion of exposed hens with broods was adjusted to reflect the probable exposure rate as if they were captured on nests. This rate is based on the proportional difference found between birds at hatch and hens with ducklings approximately 30 d old that were captured at Kashunuk River during 1993–1999. Most nest and brood locations were mapped using global positioning system coordinates and verified from field maps.

Model data. We determined the straight line distance from the nest to the nearest village and the distance by navigable waters from the nearest village to each nest. Major rivers are important transportation corridors used in summer and autumn to reach areas for hunting, fishing, and other activities. To be consistent, we treated the established all-terrain vehicle trail from the village of Hooper Bay to Kokechik Bay as navigable water because it is the primary mode of access to this region. We measured the distance of each nest to the nearest navigable water by using two criteria for navigable water: access by large rivers that could be accessed regardless of tide level and the distance to the nearest small navigable slough that could only be accessed at high tide. Navigable waters were identified from observations of biologists at the different study sites, discussions with residents of the Y-K Delta, and evidence of camp sites. Because the proportion of hens exposed to lead increased from hatch to brood rearing (Flint et al. 1997),

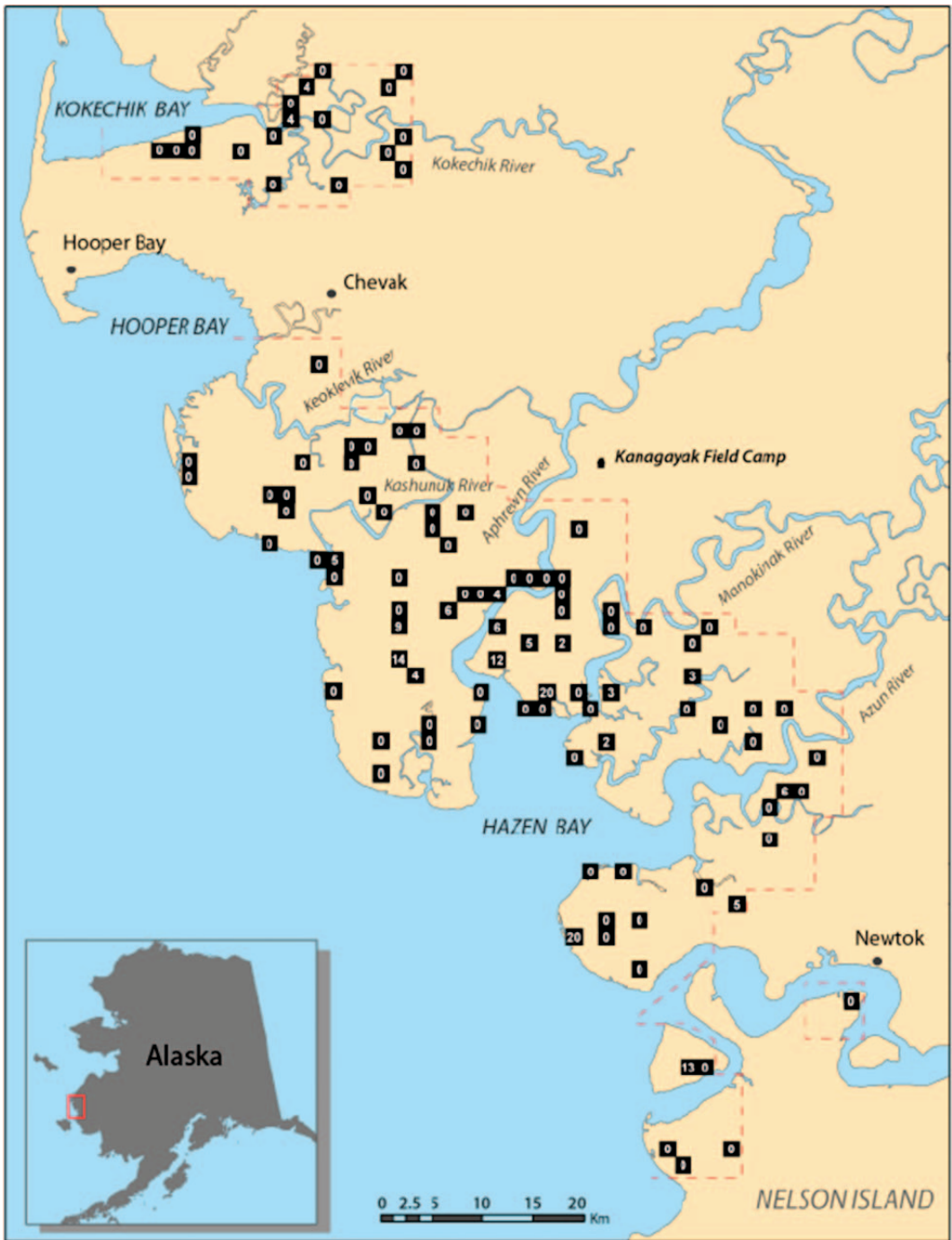


Figure 4. Locations and number of spectacled eiders *Somateria fischeri* present on 107 random plots in August 1995 on the Yukon-Kuskokwim Delta, Alaska. Numbers represent total adults and ducklings within each plot. Total birds sampled for lead analysis includes 30 adult females and 116 ducklings.

breeding status (nesting vs. 30-d-old ducklings) was included in all models.

Four species of geese (i.e., white-fronted goose, cackling goose, black brant, and emperor goose) are

present and taken by hunters on the coastal Y-K Delta (Raveling 1984; Wentworth 2007). We used relative density estimates of cackling geese from aerial surveys conducted in early summer 1998–2001



Figure 5. Location of search areas in which spectacled eiders *Somateria fischeri* were sampled for the blood lead analysis during 1993–1999 in relationship to high-density nesting areas on the Yukon-Kuskokwim Delta, Alaska. 1, Kashunuk River; 2, Tutakoke; 3, Big Slough; 4, Aphrewn; 5, Opygyarak; 6, Manokinak River; 7, Aknerkochik River; 8, Naskonat Peninsula; 9, Kigigak Island. The Tutakoke River and Big Slough sampling sites are referred to as a single location (Tutakoke & Big Slough), as are the Aphrewn and Opygyarak study areas (Opygyarak & Aphrewn).

(Platte and Stehn 2015) to represent areas with high concentrations of geese as this species is the most abundant goose species in areas where spectacled eiders generally occur. Because large colonies of

black brant also occur within the Y-K Delta (Sedinger et al. 1993), we determined the distance of each nest to the nearest major black brant colony. These parameters were used in 20 models to

describe the distribution of lead across the Y-K Delta. After examining the results of the first set of models, we added the interaction of distance to large river and distance to village, and then re-examined the models. We also examined a null model, with no covariates, resulting in 22 models in total that were considered. These models are all logistic regression models, as the explanatory variables are continuous and the response variable (presence of lead) is binomial. The data set includes birds both captured before hatch and with broods.

Model selection. The number of spectacled eiders sampled for lead at each study area varied by nearly an order of magnitude. We were concerned that such unbalanced sample sizes might bias estimates of the spatial parameters of interest. To mitigate this concern, we used a bootstrap resampling process wherein we analyzed a common sample size per area ($n = 50$). We randomly selected, with replacement, 50 birds from each study area; conducted our analysis; and then repeated the process until we achieved a set of 1,000 such analyses. By doing 1,000 iterations, we ensured that all birds at each area had an opportunity to contribute to the collective analysis and we also maintained a spatially balanced sample size. We then examined the mean of the 1,000 iterations to obtain Akaike's Information Criterion (AIC) values and parameter estimates. Confidence intervals (CIs) were derived by examining the 5th and 95th percentiles of this set of iterations. Candidate models were ranked based on AIC differences (ΔAIC), and the evidence regarding model selection was examined following Burnham and Anderson (2002). The relative importance of variables was evaluated by ranking the summed AIC weights (w_{AICs}) of models that included each variable. We examined models with as many as four variables, plus the null model. However, we present only the models with a w_{AIC} value greater than 0.01.

Densities of lead. To project lead exposure rates throughout the Y-K Delta landscape, we applied our estimates of the spatial variables to the full range of spatial values at the landscape level (Figure 6). We partitioned the Y-K Delta into 100-m grids, and the appropriate value for each variable was determined using ArcGIS. Kriging was used to interpolate distance values across the study area and to create new raster files with gradient distance values for each parameter. Once we created a raster file for each of the parameters, a probability of exposure was determined by inserting the raster values into the model. Weighted model averaging was then used to determine the overall proportion of lead exposed spectacled eiders in each of the 100-m grids.

Population on the Y-K Delta. We created an estimate of the relative density distribution of spectacled eiders on the Y-K Delta coastal zone from data

collected by the USFWS during 1993–2000 (Fischer et al. 2010). Sightings of spectacled eiders were obtained from aerial water bird surveys by using standard protocols (USFWS and Canadian Wildlife Service [CWS] 1987). Throughout the sampling area, an aerial observer recorded spectacled eiders within 200-m-wide strip transects. The survey area was then divided into 2.56-km² blocks to estimate the relative density of spectacled eiders. The number of spectacled eiders sighted within each block was summed across all years; the total area that was searched within each block was also summed across all years. The density was then calculated for each block as the total number of spectacled eiders sighted divided by the total area searched. Block-level density estimates were downscaled using a triangulated irregular network (DéFloriani and Magillo 2009). The final raster density surface was then created by sampling the triangulated irregular network at 100-m intervals to obtain estimated density values at each of those points.

Integration of lead and bird population data. We overlaid the spectacled eider density raster with the lead density raster and extracted values for each 100-m grid. We multiplied the probability of exposure by the density of spectacled eiders for each grid and summed all the grid values to obtain the annual lead exposure probability of spectacled eiders for the period 1994–1999. To evaluate the goodness of fit of our overall analyses procedure, we examined the proportion of birds likely exposed to lead based on the models with the strongest level of support to the known proportion of birds exposed to lead on the study areas by using a χ^2 test.

Results

Based on blood lead levels, at least one adult female spectacled eider was classified as exposed (i.e., blood Pb >0.2 ppm) in each study area on the Y-K Delta (Table 1). There was no significant difference among years within study sites (Table 2); thus, year was not considered further in the analysis among sites. Exposure rates at hatch varied significantly ($\chi^2 = 47.9$; $df = 6$; $P < 0.001$) among study sites (Table 1). The Kashunuk River site had the highest proportion of spectacled eiders exposed to lead, whereas less than 5% of birds were found to be exposed at the Aknerkochik River and Tutakoke and Big Slough sites.

The single best-approximating model for lead exposure probably included the variables distance to large river, distance to nearest village, and their interaction (Table 3). There was substantial support for the first model, less so for the next five models (Table 3), and considerably less for the remaining models. We thus included only the top six models in our confidence set of models. The proportions of birds predicted by the models to be exposed to

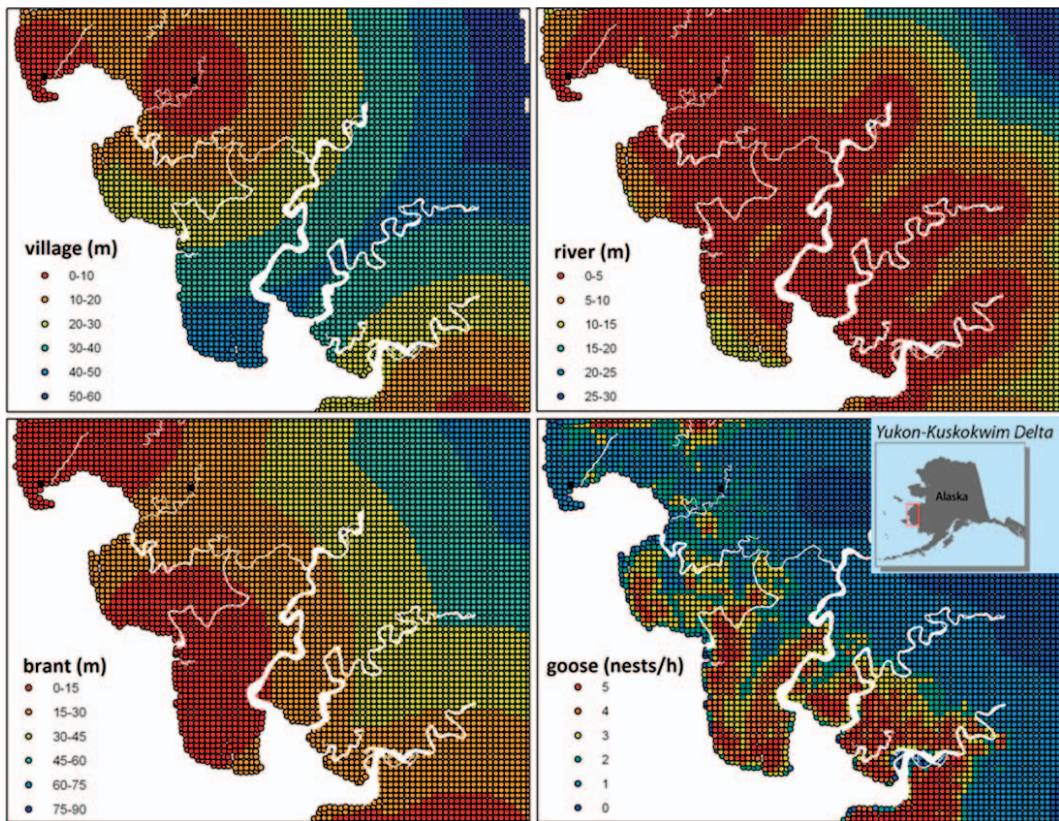


Figure 6. Density maps of four variables that influenced the probability that sampled spectacled eiders *Somateria fischeri* had been exposed to lead (i.e., blood Pb >0.2 ppm) on the Yukon-Kuskokwim Delta, Alaska. The distance to the nearest village (village), the distance to the nearest navigable slough or river (river), the distance to the nearest black brant *Brant bernicla nigricans* colony (brant), and the local goose nesting density (nests/ha) as determined by aerial surveys and ground plots across the Yukon-Kuskokwim Delta (goose). Goose and brant data from 1998-2001.

lead differed from the observed ($\chi^2 = 20.6$; $df = 7$; $P = 0.004$), based primarily on the Aknerkochik River area (Table 4). The probability of lead exposure was highest closer to villages and navigable waterways (Figure 7). Furthermore, the relationship between distance to village and navigable waterway was not constant. The effect of distance to village was strongest close to waterways and functionally negligible a couple of kilometers away from the waterway. Based on the merging of the two raster files (Figures 8 and 9; estimated bird density and distribution and estimated lead exposure rates based on the models), the estimated exposure rate of the spectacled eider population on the Y-K Delta from 1994 to 1999 was 11.8%.

Discussion

The effects of lead on spectacled eiders on the Y-K Delta are based on studies of birds within small, long-term study areas (i.e., Kashunuk River and Kigigak Island). Lead in these areas is believed to have contributed to mortality of birds during spring

and throughout the brood-rearing period (Franson et al. 1995; Flint and Grand 1997; Flint et al. 1997, 2000; Franson et al. 1998; Grand et al. 1998). Our data show that lead exposure rates were not consistent throughout the Y-K Delta. The variation in lead exposure rates among the search areas within the higher density breeding area suggests that there were factors within those general areas that influenced the probability of ingesting lead. We hypothesized that lead (in the form of spent shot) is deposited in areas with greater access, near population centers, and where there are high densities of hunted species. Our data confirm these general hypotheses; specifically, the occurrence of lead exposure in a bird was primarily a function of the distance to a major river, the straight line distance to a village, and their interaction, and less so a function of the distance to black brant colonies and goose densities. Model comparisons showed that access and distance to population centers are the most important factors influencing lead deposition into the environment.

