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Population Dynamics of Long-tailed Ducks Breeding on the Yukon-Kuskokwim Delta, Alaska

JASON L. SCHAMBER[1,2] PAUL L. FLINT,[1] J. BARRY GRAND,[1,3] HEATHER M. WILSON[1,4] and JULIE A. MORSE[1,5]

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ABSTRACT. Population estimates for long-tailed ducks in North America have declined by nearly 50% over the past 30 years. Life history and population dynamics of this species are difficult to ascertain, because the birds nest at low densities across a broad range of habitat types. Between 1991 and 2004, we collected information on productivity and survival of long-tailed ducks at three locations on the Yukon-Kuskokwim Delta. Clutch size averaged 7.1 eggs, and nesting success averaged 30%. Duckling survival to 30 days old averaged 10% but was highly variable among years, ranging from 0% to 25%. Apparent annual survival of adult females based on mark-recapture of nesting females was estimated at 74%. We combined these estimates of survival and productivity into a matrix-based population model, which predicted an annual population decline of 19%. Elasticities indicated that population growth rate (λ) was most sensitive to changes in adult female survival. Further, the relatively high sensitivity of λ to duckling survival suggests that low duckling survival may be a bottleneck to productivity in some years. These data represent the first attempt to synthesize a population model for this species. Although our analyses were hampered by the small sample sizes inherent in studying a dispersed nesting species, our model provides a basis for management actions and can be enhanced as additional data become available.

Key words: Alaska, *Clangula hyemalis*, elasticity, long-tailed duck, population dynamics, sensitivity, sea duck, vital rates, Yukon-Kuskokwim Delta

RÉSUMÉ. Les estimations de populations d’hareldes kakawis en Amérique du Nord ont chuté de près de 50 pour cent ces 30 dernières années. Le cycle biologique et la dynamique des populations de cette espèce sont difficiles à établir car ces oiseaux nichent moyennant de faibles densités dans une vaste gamme d’habitats. De 1991 à 2004, nous avons recueilli des données sur la productivité et la survie des hareldes kakawis à trois emplacements du delta Yukon-Kuskokwim. Les couvées atteignaient 7,1 œufs en moyenne, tandis que le succès de reproduction s’établissait généralement à 30 pour cent. En moyenne, 10 pour cent des jeunes canards survivaient jusqu’à l’âge de 30 jours, mais ce taux variait beaucoup d’une année à l’autre, allant de 0 pour cent à 25 pour cent. Annuellement, d’après la méthode par marquage et recapture des femelles nidificatrices, la survie apparente des femelles adultes était évaluée à 74 pour cent. Nous avons combiné ces estimations de survie et de productivité dans un modèle de population matriciel, ce qui a permis de prédire un déclin de population annuel de 19 pour cent. Selon les élasticités, le taux de croissance de la population (λ) était plus sensible aux changements dans le cas de la survie des femelles adultes. Par ailleurs, la sensibilité relativement élevée du λ par rapport à la survie des jeunes canards laisse croire que le faible taux de survie des jeunes canards pourrait présenter une embûche en matière de productivité d’ici quelques années. Ces données représentent la première tentative de synthèse d’un modèle de population pour cette espèce. Bien que nos analyses aient été gênées par la petite taille des échantillons inhérente à l’étude d’espèces de nidification dispersées, notre modèle fournit un fondement permettant d’aboutir à des mesures de gestion en plus de présenter la possibilité d’être amélioré au fur et à mesure que des données supplémentaires sont disponibles.

Mots clés : Alaska, *Clangula hyemalis*, élasticité, harelde kakawi, dynamique des populations, sensibilité, canard de mer, taux vitaux, delta Yukon-Kuskokwim

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[1] U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA
[2] Corresponding author: jschamber@usgs.gov
[3] Alabama Cooperative Fisheries and Wildlife Research Unit, Auburn, Alabama 36849, USA
[4] U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska 99503, USA
[5] The Nature Conservancy, 410 North 4th Street, Mount Vernon, Washington 98273, USA

INTRODUCTION

The long-tailed duck (*Clangula hyemalis*), a sea duck (Mergini) species with a circumpolar distribution, nests in tundra habitats and winters along sub-Arctic and temperate coastlines. In North America, the ducks' breeding range includes western Alaska, the Arctic coastal plain of Alaska, and Arctic Canada; their wintering areas are located primarily along the Pacific and Atlantic coastlines, but also in the Great Lakes region (Robertson and Savard, 2002). Like many species of sea ducks in North America, long-tailed ducks have declined dramatically in number in recent decades without apparent cause. Population size estimates based on aerial counts of breeding birds in both Alaska and Canada's Yukon Territory are nearly 50% lower than estimates from the mid-1970s (Conant and Mallek, 2006). Difficulty identifying causal factors for this decline was largely attributed to the paucity of available biological information for the species. Despite the widespread distribution of long-tailed ducks, few studies have focused on them, principally because they often winter offshore and nest at very low densities in regions that seldom are accessible or surveyed (Robertson and Savard, 2002). Consequently, life-history attributes of long-tailed ducks are poorly understood because few estimates for basic vital rates (e.g., annual adult survival, nest success, duckling survival) are available (Alison, 1975; SDJV Management Board, 2001). In response to these data gaps, the SDJV (Sea Duck Joint Venture) Management Board (2001) has listed study of long-tailed duck population dynamics as a high priority.

