Lesser scaup breeding ecology in the Canadian parklands
by David Nelson Koons

Abstract:
Neutrophils play an essential role in fighting bacterial infections. Many neutrophil functions are the result of an interplay between cell surface receptors and their ligands. Formyl peptide receptor (FPR), through the action of its ligand, fMLF, has been shown to mediate neutrophil migratory, as well as cytotoxic functions. This receptor is believed to be organized into seven-transmembrane regions and is coupled to guanosine triphosphate-binding protein (G protein), which is a key component in FPR-mediated signal transduction. Previously, numerous attempts have been made to purify the receptor. In this work, we describe the expression and partial purification of FPR expressed in insect cells infected with recombinant baculovirus. The receptor expressed in these cells had a significantly decreased ligand binding affinity with a dissociation constant of 70 nM, as compared to the receptor on neutrophils with dissociation constant of 3 nM, suggesting that the processing of the receptor may be different. We, therefore, shifted our effort to purify FPR from Chinese hamster ovary (CHO) cells, which were found to bind ligand with a similar affinity as human neutrophils.

The purified receptor, as well as intact CHO cells expressing FPR (CHO-FPR), was used in the selection of phage peptide library in order to identify sequences that bind to the receptor. Although no consensus sequence was identified, the use of CHO-FPR cells in affinity purification of phage peptide library allowed the selection of phage that had binding characteristics different from the phage selected using wild-type CHO cells. This was demonstrated by flow cytometry, which proved to be a rapid and efficient method for screening the selected phage.

Finally, to further explore the protein-protein binding sites on FPR, and more specifically the interaction between the receptor and G protein, two cytoplasmic tail deletion mutants of FPR were constructed and analyzed for their signal transduction capabilities. Partial calcium release and suppressed chemotaxis by the deletion mutants suggest that the deleted regions are not absolutely necessary in eliciting the FPR-mediated response. Our results support the notion that there are several binding sites between FPR and G protein.

LESSER SCAUP BREEDING ECOLOGY IN THE CANADIAN PARKLANDS

by

David Nelson Koons

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

The continental population of lesser scaup (*Aythya affinis*) has declined over the past 20 years and causes of the decline have not been identified. To identify factors possibly related to the decline, I designed and conducted a study to estimate demographic vital rates of lesser scaup and to compare those rates to historic vital rates for a local population (Erickson, Manitoba). The local population had been well studied before the recent declines of scaup numbers occurred. I also developed a model to examine population growth and its relation to vital rates. For my study population, I found that nesting success, duckling survival, and possibly breeding-season survival of mature females were lower than historical estimates. I found that nesting success increased with period-of-year, was higher for over-water nests, and was negatively related to vegetation density. The majority (86%) of duckling mortality occurred during the first week post-hatch. Eighty-three percent of female mortality occurred during the nesting period, and female survival during the nesting period was negatively related to vegetation density. Further, analytic perturbation of my population model indicated that the local population is declining, and that breeding-season survival of mature females and nesting success have the strongest potential to affect population growth. Thus, declines in these vital rates have likely caused the local decline of scaup numbers. Strategies designed to increase breeding-season survival of mature females and nesting success will likely have a bigger impact on lesser scaup population growth rate at Erickson than strategies designed to manage other vital rates.

INTRODUCTION

Once among the most abundant waterfowl species, the continental lesser scaup (*Aythya affinis*; hereafter scaup) population has been declining for over 20 years (Allen et al. 1999) and is currently near the lowest level ever recorded (U.S. Fish and Wildlife Service 2000; hereafter USFWS). Furthermore, surveys conducted each May by the USFWS indicate that declines have taken place in both the boreal forest and prairie-parkland regions, where 68% and 25% of scaup breed, respectively (Austin et al. 1998).

Although basic life history of scaup is well known (Austin et al. 1998), a complete set of vital-rate estimates (i.e., survival and reproductive rates) exists only for the parklands of Manitoba (Afton 1984). Further, even these estimates are inadequate to evaluate causes of population declines as the estimates are approximately 20 years old, and no research results have been published on scaup vital rates since. Given the current status of the continental scaup population and lack of current information on vital rates, better information is needed for understanding causes of the apparent declines across both the boreal and prairie-parkland regions.

Several hypotheses have been proposed to explain population declines, and all hypotheses pertain to changes in the environment and corresponding changes to scaup vital rates (Afton and Anderson unpublished ms cited in Austin et al. 2000). Given the lack of recent data on scaup vital rates, comparisons of past versus current vital rates and of resulting population dynamics have not been possible. Such an analysis would, however, be useful for evaluating (1) which vital rates, if any, have changed and (2) what actions might help reverse population declines. Obviously, data collection for a past-versus-present analysis should be conducted in the same location where past vital-rate information was collected and at a location where the local population has declined.

The only area offering such an opportunity is in the parklands of southwestern Manitoba, Canada, where Rogers (1964), Hammell (1973), and Afton (1984) conducted research near Erickson, Manitoba prior to the continental decline of scaup (pre-1981). Afton's (1984) work is particularly useful as it provided estimates of all the vital rates that compose the fundamental life cycle of lesser scaup. Furthermore, the number of scaup near Erickson declined between 1955 and 2000 (Fig. 1). By conducting new research in Erickson, Manitoba, comparisons can be made for several vital rates simultaneously, and changes in rates can be estimated. Additionally, possible causes of vital-rate changes could be evaluated if factors potentially related to each vital rate were measured and used to model vital rates (Burnham and Anderson 1998). Finally, past and current data could be used in a model of population dynamics to evaluate which vital rates most influence scaup dynamics (e.g., Rockwell et al. 1997, Wisdom and Mills 1997, Flint et al. 1998, Saether and Bakke 2000).

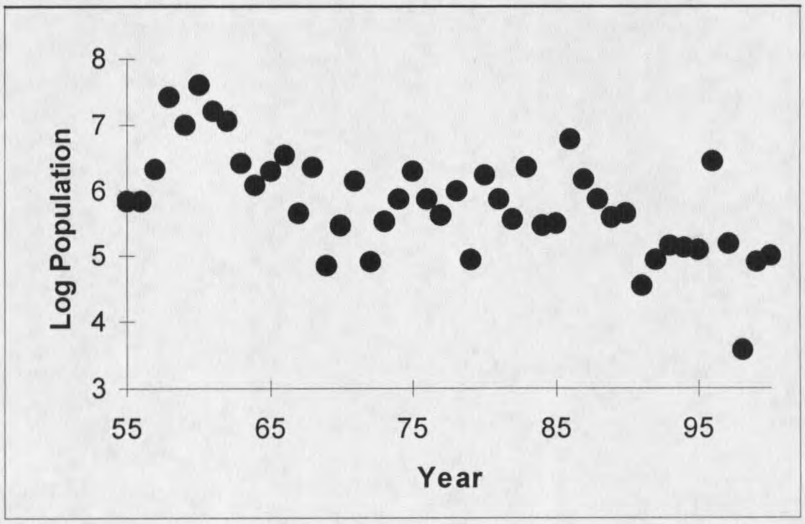
Accordingly, I designed and conducted a study of breeding scaup in Erickson, Manitoba with the following objectives: (1) estimate vital rates and compare them with past estimates; (2) evaluate the relationships between vital rates and various attributes of individual birds and environmental covariates; (3) use analytic perturbation of a population model to examine effects of changes in vital rates on population growth rate for scaup in both the current and pre-1981 eras (Caswell 1997, 2000a); and (4) assess the implications of my study to future research and management of scaup.

STUDY AREA

I conducted research 4.8 km south of Erickson, Manitoba (50º 30' N, 99º 55'W) on the Riding Mountain plateau in the parkland region of the province. Land cover consisted of numerous small wetlands (12-19 wetlands / km^2), patches of aspen (*Populus tremuloides* and *Populus balsamifera*), and a mosaic of cereal grain agriculture, hayland, pasture, and grasslands.

I conducted work on a 28.5 km^2 site, which included the site used for previous scaup work (Rogers 1964, Hammell 1973, Afton 1984, and Austin 1986). Vegetation on the site was 42% cultivated (wheat, barley, canola, and flax fields), 17% grassland and pasture, 15% hayland, 14% wetland and wetland margin, and 12% woodland (data acquired from 1994 aerial photographs).

Figure 1. Erickson Population of Lesser Scaup (1955 – 2000) – Data Comes From The USFWS May Breeding Pairs Survey (Stratum 40; transect 6, segments 3 and 4; transect 4, segment 4).