Table 1. Blood lead exposure rates (>0.2 ppm) of spectacled eiders *Somateria fischeri* on each of eight sampling areas on the Yukon-Kuskokwim Delta, Alaska, from 1995 to 1998. The proportion exposed is calculated as the number exposed/total.

Study site ^a	Status ^b	No. unexposed	No. exposed	Proportion exposed
Aknerkochik River	Hatch	63	2	0.031
Opyagyarak & Aphrewn	Hatch	19	2	0.095
Kashunuk River	Hatch	206	82	0.285
Kigigak Island	Hatch	272	45	0.142
Manokinak River ^c	Brood	32.3	5.7	0.151
Naskonat Peninsula	Hatch	42	5	0.106
Tutakoke & Big Slough	Hatch	105	4	0.037
Y-K Delta random plots ^c	Brood	29.2	0.8	0.028

^a See Figure 5 for location of study sites.

^b Hatch, adult females on nests within 7 d of hatch; brood, adult females with ducklings approximately 30 d old.

^c Adjusted to reflect the number and proportion of females that would have been exposed to lead if captured at hatch. Estimate is based on a 0.344 exposure rate of females with broods and a 0.285 exposure rate of hens at hatch (see Table 2) at Kashunuk River.

Overall, our model of the variables that influence lead exposure fit well, with the exception of the Aknerkochik River site. We were unable to develop an ease of access variable, although it is likely a key factor in the decision a hunter would consider when

selecting an area in which to hunt. Few people access the Aknerkochik River from Hazen Bay because of the difficulty in navigating the tidal mudflats to reach the area. Instead, people tend to go up the Manokinak River and access the

Table 2. Annual variation in the proportion of spectacled eiders *Somateria fischeri* exposed to lead (blood Pb >0.20 ppm) at the two long-term study sites, Kashunuk River and Kigigak Island on the Yukon-Kuskokwim Delta, Alaska, from 1993 to 1999.

Study site ^a	Status ^b	Year	No. unexposed	No. exposed	Proportion exposed
Kashunuk River	Hatch	1993	1	1	0.500
		1994	22	6	0.214
		1995	45	17	0.274
		1996	20	16	0.444
		1997	31	13	0.295
		1998	59	16	0.213
		1999	28	13	0.371
Kigigak Island	Hatch	1994	43	4	0.085
		1995	39	9	0.188
		1996	46	8	0.148
		1997	51	12	0.190
		1998	49	4	0.075
Kashunuk River	Brood	1993	13	6	0.316
		1994	17	7	0.292
		1995	16	10	0.385
		1996	12	6	0.333
		1997	16	12	0.429
		1998	16	8	0.333
		1999	11	4	0.267

^a See Figure 5 for locations of sampling areas.

^b Hatch, adult females on nests within 7 d of hatch; brood, adult females with ducklings approximately 30 d old.

Table 3. Model structure of the top 6 of 22 models examined to describe lead exposure for spectacled eider *Somateria fischeri* females at eight study sites on the Yukon-Kuskokwim Delta, Alaska, based on samples collected between 1993 and 1999.

Model ^a	AIC	ΔAIC	W _{AIC}	Deviance
Village, river, village*river, status	260.89	0.00	0.61	125.5
River, status	264.40	3.51	0.11	129.2
Village, river, status	264.45	3.56	0.10	128.2
Brant, river, status	265.30	4.41	0.07	128.7
Goose, river, status	265.54	4.65	0.06	128.8
Goose, brant, river, status	266.43	5.54	0.04	128.2

^a Village, straight line distance from the nest to the nearest village; river, straight line distance from the nest to the nearest large (navigable at low tide) slough; brant, straight line distance from the nest to the closest edge of the nearest brant colony; goose, relative cackling goose density at the nest site; status, bird was captured either on a nest or with a brood.

Aknerkochik River via a narrow slough that is only navigable at high tide. Although the Aknerkochik River area is relatively close to a village and is a navigable slough, it likely receives less hunting pressure than expected, so our model overestimated the exposure rate at this site.

We were unable to sample birds in large areas with very low densities of spectacled eiders. The extremely low density or lack of nesting spectacled eiders available to sample could be, in part, a result of poor (marginal) nesting and brood rearing habitats. Alternatively, high densities of lead may have resulted in the elimination or a significant reduction of breeding birds in these areas. Our models suggest that the probability of a bird ingesting lead in some areas with few or no birds, particularly near villages, is high. Based on our models, a plausible explanation is that birds that would have occurred near villages were eliminated by very high lead poisoning rates. However, the correlation of the lack of birds available to sample and distance to village does not necessarily reflect causation; there could be few birds in these areas due to a combination of additional factors (e.g., no suitable nesting, no brood rearing habitat, or disturbance). The estimate of the exposure rate

across the Y-K Delta relies on an estimate of the distribution and numbers of birds. Although high lead exposure rates are predicted at some locations, the lack of birds in these areas precludes further analysis. Regardless of why these areas are devoid of birds, the estimate of lead exposure rates only includes areas where spectacled eiders occur. Thus, the predicted exposure rate where there are no breeding birds is irrelevant in this estimate.

Spectacled eiders begin to ingest lead shot upon their arrival to the nesting grounds (Flint et al. 1997). It is apparent that female spectacled eiders at Kashunuk River during 1993–1999 maintained a constant exposure rate to lead from spring (28.2%; $n = 71$) until hatch (28.3%; $n = 286$). Flint et al. (1997) reported a 13.0% ($n = 23$) exposure rate of birds captured before nesting and a 25.3% ($n = 91$) exposure rate at hatch. Their data are from 1993 to 1995, and the difference in the spring estimate could be an artifact of the analysis of the relatively small sample size during those years. Female spectacled eiders begin feeding on the nesting grounds in spring as soon as habitats become available and likely consume lead during this short period before incubation. Our lead exposure rate at

Table 4. Observed numbers of female spectacled eiders *Somateria fischeri* exposed to lead (i.e., blood Pb >0.2 ppm) at eight study sites on the Yukon-Kuskokwim Delta, Alaska, between 1993 and 1999 and expected number exposed to lead based on the best supported model.

Area ^a	Total sampled	No. observed exposed	No. expected exposed	(OBS – EXP) ² /EXP
Aknerkochik River	65	2	14.14	10.424
Big Slough	109	4	4.70	0.103
Aphrewn	15	1	2.16	0.623
Naskonat Peninsula	47	5	1.53	7.869
Opygyarak & Aphrewn	8	1	0.32	1.451
Kigigak Island	317	45	44.16	0.016
Manokinak River	38	5.7	5.01	0.096
Kashunuk River	288	82	79.98	0.051

^a See Figure 5 for locations of sampling areas.

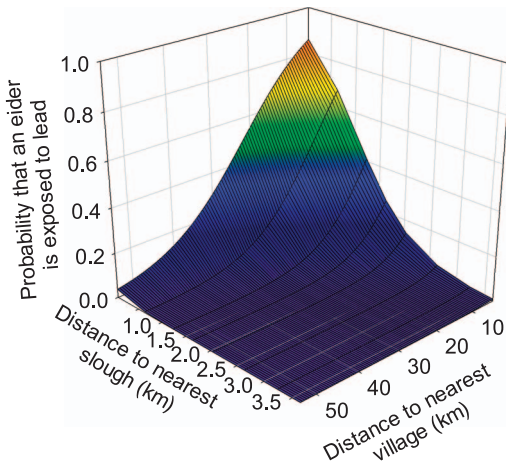


Figure 7. Interactive effect of the straight line distance from the nest to the nearest village and distance to the nearest slough on the probability a spectacled eider *Somateria fischeri* will exceed the 0.20 ppm blood lead concentration threshold (exposed) on the Yukon-Kuskokwim Delta, Alaska. Results based on samples collected between 1993 and 1999. The likelihood of lead exposure increased closer to villages and travel corridors.

30 d after hatch (with broods) is similar to that reported by Flint et al. (1997) at the Kashunuk River. Flint et al. (1997) reported an exposure rate of 35.8% ($n = 67$) for 3 y of data (1993–1995), whereas with an additional 4 y of data, we found the exposure rate to be 34.4% ($n = 154$).

Nest Success

We defined nesting success as the proportion of breeding females that hatched at least one duckling each year. Because spectacled eiders rarely re-nest (Grand and Flint 1997), we assumed that nesting success equates to the proportion of nests that hatch each year. Most published estimates of nest success for spectacled eiders used apparent success rates; these rates were defined as the portion of a sample of nests that hatched or were active at the time of discovery. This simplistic approach was cost-effective, because it required only one visit to each nest; however, the estimates are of limited utility because they fail to account for the difference in detection rates among nests that were being incubated, those nests containing eggs that had already hatched, and nests already destroyed by predators at the time the search was conducted (Mayfield 1961; Johnson 1979). Grand and Flint (1997) examined sources of variation in spectacled eider nest success 1991–1995 along the Kashunuk River. They found that females initiating laying early in the nesting season were more likely to succeed. Nest initiation dates and success

rates are age related in female common eiders (Baillie and Milne 1982); unfortunately, age-specific information about spectacled eider nest initiation dates and success was not available. Nest success of spectacled eiders varies dramatically among years (Stehn et al. 1993; Grand and Flint 1997).

Methods

To estimate nest success, we cast models that incorporated annual and intra-annual variation in nest survival that were continuous or discrete based on the following criteria adapted from Grand et al. (2006):

1. We considered models that included differences in daily survival rate (DSR) of nests among years. Our assumption was that nest survival varied among years, and our ability to discriminate among those differences was limited only by sample sizes.
2. We included models that estimated different DSRs between sites each year without any constraints on the difference between sites (i.e., interaction between site and year). We included models that allowed DSR to vary among years with a constant difference between sites (i.e., additive effect of sites and years).
3. In addition to variation among sites and years, we examined the effects of female experience, timing of nest initiation, and date.
4. We included models where nest survival varied by nest age to account for hypothesized variation in female behavior across stages of incubation and heterogeneity in female and nest site quality. We assumed that if nest age was an important source of variation in DSR, the effect would be consistent (i.e., additive) among years and dates or initiation dates, but it could be either linear or quadratic in form.
5. We included models of DSR that varied with nest initiation date to incorporate hypothesized differences related to condition and experience of nesting females. We also hypothesized that these effects could be either linear or quadratic.
6. We also included models of DSR that varied by calendar date, to incorporate hypothesized variation in predator distribution and abundance. We hypothesized that these effects could be either linear or quadratic.
7. Because we observed differences in phenology among years, we included models with patterns of DSR across initiation dates or calendar dates that varied among years.

For discrete-time models, we used 10-d intervals for both calendar date and initiation date and 7-d intervals for nest age. We used shorter intervals for age categories because our sample contained a relatively even distribution of nest exposure days

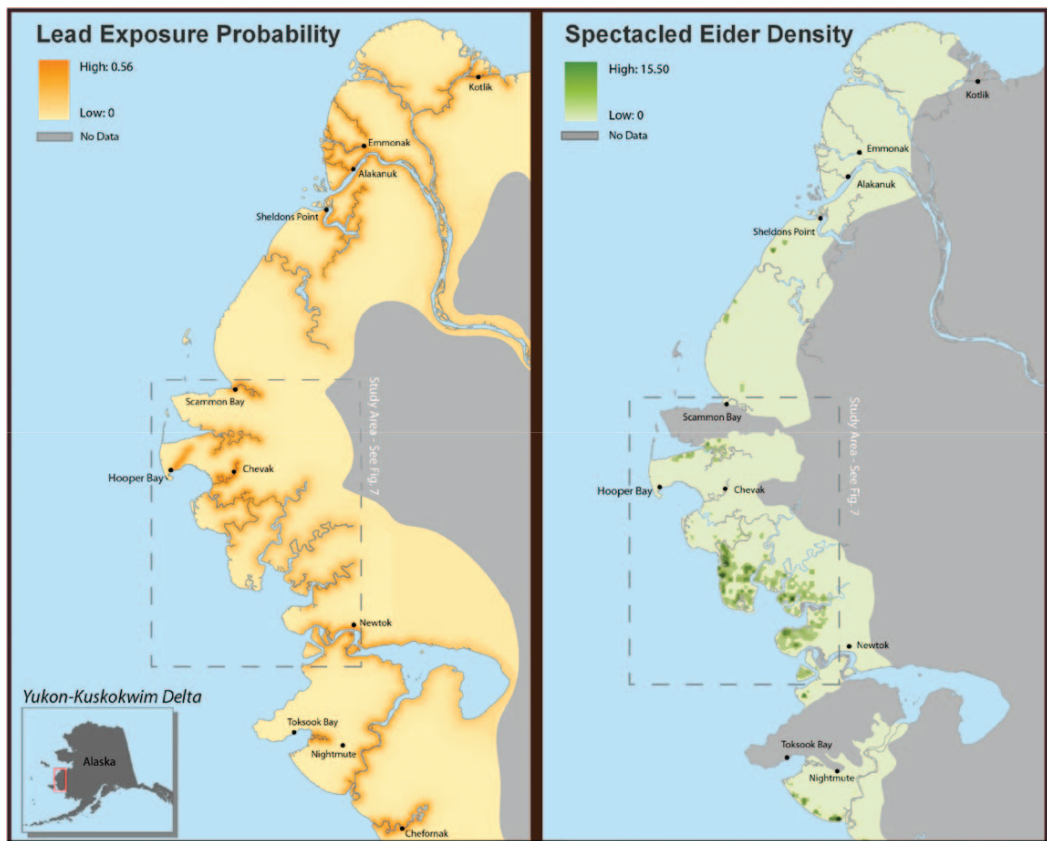


Figure 8. Expected probability of lead exposure (i.e., blood Pb > 0.2 ppm) relative to distance to nearest slough and village based on data from 1994 to 1999 and estimated spectacled eider *Somateria fischeri* density on the Yukon-Kuskokwim Delta, Alaska, based on random plot and aerial survey data from 1993 to 2000. Dashed boxes represent the primary nesting area (see Figure 9). Density is plotted as number of nests per 2.54 Km² block.

across all categories. We pooled data in the first two and last two calendar date intervals and the last three initiation date intervals each year because they included fewer than 10 nests. This approach resulted in six calendar date intervals, four initiation date intervals, and five nest age intervals. Data were standardized across all years by Julian date, and the first interval began with the earliest observed nest exposure date (27 April) and initiation date (24 April). We then cast continuous-time models equivalent to our discrete-time models replacing the discrete-time covariates of date, initiation date, and nest age with linear and quadratic functions of the three covariates (Table 5). Our global model included the interaction between year and date interval and an additive effect of nest age.

We examined variation in DSR and estimated nest survival by using the maximum likelihood estimators in Program MARK (White and Burnham 1999). Thus, we were able to construct models with DSR estimates that differed among intervals. We used a logit link to constrain estimates between 0 and

1, and we used AIC corrected for small-sample bias (AIC_c) to select among our set of candidate models (Burnham and Anderson 2002). Output from Program MARK allowed us to examine the effects of each parameter in our best model via the coefficients in the logit equation (β s) and their standard errors. Although this was a useful method to obtain estimates of the real parameters of interest, variances were estimable only by approximation through the delta method or bootstrap simulation. We used bootstrap resampling of the encounter history data (500 samples with replacement up to the original sample size for each of the 4 y; Efron and Tibshirani 1994). Because MARK does not provide a convenient method to run large numbers of analyses by using different data sets, we analyzed bootstrap samples in MATLAB release 13 (The Mathworks, Inc.) and used a quasi-Newton optimization routine to obtain maximum likelihood estimates based on the same estimator used in MARK (Dinsmore et al. 2002).