Current management of long-tailed ducks is based largely on analyses of long-term aerial survey data of breeding pairs, from which estimates of population growth rate (λ) are derived. However, traditional coverage of sea duck breeding areas during the breeding pair survey was incomplete and mistimed relative to sea duck breeding chronology. Thus, reliable data are available only for portions of their range where intense aerial surveys have been conducted, such as the Yukon-Kuskokwim Delta (YKD), Alaska (Platte and Stehn, 2006). Although these survey data are useful for determining population trends, in the absence of a demographic model, managers are unable to distinguish among the intrinsic processes underlying apparent trends. Demographic models integrate probabilities of vital rates into an estimate of λ, thereby providing a functional link between life history and population dynamics. This link is important because managers often can manipulate λ in accordance with management goals by altering extrinsic factors linked to vital rates. Thus, demographic models enable managers to identify critical vital rates and develop focal management strategies to meet specific goals—in this case, the potential reversal of the apparent long-tailed duck population decline.

We developed a heuristic demographic model for a dispersed population of long-tailed ducks breeding on the YKD, Alaska. The YKD supports an estimated 30% of the breeding population in Alaska (Bellrose, 1980; Hodges et al., 1996; Mallek et al., 2006). We estimated variability in clutch size, nesting success, duckling survival, and apparent adult female survival from three disjunct study areas on the YKD and then integrated these estimates into a stage-based matrix model to examine the relative importance of each vital rate to λ.

METHODS

Study Areas

We studied long-tailed ducks at two coastal sites and one inland location on the YKD, Alaska (Fig. 1): the lower Kashunuk River (61˚20′ N, 165˚35′ W), Kigigak Island (60˚50′ N, 165˚50′ W), and Aropuk Lake (61˚07′ N, 163˚53′ W). The Kashunuk River (KR) study site, located approximately 5 km from the Bering Sea coast, was described in detail by Grand et al. (1997). The Kigigak Island (KI) study area, located approximately 60 km south of the KR site, encompassed nearly the entire island, as described in detail by Moran (2000). At both sites, long-tailed ducks nested primarily in sedge meadow habitats that contained countless small, high-saline ponds and lakes. Specific nest sites included grass flats, slough banks, and pond edges. In contrast, the Aropuk Lake (AL) study site was located nearly 70 km inland from the Bering Sea coastline. Habitat surrounding AL consisted predominantly of dry lichen tundra interspersed with numerous freshwater lakes and low, wet sedge/graminoid marshes interconnected by an extensive system of drainages. Dense, dwarf shrub vegetation thrived along these drainages and lake margins, characterizing the edge between dry and wet habitats. Long-tailed ducks preferred to nest on dry lichen tundra or along habitat edges in dwarf shrubs. At both KR and AL, long-tailed duck broods typically moved from nesting areas to large freshwater lakes in upland habitats immediately following hatch.

Field Methods

The search methods we used to locate long-tailed duck nests varied slightly among sites, but study areas at each site were searched for nests at least twice each year. At KR, in 1991–2002, five to seven people searched an area approximately 15–27 km^2, in conjunction with searches for nests of northern pintail (*Anas acuta*, Flint and Grand, 1996) and spectacled eider (*Somateria fischeri*, Grand and Flint, 1997). At KI, in 2003–04, two to three people searched nearly the entire island (32.5 km^2) in conjunction with searches for nests of common eider (*Somateria mollissima*) and spectacled eider. At both KR and KI, searches were conducted from mid-May through mid-June. At AL, in 2002–04, four to six people searched an area approximately 54 km^2 in conjunction with searches for nests of black scoter (*Melanitta nigra*); searches were conducted from early June through mid-July. Here, we systematically searched all dwarf shrub habitat along wetland drainages and lake margins and opportunistically searched dry lichen tundra.

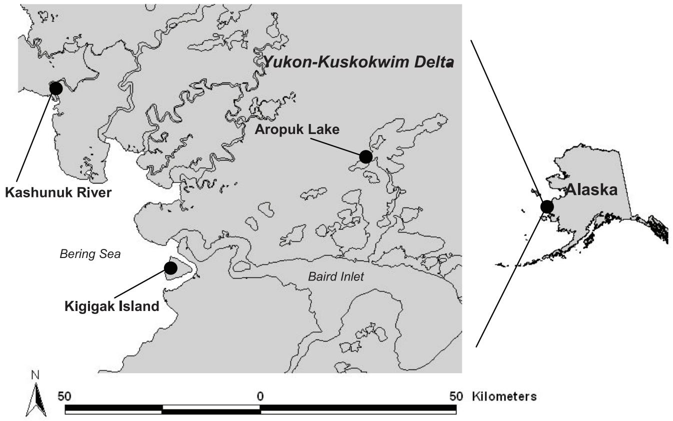

FIG. 1. Map of the Yukon–Kuskokwim Delta, Alaska, showing locations of the Kashunuk River, Kigigak Island, and Aropuk Lake sites used for the demographic study of long-tailed ducks.