METHODS

Population Counts

To facilitate future comparison with the Erickson scaup population of 1999 and 2000, I counted the number of scaup on each wetland within a 20.7 km^2 core area each week from mid-May until 1 June, and bi-weekly from 1 June to mid-July. I recorded the number of pairs, lone males, lone females, and groups as well as group composition. I estimated the number of breeding pairs using the following *ad hoc* formula: Total Breeding Pairs = [# Observed Pairs] + [# Lone Females]. Scaup recorded in a group or as a lone male were not used in estimation of breeding pairs. However, all scaup counted on each survey were used to calculate a sex ratio of males to females. I estimated the number of resident breeding pairs and sex ratio in mid-June each year, which was when I judged migrant birds had left the study area, and resident females had not yet begun incubation (e.g., Rogers 1964, Afton 1984, pers. obs.).

Trapping and Telemetry

To facilitate estimation of nesting success, clutch size, duckling survival, and female survival, I trapped, radiomarked, and followed females during 15 May – 1 September in 1999 and 2000. I captured some females each spring before females initiated nests using decoy traps. Each trap contained a live captive female (Anderson et al. 1980) or plastic decoy and mirrors. I also trapped females on nests using Weller nest traps (1957). Nests of unmarked females were located using systematic foot searches, an ATV chain drag (Klett et al. 1986), a rope drag, by observing behavioral cues of the female, or combinations of these methods. Nest-trapped birds were anesthetized with propofol after handling to reduce nest abandonment (K. Machin DVM, pers. commun.).

For each female trapped, I recorded morphometrics and body mass (nearest 2 g), and used eye color to determine age (Trauger 1974). I outfitted each female with a 9-g prong-and-suture radio transmitter containing a 12-hour motion-mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a USFWS aluminum leg band. Each female was also outfitted with a unique combination (color and shape) of nasal disks (Bartonek and Dane 1964). Birds were released at the place of capture within 20 minutes of being removed from a trap.

To find nests of radiomarked females, I estimated each female's location once per morning until a nest was found or the nesting season ended. I used a null-peak or hand-held antenna system to estimate a female's location and checked the mortality-pulse-rate of the radio to monitor female fates. Once a female was known to be nesting, I continued to locate her daily to monitor survival of her and the nest. For each female that hatched a brood, I continued to monitor the female up to 28 days post-hatch to monitor survival of her and the ducklings. For each unsuccessful female, I continued to locate the female daily to determine if she renested and to monitor her survival.

Nesting Success and Clutch Size

To attain estimates of (1) nesting success and (2) mean clutch size for comparison to the past, I (1) monitored nest fates throughout the nesting season and (2) recorded total clutch size at each nest that survived to incubation. If a radiomarked female was not located at her nest for ≥ 24 hours, I checked the nest to determine its status. Nests of non-radiomarked females were visited approximately every 4 to 6 days to monitor nest fate (Bart and Robson 1982). I defined a successful nest as one that hatched at least one egg (Klett et al. 1986).

Further, I measured factors potentially related to clutch size and nesting success. Because nesting chronology can affect both clutch size and nesting success, I recorded the stage of incubation when a nest was found (Weller 1956), which I used to estimate nest-initiation date and the expected date of hatch. I also measured length and breadth of each egg to estimate mean-within-clutch egg volume following Hoyt (1979) because mean-within-clutch egg volume can potentially affect a female's total clutch size. I recorded habitat at each nest to acquire potential nesting success covariates and to quantify the habitat used by nesting female scaup for comparison to past habitat use. Specifically, I measured the following vegetation characteristics at each nest 0 to 5 days after the estimated hatch date: genus of dominant plant species, visibility obstruction reading (VOR) from four cardinal directions (Robel et al. 1970), maximum vegetation height, percent canopy cover (Daubenmire 1959), and water depth for over-water nests. I also recorded the distance from each nest to the nearest vegetative edge (definitive transition in vegetation cover type [e.g., the border between cattail and sedge in a wetland]) or man-made edge (a road, building, fence, or railway), and to the nearest wetland (boundary of water and dry land).

Duckling Survival

To acquire estimates of duckling survival for comparison to past estimates, I followed marked females that hatched nests and attempted brood counts every two days until total brood mortality occurred or up to 28 days post-hatch. Almost no duckling mortality occurs after four weeks of age (Afton 1984, Dawson and Clark 1996). Whenever I suspected that a female had lost her brood, I repeatedly watched the wetland(s) being used by that female and radiotracked her intensively for a week. I concluded that a female had lost her brood if she was never seen with ducklings during that week. If a brood was not readily visible during a brood count, I made noise from a distance, which usually caused the brood to swim to the middle of the pond. To alleviate bias associated with brood mixing, I verified that the size of each duckling was consistent with the age of the brood.

Data Analyses

Physical Condition

To attain an index of physical condition for use as a covariate in survival, fecundity, and fertility models, I used principle components analysis of the correlation matrix on the following morphometrics: total length, keel length, bill length, culmen, wing chord, and right tarsus (Afton and Ankeny 1991). I used first principle component (PC1) scores as a measure of body size for each bird (Alisauskas and Ankeny 1987). (PC1 explained 36% of the overall variation among morphometrics, and all factor loadings were positive and ranged from 0.33 to 0.49. Other principle components were not used because they were interpreted as body shape components.) I used a regression model to correct body mass for capture date. I then regressed body mass, corrected for capture date, on PC1 and used the residual scores as an index to physical condition (Olsen and Afton 2000).

Nesting Success

To estimate scaup nesting success and to evaluate factors related to nesting success, I used data on daily nest fates (survived or died) for nests of all radiomarked females and on nest fates for 4-to-6-day intervals for nests of non-radiomarked females. I did not use data from island nests because a small fraction of the population used islands as nest sites. Nesting success was estimated by raising the maximum-likelihood estimate of daily survival rate of nests (Bart and Robson 1982) to the 36th power, i.e., the average number of days it takes a scaup to lay and incubate a clutch. To evaluate factors potentially related to nesting success, I used generalized linear models (McCullogh and Nelder 1989; binomial errors on fate and log-link function), which considered observer-effects (Rotella et al. 2000) as well as other covariates. The following covariates were considered as factors potentially related to daily survival of scaup nests: habitat type, vegetation density, canopy cover, distance to nearest edge, distance to nearest wetland boundary, period of year (early [12 June to 2 July], middle [3 July to 24 July], and late [25 July to 15 August] parts of the nesting season), and year.

Using these covariates, I developed an *a priori* list of candidate models based on my hypotheses of interest and the literature on nesting success (Burnham and Anderson 1998). The model list (see Results) was constrained by covariates measured in the field and by the amount of data available. To select models from the candidate list, I used Akaike's Information Criterion adjusted for sample size (AIC_c), or the information criterion adjusted for sample size and overdispersion ($QAIC_c$), and Akaike Weights (the weight of evidence for a model compared to other models in the candidate list) (Akaike 1973, Burnham and Anderson 1998). This statistical method emphasizes parsimony and considers the most parsimonious model to be that with the lowest information criterion value. I used AIC_c or $QAIC_c$ values to calculate, ΔAIC_c, or Δ $QAIC_c$, which are a measure of the difference between the AIC_c, or $QAIC_c$, value for a given model and that of the most parsimonious model. Thus, the most parsimonious model has an ΔAIC_c or $\Delta QAIC_c$ value of 0.0. I restricted my selection of models to those with ΔAIC_c values of less than two and further restricted selection to model covariates that accounted for at least 25% of the Akaike weight (Burnham and Anderson 1998). Because modeling was done on a transformed response variable, I estimated survival by back-transforming estimates of the response variable using estimated slopes (ßs) and the proper link function. For models containing multiple slope estimates (ßs), I estimated the variance of daily survival using the delta method (Seber 1982). To estimate precision of point estimates of daily survival, I constructed 95% confidence intervals using back-transformation. Standard errors were not attainable for survival estimates that were transformed daily survival estimates (e.g., nesting success = daily survival rate ^{36}).

Once the most parsimonious models of nesting success were selected, I used estimated coefficients for those models to estimate daily survival rate for each level of categorical explanatory covariates and across the range of continuous explanatory covariates. Because daily survival rate may have differed by nesting stage, I used PROC

NLIN (SAS Institute) to test for differences of daily survival rate between incubation and laying stages (see Stanley 2000).

I also modeled nesting success of all duck species and checked for differences among species using model-selection methods described above. I was able to consider more complex models for the data set containing nest-fate observations for all duck nests (scaup, canvasback [*A. valisineria*], redhead [*A. americana*], ring-necked duck [*A. collaris*; hereafter ring-neck], ruddy duck [*Oxyura jamaicensis*], mallard [*Anas platyrhynchos*], gadwall [*A. strepera*], northern shoveler [*A. clypeata*], green-winged teal [*A. crecca*], and blue-winged teal [*A. discors*]. After I selected explanatory models of nesting success of all ducks species and identified differences of nesting success among species, I created exploratory models of duck nesting success that considered environmental covariates and differences among species (see Results for list of models). Model selection was performed using AIC_c values as described above.