We calculated the real parameter estimates of DSR for each combination of nest age, date, and

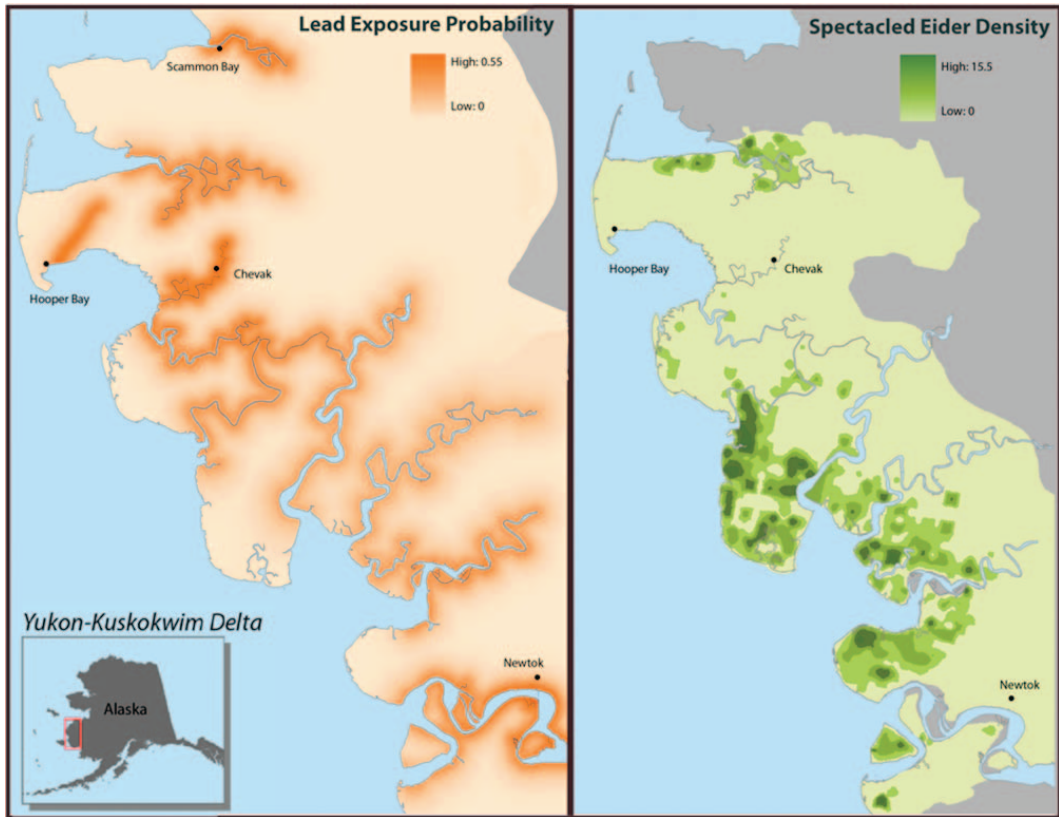


Figure 9. Lead exposure probability (i.e., blood Pb >0.2 ppm) and spectacled eider *Somateria fischeri* nest density maps of the primary nesting area on the Yukon-Kuskokwim Delta, Alaska, during 1993–1999 and 1993–2000, respectively. Density is plotted as number of nests per 2.54 Km² block.

year in the study period. When initiation dates fell before the first date for which nests were monitored, we estimated survival during that period as follows:

$$\prod_{i=1}^j \text{DSR}_i, \quad (1)$$

where DSR_i is the DSR of a nest of age i on the first day of the period of nest observations.

Results

Nest success varied across sites and years of the study (Table 6). We found weak support for an effect of nest initiation date on hatching success. Generally, nesting success at Kigigak Island was higher than at Kashunuk River (average effect size was 21% difference in success and Kigigak > Kashunuk River in 10 of 11 y). However, there was considerable annual variation in success within sites with estimates ranging from less than 5 to more than 90% at both locations. The difference among sites was not consistent and was represented by a site*year interaction term (Table 5). As such, there was no general correlation in success among sites. However,

the lowest estimates at both sites occurred in the same year (i.e., 2001).

Discussion

It seems that both regional and local-scale factors influence nesting success. We interpret these patterns to indicate that site-specific nesting success is primarily determined by localized predator populations. However, in some years broad-scale predator dynamics may become dominant. For example, in 2001, the arctic fox *Alopex lagopus* population size was very high and potential alternative prey (i.e., microtines) was low, resulting in high levels of fox predation on bird nests across the Y-K Delta. It is unclear why Kigigak Island had consistently higher nesting success. Because Kigigak it is an island, access by arctic foxes may have been precluded in some years. Alternatively, the relatively high density of other species of nesting birds may have contributed to predator swamping. Kigigak Island also suffered less frequent tidal flooding. Nonetheless, our data make it clear that substantial spatial heterogeneity in reproductive success exists within regional subpopulations, making it questionable to expand

Table 5. Models used in the overall estimation of success for spectacled eider *Somateria fischeri* nests at Kigigak Island and Kashunuk River on the coastal fringe of the Yukon-Kuskokwim Delta, Alaska, 1992–2004.

Model ^a	AIC _c	ΔAIC _c ^b	w ^c	k ^d	Deviance
DSR (site*year l)	2,900.06	0	0.404	25	2,850.01
DSR (site*year A l)	2,900.62	0.562	0.305	26	2,848.57
DSR (site*year D yrinit)	2,902.97	2.916	0.094	26	2,850.93
DSR (site*year yrinit)	2,903.01	2.950	0.092	25	2,852.96
DSR (site*year A yrinit)	2,903.70	3.643	0.065	26	2,851.65
DSR (site*year yrinit yrinit2)	2,904.96	4.904	0.035	26	2,852.92
DSR (site*year i)	2,910.50	10.447	0.002	30	2,850.44
DSR (site*year*i)	2,911.38	11.327	0.001	48	2,815.23
DSR (site*year A A2)	2,912.27	12.213	0.001	26	2,860.22

^a DSR, daily nest survival rate; l, initiation date (continuous); A, age (continuous); D, date (continuous); i, 10-d nest initiation periods; yrinit, relative initiation date within years. A 2 after a term indicates a quadratic effect.

^b Difference between each models' Akaike's Information Criterion and the lowest AIC value.

^c $\exp(-1/2 \Delta AIC_c) / \sum(\exp(-1/2 \Delta AIC_c))$.

^d Number of estimated parameters.

estimates from a single study location to larger population segments.

Female Offspring Produced

Clutch size is defined as the number of eggs laid by a female into a nest. Aside from anecdotal information published or cited in life history accounts, Dau (1974, 1976b) provided the first detailed study that examined clutch size of spectacled eiders on the Y-K Delta. Dau (1974, 1976b)

found inter- and intra-annual variation in clutch size and proposed that both types of variation are largely age related, but data from known-aged individuals were not available to produce estimates. Stehn et al. (1993) compared 1986–1992 estimates to Dau (1974), and they suggested that the apparent increases in clutch size were due to either poor detection of small clutches or changes in the age structure of the population, but again without supporting data. Also, Grand and Flint (1997) found that average clutch sizes at their study site on the

Table 6. Estimates of success for spectacled eider *Somateria fischeri* nests at Kigigak Island and Kashunuk River on the coastal fringe of the Yukon-Kuskokwim Delta, Alaska, 1992–2004.

Year	Kashunuk River		Kigigak Island	
	Success	SE	Success	SE
1992	0.61	0.14	0.92	0.05
1993	0.39	0.08	0.70	0.08
1994	0.19	0.06	0.82	0.06
1995	0.78	0.05	0.83	0.05
1996	0.47	0.07	0.92	0.03
1997	0.33	0.06	0.83	0.04
1998	0.71	0.06	0.87	0.04
1999	0.56	0.08	0.71	0.06
2000	0.80	0.07	0.82	0.05
2001	0.04	0.03	0.02	0.02
2002	0.92	0.04	0.77	0.05
2003	—	—	0.47	0.07
2004	—	—	0.81	0.05
Average	0.53	0.07	0.73	0.06

Y-K Delta spanned the range of historic estimates, suggesting that there has not been a long-term trend in clutch size.

Like Dau (1974, 1976b), Grand and Flint (1997) found that the number of eggs laid in nests declined with nest initiation date (i.e., later initiated nests contained fewer eggs). Furthermore, they discovered that this seasonal decline did not vary among years and suggested that seasonal declines in clutch size were age related, although marked populations of known-age individuals were not available to estimate age-specific nest initiation dates or clutch sizes. Grand and Flint (1997) reported that approximately 10% of eggs laid into successful nests were taken by predators and that proportion did not vary among years. Furthermore, they found that approximately 10% of the eggs in successful nests did not hatch due to infertility or embryonic mortality. Consequently, Grand and Flint (1997) estimated 4.3 ducklings produced per successful nest. In spite of variation in clutch size, the estimate of ducklings produced (eggs hatched) per nest did not vary within or among years. We reanalyzed those clutch size data in conjunction with an additional 7 y of data from Kashunuk River and 13 y of data from Kigigak Island to better estimate female ducklings produced per successful nest.

Methods

We used data from nests discovered following the search protocols described above. We numbered and candled each egg to determine viability and stage of incubation (Weller 1956). During each visit to a nest, we recorded the presence of the female, condition and number of eggs, and stage of incubation. In most years, nests were visited at 7- or 10-d intervals and within 2 d after hatch to determine egg fates from nest contents. We subtracted depredated and unhatched eggs from the number of eggs laid into the nest to determine the number of ducklings produced. The variance associated with annual estimates of the mean includes both sampling variation, due to the observation and experimental error, and process variation (σ), which reflects the true annual variation in number of ducklings hatched per nest. We estimated process variance using techniques outlined by Burnham et al. (1987).

Results

The mean clutch size hatched at Kashunuk River and Kigigak Island across all years was 4.6 ($\sigma = 0.34$) and 4.4 ($\sigma = 0.44$), respectively (Table 7). Sex ratios determined from ducklings captured in broods at 30 d posthatching were 0.49 female: 0.51 male ($n = 1,038$). Thus, we used an estimate of one-half of the number of ducklings produced to approximate the number of females hatched per nest.

Discussion

Clutch size hatched shows very little variation compared to other reproductive parameters. Given that spectacled eiders rely heavily on stored nutrient reserves for egg production, this implies relatively consistent prenesting foraging conditions, or that females unable to achieve a minimum body condition threshold skip breeding. We have no data to distinguish among these competing explanations. The causes of the relatively high rates of egg infertility are unknown. Previous studies failed to find a link between egg fertility and contaminants (Grand et al. 2002). The equal sex ratios for duckling captured at 30 d of age implies that any subsequent variation in sex ratio results from differential survival of older age classes.

Duckling Survival

Duckling survival is defined as the proportion of young hatched that survive until 30 d after hatch (Flint and Grand 1997). Dau (1974) provided information on declines in brood size, but this information cannot be used to estimate duckling survival, because the proportion of broods that were completely lost was not estimated. We used Flint and Grand (1997) estimates in conjunction with the additional results provided by Flint et al. (2006b) of 45% duckling survival from hatch through 30 d of age at Kashunuk River. Using the same techniques used at Kashunuk River, we estimated 67% duckling survival from hatch through 30 d of age at Kigigak Island based on 2 y of data. Flint et al. (2006b) found evidence of annual variation in duckling survival at the Kashunuk River site. Furthermore, they found an overall correlation between duckling growth and overall site-specific survival rates, suggesting that habitat conditions simultaneously influence both growth and survival (Flint et al. 2006b), despite relatively large fluctuations in habitat conditions. Thus, we allowed duckling survival to vary among years at the Kashunuk River site.

We defined brood survival as the proportion of females hatching a clutch that fledged at least one duckling in a brood each year. Duckling mortality rates may vary among broods; thus, duckling survival does not equate to brood survival (Ringelman and Longcore 1982; Savard et al. 1991; Flint et al. 1995). The mean brood survival at Kashunuk River and Kigigak Island across all years was 0.55 ($\sigma = 0.001$) and 0.85 ($\sigma = 0.009$), respectively. We found little evidence of annual process variation, but this was likely a result of relatively few years of study and high sampling variation within each year.

Survival and Breeding Propensity

Grand et al. (1998) estimated the annual survival rate of adult female spectacled eiders based on

Table 7. Number of ducklings produced from spectacled eider *Somateria fischeri* nests at Kigigak Island and Kashunuk River on the coastal fringe of the Yukon-Kuskokwim Delta, Alaska, 1992–2004.

Year	Kashunuk River			Kigigak Island		
	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
1992	19	5.6	0.4	58	4.9	0.2
1993	16	4.1	0.4	59	4.8	0.2
1994	27	4.3	0.4	54	5.2	0.2
1995	21	4.0	0.4	69	4.3	0.2
1996	63	4.7	0.2	93	4.6	0.1
1997	42	4.4	0.2	114	4.5	0.1
1998	44	4.0	0.2	92	4.3	0.1
1999	71	4.3	0.1	93	4.4	0.1
2000	45	5.1	0.2	99	4.8	0.1
2001	3	5.7	0.3	4	2.5	0.3
2002	54	5.0	0.2	108	4.6	0.1
2003	—	—	—	68	3.7	0.2
2004	—	—	—	115	4.5	0.1

a sample of nesting females marked and resighted over a period of 4 y at Kashunuk River and Kigigak Island. They found that adult females that were exposed to lead experienced the very low annual survival rate of 44% (S_a *lead*). They also estimated annual survival rate of 78% for breeding adult females not exposed to lead (S_a *no lead*). This “unexposed” survival rate estimate is almost certainly biased low, because the sample of unexposed females undoubtedly included some females that were exposed to lead after blood levels were sampled (i.e., at hatch). Furthermore, their approach required estimating the probability of lead exposure for each individual in each year, which was logistically difficult and costly. Here, we extend those samples to include seven additional years of observations on marked females, including some individuals marked as ducklings whose ages were known exactly. These expanded models allow estimation of first-year survival as well as relative age-specific breeding propensity of 2-y-old females. We also examined the effects of winter sea ice conditions on annual survival of both adults and first-year birds. However, the estimates we present are from a composite sample of individuals for which lead exposure is unknown.

Methods

Sea ice concentrations were quantified using passive satellite data. We used bootstrap sea ice concentration estimates from the Special Sensor Microwave Imager sensors for the four 25 × 25 km pixels defined by Petersen and Douglas (2004) as the core wintering area (Comiso et al. 1997; Comiso 2002). Winter was defined as 1 November until 30 April. We used three indices to describe ice severity:

1) mean percentage of ice cover, 2) total number of days when ice cover was 95% or more, and 3) a severity index that emphasized long periods of ice cover equal to or greater than 95%. In developing this index, we determined length of contiguous periods of days in which ice concentration was equal to or greater than 95%, allowing for 1-d drops below the 95% threshold. Thus, 3 d of ice concentration equal to or greater than 95%, followed by 1 d of ice at 94%, then three more days of equal to or greater than 95% ice would be recorded as a single period of 7 d of severe ice. Conversely, if the intermediate interval of less than 95% ice had been 2 d, the data string would have been recorded as two periods of 3 d with extreme ice. Our allowance for 1-d drops below the threshold accounts for the fact that daily sea ice concentrations are estimated. Similarly, 1-d events of equal to or greater than 95% ice coverage were not considered. Our index followed the logic of species diversity indices and was calculated as follows:

$$\sum_{i=1}^B (D \times \ln(D)), \tag{2}$$

where *B* is the total number of periods within each year and *D* is the length of each period in days. This index accounts for variation in total number of days with ice concentration equal to or greater than 95% across years and gives higher weight to years in which these days were more contiguous. Thus, a high index indicates relatively severe ice conditions and a low index indicates mild ice conditions.