For each nest, we recorded date found, number of eggs, stage of embryonic development (as determined by candling; Weller, 1956), and nest status (laying, incubating, failed, or hatched). Nests found during laying or incubation were revisited at seven-day intervals until they failed or hatched. We calculated clutch size for each nest as the number of eggs surviving to incubation, accounting for partial predation. We considered nests successful if one or more eggs hatched, as indicated by the presence of egg membranes or ducklings in the nest bowl. For nests found during egg-laying, we calculated nest initiation dates by subtracting one day for each egg laid from the date the nest was found (Alison, 1975). For nests found during incubation, we calculated nest initiation dates in two ways, depending on nest fate. For nests that hatched, we calculated initiation dates by subtracting the 26-day incubation period (Robertson and Savard, 2002) plus clutch size from the hatch date. For nests that failed, we calculated the initiation date by subtracting the estimated age of eggs (based on stage of embryonic development) plus clutch size from the date found. Olson and Rohwer (1998) suggested that increased visits may reduce nest success. We assumed that in our case, observer effects on nest success (e.g., increased predation rates) were minimal because nests were visited infrequently. However, because of our small sample sizes, we were unable to assess this potential source of bias. Nests that were potentially abandoned because of observer activity and found after hatching or failure were excluded from all analyses.

We examined survival of ducklings in broods of radio-marked females at KR in 1998–2000 and at AL in 2002–04. We trapped females on the nest in early to mid-incubation at KR and near hatch at AL, using string-activated or remotely triggered bow-nets (Sayler, 1962), dip-nets, or mist-nets. Each trapped female was marked with a VHF transmitter: a subcutaneously anchored radio transmitter at KR, and an external prong-and-glue-anchored transmitter at AL (Pietz et al., 1995). To determine initial brood size, we inspected nests after broods departed and counted the number of egg membranes remaining in the nest bowl. Broods of radio-marked females were relocated every seven days until 30 days after hatch in order to count the number of ducklings remaining. When radio-marked females remained within the study area, we used hand-held yagi-antennas for relocation; if broods moved outside of the study area, we relocated them from fixed-wing aircraft. We assumed random variation in error associated with our brood counts (Flint et al., 1995). Additionally, we used the mean number of ducklings per hen as the duckling count for two radio-marked broods that were observed in a crèche.

To examine annual adult female survival, we trapped females on their nests at KR in 1994–2002, using the same methods as for radio-marking. At capture, we marked females with a U.S. Geological Survey metal band or recorded band numbers of recaptured females.

Analytical Methods

For all analyses of productivity, we combined each study site with each respective year of study to create a 17-level class variable we called “site-year.” While use of this variable confounded interpretation of spatial and temporal variation, it reduced the complexity of models relative to our small sample sizes. We used Akaike’s Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson, 2002) to rank models within a candidate model set. We calculated model weights (w_i) as evidence of relative model importance. Additionally, we used the sum of AIC_c weights for all models that included a parameter of interest (hereafter called “parameter weight”) as the basis for statistical inference regarding individual parameters. To account for model-selection uncertainty among nest success and duckling survival model sets, we calculated model-averaged estimates across all candidate models within a set. We then estimated standard errors for model-averaged estimates of nest success and duckling survival by performing 500 bootstrap-resample simulations of our data in SAS (v.8.0, SAS Institute, 2003). We obtained a single model-averaged mean estimate and associated standard error for each productivity vital rate, using the analytical methods described above on pooled data for all respective site-years, and used them as input parameters in our demographic model.

Nesting: We examined variation in clutch sizes using general linear models in SAS (v.8.0, SAS Institute, 2003). We considered only two factors, site-year and initiation date, when constructing models of clutch size because of sample size limitations in our data set. Thus, we compared all permutations of our global model, which included site-year + site-year • initiation date, as well as an equal means model (null).

We estimated daily survival rate (DSR) of nests (DSR_{NS}) using the nesting model (Dinsmore et al., 2002) in program MARK (v. 4.3, White and Burnham, 1999) and calculated nest success as the product of DSR_{NS} across the nesting period of 33 days (average 7-day laying + 26-day incubation; Robertson and Savard, 2002). We used a logit-link function to constrain estimates of DSR between 0 and 1 (Lebreton et al., 1992). We compared the fit of four candidate models, using AIC$_c$ to examine temporal variation in DSR$_{NS}$ across nest ages (i.e., from initiation through hatch) among site-years. We considered models for which site-year DSR$_{NS}$ 1) was constant over the nesting period, 2) included a linear trend across the nesting interval, or 3) showed a quadratic trend over the nesting interval (Dinsmore et al., 2002). Our fourth model included an initiation date covariate added to the best model (site-year + linear-age) of those we initially considered because a seasonal decline in nest success was detected in other sympatric nesting ducks on the YKD (Flint and Grand, 1996; Grand and Flint, 1997; Flint et al., 2006a). We could not estimate a variance inflation factor ($\hat{c}$) because MARK does not include a goodness-of-fit test for nest survival data (Dinsmore et al., 2002).

