

# NEST SURVIVAL OF SCAUP AND OTHER DUCKS IN THE BOREAL FOREST OF ALASKA

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**Abstract:** We estimated variation in nest survival of lesser scaup (*Aythya affinis*), greater scaup (*A. marila*), and other common duck species at Minto Flats, Alaska, USA, during 1989–1993 and 2002–2003. Daily survival probability of scaup nests, as well as nests of all other duck species, varied with year, date, and nest habitat. Daily survival probability was unrelated to nest age and distance from the nest to water. Average, year-specific nest survival of all ducks at Minto Flats was 0.11 (95% CI: 0.05 to 0.22), comparable to nest survival of ducks breeding in mid-continent regions (i.e., the prairie pothole region and the Canadian prairie-parklands). Nest survival of scaup was variable among years, ranging from 0.01 (95% CI: 0.00 to 0.06) in 1992 to 0.61 (95% CI: 0.50 to 0.74) in 1993 and was probably related to variation in predation risk and water levels. Scaup production could have been limited by low nest survival during most years of this study; nest survival exceeded 20% only in 1993 and 2002. Because of the high densities of breeding scaup and other waterfowl species at Minto Flats, we recommend management to maintain existing habitat for breeding scaup and other duck species. This management could be most effectively informed by yearly monitoring of production to more accurately understand spatial and temporal variation in recruitment and to identify potential effects of proposed oil and gas exploration on recruitment of ducks at Minto Flats.

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**Key words:** Alaska, *Aythya affinis*, *Aythya marila*, boreal forest, ducks, nest success, nest survival, population dynamics, scaup.

Management of North American waterfowl is largely based on surveys of breeding pairs conducted during the spring (Bellrose 1980, Nichols et al. 1995). An assumption of this approach to management is that breeding pairs have the same potential for production regardless of where these birds breed; however, knowledge of reproduction and variation in reproduction is limited for many species in some of their major breeding areas. This information gap is quite apparent for lesser scaup and other species of waterfowl breeding in the boreal forest of Alaska and Canada, which is a major breeding area for waterfowl that is also threatened by development activities (e.g., Hobson et al. 2002).

The total abundance of the North American populations of lesser and greater scaup declined at the annual rate of 150,491 (SE = 25,100) individuals/year during 1978–1997 (Afton and Anderson 2001). As of 2003, scaup abundance remained well below the long-term average (1955–2003) of 5.3 million and the North American Waterfowl Management Plan goal of 6.3 million (Wilkins and Otto 2003). There is evidence that the decline in abundance has not been consistent between species; scaup abundance has declined most in the western boreal forest of Canada and has increased or remained stable in tundra regions of Alaska and Canada (Afton and Anderson 2001). Because most scaup that breed in tundra regions are greater scaup (Kessel et al. 2002), some researchers have speculated that the decline in scaup abundance is primarily related to declines in the number of lesser scaup breeding in the western boreal forest of Canada (Afton and Anderson 2001, Koons and Rotella 2003). Declines in the ratio of juvenile to adult lesser scaup in the fall harvest from 1961 to 1996 indicate that scaup abundance in North America is related to declines in recruitment of