Clutch Size

I evaluated the effects of nest-initiation date, female age, female physical condition, mean-within-clutch egg volume, and year on scaup clutch size using multiple linear regression (Neter et al. 1996). Because full clutch size could not be determined for nests that were terminated prior to incubation, parasitized by redheads (Sayler 1985), or found after a flooding event, I excluded these nests and known re-nests of radiomarked females from clutch size analyses.

When evaluating competing models, I only used the subset of my clutch-size data that contained complete data for all individuals so that sample sizes were consistent for all models, which ensured comparable likelihoods among the models. Model selection was performed using AIC_c values and methods described above.

Duckling Survival

I estimated duckling survival as the proportion of all ducklings in all broods that survived from hatch to 28 days of age. I assumed that brood amalgamation did not occur because I never saw a brood size increase. I evaluated factors related to duckling survival using generalized linear models (known-fate models with the logit-link function, binomial errors on fate) with Program Mark (White and Burnham 1999) and treated ducklings as independent sampling units. I evaluated the effects of duckling age, year, and hatch date on duckling survival by evaluating candidate models using AIC_c values and methods described above. Further, I evaluated how estimated standard errors changed when I relaxed the assumption of independence among brood mates by applying cluster sampling (Flint et al. 1995). Flint et al. (1995) used brood size as the cluster size. In my analyses, I evaluated a variety of cluster sizes i.e., I changed the cluster size from the duckling to the mean brood size in separate analyses, because I suspected that fates of brood mates were neither completely dependent nor completely independent. I did this by changing the over-dispersion factor in Program Mark from 1 to 6, which was the mean brood size.

I also used generalized linear models (known-fate models with the logit-link function, binomial errors on fate) with Program Mark to estimate brood survival, the proportion of broods that had at least one duckling survive to 28 days of age. I assumed that fates of broods were independent, and subsequently, did not address over-dispersion for brood-survival estimation. Models with covariates were not considered.

Female Survival

I estimated daily survival rates of female scaup on the breeding grounds for three distinct periods: (1) the non-maternal period (i.e., not nesting or rearing a brood), (2) the nesting period, and (3) the brood-rearing period. To test for daily survival rate differences among the three periods, I used AIC$_c$ and methods described above.

To estimate breeding-season survival from estimates for the three distinct periods, I first weighted period-specific estimates by the percent of the population that consisted of non-breeders, unsuccessful nesters, and successful nesters. I used Afton's (1984) four-year average non-breeding rate as the percent of the population that did not breed (15.7%) (my data were inadequate for estimating this parameter). I then used my field estimates of female success to calculate the percent of the population that consisted of unsuccessful nesters and successful nesters.

Survival of females at the nest may be affected by similar factors that affect survival of the nest itself. Therefore, I examined the relationships between daily survival rate of nesting females and vegetation density, habitat type, incubation stage, female physical condition, period of year, and year using AIC$_c$ values and methods described above.

Population Modeling

I created a matrix population model for the scaup population on my study area to estimate population growth for 1999 and 2000 and to evaluate the growth rate's relationship with measured vital rates. Because the number of females in the local population was more limiting than the number of males (see Results), I created a model that represented females only. To parameterize the model, I used my vital-rate estimates for as many vital rates as possible and used published estimates for rates that I was unable to estimate.

I used a two age-class extended Leslie matrix model (Leslie 1945, 1948, Caswell 2000a). The model used a pre-breeding census, and thus, females entered the second year (SY) and after second year (ASY) age classes at the start of their first and second breeding seasons, respectively. For simplicity, I assumed that females that were two years old and older experienced similar survival and reproduction (Afton 1984). I also assumed exponential population growth, independence among vital rates, density independence, and a stable age distribution (Caswell 1989, 2000a).

I used a prospective analytic perturbation approach to estimate population growth rate from the model and to explore the relative influence of vital rates on population growth (Horvitz et al. 1997). I calculated asymptotic population growth rate (λ) as the dominant eigenvalue of the matrix. Both sensitivity and elasticity were calculated for each matrix sub-element of the mean matrix using partial differentiation of the matrix (Caswell 1989). The mean Leslie matrix was composed of fertility F_X (top row) and survival S_X (bottom row in a 2 x 2 matrix) values for each age class, where *x* refers to an age class

$$\begin{pmatrix} F_{SY} & F_{ASY} \\ S_{SY} & S_{ASY} \end{pmatrix}$$

Fertility and survival transition paths for each age class were reduced to:

$$F_{SY} = BP_{SY} \cdot (NS + (1 - NS) \cdot RN_{SY} \cdot NS) \cdot CS \cdot DS \cdot JS$$

$$F_{ASY} = BP_{ASY} \cdot (NS + (1 - NS) \cdot RN_{ASY} \cdot NS) \cdot CS \cdot DS \cdot JS$$

$$S_{SY} = BS \cdot NBS$$

$$S_{ASY} = BS \cdot NBS$$

Non-subscripted parameters in the fertility and survival equations were the same between age classes. BP_{SY} and BP_{ASY} are the breeding probabilities for each age class, respectively, that attempt nesting at least once per year; NS is nesting success; RN_{SY} and RN_{ASY} are the probabilities of producing a second clutch given total failure of the first clutch for each age class, respectively. I estimated RN for surviving females only. Thus, I had to adjust the rate downward to make it representative of all females. To do this, I multiplied the published renesting rate by female survival during the nesting period. CS is the clutch size of eggs that contain female embryos assuming a 50:50 primary sex ratio within a clutch; DS is duckling survival; JS is juvenile survival or the proportion of fledged birds that survive to the start of the next breeding season; BS is breeding-season survival of females; and NBS is non-breeding-season survival of females.

The functional relationships of demographic parameters in each pathway equation are believed to strongly influence population dynamics. Fertility equations represent the pathway of recruitment of second-year age class individuals into the population during each time step. Although some data (e.g., Afton 1984) suggested age-specific variation in NS and DS, I limited age-structure in my fertility equations because differences appeared to be rather small, and I believed that increases in model realism were small compared to the increases in complexity. The S_x matrix transitions represent the probability of adults surviving a time step (Caswell 2000a). Because adult survival can be affected by different factors between seasons, I broke adult survival into seasonal components.

RESULTS

In 1999 and 2000 I captured and radio-marked a total of 34 females. This sample provided data for 34 nests (1 known re-nesting attempt), 9 broods, and daily survival for 34 females. Twenty-two additional nests were found. Thus, I obtained data for 56 scaup nests and used 49 of these nests in nesting-success analyses. Further, I found 278 nests of other duck species and used these to compare nesting success among species.

Population Counts

I estimated that there were 43 (2.08 pairs / km^2) and 30 (1.45 pairs / km^2) breeding pairs present on the study area in 1999 and 2000, respectively. The sex ratio of males to females during the second week of June was 2.62:1 in 1999 and 1.60:1 in 2000.

Nesting Habitat Use

I found 52.7%, 40%, and 7.3% of scaup nests (n = 55) in overwater, upland, and island locales, respectively. Over-water nests consisted of both floating-platform nests and nests built on sedge hummocks, and the mean depth of water at these nests was 0.22 m (n = 29, SE = 0.02, range = 0.01 - 0.5 m). I found the majority (60%) of scaup nests (n = 55) in sedge (C*arex* spp.), 18.18% in grasses, 7.27% in phragmites (*Phragmites communis*), 5.45% in forb, 5.45% in sedge and cattail (*Typha* spp.) mixed cover, and 3.64% in sedge and phragmites mixed cover. Mean height of vegetation at scaup nests was 0.83 m (SE = 0.04, range = 0.25 – 2.00 m), and mean canopy cover over nests was 56.8% (SE = 3.74, range = 0 – 100%). The mean Visibility Obstruction Reading (VOR), an index of vegetation density, was 5.7 dm (SE = 0.30, range = 0.4 – 13.8 dm). Mean distance to wetland boundary for over-water nests was 9.8 m (*n* = 29, SE = 1.17, range = 2.1 – 26 m), 10.5 m for upland nests (*n* = 22, SE = 5.57, range = 0.1 – 115 m), and 2.0 m for island nests (*n* = 4, SE = 0.649, range = 0.3 – 3 m). Additionally, the mean distance from a scaup nest to a man made, or vegetative edge was 5.3 m (*n* = 55, SE = 0.896, range = 0 – 38 m).