Statistical analyses. We used a Cormack–Jolly–Seber maximum likelihood approach to estimate

annual survival (ϕ) and resighting probabilities (p) from the mark–resighting data (Lebreton et al. 1992). We included observations of incubating females identified by nasal markers or plastic or metal tarsus bands in the analysis. We used MARK for the analysis with a logit link function and estimated variance using the second partial derivative. We considered females observed at Kashunuk River and Kigigak Island as separate populations because we never observed exchange between the two sites. We used AIC corrected for small-sample bias and overdispersion ($QAIC_c$) to identify suitable models for estimating survival and resighting probabilities (Anderson et al. 1994). The overdispersion parameter (i.e., \hat{c}) was estimated from the ratio of the deviance in the real data, divided by the deviance from simulated data that was binomially distributed.

We considered models that included variation in ϕ and p between sites, among age classes, and over time. Females marked as ducklings never returned at 1 y of age; thus, recapture rates for these females were fixed at 0. We used an age graduation model and assumed that second-year survival rates (i.e., from 1 to 2 y of age) for females marked as ducklings was equal to adult (i.e., >2 y of age) survival rates for the same calendar year. Thus, for females marked as ducklings, we only observed the product of first-year survival (i.e., survival from 30 d of age to 1 y) and second-year survival, but under the assumption that second-year survival is equivalent to adult survival, the first-year survival rate is estimable. However, because adult survival rate varied annually, first-year survival could only be estimated as being constant across years.

We estimated breeding propensity of 2-y-old females as the ratio of recapture probabilities between 2-y-old females and all other females within site-years. This approach is based on the fact that failure to breed is functionally a form of temporary emigration, which biases recapture rates. Assuming all else is equal, lower recapture rates for 2-y-old females relative to older birds would reflect this temporary emigration and thus be indicative of lower breeding propensity. Thus, we modeled recapture rates for 2-y-old birds as being equal to older birds for the same site-year, but we included an additional parameter that we defined as the breeding propensity. We based all our model selection on a logit-linked model, but we reconsidered the best models under a log link to actually estimate the breeding propensity. Changing links allowed us to directly estimate the breeding propensity as the proportion of 2-y-old females breeding relative to older females. Breeding propensity is reported as the inverse log of the beta values and associated CIs.

We tested three possible sea ice covariates: mean ice concentration in the core area, total number of

days when ice concentration was equal to or greater than 95%, and an index to periods of severe ice conditions. Because these covariates were all correlated, we only included them individually in models to assess which covariate might best describe the influence of ice. Given that we had high variation in nesting success across years and sites, we included nesting success as a covariate to address questions regarding costs of reproduction on subsequent survival as well as mortality of hens associated with predation on nests. If successful reproduction by females entails a subsequent reduction in future survival as a result of presumed physiological stress, then at the cohort level, years of high nesting success should be followed by years of relatively low survival. That is, survival from year i to year $i+1$ should be negatively related to nesting success in year i . Conversely, if predators destroying nests are also killing hens, then years of relatively low nesting success should correspond with relatively low annual survival. Because most hens are “recaptured” at hatch, we would expect a positive relationship between survival from year i to year $i+1$ and nesting success in year $i+1$. Thus, for both of these analyses, to conclude support for these hypotheses, the defined models would have to show AIC based support and the beta value would have to show the expected direction of the relationship (i.e., + or –). Finally, we suspected that much of the variation in recapture rate across sites and years was related to nesting success. Thus, we included nesting success as a covariate influencing recapture rate in an attempt to reduce parameter space. The variance associated with annual estimates of survival includes both sampling variation, due to observation and experimental error, and σ , which reflects the stochastic variation in survival. We estimated process variance using techniques outlined by Burnham et al. (1987).

Results

For females originally marked as adults, we analyzed 297 recaptures of 341 females marked at Kashunuk River and 612 recaptures of 386 females marked at Kigigak Island during 1992–2004. For birds originally marked as ducklings we analyzed 30 recaptures of 274 females marked at Kashunuk River and 43 recaptures of 241 females marked at Kigigak Island. There was little evidence of overdispersion and \hat{c} was estimated at 1.064. The model that best fit our data allowed survival to vary among ages and sites with an additive effect of years; this model also allowed resighting rates to vary among years and sites with no difference in breeding propensity among sites (Table 8). However, this model was very similar in w_{AIC} ($\Delta QAIC_c = 0.02$) to a model that replaced the additive year effect (10 parameters) with an index of sea ice severity applied

Table 8. Most parsimonious models of survival and resighting probability for spectacled eiders *Somateria fischeri* at Kigigak Island and Kashunuk River on the Yukon-Kuskokwim Delta, Alaska 1993–2004.

Model ^a	QAIC _c ^b	ΔQAIC _c ^c	w	k ^d	Deviance
$\phi_{\text{site+age+time}} p_{\text{site*time}} \text{BP}_1$	3,507.87	0.00	0.18	36	935.547
$\phi_{\text{site+age+(ICE*age)}} p_{\text{site*time}} \text{BP}_1$	3,507.89	0.02	0.18	28	952.117
$\phi_{\text{age+(ICE*age)}} p_{\text{site*time}} \text{BP}_1$	3,508.68	0.80	0.12	27	954.966
$\phi_{\text{site+age+(ICE*age+site)}} p_{\text{site*time}} \text{BP}_1$	3,508.83	0.96	0.11	29	950.996
$\phi_{\text{site+age+(DAYS ICE*age)}} p_{\text{site*time}} \text{BP}_1$	3,509.01	1.13	0.10	28	953.230
$\phi_{\text{site+age+time}} p_{\text{site*time}} \text{BP}_2$	3,509.45	1.57	0.08	37	935.037
$\phi_{\text{site+age+(ICE*adults)}} p_{\text{site*time}} \text{BP}_1$	3,509.81	1.94	0.07	27	956.097
$\phi_{\text{age+time}} p_{\text{site*time}} \text{BP}_1$	3,509.82	1.94	0.07	35	939.568
$\phi_{\text{site+age+(ICE*age*site)}} p_{\text{site*time}} \text{BP}_1$	3,510.20	2.32	0.06	30	950.298
$\phi_{\text{site+age+(mean ICE*age)}} p_{\text{site*time}} \text{BP}_1$	3,511.04	3.16	0.04	28	955.265
$\phi_{\text{site+age*time}} p_{\text{site*time}} \text{BP}_1$ random effects	3,513.60	5.72	0.01	41.1	930.632
$\phi_{\text{site+age*time}} p_{\text{site*time}} \text{BP}_1$	3,516.61	8.73	0.00	44	927.58

^a Notation follows that of Lebreton et al. (1992). ϕ , P(survival); p, P(resighting); ICE, ice index; DAYS ICE, number of days with equal to or greater than 95% ice cover; mean ICE, average percentage of ice cover over the winter period.
^b Akaike's information criterion corrected for small sample bias and variance inflation (Anderson et al. 1994).
^c Increase in QAIC_c over the lowest observed value of QAIC_c.
^d Number of parameters estimated.

separately to each age class (two parameters). The sea ice severity model suggests that when sea ice conditions were severe survival was 10–22% lower than survival when ice conditions were mild (Figure 10). At Kashunuk River, annual estimates of survival varied from 0.63 to 0.94 ($\bar{x} = 0.78$, $\sigma = 0.007$); at Kigigak Island, annual estimates of survival varied from 0.55 to 0.95 ($\bar{x} = 0.81$, $\sigma = 0.009$; Table 9). First-year survival at Kashunuk River was 0.22 (95% CI = 0.15–0.31) and at Kigigak Island was 0.27 (95% CI = 0.19–0.37). Breeding propensity of 2-y-old females was estimated at 0.29 (95% CI = 0.14–0.55), with weak evidence for variation among sites (Kashunuk River = 0.16, Kigigak Island = 0.37, $\Delta\text{QAIC}_c = 1.57$). We found essentially no support for hypothesized effects of nesting success on survival. In our analyses of the potential physiological effects that may reduce subsequent survival, although the beta value was in the predicted direction, support for the overall model was negligible (model likelihood 0.01). In the analyses that examined predation on nests, the beta value was in the opposite direction from that predicted and support for this model was also negligible (model likelihood = 0.02).

Discussion

Similar to Grand et al. (1998), we found support for variation in survival rates across study sites, with Kigigak Island having higher survival than Kashunuk River. Our current analyses support this site-specific variation for both adult and first-year female survival. However, variation among sites seems to be

related to winter sea ice conditions because geographic variation in survival is greatest during years of heavy sea ice. Models predict little variation in survival in years of mild sea ice conditions. We suspect that the mechanism causing this variation may be lead poisoning from ingestion of spent shot. Previous studies have demonstrated variation in lead exposure across study areas as well as reduced annual survival of lead-exposed birds. Grand et al. (1998) concluded that most mortality associated with the lead exposure they documented must occur at sea (i.e., after birds left the breeding grounds). Our current analyses support this conclusion and suggest that this lead effect may be most pronounced in years of severe sea ice concentration.

We tested three possible sea ice covariates: mean ice concentration in the core area, total number of days when ice concentration was equal to or greater than 95%, and an index to periods of severe ice conditions. The index gives more weight to continuous periods when ice coverage was greater than 95%. The logic being that during longer periods of limiting ice conditions, birds would require more stored reserves, which might then influence their survival. Although all of these covariates are correlated across years, we found the strongest support for models using the index. We conclude that the presence of ice in the core wintering area is not detrimental to spectacled eiders. In fact, it may have positive effects by providing roosting habitat and reducing wave height under high wind conditions (Petersen and Douglas 2004; Lovvorn et al.

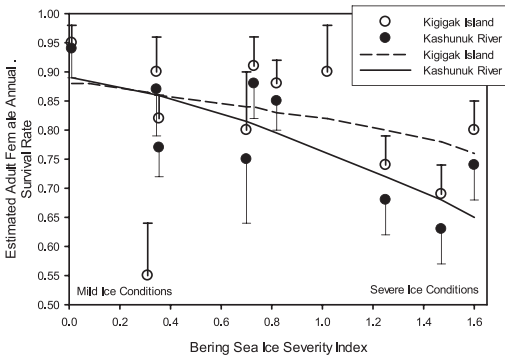


Figure 10. Estimated annual survival rates (circles) of adult female spectacled eiders *Somateria fischeri* from the Kashunuk River and Kigigak Island study sites on the Yukon-Kuskokwim Delta, Alaska, in relation to an index of ice severity in the Bering Sea from 1992 to 2002. Lines show the predicted relationship between survival and ice severity index for each study site. The ice severity index gives higher scores to years with more frequent and longer continuous periods of ice cover equal to or greater than 95%.

2009). However, continuous periods of heavy ice seem to have negative effects on survival, implying that under these conditions forage is likely limiting.

Given that winter ice conditions influenced survival of adult females, we expected even stronger

effects on first-year-survival. However, beta values indicate a positive effect of ice conditions on first-year survival. Because we only observed the product of first- and second-year survival and given a negative effect of ice on second-year (i.e., adult) survival, we might expect a negative covariance between first- and second-year survival. Under such conditions, however, we would not expect completely different trends in the effects of ice conditions on survival among age classes. In fact, our results indicate that first-year survival is positively related to our sea ice severity index. This relationship led us to hypothesize that perhaps there is age-based segregation in wintering spectacled eiders and that subadult birds are not present on the core wintering area. Petersen et al. (1999) conducted a photo census of wintering spectacled eiders and reported a flock composition of 56% birds in adult male plumage. At the time of the survey, male first-year birds were indistinguishable from females. Thus, if the population is close to stability (i.e., recruitment \cong annual mortality), we would expect to see more dark-colored birds than adult males, even though males likely have a higher survival rate. Application of a simple balance equation assuming a stable population and the adult survival rates estimated in this study suggests that approximately 50% of the brown birds observed (i.e., the nonadult males) would be first-year birds. Under these conditions, only approximately 22% of

Table 9. Estimates, SEs, and 95% CIs for survival of spectacled eiders *Somateria fischeri* at Kigigak Island and Kashunuk River (model ϕ_s , p_{2t}) on the Yukon-Kuskokwim Delta, Alaska, 1993–2004.

Parameter	Kashunuk River	SE	Kigigak Island	SE
Survival (ϕ_s)				
1992	0.7468	0.1150	0.7984	0.0971
1993	0.8774	0.0810	0.9057	0.0637
1994	0.7444	0.0624	0.7963	0.0530
1995	0.8464	0.0480	0.8809	0.0387
1996	0.7704	0.0457	0.8183	0.0388
1997	0.8806	0.0604	0.9082	0.0478
1998	0.6845	0.0582	0.7444	0.0488
1999	0.6271	0.0574	0.6930	0.0480
2000	0.9398	0.0456	0.9545	0.0345
2001			0.9001	0.0750
2002			0.5524	0.0895
Parameter				
Estimate				
SE				
Lower 95% CI				
Upper 95% CI				
Breeding propensity of 2 y olds				
Kashunuk River	0.1601		0.0396	0.6505
Kigigak Island	0.3679		0.1666	0.8058
First-year survival				
Kashunuk River	0.2171	0.0411	0.1472	0.3082
Kigigak Island	0.2713	0.0476	0.1884	0.3738

the observed population would be adult females, and the ratio of adult males to adult females would exceed 2.5:1. This sex and age structure is functionally unattainable in a viable population. Thus, the age ratio data seem to support our post hoc hypothesis that first-year birds may be segregated from adults during winter. This segregation would explain the anomalous relationship between our sea ice index and first-year survival. We believe the potential for age-based population segregation during winter deserves further study.

We found evidence that both first-year survival rates and 2-y-old breeding propensity varied among study sites; both parameters being higher at Kigigak Island compared to Kashunuk River. Flint et al. (2006b) found that ducklings at Kigigak Island both grew faster and survived at a higher rate than ducklings at Kashunuk River and concluded that this was likely caused by variation in habitat conditions. Sedinger et al. (1995, 2004) reported that black brant goslings that grew at a higher rate were more likely to survive and breed at a younger age. Overall, our data seem to fit this pattern where the higher growth rates observed at Kigigak Island (Flint et al. 2006b) are correlated with higher first-year survival and lower age of first reproduction. This correlation supports the conclusion that despite the reduced population size, habitat conditions may be limiting in some breeding locations.

For the purposes of our model, we defined breeding propensity (bp_i) as the proportion of females in age class i that attempted to nest each year. Baillie and Milne (1982) found that for common eiders, 1-y-old females never nested, only 26% of the 2-y-old females nested, 42% of 3-y-old females nested, and most females more than 3 y old nested each year. Similarly, we have never observed 1-y-old female spectacled eiders attempting to nest, and we assumed that $bp_1 = 0$. We used separate estimates of breeding propensity for 2-y-old females at each of our study sites as described above (i.e., $bp_2 = 0.37$ at Kigigak Island and $bp_2 = 0.16$ at Kashunuk River). Because failure to breed is the functional equivalent of temporary emigration and temporary emigration is confounded with detection probability (Grand et al. 1998), we were forced to assume that $bp_3 = 1.0$ at both study sites. If bp_3 is actually less than 1, then we will underestimate overall productivity and our estimate of bp_2 would represent the breeding propensity relative to that of adults.