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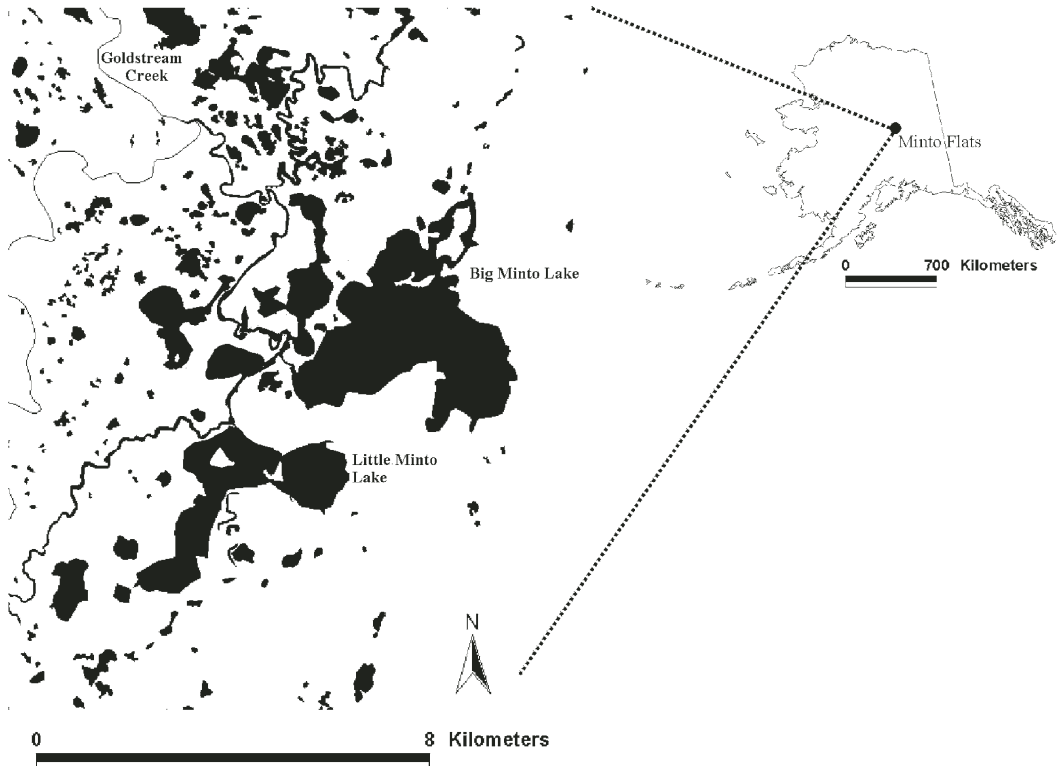


Fig. 1. Minto Lakes study site at Minto Flats, Alaska, USA. Black areas represent open water, and white areas represent land, at average water levels.

juvenile lesser scaup to the fall population (Austin et al. 2000, Afton and Anderson 2001).

Nest survival, the probability that a nesting attempt results in  $\geq 1$  egg hatching, has been identified as one of the most influential components of recruitment, and ultimately the rate of population change ( $\lambda$ ) for many duck species. Nest survival and hen success (i.e., the product of nest survival probability and renesting probability) are the most influential parameters in models of the reproductive success of mallards (Johnson et al. 1992, Hoekman et al. 2002). Hen success strongly influences the local dynamics of canvasback (*Aythya valisineria*) populations (Anderson et al. 1997), and nest survival has considerable effect on local population dynamics of lesser scaup in the boreal forest of Northwest Territories (Brook 2002) and the parklands of Manitoba (Koons and Rotella 2003). Therefore, knowledge of patterns of variation in nest survival is highly useful to managers of duck populations.

We studied nest survival of scaup and other species of breeding ducks during 1989–1993 and again during 2002–2003 at Minto Flats State Game

Refuge in the boreal forest of interior Alaska. Our primary objective was to estimate nest survival and characterize factors affecting nest survival for ducks breeding in the boreal forest of Alaska. This information could be used to inform local and continental management actions that are currently based on limited information for waterfowl breeding in the boreal forest.

## STUDY AREA

Minto Flats State Game Refuge (64°50'N, 148°50'W) is located in the boreal forest of interior Alaska, approximately 55 km northwest of Fairbanks and 220 km south of the Arctic Circle (Fig. 1). The refuge includes 145,000 ha of forests and rivers interspersed with semi-permanent wetlands and eutrophic lakes (Petrula 1994).

Climate at Minto Flats is best described as continental sub-arctic with high annual variation in average daily temperature (range: -26°C to 16°C) and low average annual precipitation (range: 29 cm to 43 cm; Petrula 1994). The Minto Flats watershed is drained by the Chatanika, Tatalina, and Tolovana rivers and by Goldstream Creek (Petrula 1994),

has little topographic relief (<15 m; Petrula 1994), and is subject to large fluctuations of water depth within and among seasons (Petrula 1994).