Duckling Survival: We used the known-fates model in program MARK with a logit-link to examine duckling DSR (DSR$_{DS}$) and calculated duckling survival as the product of DSR$_{DS}$ across 30 days. We considered two factors, site-year and duckling age, and compared the models: 1) DSR$_{DS}$ varied with site-year and was invariant with age; 2) DSR$_{DS}$ varied with site-year and exhibited a geometric trend with age; and 3) DSR$_{DS}$ was constant among site-years and showed a geometric trend with age. We tested the fit of a hatch date covariate to the best model (site-year + geometric age) because later hatching ducklings tend to survive less well (Grand and Flint, 1996; Flint et al., 2006b). We did not consider models where DSR$_{DS}$ showed a linear trend over duckling age; rather, we assumed DSR$_{DS}$ changed in a geometric manner (Gunnarsson et al., 2004, 2006). However, we assessed the slope that best fit our data using the equation:

$$DSR_{DS} = A \bullet (1 - x^{a})$$

where A = age at which DSR becomes asymptotic (assumed to be 30 days), x = a constant non-linear slope parameter varying from 0.5 to 0.9, and a = duckling age varying from 1 to 30 (Gunnarsson et al., 2004, 2006). Because MARK does not support goodness-of-fit tests for known-fate models, we accounted for lack of independence among brood mates by estimating the amount of over-dispersion (i.e., $\hat{c}$) in our sample. Using Winterstein's (1992) second goodness-of-fit test, we calculated $\hat{c}$ by comparing the observed number of surviving ducklings in each brood to the expected number of survivors based on our 30-day survival estimate for individual site-years (Chouinard and Arnold, 2007). We adjusted the estimated sampling variance of all models accordingly and selected among models using quasi-likelihood Akaike's Information Criterion (QAIC$_c$) to correct for small sample size and overdispersion.

Adult Female Survival: We used the live recaptures model in program MARK to estimate annual apparent survival rate (Φ) and encounter probability (*p*). Because of our small sample size, we could not estimate survival and encounter probability from a full time-varying model (Φ_t, p_t). We also did not consider models with constant encounter rates ($p.$) because our annual recapture rates varied with differences in nest survival and trapping effort. Instead, we considered only two models. We compared the fit of a model for time-invariant survival probability and time-varying encounter rate ($\Phi.$, p_t) to a random effects time-varying model ($\Phi_{\mu\sigma}$, p_t) and selected the best approximation between them using QAIC$_c$ (Burnham and Anderson, 2002). The random effects model is an intermediate model between the time-invariant and full time-varying models. Using the bootstrap goodness-of-fit test in MARK, we estimated the over-dispersion parameter ($\hat{c}$) as the ratio of the deviance from our best model to the mean deviance from 100 simulated encounter histories.

Demographic Model: We developed a heuristic, stage-based (1st stage: 1 year old; 2nd stage: ≥ 2 years old) matrix model (Caswell, 2001) using PopTools (v. 2.7.5; Hood, 2006) and model-averaged mean estimates of annual survival and productivity for long-tailed ducks from KR, KI, and AL. We lacked data on first- and second-year survival, so we assumed that first-year survival was 85% of adult survival (Johnson et al., 1992) and used the estimate of adult female survival for the proportion of females surviving from one to two years old. We also assumed that females delayed breeding until two years old (Robertson and Savard, 2002). To estimate λ, we used the dominant eigen value of the mean matrix, assuming a stable age distribution and density independence in a closed population (Caswell, 2001). For mean parameter values, we calculated sensitivities and elasticities numerically to assess the response of λ to changes in vital rates (Caswell, 2001). We predicted the absolute change in λ due to a minute (.001) change in vital rates (sensitivity) and the proportional change in λ in response to a minute (.001) proportional change in vital rates (elasticity). We used Monte Carlo simulation in PopTools (v. 2.7.5; Hood, 2006) to compute stochastic model estimates of λ and associated confidence limits based on two approaches. The first used a projection matrix dependent upon random variables selected from our estimates of productivity (i.e., clutch size, nest success, and duckling survival). The second used a projection matrix dependent upon random variables selected from our estimates of productivity and a standard normal deviate of the *logit* of our annual survival estimate and associated standard error. Additionally, we examined the sensitivity and elasticity from changes in parameter sets of survival and productivity required to achieve stable population growth. Specifically, we adjusted parameter values to achieve $\lambda = 1.0$, which included an absolute increase of 0.19 to adult survival only, proportional increases (2.25) to productivity (i.e., nest success and duckling survival), or equal, proportional increases of 1.22 to survival, nest success, and duckling survival. In each case, we re-calculated sensitivities and elasticities for comparison with those from our base model to assess the robustness of our inference.

TABLE 1. Akaike Information Criterion (AIC$_c$) adjusted for small sample for models of clutch size, nest survival, and duckling survival of long-tailed ducks on the Yukon-Kuskokwim Delta, Alaska. Also included are the number of model parameters (K), the difference in AIC$_c$ score between each model and the best model (Δ_i), the likelihood of each model in a set (w_i), and model fit (r^2).

Model	K	AIC$_c$	Δ_i	w_i	r^2
Clutch Size:					
initiation date	3	59.93	0.00	0.90	0.02
null	3	65.20	5.27	0.06	0.00
site-year, initiation date	19	66.98	7.05	0.02	0.13
site-year	18	70.56	10.63	< 0.01	0.16
site-year, initiation date, site-year·initiation date	35	77.07	17.14	< 0.01	0.23
Nest Survival:					
site-year, nest age	18	587.70	0.00	0.42	
site-year	17	588.68	0.97	0.26	
site-year, nest age, quadratic nest age	19	589.69	1.98	0.15	
site-year, nest age, initiation date	19	589.72	2.01	0.15	
constant DSR	1	622.48	34.77	0.00	
Duckling Survival:					
site-year, geometric age trend, hatch date	8	282.94	0.00	0.50	
site-year, geometric age trend	7	282.98	0.03	0.49	
site-year	6	292.11	9.16	< 0.01	
constant DSR, geometric age trend	2	301.29	18.34	< 0.01	