Effects of Lead Exposure on Annual Survival

Based on a sample of nesting females marked and resighted over a period of 4 y, Grand et al. (1998)

estimated the annual survival rate of adult female spectacled eiders at two sites on the Y-K Delta. They found that adult females that were exposed to lead experienced the very low annual survival rate of 44% ($S_{a \text{ lead}}$). They also estimated annual survival rate of 78% for breeding adult females not exposed to lead ($S_{a \text{ no lead}}$). However, this estimate is biased low, because the sample of unexposed females undoubtedly included some females that were exposed to lead after hatch, when lead exposure levels were sampled.

We used an ad hoc procedure to correct for this known bias. We assumed that all of the difference in estimated annual survival between Kashunuk River and Kigigak Island resulted from differences in lead exposure rate. We estimated the difference in lead exposure rate between sites after accounting for time spent on the breeding grounds (Flint et al. 1997). Females that fail to hatch a clutch or rear a brood return to sea soon after reproductive failure. Hence, females that lose their nests depart the breeding grounds first, followed by females that lose their broods; the last females to depart the breeding grounds are those that successfully rear broods (Petersen et al. 1999). Thus, lead exposure rates are expected to be highest for successfully breeding females.

Flint et al. (1997) estimated the portion of nesting females exposed to lead shot at the Kashunuk River area (θ) was 0.25–0.35 each year by using the following equation:

$$\theta = ((1 - ns)x_1) + (ns(1 - bs)x_2) + (ns \ bs \ x_3), \quad (3)$$

where x_1 (0.13) is the predicted lead exposure rate for females that nest unsuccessfully; x_2 (0.25) is the predicted exposure rate of females that nest successfully, but lose their entire brood and depart the study area; and x_3 (0.36) is the predicted exposure rate of females that successfully rear a brood before departing the study area. We produced new estimates of x_1 , x_2 , and x_3 and recalculated θ (Table 10) by using additional data on exposure rates of females during early incubation (Grand et al. 2002).

These proportions, x_1 , x_2 , and x_3 , were specific to the Kashunuk River study area. We estimated lead exposure at Kigigak Island, but only by sampling females captured at hatch. Therefore, we lacked the data necessary to estimate the values for x_1 and x_3 specific to Kigigak Island. To scale estimates of lead exposure for other areas, we estimated l_a , the exposure rate relative to the exposure rate at Kashunuk River. Thus, l_a for Kigigak Island was the lead exposure rate of females sampled during hatch on Kigigak Island divided by the lead exposure rate of females sampled during hatch at Kashunuk River. We

Table 10. Vital rates used in simulations of Yukon-Kuskokwim Delta, Alaska, spectacled eider *Somateria fischeri* populations (see text for sources and definitions).

Parameter	Population	
	Kashunuk River	Kigigak Island
Breeding propensity		
2 y olds (bp_2)	0.16	0.37
3 y olds (bp_3)	1.00	1.00
Nest success (ns)	0.53	0.73
Range	0.04–0.92	0.02–0.92
Females hatched (fh)	2.29	2.19
Duckling survival (ds)	0.39	0.67
Immature survival (\hat{S}_a)	0.22	0.27
Adult survival		
Not exposed to lead ($\hat{S}_{a \text{ no lead}}$)	0.88	0.88
Exposed to lead ($\hat{S}_{a \text{ lead}}$)	0.44	0.44
Relative lead exposure (l_a)	1.00	0.47
Lead exposure rates of females		
Unsuccessful nesters (x_1)	0.26	0.12
Successful nesters (x_2)	0.30	0.14
Successful brood rearing (x_3)	0.35	0.16
Lead exposure (θ)	0.29	0.16
Population growth rate (λ)		
Deterministic	0.8883	1.0359
Stochastic ^a	0.8812	1.0261
95% CI	(0.8566–0.9048)	(0.9865–1.0609)
Stable age distribution		
Age 1	0.096	0.196
Age 2	0.095	0.166
Age 3+	0.809	0.637

^a Stochastic growth rate estimated assuming no decline in lead exposure rate.

then recalculated the lead exposure rate for Kigigak Island as follows:

$$\theta = \frac{((1 - ns)x_1l_a) + (ns(1 - bs)x_2l_a) + (nsbsx_3l_a)}{l_a[((1 - ns)x_1) + (ns(1 - bs)x_2) + nsbsx_3]} \tag{4}$$

Given these θ values for each site and year, we calculated the difference in θ between sites for each year (i.e., $\Delta\theta$). Under our assumption that all of the estimated site effect is caused by differences in lead exposure, then, the site effect beta (i.e., β_{site}) value from the mark-recapture analysis is relative to this $\Delta\theta$. By scaling the β_{site} by $\Delta\theta$, it becomes possible to estimate survival as if no individuals were exposed to lead (i.e., $\theta = 0$) and as if all individuals were exposed to lead (i.e., $\theta = 1$). Using this approach, we estimated survival of females not exposed to lead ($S_{a \text{ no lead}}$) as 88% ($\sigma = 0.06$) and survival of females exposed to lead ($S_{a \text{ lead}}$) as 48% ($\sigma = 0.14$).

Calculating the effect of lead exposure

We also assumed that the availability of lead shot, and thus lead exposure rates of spectacled eiders, would decline across years, even though the proportion of lead available to ducks in tundra wetlands at Kashunuk River had not declined measurably after 3 y (Flint 1998). However, further study by Flint and Schamber (2010) demonstrated that lead pellets were slowly settling into wetland sediments and would eventually become unavailable to feeding spectacled eiders. Therefore, we assumed that, in the absence of additional shot deposition, lead exposure would eventually decline exponentially as described by

$$w_t = (0.5^{(1/y)})^t \tag{5}$$

where w_t is the relative exposure rate of adult females in year t and y is the number of years required for

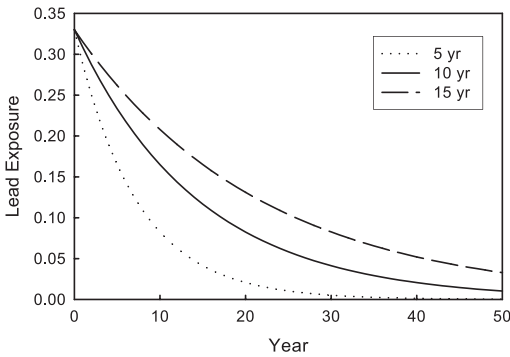


Figure 11. Lead exposure rates of adult female spectacled eiders *Somateria fischeri* nesting at Kashunuk River on the Yukon-Kuskokwim Delta, Alaska, predicted from an exponential decay in lead availability that declined to 50% of its original value in 5, 10, or 15 y.

lead availability to decline to 0.5 of the original value. This is synonymous with a half-life decay function. In our simulations of lead exposure effects on spectacled eider populations, we used $y = 5, 10, \text{ and } 15$ y (Figure 11).

To incorporate adjustments for differences in exposure rates among areas and the anticipated decline in lead availability across years, we modified the Flint et al. (1997) equation and estimated the exposure rate of nesting females at location a in year t of a simulation as follows:

$$\theta = w_t I_a [((1 - ns)x_1) + (ns(1 - bs)x_2) = (ns \cdot bs \cdot x_3)] \tag{6}$$

Thus, we estimated the survival rate for population a at time t by using a weighted average survival rate (\hat{S}_a^*) as

$$\begin{aligned} \hat{S}_a^* &= (\theta_{at} \times \hat{S}_{a \text{ lead}}) + ((1 - \theta_{at}) \times \hat{S}_{a \text{ no lead}}) \\ &= (\theta_{at} \times 0.48) + ((1 - \theta_{at}) \times 0.88). \end{aligned} \tag{7}$$

Consequently, for populations not exposed to lead we estimated $\hat{S}_a^* = 0.88$. When we simulate populations suffering from lead exposure, average annual survival is reduced as in equation (7), but as lead exposure declines through time, the survival rate increases and asymptotically approaches $\hat{S}_{a \text{ no lead}}$ (Figure 12).

Estimating juvenile, 1-y-old, and 2-y-old survival

Little is known about the survival rates of juvenile and subadult spectacled eider females. Recall that our estimates of duckling survival include only the period from hatch through 30 d of age. In a separate study at Kashunuk River, Flint et al. (2000) estimated 71% of spectacled eider ducklings survived

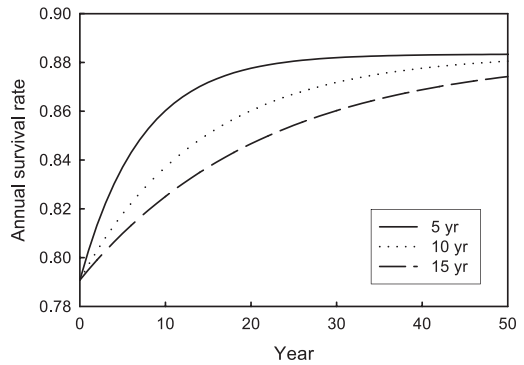


Figure 12. Annual survival rates of adult female spectacled eiders *Somateria fischeri* nesting at Kashunuk River on the Yukon-Kuskokwim Delta, Alaska, predicted from an exponential decay in lead availability that declined to 50% of its original value in 5, 10, or 15 y.

from 30 d posthatching until departure from the breeding grounds. Using our mark-recapture data, we were able to estimate first-year survival from the time of banding (i.e., 30 d) until the next breeding season (\hat{S}_0). We found support for variation in \hat{S}_0 among sites (Kashunuk River = 0.22 and Kigigak Island = 0.27), but due to model constraints, we were unable to estimate annual variation in this parameter.

We assumed that the survival rate of 1-y-old females was greater than that of juveniles. Given that there is no opportunity for exposure to lead poisoning (because breeding propensity was 0 and these 1-y-old females were never observed on breeding areas), we assumed that their survival rate (\hat{S}_1) was equal to $\hat{S}_{a \text{ no lead}}$. Only the portion of 2-y-old females that arrive on the breeding grounds to nest (bp_2) are potentially exposed to lead poisoning. Therefore, we estimate the annual survival rate of 2-y-old females by using the weighted average

$$\hat{S}_2 = ((1 - bp_2) \times \hat{S}_{a \text{ no lead}}) + (bp_2 \times \hat{S}_a^*). \tag{8}$$

Deterministic Model of Population Dynamics

To construct an accurate population model in the absence of emigration or immigration required an understanding of only two basic processes: survival and recruitment. We used the available demographic data and constructed an explicit model based on our knowledge of life history processes contributing to survival and recruitment of females (Figure 13). We sought to construct a model that would provide estimates of population size that were comparable to

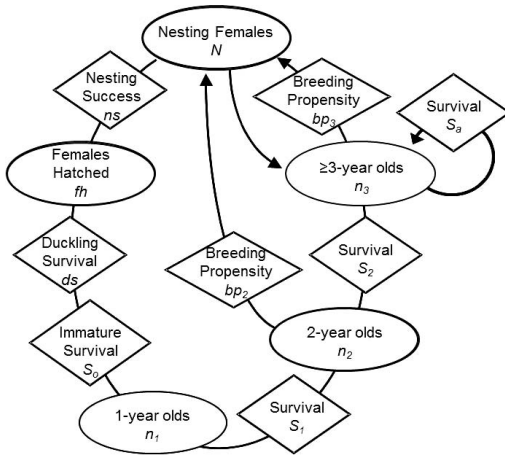


Figure 13. Explicit population model of spectacled eider *Somateria fischeri* life history. Diamonds represent vital rates and ovals represent age classes or states. Predicted population trends are based on the number of nesting females.

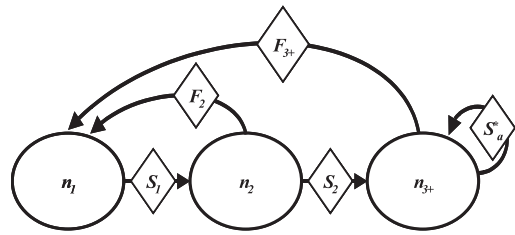


Figure 14. Three-stage, prebreeding census, birth-pulsed model used for spectacled eider *Somateria fischeri* populations. Circles denote stages in the age-structured model. Boxes indicate transition probabilities.

growth rate using an elasticity analysis of the matrix (Caswell 2001). For the Kashunuk River projection matrix, the elasticity matrix is

$$E = \begin{bmatrix} 0 & 0.0017 & 0.0924 \\ 0.0942 & 0 & 0 \\ 0 & 0.0924 & 0.7192 \end{bmatrix}. \quad (11)$$

breeding ground surveys. Therefore, we simplified the explicit demographic model into a three-state, prebreeding census, birth-pulsed population model (Figure 14). The prebreeding census model allowed us to project the population growth rate and age distribution just before nesting. The three age classes used in our model include individuals not yet age-1 (n_1); at least age-1, but not yet age-2 (n_2); and age-2 and older (n_3). Using this three-stage model, we developed population projections and explored the relative contribution of demographic variables to the predicted population growth rate.

The demographic data were summarized in a Leslie-style matrix (Caswell 2001). We estimated the fertilities as follows:

$$F_i = bp_i \times ns_i \times fh_i \times ds_i \times S_0. \quad (9)$$

In our case, the matrix values for the Kashunuk River subpopulation derived from the values in Table 10 are as follows:

$$A = \begin{bmatrix} 0 & 0.017 & 0.103 \\ 0.8785 & 0 & 0 \\ 0 & 0.8638 & 0.7908 \end{bmatrix}. \quad (10)$$

The predicted growth rates for the populations we studied were $\lambda = 0.8883$ for Kashunuk River and $\lambda = 1.0359$ for Kigigak Island. Thus, our model predicts substantially different trends for these two breeding areas (Figure 15).

We estimated the relative contribution each of the demographic variables makes to the population

Because the nonzero values in the lower two rows are the probabilities of individuals surviving from age class 1 to 2, 2 to 3, and in age classes 3 and greater, we sum these elasticities and conclude that these survival rates determine 90.6% of the population growth rate, whereas the projection elements related to fertility only determine 9.4% of λ .

The elasticities of S_2 and S_3 depend on effects of S_a no lead, S_a lead, bp_i , nest success (ns), and x_1-x_3 . Changes in any of these parameters could alter λ through their effect on S_2 and S_3 . Similarly, the effect of an alteration of nesting success on λ would operate through changes in F_2 , F_3 , S_2 , and S_3 . The relative effects of individual demographic parameters on the population growth rate are termed lower level elasticities (Caswell 2001). We estimated lower level elasticities with perturbations of computer projections by using a proportionate change set at $p = 0.01$ (e.g., Schmutz et al. 1997).

The lower level elasticities for S_a no lead and the composite S_a no lead + S_a lead had, by far, the most profound effect on the dynamics of both subpopulations (Figure 16). Our model is unusual in that survival probabilities are influenced by the lower level elasticities of bp , ns , and duckling survival (ds). These three parameters are linked to survival through their effect on lead exposure rates. For example, a change in nest success not only influences F_i but also S_2 and S_a^* . We explicitly parameterized a study site-specific lead exposure rate; thus, we could estimate the associated elasticity. As expected, the lower level elasticity of the lead exposure rate was negative, because increases in lead exposure result in decreases in λ . Elasticities and lower level elasticities are both specific to the exact values of the

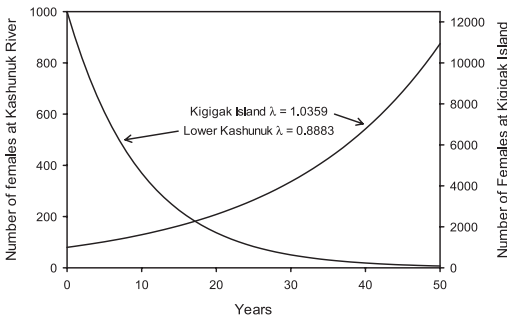


Figure 15. Projected population trends of female spectacled eiders *Somateria fischeri* at Kashunuk River and Kigigak Island on the Yukon-Kuskokwim Delta, Alaska, predicted using the deterministic model. Both populations were started at an initial population of 1,000 individuals.

elements of the projection matrix. Therefore, we expected some variation among the lower level elasticities of the demographic variables between Kigigak Island and Kashunuk River, owing to differences in lead exposure, nesting success, and duckling survival. However, adult survival has the largest effect on dynamics for both subpopulations. The fact that elasticities were similar for two populations with substantially different trends suggests that these results are relatively robust to variation in the specific values in the projection matrix. Thus, we conclude that adult survival probably has the largest impact on population dynamics under a wide range of biological conditions.