Nesting Success

Forty-nine scaup nests yielded 288 interval-specific fates for intervals ranging from 1 to 7 days long. Estimated daily survival rate for scaup nests was 0.940 (95% CI = 0.913 to 0.967), and 0.943 (95% CI = 0.910 to 0.976) in 1999 and 2000, respectively. Corresponding estimates of nesting success were 10.8% and 12.1%, respectively. Daily survival rate pooled among years was estimated as 0.941 (95% CI = 0.921 to 0.962, 11.2% nesting success). Estimated daily survival rates were similar for laying (0.938, 95% CI = 0.881 to 0.995) and incubation stages (0.942, 95% CI = 0.915 to 0.969).

The most parsimonious model of daily survival rate of scaup nests contained no environmental covariates and no observer effects. However, a number of other models were within 2 AIC_c units of the best model. A model that considered period-of-year received some support ($\Delta AIC_c = 0.66$, accounted for 29% of the Akaike Weight; Table 1) and indicated a positive trend in daily survival rate over the three periods (estimated ß = 0.023, SE = 0.0184). Estimates of daily survival rate, which were imprecise, in the early, middle, and late parts of the year were 0.921 (95% CI = 0.878 to 0.963), 0.941 (95% CI = 0.921 to 0.962), and 0.963 (95% CI = 0.926 to 0.999), respectively.

Table 1. An Evaluation of Generalized Linear Models for Lesser Scaup Nesting Success: Comparisons of Environmental Covariate Effects.

Rank	Model	AICc	Δ AICc	Akaike weight
1	Null model	175.78	0.00	0.14
2	Trend date	176.44	0.66	0.10
3	Habitat type	176.86	1.08	0.08
4	Habitat type and VOR	176.98	1.20	0.08
5	Habitat type and Trend date	177.01	1.24	0.08
6	VOR	177.36	1.58	0.06
7	Canopy cover	177.57	1.79	0.06
8	Wetland edge	177.72	1.94	0.05
9	Edge	177.74	1.97	0.05
10	Observer effects	177.77	1.99	0.05
11	Year	177.79	2.01	0.05
12	VOR and Trend date	178.22	2.44	0.04
13	Wetland edge and Trend date	178.42	2.64	0.04
14	VOR and Observer effect	178.42	2.65	0.04
15	Habitat Type and Wetland edge	178.86	3.09	0.03
16	VOR, Trend date, and Interaction	179.19	3.41	0.03
17	Canopy cover and VOR	179.29	3.52	0.02
18	Global[a]	187.18	11.40	0.0005

[a] The Global model contains all hypothesized covariates: Trend date – estimates allowed to vary by period of year, which treats period of year as a class variable modeled in a trend fashion; Habitat type – estimates allowed to vary by nesting habitat (upland vs. over-water nesting habitats; VOR – estimates allowed to vary by Visibility Obstruction Reading, an index of vegetation density at the nest; Canopy cover – estimates allowed to vary by canopy coverage of vegetation at the nest; Wetland edge – estimates allowed to vary by distance from nests to wetland boundaries; Edge– estimates allowed to vary by distance from nests to nearest man-made or vegetative edges; Observer effects – estimates effect of observer on daily survival rate; Year – estimates allowed to vary by year.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

There was some evidence that habitat type was related to daily survival rate; habitat-type was in three of the top six models, all three models had $\Delta AIC_c < 2$, and models with habitat-type accounted for 27% of the total Akaike weight (Table 1). Using the model that simply contained habitat type for estimation, daily survival rate for over-water nests was

0.950 (95% CI = 0.925 to 0.975), and daily survival rate for upland nests was 0.928 (95% CI = 0.892 to 0.965). The estimated effect of habitat was imprecise, however, and 95% confidence intervals overlapped. VOR also received some support (in two of the top six models, each with $\Delta AIC_c < 2$, accounted for 27% of Akaike Weight; Table 1). VOR had a weak, negative relationship with daily survival rate of scaup nests (estimated ß = -0.0091, SE = 0.0065). Fisher's pairwise comparisons indicated that sedge vegetation had the highest VORs ($P < 0.01$). Additionally, VORs were higher for over-water nests than for upland nests ($P < 0.001$). Indicating a possible interaction between VOR and habitat type. Given the sparse data set, however, I was unable to evaluate such complex models.

When all 327 duck nests (947 interval fates) were considered, the most parsimonious model of nesting success included habitat type, VOR, an interaction between habitat type and VOR, and distance to nearest edge as covariates (Table 2). Similar to the scaup results, daily survival rate was higher for over-water nests (0.957, 95% CI = 0.945 to 0.968) than for upland nests (0.937, 95% CI = 0.927 to 0.947). Daily survival rate was negatively related to VOR for over water nests (estimated ß = -0.0065, SE = 0.0018), but not for upland nests (Fig. 2). Daily survival rate was positively related to distance to nearest edge (estimated ß = 0.0005, SE = 0.0002, Fig. 3). No other model was within 2 AIC_c units of the most parsimonious model (Table 2).

Daily survival rate of ring-neck nests (0.969, 95% CI = 0.951 to 0.986; 0.322 nesting success) was higher than estimated daily survival rate of other species (0.943, 95% CI = 0.935 to 0.951; 0.121 nesting success); however, daily survival rate was similar among other species (Table 3). When environmental covariates and differences among species were

Table 2. An Evaluation of Generalized Linear Models for Duck Nesting Success (all species): Comparisons of Environmental Covariate Effects.

Rank	Model	AICc	Δ AICc	Akaike weight
1	Habitat type, VOR, Interaction & Edge	892.08	0.000	0.61
2	Habitat type, VOR & Edge	894.76	2.673	0.16
3	Habitat type, VOR, Edge & Year	895.76	3.677	0.10
4	Habitat type, VOR & Interaction	896.88	4.796	0.06
5	Global[a]	896.88	4.796	0.06
6	Habitat type & VOR	899.36	7.275	0.02
7	Habitat type	903.54	11.457	0.002
8	Habitat type & Date of year	905.29	13.207	0.001
9	Year	905.53	13.443	0.001
10	Edge	906.03	13.949	0.001
11	VOR & Year	907.02	14.934	0.000
12	Null	907.82	15.734	0.000
13	VOR	907.87	15.790	0.000
14	VOR, Year & Interaction	908.90	16.816	0.000
15	Trend Date	909.19	17.107	0.000
16	VOR & Date of year	909.46	17.377	0.000
17	Observer effects	909.77	17.690	0.000
18	Wetland edge	909.79	17.704	0.000

a The Global model contains all hypothesized covariates: Trend date – estimates allowed to vary by period of year, which treats period of year as a class variable modeled in a trend fashion; Habitat type – estimates allowed to vary by nesting habitat (upland vs. over-water nesting habitats; VOR – estimates allowed to vary by Visibility Obstruction Reading, an index of vegetation density at the nest; Interaction – an interaction term between Habitat type and VOR; Wetland edge – estimates allowed to vary by distance from nests to wetland boundaries; Edge– estimates allowed to vary by distance from nests to nearest man-made or vegetative edges; Observer effects – estimates effect of observer on daily survival rate; Year – estimates allowed to vary by year.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

considered, the most parsimonious model again included habitat type, VOR, an interaction between habitat type and VOR, and distance to nearest edge as covariates (Table 4). The model containing these covariates and a covariate that considered daily survival rate differences between ring-necks and other species also received support ($\Delta AIC_c = 1.27$). Ring-necks had higher daily survival rate than other over-water nesting species (Table 3).

Similar to scaup, ring-necks predominantly nested in sedge cover. VOR readings were similar for ring-neck nests and nests of other over-water nesting species (P > 0.10).

Figure 2. Estimated Daily Survival Rates of Duck Nests (all species) Across A Range of VORs (an index of vegetation density).

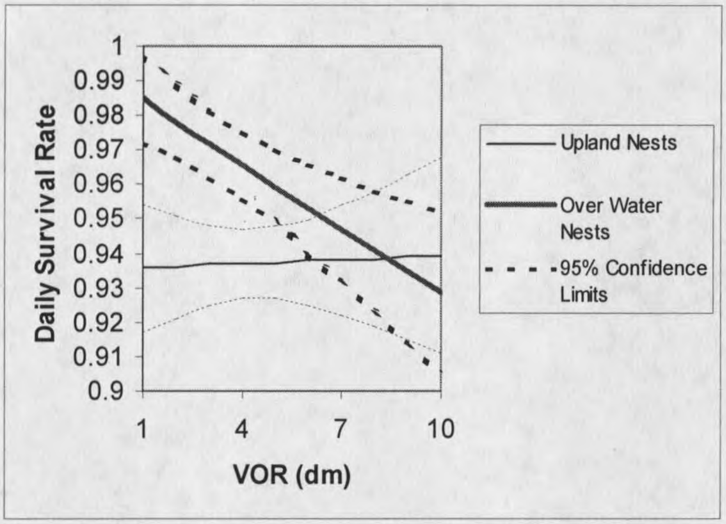


Figure 3. Estimated Daily Survival Rates of Duck Nests (all species) Across A Range of "Distance From Nest To Edge" Readings.

