



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

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in  
Microbiology  
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**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.

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APPROVAL

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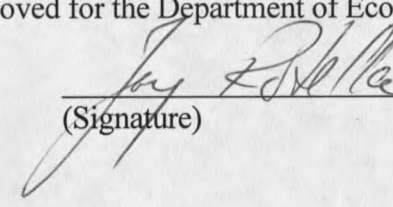
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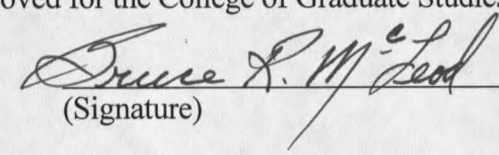
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## ABSTRACT

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).

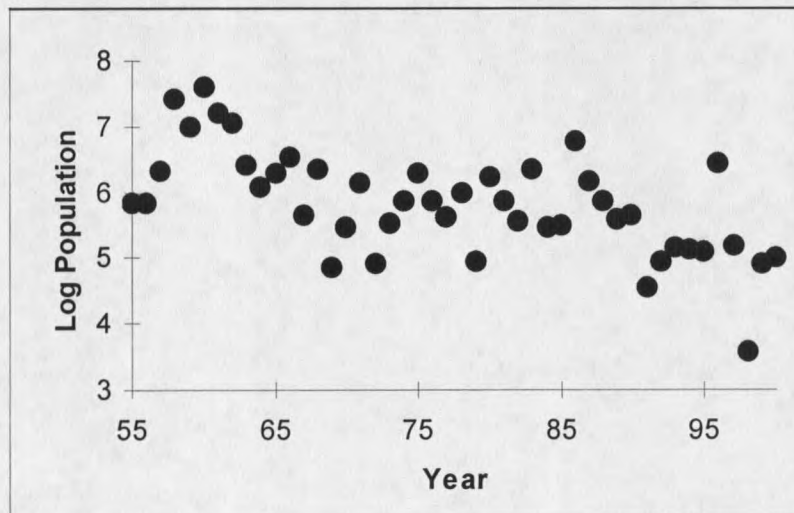
Accordingly, I designed and conducted a study of breeding scaup in Erickson, Manitoba with the following objectives: (1) estimate vital rates and compare them with past estimates; (2) evaluate the relationships between vital rates and various attributes of individual birds and environmental covariates; (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 (50° 30' N, 99° 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<sup>2</sup>), 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<sup>2</sup> 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<sup>2</sup> 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 re-nested 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  $\geq 24$  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 36<sup>th</sup> 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 (McCulloch 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<sub>c</sub>), 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<sub>c</sub> or QAIC<sub>c</sub> values to calculate,  $\Delta$ AIC<sub>c</sub>, or  $\Delta$ QAIC<sub>c</sub>, which are a measure of the difference between the AIC<sub>c</sub>, or QAIC<sub>c</sub>, value for a given model and that of the most parsimonious model. Thus, the most parsimonious model has an  $\Delta$ AIC<sub>c</sub> or  $\Delta$ QAIC<sub>c</sub> value of 0.0. I restricted my selection of models to those with  $\Delta$ AIC<sub>c</sub> 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 ( $\beta$ s) and the proper link function. For models containing multiple slope estimates ( $\beta$ s), 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<sup>36</sup>).

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<sub>c</sub> 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 ( $\lambda$ ) 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 re-nesting 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<sup>2</sup>) and 30 (1.45 pairs / km<sup>2</sup>) 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 (*Carex* 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  $\beta = 0.023$ , 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	$\Delta$ 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 <sup>a</sup>	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<sub>c</sub> 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<sub>c</sub> < 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









































