The negative relationship between nesting success, adult survival, and population growth at Kashunuk River is mediated through lead and its effect on the survival of lead-exposed females during nesting and brood rearing. From equations (7) and (8), it is clear that as nesting success improves, lead exposure increases, and more of the population survives at the lower, $S_{a\ lead} = 0.48$, annual survival rate. Conversely, a reduction in nesting success results in reduced lead exposure rates and more individuals with the higher, $S_{a\ no\ lead} = 0.88$, annual survival rate. Given this relationship, and the result that adult female survival has the greatest influence on population dynamics, it is possible that beyond some point, increases in nesting success could have a negative effect on population dynamics. The fact that the lower level elasticities were positive implies that this negative relationship does not exist for the parameter values in our matrix. To further assess this relationship for other potential parameter values, we examined the relationship between nesting success and population dynamics by predicting S_a^* and λ for the Kashunuk River subpopulation by using values of nest success ranging from 0 to 100% in the presence of the lead effect on adult survival (Figure 17). Although S_a^* declines as

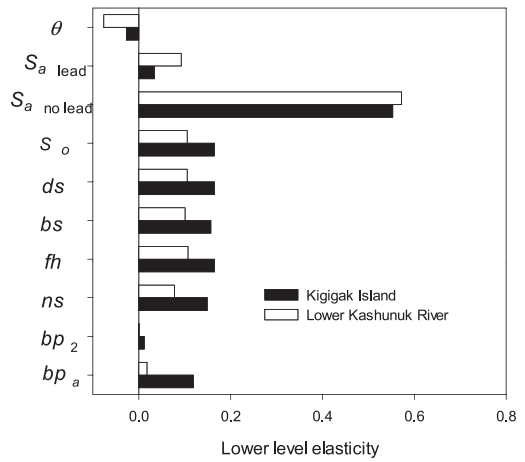


Figure 16. Lower level elasticities for demographic components from the deterministic model of female spectacled eider *Somateria fischeri* populations at Kashunuk River and Kigigak Island on the Yukon-Kuskokwim Delta, Alaska. θ , population level lead exposure rate; $S_{a\ no\ lead}$, survival rate of adult females not exposed to lead; $S_{a\ lead}$, survival rate of adult females exposed to lead; $S_{a\ no\ lead} + S_{a\ lead}$, survival rate of all adult females; S_o , survival rate of 1 y olds; bp_2 , breeding propensity of 2 y olds; bp_a , breeding propensity of adults; ns , nest success; ds , duckling survival; fh , females hatched per nest.

nest success improves, we found that increases in nesting success continued to yield increases in λ .

Interestingly, the lower level elasticity for breeding propensity (for both age classes) was functionally 0 at the Kashunuk River, but not at Kigigak Island. This difference among sites is primarily related to the differences in lead exposure. Thus, at Kashunuk River increases or decreases in breeding propensity would have little effect on λ because the net change in productivity is functionally offset by the change in survival resulting from the change in lead exposure. Accordingly, in areas with greater lead exposure than the Kashunuk River, we suspect that the elasticities for breeding propensity would be negative, implying that the highest λ would be obtained when breeding propensity was 0. Populations that fail to reproduce are destined to decline, so this is functionally looking for the minimum rate of decline. Overall, these results imply that lead exposure rates greater than those we found along the Kashunuk River would result in localized extirpation.

Variance components of the deterministic model

We estimated the variance in our deterministic λ based on process variance (Flint 2015). In cases where we had suites of estimates for a given parameter, each with its own estimate of sampling error, we first computed total parameter variance

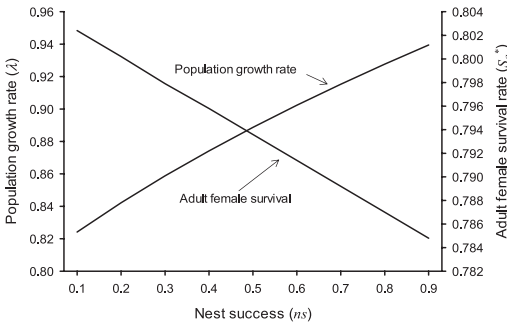


Figure 17. Predicted relations among population growth rate, survival rate of adult females, and nesting success with the effects of lead exposure for spectacled eiders *Somateria fischeri* breeding the Kashunuk River on the Yukon-Kuskokwim Delta, Alaska.

then decomposed process variance following Burnham et al. (1987). Sampling variance was then estimated by subtracting process variance from total variance. For several parameters we could only estimate sampling error (i.e., for example, in estimating first-year survival and breeding propensity, we could not consider temporally varying parameter structure), and thus we could not estimate process or total variance. Because the estimate of second-year survival is based on weighted values of $S_{a\ no\ lead}$ and $S_{a\ lead}$ we had no estimates of any form of variance. For these estimates, we assumed the sampling and process variance estimates from the adult female survival analyses applied. We then used the approach described by Caswell (2001) to estimate the variance in λ as follows:

$$V(\lambda) = \sum \text{Lower level sensitivity}^2 * \text{process variance.}$$

Proportional contributions of each parameters variance to the total were calculated as follows:

$$\text{Lower level sensitivity}^2 * \text{process variance} / V(\lambda).$$

Table 11. Confidence limits and variance decomposition of the deterministic λ for the modeled spectacled eider *Somateria fischeri* populations at Kigigak Island and Kashunuk River on the coastal fringe of the Yukon-Kuskokwim Delta, Alaska, by using data collected from 1992 to 2004.

	Kashunuk River	Kigigak Island
λ Upper confidence limit	1.064	1.245
λ Lower confidence limit	0.719	0.833
Clutch size	0.01 ^a	0.06
Nesting success	0.24	0.28
First-year survival	0.13	0.28
Second-year survival	0.01	0.03
Adult survival	0.60	0.36

^a Proportion of the variation in λ attributable to annual variation in each of the life history parameters.

In our data sets, process error results in considerable uncertainty in the potential realized λ values for both populations (Table 11). Based on 95% CIs, both estimates include stability (i.e., $\lambda = 1.0$). Given that our estimates of process variance functionally represent annual variation in the input parameters, the CIs represent the range of potential λ values that might be realized across any specific set of years. However, we did not have estimates of variance for all input parameters; thus, our overall variance of λ is almost certainly underestimated. The relative contributions of process variance in each lower level parameter to the total variance differed among study areas (Table 11). For example, variance in adult survival was the largest contributor to total variance for the Kashunuk River subpopulation, but it was far lower for Kigigak Island. Most of the differences in variance contributions among study areas were related to differences in sensitivities as opposed to differing patterns of process variance.

Population Growth in Stochastic Environments

Spectacled eiders live in an environment where weather, habitat conditions, and predator populations vary, both functionally and numerically, among years. Because the expression of life history characters affecting reproductive success and survival depends on the environment, the use of deterministic models that assume demographic variables are constant might not realistically demonstrate all aspects of population dynamics. Even for large populations, random variation in demographic variables has an impact on overall dynamics, such that populations grow at rates lower than those expected from the long-term means of demographic variables (Tuljapurkar 1990; Caswell 2001). Because some populations of spectacled eiders are small, stochastic variation can have a profound impact on short- and long-term dynamics. With small populations, even for demographic variables

that suggest a positive growth rate, stochastic fluctuations can lead to extinction. We examined population growth rate, and the elasticity of growth rate under conditions of stochasticity. We developed a stochastic model built on the deterministic model. We then examined the interplay of stochastic variation in nesting success and survival on the basic dynamics of the system and their joint effect on potential management options. Finally, we evaluated the impact of stochasticity on the persistence of small subpopulations of spectacled eiders.

We began our examination of growth in stochastic environments with a model based on the demographics of the Kashunuk River subpopulation, and we assumed no change in lead effects on survival. We generated demographic variables from the baseline data set in which nesting success, clutch size, and adult survival were drawn from a beta distribution using the mean and process variance and limited by the range of estimates (Table 10). We included correlations among input parameters as estimated from the original data. As seen with the deterministic model, the Kashunuk River subpopulation is predicted to decline rapidly; however, the influence of variation in vital rates is clearly seen in the variation among projections (Figure 18). Because our projections did not start at $N_0 = 1$, we used the more general maximum likelihood equation for estimating λ from Heyde and Cohen (1985):

$$\lambda = e^{\left(\frac{\ln N_t - \ln N_1}{t - 1}\right)}. \quad (12)$$

We used Monte Carlo methods to simulate stochastic population growth for various sets of demographic variables and conditions (e.g., relative lead exposure rate). In each simulation, we calculated the mean and determined 95% confidence limits (upper and lower 2.5 percentiles) of 1,000 trials.

Elasticities of the stochastic model

We calculated elasticities for the stochastic model by using a slight variation of the approach we used for finding lower level elasticities of the deterministic model. We altered each demographic variable in turn by a constant proportion and calculated the relative change in the population growth rate and scaled that by the proportion (Schmutz et al. 1997). Although there are some small numerical differences between the lower level elasticities for the stochastic and deterministic models, the patterns are essentially the same (Figure 19). This finding is consistent with that of Dixon et al. (1997), who concluded that deterministic elasticities are reasonable estimators of stochastic elasticities under many conditions. The

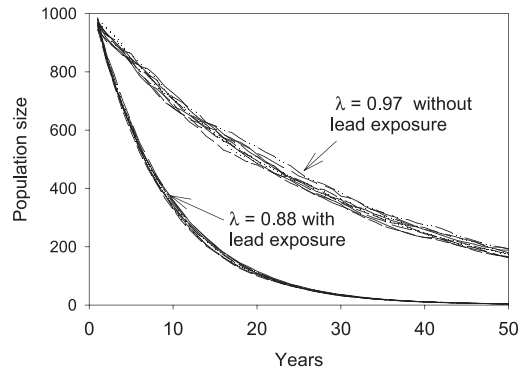


Figure 18. Theoretical stochastic population trends of female spectacled eiders *Somateria fischeri* at Kashunuk River on the Yukon-Kuskokwim Delta, Alaska, in the presence ($n = 10$ trials) and absence ($n = 10$ trials) of lead effects.

overall pattern of lower level stochastic elasticities for spectacled eiders is typical for populations of long-lived species: adult survival has the largest impact on population growth rate.

We considered the effects of lead poisoning in two ways: 1) assuming effects of lead remained constant over time and 2) assuming that lead exposure rates declined through time. When lead effects are introduced at some constant level, the model can still be viewed as the basic stochastic model with a single λ . When the level of lead affecting one or more demographic variables changes systematically over time, the result is a series of outcomes that are themselves a functional relationship. Under this changing scenario, λ is represented as line where the specific value changes through time.

Constant lead levels

We examined the effects of lead exposure on the stochastic dynamics of spectacled eiders. We used a stochastic model with the baseline data set for Kashunuk River and compared that with a model where $\theta = 0$ (i.e., no lead effects). Clearly, lead exposure has a negative effect on $\tilde{\lambda}$ (Figure 18). With lead exposure and its effect on adult survival, $\tilde{\lambda} = 0.8929$ (95% CI = 0.8897–0.8958) for the spectacled eiders at Kashunuk River and $\tilde{\lambda} = 1.0373$ (95% CI = 1.0340–1.0405) at Kigigak Island. There was less variation among replicate trials that included the effect of lead exposure. This reduction in variation resulted from two simultaneous processes. First, the negative feedback between nesting success and adult female survival tended to remove the extremes. That is, the effects of years of good production were dampened by poor survival. Second, the reduction in variation reflects the reduction over time in the size of any population whose stochastic growth rate was less than 1 because the apparent reduction in variation is relative. As the population size declines

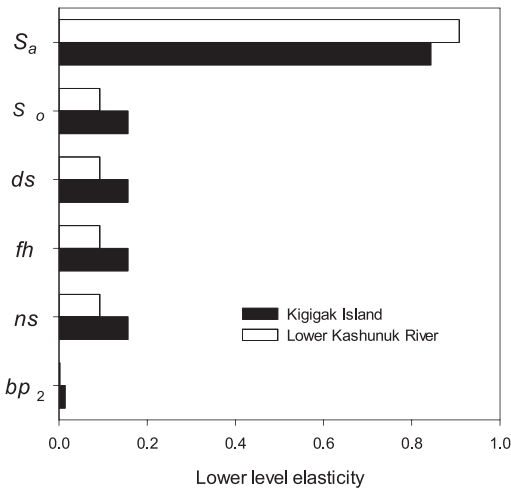


Figure 19. Lower level elasticities for demographic components from the stochastic model of spectacled eider *Somateria fischeri* dynamics for birds from Kigigak Island and Kashunuk River on the coast on the Yukon-Kuskokwim Delta, Alaska. S_a , survival rate of adult females; S_o , survival rate of 1 y olds; bp_2 , breeding propensity of 2 y olds; ns , nest success; ds , duckling survival; fh , females hatched per nest.

asymptotically through time, similar rates of variation have a smaller impact on the change in the expected population size among years and trials. Regardless of the level of lead exposure, the basic patterns of the lower level elasticities of the demographic variables (Figure 19) were the same as those estimated from deterministic models. Adult survival had the greatest effect on λ ; however, the elasticity of survival in the model without lead exposure effects was substantially greater than for models incorporating lead exposure. Lead exposure had no effect on the pattern of lower level elasticities of the demographic variables contributing to fertility.

Declining lead levels

Flint and Schamber (2010) hypothesized that the availability of lead shot in the environment declines through time. We assumed that the reduction in availability would lead to a reduction in lead exposure rates and a subsequent increase in adult female survival. We examined the behavior of the model under three different scenarios for lead exposure: 1) current lead exposure rate constant through time; 2) starting at the current lead exposure rate and assuming a 10-y half-life decay rate in exposure; and 3) no lead exposure, but all other parameters remain the same (Figure 20). Comparison of these curves demonstrates the overall negative effect of the measured lead exposure on population trends. The 10-y half-life scenario demonstrates the effect of nonconstant rates on population trajectories. Recall that stochastic growth

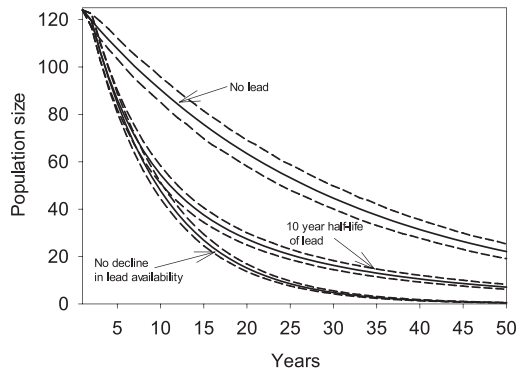


Figure 20. Stochastic growth rates and number of female spectacled eiders *Somateria fischeri* at Kashunuk River on the Yukon-Kuskokwim Delta, Alaska, by year as estimated using the stochastic model with no decline in lead exposure rate over time, with lead exposure half-life of 10 y (i.e., exposure declines by 50% over a 10-y interval) and no lead exposure. Average population size and 95% confidence interval is presented.

rates are estimated according to equation (3) of Heyde and Cohen (1985). Because lead levels declined, the 1-y growth rate over the interval $t \rightarrow t+1$ was less than that over the interval $t+1 \rightarrow t+2$. The estimate over the entire interval of T years was the average of those changing estimates and therefore specific to the interval T . Hence, the shape of the 10-y half-life function is different from the two constant-rate scenarios.