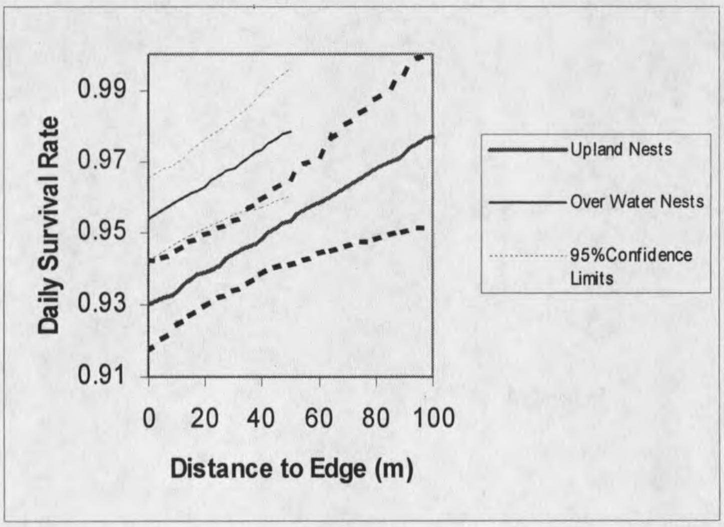


Table 3. An Evaluation of Generalized Linear Models for Nesting Success Among Species: Comparisons of Competing Models.

Rank	Model	AICc	Δ AICc	Akaike weight
1	Ring-necks different than all others [a]	909.80	0.00	0.649
2	Divers different than dabblers [b]	912.81	3.01	0.144
3	All species the same [c]	912.84	3.04	0.142
4	Scaup different than all others [d]	914.65	4.85	0.057
5	All species different [e]	918.73	8.93	0.007

a This model estimated daily survival rate separately for ring-necked duck and combined data for all other species.

b Model b estimated daily survival rate for diving ducks separately from dabbling ducks.

c Model c combined data for all species.

d Model d estimated daily survival rate separately for lesser scaup and combined data for all other species.

e Estimates of daily survival rate were allowed to vary by individual species.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

Table 4. An Evaluation of Generalized Linear Models for Duck Nesting Success That Explore Both Differences Among Species And Environmental Covariates.

Rank	Model	AICc	Δ AICc	Akaike weight
1	Habitat type, VOR, Interaction & Edge	892.08	0.00	0.397
2	Habitat type, VOR, Interaction, Edge + Ring [a]	893.35	1.27	0.211
3	Habitat type, VOR & Edge	894.76	2.67	0.104
4	Habitat type, VOR, Edge, + Ring	895.32	3.24	0.078
5	Habitat type, VOR, Edge & Year	895.76	3.68	0.063
6	Habitat type, VOR, Edge, Year + Ring	896.50	4.42	0.043
7	Habitat type, VOR & Interaction	896.88	4.80	0.036
8	Global [b]	896.88	4.80	0.036
9	Habitat type, VOR, Interaction + Ring	898.48	6.40	0.016
10	Global + Ring	898.59	6.51	0.015

a Ring – A covariate that allows daily survival rate to vary between ring-necked duck and combined data for all other species.

b In addition to the Ring covariate, the Global model contains the following covariates: Habitat type – estimates allowed to vary by nesting habitat (upland vs. over-water nesting habitats); VOR – estimates allowed to vary by Visibility Obstruction Reading, an index of vegetation density at the nest; Interaction - an interaction term between Habitat type and VOR; Edge – estimates allowed to vary by distance from nests to nearest man-made or vegetative edges; Year – estimates allowed to vary by year.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

Clutch Size

Estimates of mean clutch size were 9.9 (*n* = 26, SE = 0.33, 95% CI = 9.3 to 10.6) and 9.4 (*n* = 13, SE = 0.31, 95% CI = 8.8 to 10.0) in 1999 and 2000. The most parsimonious model of clutch size indicated a negative relationship between clutch size and nest initiation date (*n* = 27, estimated ß = – 0.07, SE = 0.02, R^2 = 25%; Table 5). A model that considered both nest initiation date and female condition also gained some support; however, the relationship with female condition was weak and imprecisely estimated (estimated ß = 0.006, SE = 0.006; Table 5).

Table 5. An Evaluation of Generalized Linear Models for Clutch Size: Comparisons of Environmental and Individual Covariate Effects.

Rank	Model	AICc	Δ AICc	Akaike Weight
1	Initiation date	83.88	0.00	0.52
2	Initiation date and Female condition	85.54	1.66	0.23
3	Global[a]	86.39	2.51	0.15
4	Null only	89.39	5.51	0.03
5	Year	89.87	5.99	0.03
6	Female condition	90.98	7.10	0.02
7	Female age	91.60	7.72	0.01
8	Mean-within-clutch egg size	91.70	7.82	0.01
9	Egg size and Female condition	93.52	9.64	0.004

[a] The Global model contains all hypothesized covariates: Nest initiation date – estimates allowed to vary by the nest-initiation date; Female condition – estimates allowed to vary by the physical condition of the nesting female; Year – estimates allowed to vary by year; Female age – estimates allowed to vary by the age of the nesting female; Mean-within-clutch egg size – estimates allowed to vary by the average egg size in the clutch.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

Nest-Initiation Date

Nest-initiation date was determined for 33 and 21 scaup nests in 1999 and 2000, respectively. Corresponding mean nest-initiation dates were 24 June (95% CI = 20 June to 28 June) and 25 June (95% CI = 21 June to 29 June).

Duckling Survival

Over two years, 8 different radiomarked females hatched 9 broods and 54 ducklings (4 broods and 22 ducklings in 1999; 5 broods and 32 ducklings in 2000). The most parsimonious model (s{7}) indicated a relationship between duckling age and duckling survival, and model s{7} further gained support when the over-dispersion parameter was increased (Table 6). Under the scenario of no over-dispersion, estimated 28-day duckling survival associated with model s{7} was 0.193 (SE = 0.055, 95% CI = 0.108 to 0.323); first week survival was 0.315 (SE = 0.063, 95% CI = 0.206 to 0.449) and survival for each other week was 0.850 (SE = 0.056, 95% CI = 0.704 to 0.931). Over-dispersion parameter levels, or cluster sizes, of 1,2, 4, and 6 resulted in standard errors for first week survival of 0.063, 0.089, 0.126, and 0.155, respectively. Respective standard errors for survival in other weeks were 0.056, 0.079, 0.113, and 0.138.

Estimated duckling survival rate did not differ by year (1999: duckling survival = 0.182, 95% CI = 0.068 to 0.384; 2000: duckling survival = 0.272, 95% CI = 0.104 to 0.548). Estimated brood survival averaged 0.482 in 1999 and 2000 (SE = 0.176, 95% CI = 0.189 to 0.788; 1999: brood survival = 0.366, SE = 0.261, 95% CI = 0.060 to 0.839; 2000: brood survival = 0.564, SE = 0.229, 95% CI = 0.173 to 0.889).

Table 6. An Evaluation of Generalized Linear Models for Duckling Survival: Examining the Effect of Cluster Size on Model Parsimony.

Rank	Model	c-hat [g]	QAICc	Δ QAICc	Akaike Weights
1	{s(7)}[a]	1	105.22	0.00	0.274
2	{s(7 and year)}[b]	1	105.31	0.09	0.262
3	{s(T)}[c]	1	105.57	0.35	0.231
4	{s(7 and hatch date)}[d]	1	106.32	1.10	0.158
5	{s(t)}[e]	1	107.83	2.60	0.075
6	{s(.)}[f]	1	131.67	26.45	0.000
1	{s(7)}	2	54.68	0.00	0.321
2	{s(T)}	2	54.85	0.17	0.294
3	{s(7 and year)}	2	55.79	1.11	0.184
4	{s(7 and hatch date)}	2	56.29	1.62	0.143
5	{s(t)}	2	58.14	3.46	0.057
6	{s(.)}	2	66.86	12.18	0.001
1	{s(7)}	4	29.40	0.00	0.332
2	{s(T)}	4	29.49	0.09	0.317
3	{s(7 and year)}	4	31.03	1.62	0.147
4	{s(7 and hatch date)}	4	31.28	1.88	0.130
5	{s(t)}	4	33.29	3.89	0.047
6	{s(.)}	4	34.45	5.04	0.027
1	{s(7)}	6	20.98	0.00	0.317
2	{s(T)}	6	21.04	0.06	0.308
3	{s(7 and year)}	6	22.77	1.79	0.129
4	{s(7 and hatch date)}	6	22.94	1.96	0.119
5	{s(.)}	6	23.65	2.67	0.084
6	{s(t)}	6	25.01	4.03	0.042

a S(7) - The model estimates survival for the first week of duckling life separately than weeks 2-4.

b Year - The covariate allows estimates to vary by year.

c S(T) - The model estimates survival as an increasing trend over the four week period.

d Hatch date - The covariate allows survival to vary by hatching date of the brood.

e S(t) - The model estimates survival for each week (1,2,3,and 4) separately.

f S(.) - The null model that simply estimates survival over the 28 day period with years combined.

g C-hat is the overdispersion parameter in Program Mark, which I used to simulate the cluster size.