RESULTS

Clutch Size and Nest Success

We located a total of 222 long-tailed duck nests at KR (1991–2002), 20 nests at KI (2002–03), and 31 nests at AL (2002–04). We excluded from analyses a total of 10 nests suspected of human-caused abandonment and five nests found after hatching or failure. In our analysis of clutch size variation, the most parsimonious model had strong support (w_i = 0.90) and included only initiation date; clutch size declined with date (0.01 ± < 0.01 [SE] eggs/day). We found little support for variation in clutch size by site-years (parameter weight < 0.03). Model-averaged mean clutch size for all site-years was 7.1 (95% CI: 6.5–7.7) (Table 1).

In our analysis of variation in nest success, we found strong support for an effect of site-years (parameter weight = 0.98) and moderate support for an effect of nest age (parameter weight = 0.72; Table 1). DSR$_{NS}$ declined with nest age (0.01 ± < 0.01 [SE]). We calculated nest success (DSR$_{NS}^{33}$) for each site-year from model-averaged estimates of DSR$_{NS}$. Nest success was highly variable across site-years, ranging from 0.01 ± 0.01 (SD) to 0.79 ± 0.13 (Fig. 2). Model-averaged mean nest success for all site-years was 0.30 (95% CI: 0.24–0.36).

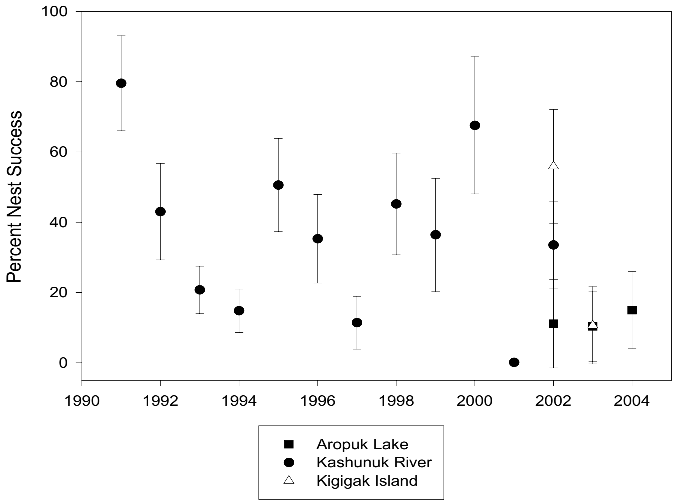

FIG. 2. Model-averaged nest success estimates of long-tailed ducks breeding on the YKD. Error bars represent SD from 500 bootstrap-resampling simulations.

Duckling Survival

At KR, we monitored the survival of 41 ducklings from seven broods in 1998, 30 ducklings from five broods in 1999, and 42 ducklings from eight broods in 2000. We found some evidence for lack of independence in survival among brood mates ($\hat{c}$ = 1.27); we therefore adjusted AIC$_c$ values to QAIC$_c$ values and inflated the estimated sampling variance of all models accordingly. No ducklings survived in 1998, and only one brood survived to 30 days post-hatching in both 1999 (2 ducklings) and 2000 (5 ducklings). At AL, we monitored duckling survival of 23 ducklings from three broods in 2002, 17 ducklings from two broods in 2003, and 20 ducklings from three broods in 2004. One brood (5 ducklings) survived to 30 days of age in 2002, but no ducklings survived in 2003 and 2004. In our analysis of variation in duckling survival, we found strong support for an effect of site-year (parameter weight > 0.99) and a geometric trend (x = 0.05) with duckling age (parameter weight > 0.99). We also found weak evidence of a hatch date effect (parameter weight = 0.50) (Table 1): DSR$_{DS}$ declined with hatch date (0.04 ± 0.02 [SE]), but effect size was poorly estimated (95% CIs: -0.08–0.01). Overall, model-averaged mean 30-day survival was very low (0.10; 95% CI: 0.06–0.14), and differed considerably between site-years, ranging from 0.01 ± 0.003 (SE) to 0.25 ± 0.08 (Fig. 3).

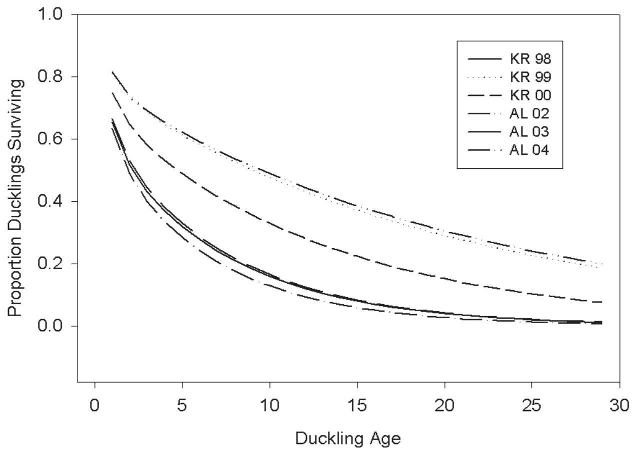

FIG. 3. Model-averaged estimates for each site-year of long-tailed duckling survival from hatch to 30 days of age on the Yukon-Kuskokwim Delta. Site-year abbreviations: KR = Kashunuk River and AL = Aropuk Lake.