Population Viability Analyses

Population viability analysis (PVA) is the estimation of the probability that a population will persist above some threshold size for a period of time. Because some spectacled eider subpopulations are relatively small, their dynamics should be examined with PVA. The PVA probability is primarily a function of size, growth rate, and variation in population growth rate. There are many forms of PVA, some based on deterministic projections and others on stochastic projections, and many authors disagree as to the minimum population size and time period on which extinction probabilities should be based (for a review, see Beissinger and Westphal 1998). We used only the stochastic growth model and the distribution of mean population sizes over time to examine the viability of the three subpopulations of spectacled eiders that compose the regional Y-K Delta population: Kashunuk River, Kigigak Island, and the remainder of the Y-K Delta.

We based our analyses on a nesting subpopulation of 100 female spectacled eiders for both Kashunuk River and Kigigak Island. Given the expected stable age distribution and breeding propensity of the Kashunuk River subpopulation, this subpopulation

corresponds to approximately 127 breeding and nonbreeding females in three age classes. We then projected these subpopulations for 50 y and assumed a minimum viable population size of 10 individuals. For the remainder of Y-K Delta subpopulation, we used a starting size of 3,664 individuals and a λ of 1.016. We did not have an independent estimate of the process variance in λ for the Y-K Delta subpopulation; thus, we used the estimate for Kigigak Island. Using these values, we simulated a time series of 50 y for each subpopulation with this mean λ and associated variance. We multiplied the associated subpopulation size by this sequence of λ 's and determined whether each subpopulation ever declined below 10 individuals (i.e., pseudoextinction threshold). We repeated this process 1,000 times and report the proportion of trials that crossed the pseudoextinction threshold. Given that the Kashunuk River subpopulation was declining, the extinction probability for this subpopulation was 1.0, with an average time to quasi-extinction of 20 y (95% CI = 18–22 y). The functional-extinction probability for the other two subpopulations was 0. To assess the sensitivity of these results to variation in λ , we increased the variance by an order of magnitude and reran the simulations for the Kigigak Island and Y-K Delta subpopulations. Under the inflated variance scenario, the quasi-extinction probability for the Kigigak Island subpopulation was 0.056 and the probability for the overall Y-K Delta subpopulation remained at 0.

All of our PVAs should be considered as worst-case scenarios because we only modeled existing conditions. That is, we have documented lead poisoning in all the populations for which we assessed viability, and recent studies suggest that, under the assumption that additional deposition of lead has ceased, lead exposure rates are likely to decline (Flint and Schamber 2010). Under declining rates of lead exposure, λ for each population would be expected to increase through time, thereby decreasing the probability of extinction. Our results demonstrate that the regional Y-K Delta population is of sufficient size that normal variation in life history parameters is unlikely to result in extirpation. However, our results show that localized subpopulations, on their own, would be susceptible to extinction. In fact, in the absence of increases in life history parameters, the Kashunuk River subpopulation declined to quasi-extinction in all simulations.

Our comparison of stochastic models demonstrated that the negative correlation between nesting success and survival resulting from exposure to lead poisoning decreased variation in λ . Therefore, if lead exposure declines, we would expect a simultaneous increase in λ and an increase in its variance. To address this potential in a worst-case scenario, we

inflated the variance by an order of magnitude and reran the simulations for the Kigigak Island and Y-K Delta subpopulations. Even under this relatively extreme case, extinction probabilities remained low. Thus, the conclusion that these subpopulations are likely to remain viable seems to be robust to a wide range of variance in λ .

Our PVA assumes that our subpopulations are closed and field studies adequately represent the full range of natural variation in demographic parameters, particularly those with high sensitivities. We have no means of assessing the potential for violating this assumption (i.e., the assumption that we documented the full range of variation), but we did document near total reproductive failure in some years and our site-specific models predict populations on markedly different trajectories. Therefore, we did find substantial variation in some cases. Our PVA cannot address the potential effects of atypical or novel catastrophic events. Infrequent large-scale die-offs have been documented for sea duck species as a result of disease outbreaks and contaminants exposure (Henny et al. 1995; Hollmen et al. 2003). Such events will likely influence population viability, but we currently lack sufficient data to model the potential for such events for spectacled eiders. However, recent outbreaks of diseases, such as avian cholera, have been shown to threaten the persistence of common eider colonies in the Canadian Arctic (Descamps et al. 2012), and cholera was recently associated with winter seabird die-offs near the wintering grounds of spectacled eiders (Bodenstein et al. 2015). Such an outbreak, when spectacled eiders are concentrated in winter, could have severe consequences for population persistence.

Metapopulation Dynamics of Spectacled Eiders on the Y-K Delta

Population dynamics is the balance of births, deaths, immigrations, and emigrations. Thus far, our analyses have considered only dynamics relative to births and deaths. This examination suggests that the subpopulation at Kashunuk River should have declined rapidly and ceased to exist. However, in each year of our fieldwork (i.e., 1991–2002) approximately 100 females nested there. One explanation for that stability is that immigration supplements this subpopulation. Spectacled eiders are not uniformly distributed across their breeding range (Figures 8 and 9), and there is little doubt that there is some dispersal among these areas because dispersal regularly occurs even among waterfowl that are highly philopatric (Blums et al. 1996; Lindberg et al. 1998). Thus, there is justification for viewing the assemblage of subpopulations on the Y-K Delta as a metapopulation, and because one of

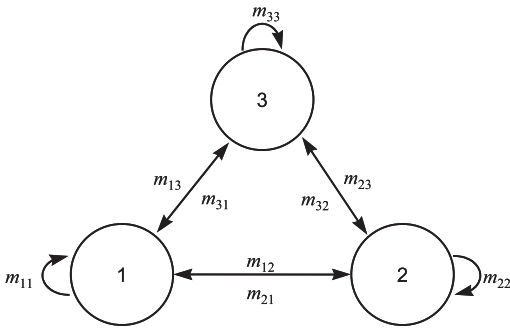


Figure 21. Structure of the three-segment metapopulation model for spectacled eiders *Somateria fischeri* on the Yukon-Kuskokwim Delta, Alaska, based on field observations from 1991-2003. The dispersal probability is represented by the letter “m” with the subscript denoting the movement from and into each segment of the population. Thus, m12 represents the probability of moving from subpopulation 1 into subpopulation 2. Fidelity to a given subpopulation is represented with the self-looping arrows and subscripts 11, 22, and 33. Model structure based on data collected from 1993-2004.

the subpopulations has an inherent growth rate of less than 1, the assemblage actually has a source-sink form of metapopulation structure.

We investigated the metapopulation dynamics of spectacled eiders on the Y-K Delta by constructing a model consisting of three subpopulations (Figure 21). To model the relationships among these segments, we used the stochastic population growth rates from Kashunuk River and Kigigak Island, estimated from our detailed demographic data, and an estimate of the population growth rate for the entire Y-K Delta from aerial surveys as described previously. Thus, our three subpopulations were Kashunuk River; Kigigak Island; and the remainder of the Y-K Delta, referred to here to as the Y-K Delta coast. We defined the subpopulations by using available spectacled eider distributions, as opposed to any knowledge of actual metapopulation structure, and these arbitrary subpopulations differ substantially in size. We examined the dynamics of the segments, relationships among them, and their impacts on the growth rate of the overall Y-K Delta metapopulation under two scenarios. The first scenario assumed constant, but different, levels of lead and concomitant growth rate in each subpopulation, whereas the second scenario assumed lead levels are declining and growth rates increasing over the projection period. In both scenarios, we assume that both growth and dispersal among the subpopulations is density independent.

Model structure

In our model, the subpopulations were connected by dispersal probabilities that are cast in a dispersal

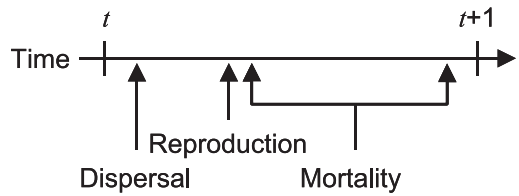


Figure 22. Time line for the processes affecting the dynamics of the spectacled eider *Somateria fischeri* metapopulation model. Timeline based on data collected from 1993-2004.

matrix (M). The elements of the matrix (m_{ij}) were defined as the probabilities that individuals in population j at time t move to segment i at time $t+1$. The diagonal elements (self-loops in Figure 21) were the probabilities that individuals did not disperse. We assumed that during dispersal the metapopulation was closed, so that all individuals dispersing from segment j were accounted for in some other segment. As such, M was constrained so that all columns sum to 1. Rows were unconstrained so that the size of each segment could change due to dispersal. In the absence of data to the contrary, we assumed that the fidelity probabilities for each segment were the same (i.e., $m_{11} = m_{22} = m_{33}$). We assumed that the emigrants from a segment dispersed equally (randomly) to the other two segments (e.g., $m_{23} = m_{13}$).

In keeping with our prebreeding census, birth-pulsed model construct, we assumed that the processes of dispersal, reproduction, and mortality occurred discretely and sequentially across the subpopulations (Figure 22). Thus, dispersal occurs before reproduction, and the number of individuals ($n_{i,t+\delta}$) in each of the subpopulations (i) at the beginning of time interval $t \rightarrow t+1$ was estimated as follows:

$$n_t + \delta = M \times n_t, \tag{13}$$

where n_t was the vector of segment sizes immediately before dispersal and δ is the number of immigrants. Also note that

$$N_t = \sum n_{it} = \sum n_{it} + \delta. \tag{14}$$

Reproduction and mortality for each subpopulation (i) was subsumed under λ_i , the inherent growth potential of the subpopulation in the absence of dispersal.

The subpopulations were then projected as follows:

$$n_t + 1 = n_t + \delta \times L_t, \tag{15}$$

where L_t is a diagonal matrix of the segment inherent growth rates (λ_i). For the scenario involving constant lead levels in each subpopulation, the

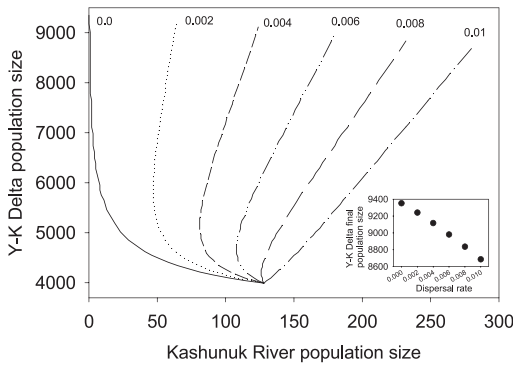


Figure 23. Population trajectories of spectacled eider *Somateria fischeri* females for two subpopulations on the Yukon-Kuskokwim Delta, Alaska, over 50 y predicted by the metapopulation model with $\lambda_{Y-K \text{ Delta}} = 1.01$ and random dispersal ranging from 0 to 1%. Dispersal value is at the end of each line. Data for model collected between 1993-2004.

growth rates were estimated as previously described. In those cases $\lambda_{i,t} = \lambda_{i,t+1}$. For the scenario involving decreases in lead levels, year-specific inherent growth rates were estimated for each subpopulation by assuming a 10-y half-life for lead exposure rates, estimating the annual survival rate for each subpopulation in each year, and extrapolating that into lambda using sensitivities. Thus, this approach assumes that only survival changes in response to decreasing lead availability. In these cases, $\lambda_{i,t} \neq \lambda_{i,t+1}$ and the matrix L_t changed each year of the projection.

Regional Y-K Delta metapopulation

We examined the dynamics of the metapopulation for a 50-y period under varying levels of random dispersal ranging from 0 to 10% from each subpopulation. We summarized the results of these trials for Kashunuk River relative to Y-K Delta. Under the current conditions, with no dispersal, the Kashunuk River segment rapidly declines toward extinction, whereas the Y-K Delta coast segment grows (Figure 23). When we increased dispersal to 0.2%, the Kashunuk River segment declined to approximately 60 pairs and then stabilized and slowly increased. Dispersal of approximately 0.8% will sustain the Kashunuk River segment at its current level given the overall Y-K Delta population size of 4,000–5,000. However, it is important to note that our simulations also demonstrate that maintenance of the Kashunuk River population via dispersal reduces the ultimate Y-K Delta population size at the end of the 50-y projection. Thus, maintenance of the sink subpopulation is possible, but it occurs at a cost to the overall regional metapopulation.

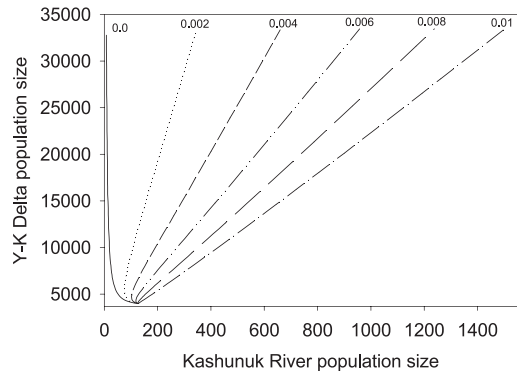


Figure 24. Population trajectories of spectacled eider *Somateria fischeri* females in two subpopulations on the Yukon-Kuskokwim Delta, Alaska, over 50 y predicted by the metapopulation model with lead exposure rates declining over a 10-y half-life and random dispersal ranging from 0 to 1%. Dispersal value is at the end of each line. Data for model collected between 1993-2004.

The overall outlook for the metapopulation improves dramatically under the model where lead availability declines through time. This result is the combination of two processes. First, the overall survival of the Y-K Delta population is increasing as lead exposure declines, and as such, the inherent λ increases through time. This same process is also occurring for the Kashunuk River subpopulation. Thus, in this source–sink situation, the negative effect of the sink is declining. Under a declining lead scenario, the 50-y projection for the entire metapopulation exceeded 30,000 nesting females (Figure 24).

Based on these results, we conclude that the disparity between λ predicted from demographic parameters and that observed in the field can be explained by dispersal. Under this scenario, dispersal from the greater Y-K Delta coast subpopulation likely maintained the Kashunuk River subpopulation. Given the observed levels of lead exposure, we suggested that maintenance of the Kashunuk River subpopulation occurred at a cost to the overall Y-K Delta metapopulation. Thus, precluding birds from breeding in the sink location would enhance the growth rate of the overall metapopulation. This is a unique situation in which it could be argued that destruction of nesting habitat along the Kashunuk River would enhance the overall population recovery. However, this conclusion changes when lead exposure is assumed to decay over time. Thus, as the magnitude of the sink decreases over time (i.e., lead becomes less available and the Kashunuk River λ increases), the cost to the overall metapopulation is mitigated.

The net result is that current population growth rate (i.e., that observed from aerial and ground

surveys) of $\lambda = 1.016$ for the Y-K Delta population is almost certainly the outcome of these metapopulation processes. Given that we estimated the Y-K Delta population level exposure to lead at 11.84%, we can calculate the potential Y-K Delta population growth rate assuming that lead availability declines. To do this, we calculated the adult female survival rate as the weighted average of the exposed and unexposed rates. Given that survival rate, we then estimated the fertility rates that yielded the observed λ . Then, keeping the fertility rates fixed, we inserted the unexposed survival rates into the matrix. Thus, if we assume that fertility remains unchanged, we have an estimate of the potential Y-K Delta population growth rate in the absence of lead exposure. Under these conditions, the potential $\lambda = 1.055$, suggesting that current lead exposure across the Y-K Delta as found during the period of our studies was depressing population growth by approximately four percentage points.