* I used $QAIC_c$ and Akaike weights to select models from the candidate list (see text).

Female Survival

During the non-maternal period, no deaths of 25 radiomarked females occurred during 943 days of observation, thus the estimated daily survival rate was 1.00 (SE = 0.0). Therefore, I checked (1) whether daily survival rates differed between the nesting period and the brood-rearing period and (2) if confidence intervals included 1.00. The model that estimated a constant survival across the nesting period and the brood-rearing period (estimated daily survival rate = 0.986, 95% CI = 0.975 to 0.997) was supported by the data ($\Delta AIC_c = 0.00$) along with the model where survival was estimated separately between the nesting period and the brood-rearing period ($\Delta AIC_c = 1.34$). During the nesting period, 5 of 29 radiomarked females died during 285 days of observation (estimated daily survival rate = 0.983, 95% CI = 0.969 to 0.998). Evidence at the nest (whole female or parts of female scaup) suggested that all 5 females were killed at the nest. By raising the nesting daily survival rate to the 26th power, the average number of days devoted to nesting by a female in each year, I estimated that 64.6% survived the nesting period (95% CI = 44.1 to 94.7%). During the brood-rearing period, 1 of 9 radiomarked females died during 126 days of observation (estimated daily survival rate = 0.993, 95% CI = 0.979 to 1.000). By raising the brood-rearing daily survival rate to the 19th power, the average number of days a brood-rearing female spent with her brood, the estimated survival of brood-rearing females was 0.875 (95% CI = 0.668 to 1.000). I used period-specific estimates of survival to estimate breeding-season survival rather than the estimates from the model that pooled the nesting and brood-rearing periods for two reasons. First, the period-specific model received support, and second, because there were biologically meaningful differences in the survival point estimates among the periods. The weighted product of the 3 period-specific survival rates yields an estimated breeding-season survival for the average female (mean = 0.694, 95% CI = 0.515 to 0.955). If estimates from the model that pooled the nesting and brood-rearing periods were used, the breeding-season survival estimate would be 0.726 (95% CI = 0.575 to 0.932).

The most parsimonious model of daily survival rate for nesting females indicated a negative relationship between daily survival rate and vegetation density, but estimates were imprecise (Table 7). Daily survival rate of females nesting in cover with a VOR ≤ 7 was higher (0.995, 95% CI = 0.986 to 1.00) than estimated daily survival rate of females nesting in cover with a VOR > 7 (0.951, 95% CI = 0.905 to 0.998; Table 7).

Table 7. An Evaluation of Generalized Linear Models for Female Daily Survival Rate During the Nesting Period: Comparisons of Environmental and Individual Covariate Effects.

Rank	Model	AICc	Δ AICc	Akaike weight
1	VOR	48.77	0.00	0.653
2	Habitat type	52.56	3.79	0.098
3	Null	52.87	4.10	0.084
4	Year	53.86	5.08	0.051
5	Period of year	54.67	5.90	0.034
6	Female condition	54.68	5.91	0.034
7	Incubation stage	54.89	6.11	0.031
8	Incubation & condition	56.71	7.93	0.012
9	Global [a]	59.81	11.04	0.003

a The Global model contains all hypothesized covariates: VOR – Visibility Obstruction Reading, an index to vegetation density at the nest, which estimates for nests with VORs > 7 and for nests with VORs ≤ 7; Habitat type – estimates for upland vs. over water nesting habitats; Year – estimates allowed to vary by year; Period of year – estimates for early and late parts of the year; Female condition – estimates for physical condition of the nesting female; Incubation stage – estimates for the incubation stage of the clutch of eggs.

* I used AIC_c and Akaike weights to select models from the candidate list (see text).

Population Modeling

Using my estimates of breeding-season survival, nesting success, duckling survival, and clutch size and published estimates of non-breeding-season survival, juvenile survival (Rotella et al. In Review), breeding probabilities, and renesting probabilities (Afton 1984), I developed the following mean matrix (**A**) for the Erickson population (Table 8).

$$\mathbf{A} = \begin{pmatrix} 0.043 & 0.062 \\ 0.570 & 0.570 \end{pmatrix}$$

The population's asymptotic λ was 0.633, characteristic of a rapidly declining population. Asymptotic λ's sensitivities and elasticities to the mean-matrix fertility and survival elements were:

$$\mathbf{S} = \begin{pmatrix} 0.093 & 0.880 \\ 0.096 & 0.907 \end{pmatrix} \qquad \mathbf{E} = \begin{pmatrix} 0.006 & 0.087 \\ 0.087 & 0.820 \end{pmatrix}$$

When the lower-level vital rates were considered, λ was most sensitive to breeding-season survival of ASY females, followed by non-breeding-season survival of ASY females, nesting success, and duckling survival and most elastic to breeding-season survival of ASY females and non-breeding-season survival of ASY females (Table 8). Elasticity values for many of the lower level vital rates were identical because of the multiplicative structure of the fertility and survival transition equations that I used. Therefore, proportional changes in λ were identical for those vital rates (Table 8). In contrast, vital-rate values entered the sensitivity analysis in an additive manner, and vital-rate impacts on λ were separated out in the analysis space.

Table 8. The Sensitivity and Elasticity Values for the Lower Level Vital Rates From Both The Current Era Model (1999-2000; $\lambda = 0.63$) and The Pre-1981 Era Model (1970, 1971, 1977-1980; $\lambda = 1.02$). (see Discussion for description of Pre-1981 Era Model)

Vital Rate	Mean Value		Sensitivity		Elasticity	
	Current	Pre-1981[c]	Current	Pre-1981	Current	Pre-1981
BP_{ASY}[b]	0.97	0.97	0.056	0.276	0.087	0.262
BP_{SY}[b]	0.71	0.71	0.006	0.205	0.006	0.143
BS_{ASY}	0.69	0.75	0.749 (1)[d]	0.452 (4)	0.820 (1)[d]	0.333 (3)
BS_{SY}	0.69	0.75	0.079	0.357	0.087	0.262
CL	4.88	4.90	0.012	0.084	0.093	0.405 (1)[d]
DS	0.19	0.62	0.304 (4)	0.669 (3)	0.093	0.405 (1)
JS[a]	0.55	0.55	0.107 (5)	0.751 (2)	0.093	0.405 (1)
NBS_{ASY}[a]	0.83	0.76	0.626 (2)	0.446 (5)	0.820 (1)	0.333 (3)
NBS_{SY}[a]	0.83	0.76	0.066	0.352	0.087	0.262
NS	0.11	0.29	0.526 (3)	1.376 (1)[d]	0.092	0.391 (2)
RN_{ASY}[b]	0.14	0.16	0.043	0.171	0.010	0.027
RN_{SY}[b]	0.06	0.07	0.003	0.098	0.0003	0.007

Vital Rate Definitions: BP_{SY} and BP_{ASY} are the breeding probabilities for each age class, respectively, that attempt nesting at least once per year; NS is nesting success; RN_{SY} and RN_{ASY} are the probabilities of producing a second clutch given total failure of the first clutch for each age class, respectively. I estimated RN for surviving females only. For the current era, I had to adjust the rate downward to make it representative of all females. To do this, I multiplied the published renesting rate by female survival during the nesting period. CS is the clutch size of eggs that contain female embryos assuming a 50:50 primary sex ratio within a clutch; DS is duckling survival; JS is juvenile survival or the proportion of fledged birds that survive to the start of the next breeding season; BS is breeding-season survival of females; and NBS is non-breeding-season survival of females.

- a Vital rate estimates that were attained from Rotella et al. (In Review).
- b Vital rate estimates that were attained from Afton (1984).
- c All vital rate estimates in the "pre-1981 era" model were attained from Hammell (1973), Afton (1984), and from Rotella et al. (In Review). Only Afton's (1984) nesting success data was used to estimate historic nesting success because his methods were similar to mine.
- d The top rankings of the sensitivities and elasticities for both the current era model and the pre-1981 era model (beginning with 1).