Adult Female Survival

We marked a total of 74 unique individual females during 1994–2002. The number of females captured varied from year to year, ranging from 0 to 16. We found some evidence of overdispersion in our data ($\hat{c}$ = 1.39) and adjusted model selection criteria and sampling variances accordingly. The model with time-invariant apparent survival and time-varying encounter probabilities was strongly supported (w_i = 0.99) as the better model. Estimated apparent survival predicted by this model was 0.74 (95% CI: 0.57–0.86), and mean encounter rate was 0.23 (95% CI: 0.10–0.50). A random effects model of time-variant survival and encounter probability performed relatively poorly (w_i < 0.01).

Demographic Model

At mean parameter values, our matrix structure for the deterministic model was:

$$\begin{matrix} 0.00 & 0.06 \\ 0.74 & 0.74 \end{matrix}$$

with λ = 0.81, predicting that the breeding population of long-tailed ducks on the YKD was declining by nearly 19% each year. Sensitivity of λ at mean values was highest for adult female survival, intermediate for duckling survival, and low for all other model parameters. Similarly, elasticity of λ was highest for adult survival, but low for all other parameters (Table 2). Stochastic model estimates were λ = 0.81 (95% CI: 0.74–1.03) for matrix structure based on randomly selected estimates of productivity and λ = 0.81 (95% CI: 0.61–1.06) for matrix structure based on randomly selected estimates of productivity and survival. At λ = 1.0, the pattern of sensitivities and elasticities was similar to the one produced by our model, although when only increases to productivity were made, the sensitivity of λ to duckling survival approached the sensitivity of adult survival (Fig. 4).

TABLE 2. Sensitivities and elasticities calculated at mean values of vital rates from a demographic model of long-tailed ducks breeding on the YKD.

Vital Rate	Sensitivity[1]	Elasticity[2]
Clutch Size	0.01	0.07
Nest Success	0.18	0.07
Duckling Survival	0.62	0.07
Adult Survival	1.01	0.93

[1] Relative change in λ from a minute absolute change in a vital rate relative to others held constant.

[2] Proportional change in λ from a minute proportional change in a vital rate relative to others held constant.

DISCUSSION

The estimates we present here for long-tailed ducks are some of the first published in North America (Robertson and Savard, 2002). Our demographic model of long-tailed ducks was based on vital rates estimated from small sample sizes of three dispersed nesting populations on the YKD; thus, we suggest cautious interpretation of our estimates of vital rates, λ, and associated confidence limits when comparing our estimates to those for other nesting populations.

Clutch Size and Nest Success

Our estimate of mean clutch size was intermediate between the estimates reported by Alison (1975) and Bengtsson (1971), and our 95% CIs overlapped their confidence limits. We did not detect variation in clutch sizes among site-years, suggesting that clutch size of long-tailed ducks may be, on average, a stable parameter across a small spatial scale. Further, the seasonal decline in clutch size was consistent with the pattern observed in most other waterfowl species (Johnson et al., 1992). Thus, our clutch size results do not suggest a change in clutch size that may have contributed to the long-term population decline.

Nest success estimates from our study were lower than apparent annual nest success estimates for long-tailed ducks breeding in northern Manitoba (52–63%; Alison, 1975), providing limited evidence for broad-scale variation in nest success. At the scale of our study, we also detected variation among site-years in nest success on the YKD, but because of our small sample size, we did not analytically partition the variation by site and year. We have few data to distinguish among sources for the variation we observed. However, predation was the apparent cause of most nest failures at all three study sites. Further, because nest remains often allowed us to identify the type of predator (avian or mammalian) responsible for nest destruction (Sargeant et al., 1998), we suspect that the predator communities differed between coastal and inland sites. Specifically, at KR and KI (coastal sites), nests were destroyed primarily by avian predators, which likely were mew gulls (*Larus canus*), glaucous gulls (*L. hyperboreus*), and parasitic jaegers (*Stercorarius*

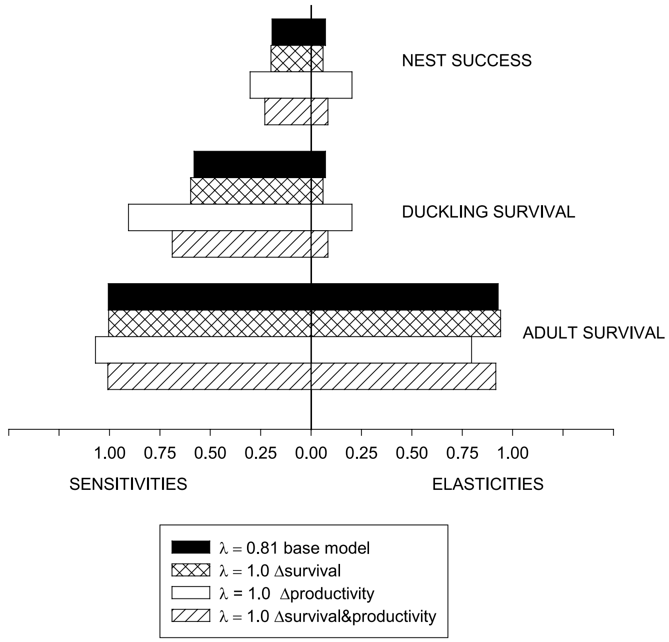

FIG. 4. Sensitivities and elasticities calculated from vital rate estimates of our base model and from adjustments to survival and productivity (adult survival, nest success, and duckling survival) to achieve $\lambda = 1.0$. Adjustments to parameter values included an absolute increase of 0.19 to adult survival only; proportional increases (2.25) to nest success and duckling survival; or equal, proportional increases of 1.22 to adult survival, nest success, and duckling survival.