Global Metapopulation Dynamics of Spectacled Eiders

As noted herein, the global population of spectacled eiders is composed of three geographically isolated breeding populations. Our current understanding of spectacled eider movements suggests that all three populations winter in the same area in the central Bering Sea (Petersen et al. 1999; frontispiece). Genetic sampling from the three breeding populations suggests that there is very little interchange of females among breeding areas, whereas males seem to move freely among breeding populations (Scribner et al. 2001). This genetic analysis supports our overall understanding of the behavior of this species. That is, females have high fidelity to specific breeding locations, a finding also supported by high resighting rates for breeding females (Grand et al. 1998). Furthermore, genetic data imply high rates of natal fidelity to specific breeding populations, a finding that is again supported by our observations regarding recruitment of ducklings marked on our study areas. Thus, we assume that all spectacled eiders winter in the same area, pair formation occurs in this mixed flock, and females return to the breeding area of origin.

From January through April, the wintering areas used by spectacled eiders are characterized by extensive coverage of sea ice, the density and southern extent of which vary greatly among years. In some years, open water is readily available in the area used by wintering spectacled eiders; in other years, ice cover approaches 99% (Petersen and Douglas 2004). Correspondingly, in years with little ice, spectacled eiders have been observed in loose flocks widely scattered over a relatively large area (Petersen et al. 1999). In years with heavy sea ice, very large flocks of spectacled eiders have been

observed concentrated in small, scattered openings in the ice. It is likely, therefore, that in years of heavy ice cover, food availability or competition for foraging sites might limit spectacled eider populations. This conclusion is supported by our survival analyses that demonstrate a negative effect of severe ice conditions on rates of annual survival. Furthermore, Flint (2013) demonstrated that population dynamics of multiple species of sea ducks in North America were related to marine regime shifts. Thus, it is quite likely that at-sea conditions are a major determinant of population processes.

We lack data on the historic levels of other breeding subpopulations from Arctic Russia and the ACP. Although the magnitude of the decline is debatable, there is general consensus that the spectacled eider subpopulation on the Y-K Delta is greatly reduced from historic levels. Given this decline, it is unlikely that density-dependent factors on the breeding grounds now limit this subpopulation. However, photographs (frontispiece) of the extremely dense flocks using small leads in nearly continuous ice cover suggest that density-dependent limitation may occur on wintering areas. Therefore, we sought to examine the effect of density-dependent limitation during winter on the dynamics and viability of the Y-K Delta breeding population.

Methods

We defined the global metapopulation of three regional breeding subpopulations with no dispersal of breeding females (Figure 1). The sizes of the regional subpopulations in Arctic Russia were assumed to be 236,493 individuals, along the ACP 10,930 individuals, and on the Y-K Delta 7,328 individuals. Because we were most interested in the effect of winter density dependence on population dynamics, we assumed that the carrying capacity was equal to the sum of the estimates of population size from the three breeding areas (i.e., 363,930).

The actual trend (i.e., λ) of the Arctic Russian breeding subpopulation is unknown; however, the ACP subpopulation is nearly stable (Larned et al. 2008). Thus, in the absence of dispersal, if one or more subpopulations are declining and the others are increasing, the declining subpopulations go extinct and the increasing subpopulations grow until carrying capacity is reached. We assumed that each of the regional subpopulations had the inherent ability to increase, and we gave all three subpopulations the same potential growth rate, $\lambda = 1.02$. We included variation around this average subpopulation growth rate and calculated subpopulation size in year $t+1$ by using the following equation:

$$N_{t+1} = N_t \times (\lambda + \psi), \quad (16)$$

where ψ is a normally distributed random variable with a mean of 0. We allowed ψ to vary

independently for each subpopulation, and examined 25 different levels of ψ from 0.05 to 0.125. We further assumed that the effects of density would influence all regional subpopulations equally. In addition, we simulated variation in ice conditions by varying K stochastically in a random uniform manner between 273,750 and 465,250 (i.e., $\pm 25\%$ of the current winter population size).

We used this stochastic model to estimate subpopulation growth over a 50-y period and repeated the simulation 1,000 times for each level of ψ . In each simulation, we tracked the size of each regional subpopulation separately. In years when the metapopulation size was less than K , all individuals were allowed to survive. In years when metapopulation size exceeded K , excess individuals were removed from each subpopulation in proportion to its size that year. The realized average annual subpopulation growth rate λ_r of each region was estimated using the equation (7) of Heyde and Cohen (1985). We estimated λ_r for each of the 1,000 trials and then estimated the variation of λ_r for each subpopulation as its standard deviation.

To examine the influence of the interaction among the three breeding subpopulations (i.e., competition), as opposed to the simple density-dependent model above, we ran 1,000 trials without competitive interaction. In these simulations the respective K for each subpopulation varied $\pm 25\%$ in a random, uniform manner. This model was intended to simulate subpopulations that were affected by density-dependent winter limitation, but they used different wintering areas. We then calculated the ratio of the variance in λ_r between the models where there was competition among subpopulations and the one where there was simple density dependence (Figure 25).

Results

Competition on the wintering grounds increases the variance in the λ 's for each of the regional subpopulations. This effect was much more pronounced for the smaller subpopulations (i.e., Y-K Delta and ACP). Because, viability is a function of subpopulation size and variation in λ (Boyce 1992), competition in winter clearly increases the extinction probability of the regional Y-K Delta subpopulation. This overall conclusion was robust over a wide range of variation in λ .

Discussion

When all subpopulations have the same inherent λ , the overall metapopulation is relatively stable (i.e., $\bar{\lambda}_r$ is ~ 1.0) and is essentially at K . That is, each of the subpopulations is at a stable equilibrium value. Thus, the model suggests that small subpopulations have a strong tendency to stay small, with little opportunity to recover, because large subpopulations can

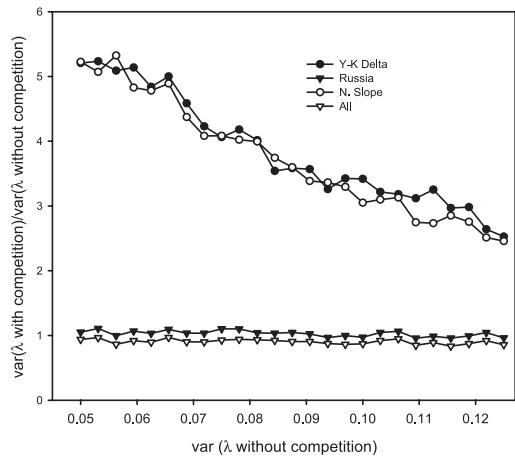


Figure 25. Relative variance in λ for spectacled eider *Somateria fischeri* subpopulations in models with and without competition in a global metapopulation. Data for model collected between 1993-2004.

respond more quickly to increases in resource availability. Furthermore, reduction of a given subpopulation will allow other subpopulations to increase until the global carrying capacity is met. Under this scenario, recovery of a reduced subpopulation is unlikely. This creates the situation where small subpopulations decrease more easily than they increase. This occurs because during years of poor productivity in the smallest subpopulation, the larger subpopulations can use any excess resources with only a small percentage increase in size. Conversely, when the larger subpopulations experience declines, the small subpopulation may not have the potential to expand to the limit of available resources.

Management Implications

Managers tasked with changing population trends are forced to consider two factors: 1) the effect of changing a given life history parameter on population dynamics and 2) their ability to change a given life history parameter in the desired manner (Caswell 2000). Our models demonstrate that proportional changes in annual survival of females would have the greatest impact on future population dynamics. Therefore, increasing annual survival of females is a viable option for increasing population growth rate. Lead poisoning has been shown to directly influence survival of spectacled eiders on the Y-K Delta. Our model demonstrates that levels of lead exposure measured across the Y-K Delta are sufficient to influence regional subpopulation dynamics. In fact, in certain specific areas (e.g., Kashunuk River), levels of exposure were likely having a dramatic influence on localized population

trends. This result justifies continued management actions to curtail further input of lead into breeding areas used by spectacled eiders. It might also be useful to explore options for reducing the availability of, or contact with, lead already in the environment. Furthermore, the persistence of lead shot in the environment has a substantial influence on predicted trends from our models. Given that lead availability seems to decline through time (Flint and Schamber 2010), our model demonstrates that management objectives can be achieved by precluding additional deposition of lead into areas used by spectacled eiders.

Subsistence harvest by residents of the Y-K Delta may have an impact on overall survival, but the level of subsistence harvest of spectacled eiders is thought to be quite low (Rothe et al. 2015). Subsistence harvest surveys have been conducted, but low levels of participation by residents of some villages may bias estimates (Wentworth 2007). Previous efforts to work with local subsistence hunters to redirect harvest from vulnerable species have been successful. In fact, for spectacled eiders harvest estimates have declined from more than 1,000 birds per year in the 1990s to approximately 200 birds in 2011 (Rothe et al. 2015). Continued efforts to minimize harvest are warranted, but given the current low levels of harvest, there is likely little effect of harvest on population dynamics.

Influencing annual survival via management actions for a species that has little harvest may be difficult. It may be more feasible to affect traits that have lower elasticity, especially those that are far from natural bounds (Wilson et al. 2012). In our stochastic simulations, variability in nest success was sufficient to have an influence on short-term trends and variation in the realized population growth rate. With an average nest success rate of 63% and a theoretical maximum of 100%, there is much room for improvement. Thus, an alternative to increasing annual survival may be to reduce the frequency of very poor years of nest success by manipulating predator populations (e.g., gulls; see Grand and Flint 1997). This would have the combined effect of raising average productivity and reducing stochastic variation in population trends, thereby enhancing population viability (Flint 2015). Based on the elasticities for our deterministic model for Kashunuk River, an 11% increase in nesting success would be required to have the same influence on population dynamics as a 1% increase in female survival. However, from a management perspective an 11% change in nesting success may be a more viable option. Furthermore, in addition to improving nest success, predator control might have the additive effect of increasing adult and duckling survival, given some proportion of nesting females and ducklings are killed by predators each year.

Similar recommendations have been made for sympatric nesting common eiders *Somateria mollissima* and long-tailed ducks *Clangula hyemalis* on the Y-K Delta (Schamber et al. 2009; Wilson et al. 2012).

When we modeled simple deterministic or stochastic projections of a single subpopulation, our model results did not match our field observations of trends at Kashunuk River. Only by invoking a metapopulation model were we able to simulate something close to what we observed in the field. We recommend researchers examine dispersal of breeding females among areas on the Y-K Delta as a test of our preferred model. It is apparent from our metapopulation analyses that no portion of the population behaves in an entirely independent manner. This result has important management implications that seem counterintuitive and may not be politically viable. One such problem is that while dispersal within a source-sink system can sustain a localized sink subpopulation, it does so at a cost to the metapopulation. If increasing the regional Y-K Delta metapopulation is the most important goal, and it is not possible to improve the vital rates of some local subpopulations, management considerations could include displacement of breeding females from sink areas that reduce the growth potential of the metapopulation as a whole. This could entail reduction or elimination of some local habitats so as to preclude nesting to maximize the growth and thus the recovery of the metapopulation.

Another management dilemma results from the potential impediment to recovery represented by density-dependent limitation during winter. Given what is known about ice dynamics in the north Bering Sea, this certainly seems plausible. If our simplistic model is valid and the global population is near an overwinter carrying capacity, then improvements in the vital rates may not result in long-term growth of the regional Y-K Delta subpopulation (Wilson et al. 2012). Furthermore, based on our model, this limitation will have the greatest influence on the smallest subpopulation segments (i.e., the ACP and Y-K Delta breeding subpopulations). Reductions in other subpopulations may be necessary to ensure an increase in the Y-K Delta subpopulation. Specifically, reduction of the largest (i.e., Arctic Russian) breeding subpopulation may be required to allow the smaller Y-K Delta and ACP subpopulations to expand in the face of winter habitat limitations. Although we examined only a few aspects of metapopulation ecology in our simulations, we conclude that future management actions for the spectacled eider could benefit by using a metapopulation approach and by considering the metapopulation dynamics of this species both on the Y-K Delta and throughout its entire distribution.

Supplemental Material

Please note: *North American Fauna* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Reference S1. Brower WAJ, Baldwin RG, Williams CNJ, Wise JL, Leslie LD. 1988. Climatic atlas of the outer continental shelf waters and coastal regions of Alaska. Volume 2, Bering Sea. Minerals Management Service OCS study MMS 87-0012. Washington, D.C.: U.S. Department of Interior.

Found at DOI: <http://www.dtic.mil/dtic/tr/fulltext/u2/a206212.pdf>.

Reference S2. Fischer JB, Stehn RA, Walters G. 2010. Nest population size and potential production of geese and spectacled eiders on the Yukon-Kuskokwim Delta, Alaska, 1985–2010. Unpublished report to U.S. Fish and Wildlife Service, Anchorage, AK.

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Archived Material

All new data presented in this monograph are publically available at <http://dx.doi.org/10.5066/F74B2ZCK>.

Five primary data files are provided along with associated metadata files.

1. Alaska and Russia waterfowl lead exposure data, 1993-1999. This file contains all the blood lead and x-ray data as linked to individuals birds band number.
2. Spectacled Eider (*Somateria fischeri*) Banding Records; Kashunuk River, Alaska, 1992-2002. This file contains all of the data associated with initial capture and banding of eiders along the Kashunuk River.
3. Spectacled Eider (*Somateria fischeri*) Capture and Resight Records; Kashunuk River, Yukon-Kuskokwim Delta, Alaska, 1995-2002. This file contains all of the recapture and resighting data for previously marked eiders along the Kashunuk River.
4. Spectacled Eider (*Somateria fischeri*) Capture, Banding, and Mark-Resight Records; Kigigak Island, Yukon-Kuskokwim Delta, Alaska, 1992-2004. This file contains all of the capture, recapture and resighting data from Kigigak Island.
5. Spectacled Eider (*Somateria fischeri*) Nest Records; Kashunuk River and Kigigak Island, Alaska, 1991-2004. This file contains all of the nest visitation data from initial discovery until determination of final nest fate. Includes data on nest initiation date as well as clutch size.

Acknowledgments

We thank M. Reardon, J. Morgart, G. Walters, and the remaining staff of Yukon Delta National Wildlife Refuge



for support and assistance necessary to carry out field research that led to this effort. We gratefully acknowledge the technicians who contributed to the collection of various portions of the fieldwork; without their efforts, and those of many others, none of this work would have been possible. D. Douglas provided information on ice dynamics in the Bering Sea. Bob Platte provided Y-K Delta-wide nest densities and distribution data. J. Schmutz and S. McCloskey assisted with portions of the analyses. We thank D. Derksen, R. Oates, R. Leedy, A. Rappaport, and R. West for support of this research and other projects that lead to this modeling effort. We sincerely appreciate the use of information collected at Kigigak Island by C. Moran and her assistants at the Yukon Delta National Wildlife Refuge. We thank E. Cooch, D. Derksen, F. S. Dobson, D. Koons, J. Pearce, E. Reed, G. Robertson, S. Gilliland, H. Wilson, and two anonymous reviewers for comments on earlier drafts of this manuscript.

Funding for this project was provided by Region 7 of the U.S. Fish and Wildlife Service, and the Alaska Science Center, U.S. Geological Survey.

Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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