DISCUSSION

Scope and Limitations

My study provides a comparison of past (pre-1981) and present (1999-2000) vital rates for a population of scaup that has declined. My data suggest that poor reproductive success may explain the decline of scaup numbers at Erickson. My estimates of nesting success (0.112), duckling survival (0.193), and possibly female breeding-season survival (0.694) were lower than estimates from the pre-1981 era (0.29, 0.617 [Afton 1984], and 0.75 [St. Denis, SK, Rotella et al. In Review], respectively; see Tables 8 and 9). My analyses indicate several important factors that were related to various vital rates, which might help explain the reasons for observed declines in the vital rates. I further estimated local population growth and explored its relationship with vital rates. Thus, my research is unique because it identifies vital rates related to lesser scaup population growth in Erickson and also identifies factors related to these vital rates.

However, when comparing vital rates between two time periods, potential biases may arise due to differences in field methodology and data analysis techniques. To mitigate potential bias, I restricted comparisons of my study results to studies that used similar field methods to mine (I compared my data to Afton (1984) for nesting success and duckling survival, Afton (1984) and Hammell (1973) for clutch size, and Rotella et al. (In Review) for female breeding-season survival). Because the most parsimonious models are the best

Table 9. Historical Estimates of Year-Specific Vital Rates for the Erickson Study Area

							Vital Rates								
Author	Year	Breeding Probability	n[c]	Nest-Initiation Date	n	Clutch Size	n	Nesting Success[a]	n	Re-Nesting Rate	n	Duckling Survival	n	Annual Survival	ess[d]
Rogers 1964	1958							0.04	26						
Hammell 1973	1970					9.0	35	0.35	23						
	1971					9.0		0.18	33						
Afton 1984	1977	0.720	25	168.2	6	10.4	5	0.177	17	0.000	14	0.518	3		
	1978	0.828	29	164.7	17	10.4	17	0.292	24	0.063	16	0.446	7		
	1979	0.977	43	169.4	31	10.2	31	0.404	47	0.389	18	0.737	19		
	1980	0.847	59	163.4	24	10.3	24	0.268	41	0.160	25	0.766	10		
Rotella et al. In Review[b]	1977-1981													0.57	197

[a] Nesting success estimates are reported for non-island nests and for years with a sample size of ≥ 15 nests. Additionally, all nesting success estimates are apparent nesting success estimates; however, Afton followed nests of marked individuals from near the time of nest initiation to nest termination.

[b] Rotella et al. (In Review) used the data set from Dr. Afton's Ph.D. dissertation (1977-1981).

[c] n = The sample size for a given study. In some cases only an overall sample-size was reported, in which case I list the overall sample size next to the first year of study.

[d] ess = effective sample size (White and Burnham 1999)

estimating models (Burnham and Anderson 1998), I used the most parsimonious models to estimate the vital rates for 1999 and 2000, whereas historical studies reported simple mean estimates and did not consider multiple covariates. Thus, disparities may exist among estimates from different studies simply due to different modeling approaches.

Further, because my study only encompassed two years, inference space of my results is limited. Inference space associated with hypothesized models was further limited by data collected in the field. The small sampling universe and associated small sample sizes often resulted in poor precision of vital rate estimates; thus, it was difficult to detect subtle effects of covariates on the vital rates. Complex relationships could not be examined and key factors related to vital rates may have been overlooked if they were not considered in the model list. Additionally, the attachment of nasal markers and radio transmitters may have led to biased estimates. However, I do not believe that this was an important problem as I rarely observed behavioral effects.

My population model was limited by lack of recent estimates of some vital rates, low precision of estimated vital rates, and two major assumptions. First, I assumed independence among vital rates, and second, I assumed density independence in the model for simplicity. I do recognize that covariation and density-dependence can strongly affect vital rates and population growth (Grant and Benton 2000, Van Tienderen 2000); however, more data are needed to establish these relations for scaup vital rates.

Nesting Success

Comparisons to the Past

My estimate of nesting success (0.11) was approximately one third of the mean nesting success estimate from the pre-1981 era (0.29, Afton 1984). Although my estimate of nesting success for scaup was imprecise, it suggests a major decline in nesting success, which could have large impacts on the population (Table 8).

Evidence from broad-scale studies of a variety of duck species suggest that nesting success of prairie-nesting ducks declined between 1935 and 1990 (Beauchamp et al. 1996), while the amount of cultivated land increased (Sargeant et al. 1993). Greenwood et al. (1995) found that nesting success of dabbling ducks generally decreased as the amount of cropland in a landscape increased. One possible explanation for these findings relates to the predator communities associated with fragmented agricultural landscapes. Increases in the amount of cultivated land cover across the prairie-pothole region has led to increased diversity and abundance of nest predators (Sargeant et al. 1993). Thus, I speculate that changes in land cover around Erickson may be one explanation for the low nesting success of scaup during 1999 and 2000. However, the lack of historic land-cover data and limited nesting success data make testing this speculation difficult. Furthermore, because I studied scaup on one study site, I was not able to test this hypothesis across a spatial gradient during the current era.

Factors Related to Nesting Success

Scaup nesting success was positively related to period of year, higher for over-water nests, and negatively related to vegetation density; however, nesting success was imprecisely estimated by these covariate models. Nesting success of all species on the study area was also higher for over-water nests, negatively related to vegetation density for over-water nests only, and positively related to distance from an edge. Thus, the two analyses tend to support the same underlying mechanisms of nesting success on the study area. However, the more powerful analysis using nests from all species indicated an interaction between habitat type and vegetation density, demonstrating that the negative relationship between nesting success and vegetation density occurred in over-water habitats, but not upland habitats.

In contrast to the positive relationship between scaup nesting success and period of year, many studies of dabbling ducks have detected negative relationships between nesting success and period of year (Greenwood et al.1995, Flint and Grand 1996). Results for scaup may differ because scaup nest later than many dabbling ducks, and thus, they may experience different ecological conditions. Specifically, I speculate that predator foraging tactics change late in the year, or that foraging efficiency of predators declines late in the year. The period-of-year relationship could also be caused by the presence of heterogeneity in nesting success among females (Natarajan and McCulloch 1999), i.e., nests with higher survival probability survive longer than others and make up a larger proportion of the nesting population later in the season.

My finding that nesting success was better over water than in uplands is consistent with results of a study done on mallards near Erickson (Arnold et al. 1993). This pattern may explain why I found a greater percentage of scaup nests over water, which contrasted previous reports of scaup nest locations in the prairie-parkland region (Gehrman 1951, Keith 1961, Hines 1977, Afton pers. comm., but see Hammell 1973 for over-water nesting). I hypothesize that natural selection has driven scaup in the Erickson region to preferentially nest over water, where nesting performance is better (Martin and Clobert 1996).

An alternative explanation for the pattern of nest placement that I observed is that flooded cover was very abundant during the course of my study and for several years before my study. Thus, the selection of over-water nest sites by scaup may have been a phenotypic plastic response to the unusually wet conditions.

Furthermore, nesting success may be heterogeneous among over-water nest sites. I found a negative relationship between nesting success and vegetation density in over-water habitats, which is contrary to findings for other bird species (Schranck 1972, Klett et al. 1988, Martin 1995, Clawson and Rotella 1998). At first, my results seem counter-intuitive, because the majority of scaup have always used (Miller and Collins 1954, Keith 1961, Townsend 1966, Hammell 1973, Hines 1977), and do use, dense vegetation for nesting. Thus, scaup may prefer to nest in dense vegetation as opposed to more sparse vegetation. If nesting success is lower in dense vegetation, then why do scaup continue to nest in dense nesting cover? One likely explanation is that selective forces, such as predation, have recently increased near wetland boundaries and scaup have not had enough time to adjust to the changing predator community (Martin and Clobert 1996, Wisdom and Mills 2000).

Over-water nests located in dense vegetation near the wetland boundary may experience higher predation rates because raccoon, skunk and mink often forage for food around wetlands (Urban 1970, Fritzell 1978, Lariviere and Messier 1998). In addition, I speculate that as native habitats are lost to agriculture or other developments, predators allocate more foraging time in dense nesting cover near wetlands.

An alternative explanation for nesting in dense vegetation is that these nest sites may incur positive trade-offs, such as increased female survival. Thus, the disadvantage of lower nesting success may be outweighed by higher survival probability in dense nesting cover (Van Tienderen 1995).

Ring-neck Nesting Performance

Nesting success estimates among most species, including scaup, were statistically similar. However, ring-necks had higher nesting success than any other species, which is notable as the breeding range of the ring-neck has expanded and populations have increased at both the continental (Hohman and Eberhardt 1998) and local scale (Hammell pers. commun., Afton pers. commun., Koons unpublished data) over the past several decades. The fact that ring-neck's nesting performance was superior to all other species implies that ring-necks must have superior nest placement or behavior or both.