parasiticus), although in some years arctic foxes (*Alopex lagopus*) were important nest predators. Contrastingly, at AL (the inland site) the primary nest predators were red foxes (*Vulpes vulpes*), but a small proportion of nests were destroyed by avian predators, either parasitic jaegers or mew gulls. Elsewhere, variation in predator composition has been linked with variation in nest success (Klett et al., 1988; Sovada et al., 1995). Thus, we hypothesize that differences in predator community between coastal and inland sites was an important factor influencing variation in nesting success in our study. However, we recognize that this hypothesis may only partially explain spatial and temporal variation in nest success. For example, numerical or functional responses in the predator community were hypothesized to be the primary source of temporal variation in nest success of sympatric nesting species on the YKD, e.g., greater scaup (*Aythya marila*), northern pintails, and spectacled eiders (Flint and Grand, 1996; Grand and Flint, 1997; Flint et al., 2006a). Accordingly, we caution that comparing estimates of nesting success based on small sample sizes for dispersed nesting species across limited geographic areas may not be instructive, as it is unlikely that study area–specific estimates represent broad-scale regional estimates at the population level. Such issues are inherent in studies of dispersed nesting species, and for adequate understanding of the true range of variation, studies must be replicated over time and a large enough space, with sufficiently large sample sizes.

Duckling Survival

Duckling survival for long-tailed ducks varied among site-years on the YKD, although we could not partition the variation between sites or years. Numerous sources likely contribute to spatial and temporal variability in duckling mortality, but these are difficult to determine (Johnson et al., 1992). However, as with many other duck species, there was some evidence that long-tailed ducklings experienced highest mortality early in the brood-rearing period (Hill and Ellis, 1984; Mendenhall and Milne, 1985; Mauser et al., 1994; Flint and Grand, 1997; Flint et al., 1998, 2006a; Hoekman et al., 2004), and thus, factors that affect mortality early may be most influential on duckling survival. Previous studies have hypothesized that the mutual effect of predation and exposure to variable environmental conditions, often associated with long-distance brood movements (Ball et al., 1975; Rotella and Ratti, 1992), is the primary cause of young duckling mortality (Mendenhall and Milne, 1985; Grand and Flint, 1996; Korschgen et al., 1996; Flint and Grand, 1997; Flint et al., 2006a, b). For the long-tailed duck broods we monitored, travel overland from nesting sites to upland brood-rearing areas averaged 2.17 km at KR and 1.71 km at AL. This travel occurred within the first week post-hatch, when ducklings are most vulnerable to predation and weather conditions because of their small size, incomplete thermoregulatory ability, and low energy reserves (Sedinger, 1992). Predation risk is likely negatively associated with duckling age and growth (Flint et al., 2006b), and older, larger ducklings may be less vulnerable to specific predator guilds (e.g., Larid spp.).

Adult Female Survival

Our results indicated minimal temporal variation in annual apparent survival of adult female long-tailed ducks breeding on the YKD. Although similar patterns of time-invariant survival have been reported for other sympatric nesting sea ducks (Grand et al., 1998; Wilson et al., 2007), we hesitate to draw any strong inference because our sample was small and our limited model set restricted our ability to detect potential temporal heterogeneity. Nonetheless, our estimate of apparent survival was lower than those reported for sympatric nesting greater scaup (0.81; Flint et al., 2006a), spectacled eiders (0.78; Grand et al., 1998) and common eiders (0.89; Wilson et al., 2007). Low adult female survival has been identified as a potential cause for decline in spectacled eiders on the YKD (USFWS, 1996), and we suggest the same may be true for long-tailed ducks. We currently cannot determine if changes in adult survival contributed to the long-term decline in long-tailed ducks on the YKD because we lack comparative historical data. However, our demographic model indicated that λ was proportionately more sensitive to adult annual survival than to reproductive parameters (see discussion below), signifying that adult survival was likely an integral factor affecting population decline. We caution that our estimate of survival was based solely on live recaptures, and therefore, estimated mortality is confounded with permanent emigration. Because our sample sizes were small, if marked females permanently emigrated from our study area, then our estimate of survival would be biased low by a relatively large amount. However, because there were no dead-recoveries of our banded females, we have no data to assess this potential bias.

Potential causes for the apparent high annual mortality we estimated are numerous. Small sample size prohibited us from considering multiple hypotheses, and therefore, we can only speculate about causal factors. We consider two possible mortality factors that occur during the breeding season that may be of primary importance to managers. First, we suggest that adult survival was negatively influenced by the presence of lead shot at KR. Grand et al. (1998) demonstrated that ingestion of lead shot reduced survival of female spectacled eiders breeding at KR by 44%, and Flint et al. (1997) estimated that more than 20% of nesting female long-tailed ducks were exposed to lead, an exposure rate slightly lower than that of spectacled eiders. For spectacled eiders, rates of exposure were higher at KR than elsewhere on the YKD (Grand et al., 1998). Thus, because most of our mark-recapture data originated at the KR area, our apparent survival estimate for long-tailed ducks may not be applicable to other nesting populations. The influence of lead exposure on annual survival rates of long-tailed ducks on the YKD deserves further empirical attention.