All ring-necks nested over water, which may partly explain their high nesting success. However, they still performed better than scaup and other over-water nesters that nested in similar vegetation and vegetation density. Differences may be related to microhabitat nest-placement patterns, such as nesting near beaver (C*aster canadensis*) runs (27% of ring-necks nested next to a beaver run) and differences in nest attentiveness behavior (Martin and Ghalambor 1999). I speculate that by nesting near a beaver run, ring-necks are able to reduce predator detection of their nests when leaving and returning to their nests during incubation breaks. Thus, this adaptive behavior may increase a ring-neck's probability of hatching a nest. Alternatively, ring-necks may enter nesting in better physical condition than other over-water nesting ducks, which may lead to higher nest attendance rates, and thus, a higher probability of hatching a nest.

Duckling Survival

My estimate of duckling survival (0.193) was less than one third of the pre-1981 estimate (0.617, Afton 1984), and such a change could have obvious impacts on the population. Additionally, my estimate of duckling survival rate is among the lowest reported for northern latitude nesting ducks (see Rotella and Ratti 1992, Grand and Flint 1996). Low duckling survival may have been linked to the prolonged wet conditions on the study area prior to and during my study. Prolonged wetness may have led to increased abundance of mink (*Mustela vison*), which are known to forage for ducklings (Arnold and Fritzell 1987).

An alternative explanation is that scaup in 1999 and 2000 were nesting a full week later than they did in the pre-1981 era (Afton 1984; Table 9) and delayed nesting may affect duckling survival in a number of ways. Given my small sample of broods, I was unable to detect a relationship between duckling survival and hatch date. However, further study of this relationship seems warranted given patterns detected in scaup (Dawson and Clark 1996) and other duck species (Rotella and Ratti 1992, Grand and Flint 1996, Dzus and Clark 1998, Guyn and Clark 1999). Further, the majority (86%) of duckling mortality occurred during the first week post-hatch, which has also been found by many other studies (e.g., Dawson and Clark 1996, Grand and Flint 1996, Guyn and Clark 1999).

Female Survival

Using mark-resight estimates of annual survival and non-breeding-season survival, Rotella et al. (In Review) estimated that a large amount of female scaup mortality occurs on the breeding grounds. Until my study, however, a direct estimate of breeding-season survival of female scaup did not exist. My estimate of local breeding-season survival (69%) is the lowest reported direct measure for all northern latitude breeding ducks (Ringleman and Longcore 1983, Cowardin et al. 1985, Kirby and Cowardin 1986, Petrie et al. 2000) and is likely lower than past survival of scaup. For comparison, breeding-season survival of female scaup at St. Denis, Saskatchewan during 1992 to 1998 was 75% (Rotella et al., In Review). Breeding season mortality of females can limit recruitment via two pathways: first, a female that dies during the breeding season does not produce young in that year; and second, lowered breeding-season survival reduces the number of females that survive to breed in following years. Thus, high female mortality during the breeding season can have substantial effects on λ (Table 8).

Of female mortality that occurred during the breeding season, 83% occurred while females were nesting. I found that nesting female survival was negatively related to vegetation density. Thus, I did not detect an advantage for the clutch or the female for females that nested in dense nesting cover. In my study, nesting in dense cover may have been more dangerous because the dense vegetation occurred near the wetland boundaries where high levels of predator activity are expected (Urban 1970, Fritzell 1978, Lariviere and Messier 1998). It would be useful to know if the pattern persists throughout wet and dry cycles. If so, natural selection may currently be working against nesting in dense vegetation (Clark and Shutler 1999).

Population Modeling

The May Breeding Pairs Survey data (USFWS; see Fig. 1) indicated a recent decline in the local population from 1981 to 2000 (population dropped 31%). My estimate of the population's growth rate ($\lambda = 0.6302$, stochastic estimate of $\lambda = 0.628$, 95% CI = 0.50 to 0.75, $n = 5000$ simulations) further supported the local decline; however, my data estimated a much more rapid decline. In contrast, when I used vital rates solely from the pre-1981 era in my population model (Table 9, I only used Afton's (1984) estimates of nesting success, which used methods similar to mine) the estimated λ was 1.02, indicative of an increasing population. Thus, the pre-1981 model indicated a slightly increasing population, whereas the population model that used current data indicated a declining population. Only nesting success, duckling survival, and female breeding-season survival were substantially different between the two time-period models.

Simultaneous changes in the mean values of the vital rates resulted in a re-ordering in rank of sensitivities and elasticities (Table 8). Results from the sensitivity and elasticity analysis indicated that both breeding-season and non-breeding-season survival of ASY females have, and likely have had, the most potential to impact λ. Sensitivity was intermediate for nesting success, duckling survival, and juvenile survival, whereas elasticity was low for all other vital rates. Sensitivity results from the pre-1981 model indicated that nesting success has the most potential to impact λ, followed by juvenile survival, duckling survival, and then breeding-season and non-breeding-season survival of ASY females. Elasticity results from the pre-1981 model indicated that juvenile survival, duckling survival, and clutch size have the most potential to impact λ, followed by nesting success, and then breeding-season and non-breeding-season survival of ASY females. However, clutch size generated a high elasticity merely because of its large magnitude relative to the other rates. On the other hand, clutch size generated one of the lowest sensitivities because a constant additive change to a set of rates will change the largest rate by the smallest proportion.

While sensitivities and elasticities are robust to large changes in a single vital rate (deKroon et al. 2000), more work is needed to examine the effects of simultaneous changes in vital rates on sensitivity and elasticity. Because fertility was so low in the "current" population model, I hypothesize that as fertility declines towards zero the importance of survival pathways in a model becomes increasingly important, regardless of life history.

Despite differences in rank of importance, models from both time periods indicated the same five vital rates as important contributors to population growth rate. Breeding-season survival (current era) and nesting success (pre-1981 era) appear to be most influential in changing λ. Further, breeding-season survival and nesting success are likely correlated because much of the female mortality occurs while nesting, and because both vital rates were negatively affected by vegetation density at the nest site (Darwin 1859, Caswell 2000b).

In summary, observed changes in nesting success, duckling survival and likely female breeding-season survival were the only vital rates that I was able to identify as possible causal agents behind the local population decline. Furthermore, sensitivity and elasticity results indicated that changes in nesting success, female breeding-season survival, and duckling survival could have substantial effects on λ. However, more work is needed to acquire current estimates of breeding propensity, re-nesting capability, juvenile survival, and non-breeding-season survival of scaup before definite conclusions about the causes of the population decline can be made.

RESEARCH AND MANAGEMENT IMPLICATIONS

My population model would indicate that the Erickson scaup population is declining because of declines in nesting success, duckling survival, and breeding-season survival. These vital rates may have been at low levels during my study due to habitat fragmentation or prolonged wet conditions on the study area, both of which may cause an increase in predator abundance. Given that nesting success and breeding-season survival were low, and that most female mortality occurred at the nest, it is likely that management aimed toward increasing the security of nests will benefit both nesting success and survival of females. However, reduction of nesting habitat around Erickson may have constrained nesting scaup into an ecological trap (Gates and Gysel 1978), i.e., scaup prefer to nest in areas where predators actively forage. Because of reductions in native habitat, predators have likely been forced to forage around wetlands; the only areas that still contain adequate numbers of prey.

I believe that active control of meso-predators will not benefit nesting scaup or other avian species in Erickson because the predator community is diverse (> 20 potential predators), and thus, the potential for remaining predators to compensate for the open niche space would be strong. Rather, management should focus on making the landscape less suitable for the predator community as a whole. Much of the remaining attractive, or dense, nesting cover is located around wetlands where scaup prefer to nest. Further, predators are likely focusing their foraging efforts in the remaining nesting-cover around wetlands, which creates an ecological trap for nesting scaup. Thus, increasing the amount of nesting habitat in the landscape past a theoretical threshold may alter predator foraging tactics or even decrease the abundance of predators (Dijak and Thompson 2000), thus, mitigating predation pressures on scaup and other nesting birds (Tewksbury et al. 1998).

So that management can prevent continued declines of scaup at a continental scale, demographic parameters of scaup population growth need to be identified across a broader spatial and temporal scale. Thus, future studies should be designed with the aforementioned inference space in mind. Additionally, covariation and density dependence of vital rates requires study because ignorance of their presence can lead to incorrect conclusions regarding the relative importance of individual vital rates to population growth (Van Tienderen 2000). Furthermore, research is needed to examine effects of landscape fragmentation and precipitation cycles on predator population dynamics. Lastly, I suggest that future research address physiological and cross-seasonal factors related to lesser scaup breeding chronology (Afton and Anderson, In Review).

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