Secondly, subsistence harvest is ostensibly an important source of mortality for long-tailed ducks on the YKD. Annual harvest surveys conducted on the YKD indicated that long-tailed ducks were harvested at higher rates in proportion to population numbers than many other duck species (Wentworth and Seim, 1996). Currently, the impact of this harvest on survival rate is unknown, but we suggest that spring hunting of breeding adults is likely an additive source of mortality. Our demographic model indicates that population dynamics of long-tailed ducks would be very sensitive to additive sources of mortality, because they are most sensitive to adult survival. Thus, we encourage further quantitative study of the influence of subsistence harvest on the survival rate of long-tailed ducks on the YKD, as was suggested for other YKD waterfowl species (King and Derksen, 1986; Wilson et al., 2007).

Demographic Model

Our model predicted that the number of long-tailed ducks breeding on the YKD is declining; however, the rate of decline that we estimated (19%) is much steeper than the average decline over a 30-year period (~2.5–4%) reported by the North American Breeding Waterfowl Survey (NABWS) for long-tailed ducks counted in Alaska and the Yukon, Canada (Conant and Mallek, 2006). Moreover, our estimated trajectory differs from the relatively stable trend (λ =1.02) indicated by the YKD coastal-specific survey data collected during the period of our studies, 1988–2006 (Platte and Stehn, 2006), even though the CIs we estimated for λ included this estimate. However, direct comparison of our model predictions to survey data are likely invalid because of differences in spatial and temporal scales between the sampling methods. That is, the entire YKD population may be stable, while the local population on our study areas may be declining. Certainly, we cannot exclude the possibility that localized factors, such as the impact of lead poisoning on survival or observer disturbance on nest success, may have biased our parameter estimates. Thus, if we assume that aerial surveys are accurate (e.g., with regard to timing and detection rate), the discrepancy between survey trends and our model may be explained by bias in one or more of our parameter estimates. On the basis of iterative proportional changes to survival and productivity, we would predict a stable population if our parameter estimates were biased low by as much as 0.17; our model predicts that a survival rate of 0.91, a nest success rate of 0.36, and a duckling survival rate of 0.12 would be required to obtain stability. Nonetheless, our model demonstrates the relative importance of vital rates to λ, and generally supports life-history patterns observed in other sea ducks, which are characterized by high adult survival and low, variable productivity (Alisauskas et al., 2004). Such patterns of relative importance are caused by the inherent model structure required to fit long-tailed duck life history. Accordingly, these patterns of relative importance are robust to variation in input parameter values (Fig. 4) (Schmutz et al., 1997; Flint et al., 1998). For example, if only fertility is increased enough to stabilize the population, the influences of productivity and survival on λ remain relatively unchanged (Fig. 4). Thus, even if our input parameters are biased relative to the true population values, our estimated sensitivities and elasticities are likely still valid for management inference.

Sensitivity of adult female survival in our model exceeded that of reproductive parameters, as in other demographic models of waterfowl (Schmutz et al., 1997; Flint et al., 1998, 2006a). Altering adult survival of long-lived species most often has greater proportionate effects on λ than equivalent changes to reproductive parameters (Schmutz et al., 1997; Sæther and Bakke, 2000; Flint et al., 2006a). Thus, increases to adult female survival of long-tailed ducks will likely have the greatest impact on population dynamics. Specifically, management actions directed toward increasing adult survival during the breeding season likely would be most beneficial, since mortality tends to be higher during this period and is likely correlated with production-related rates (Ringelman and Longcore, 1983; Cowardin et al., 1985). Unfortunately, our inability to model hypothesized mortality factors precludes our suggesting specific management activities. However, we have presented two hypothesized mortality factors (i.e., lead poisoning, subsistence harvest) that we deem significant to breeding long-tailed ducks and encourage their consideration in future management decisions.

Despite indications that annual survival is the most important determinant of population trends, effective management of survival may be difficult or impossible: given our estimates of productivity, survival would have to be over 0.93 to obtain population stability. Therefore, we also suggest that attention be focused on components of recruitment. The high duckling mortality we estimated and associated high sensitivity of this parameter in our model may indicate that duckling survival is a bottleneck to recruitment. Our model suggests that proportional changes in duckling survival and nest success would have equivalent influences on λ. However, absolute changes (i.e., fixed percentage point changes) in duckling survival would have greater effects on population dynamics than equivalent changes in nesting success. Thus, management efforts would be best aimed at increasing duckling survival to obtain increases in recruitment. However, Flint et al. (2006b) suggested that duckling survival of spectacled eiders was proximately influenced by predation, but ultimately may have been constrained by habitat characteristics such as wetland salinity or foraging conditions. This view is consistent with Pehrsson and Nyström's (1988) finding that increasing nest success of long-tailed ducks did not result in increased recruitment because duckling abundance was limited by inadequate forage in brood-rearing habitat. Given that foraging conditions may be difficult to manage, few options may be currently available to managers for improving recruitment of long-tailed ducks. Thus, we suggest that future studies delineating the relative impact of predators versus environmental factors on long-tailed duckling survival are warranted to examine possible management actions.

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