Habitat for nesting ducks at Minto Flats was composed of low-lying meadows, forested uplands, grass-shrub thickets, mats of floating vegetation, and islands. The most common plant species in meadows was bluejoint grass (*Clamagrostis canadensis*), manna grass (*Glyceria* spp.), and, in wetter areas, sedges (*Carex* spp.). Forested uplands were dominated by birch (*Betula papyrifera*) with an understory of wild rose (*Rosa* spp.) or spruce (*Picea* spp.) with an understory of dwarf birch (*Betula nana*) and Labrador tea (*Ledum decumbens*). Floating mats were generally composed of buckbean (*Menyanthes trifoliata*) and water parsnip (*Sium suave*). Grass-shrub thickets were dominated by willow (*Salix* spp.) and alder (*Alnus* spp.) with bluejoint grass in the understory. Islands were generally characterized by similar vegetation as floating mats and meadows. Larsen (1997), and Petrula (1994) provided a comprehensive description of vegetation communities and nesting habitat at Minto Flats.

During the nesting season, Minto Flats hosted a diverse group of waterfowl species in addition to greater and lesser scaup. Trumpeter swans (*Cygnus buccinator*), white-fronted geese (*Anser albifrons*), and several common North American duck species (e.g., mallards and American wigeon [*Anas americana*]) nested at Minto Flats (Petrula 1994). Previous research indicated that both species of scaup comprised approximately 40% of the breeding duck community at Minto Flats (Petrula 1994). Spring surveys further revealed that the density of breeding scaup at Minto Flats has been among the highest in North America (Hodges et al. 1996). Species of duck nest predators at Minto Flats included red fox (*Vulpes vulpes*), mink (*Mustela vison*), common ravens (*Corvus corax*), mew gulls (*Larus canus*), and herring gulls (*L. argentatus*; Petrula 1994).

Our study site was a 30-km<sup>2</sup> area immediately surrounding Big and Little Minto Lakes (Fig. 1). This area has been associated with the highest spring densities of ducks at Minto Flats (Petrula 1994) and was the primary site of previous research on duck production.

## METHODS

### Data Collection

We searched for nests daily from the third week of May until the second week of July during 2002–2003. We systematically rotated through vari-

ous locations on the study site defined by the shoreline of adjacent lakes, ponds, and channels (Fig. 1; Petrula 1994). Locations were searched 3 or more times per season (every 7–15 days). Our objectives were to search as much of the study site as possible and obtain a representative sample of nests across search occasions and habitat types. We systematically searched meadows, islands, and mats of floating vegetation by dragging a 30-m rope through the cover to flush females from nests. When dense shrubs or trees prevented us from using the rope, we walked through the entire area, using sticks and loud conversation to create as much disturbance as possible (Petrula 1994). Trained dogs also assisted with nest searching and found many nests when the female was not present.

We assigned each nest a unique number, recorded its location using a handheld Global Positioning System receiver, marked it with 15–30 cm of flagging tape placed 5 m north of the nest, and recorded several variables describing the nest: species of duck, date, number of eggs, stage of incubation, habitat type, and distance from the nest to the nearest open water.

We determined species by identifying the female as she flushed or, if the female was not present, by egg and down characteristics (Klett et al. 1986). We distinguished the 2 species of scaup by using egg measurements (Bellrose 1980). We estimated the stage of incubation by candling several eggs from each nest (Weller 1956). We recorded the habitat type as meadow, floating vegetation, upland (forested or shrub), or island, and we estimated the distance from the nest to the nearest open water (Petrula 1994).

We returned to each marked nest at arbitrary intervals from 1 to 14 days until the nest was destroyed, abandoned, or successful ( $\geq 1$  egg hatched; Klett et al. 1986). During visits when the nest was active, we recorded the current number of eggs and their incubation stage. If the nest had been destroyed (i.e., several or all eggs missing, broken, or underwater and no female was in attendance), we attempted to determine and record whether a predator or flooding was responsible. We assumed that the nest had been abandoned when the clutch was intact but the eggs were cold and the female was not present. We did not record the nest fate as abandoned until the eggs remained cold and unattended for at least 2 visits. In such cases, we dated the failure to the first date when the eggs were found cold and unattended. If the nest had been abandoned between its discovery and the first revisit, we assumed that it was abandoned at discov-

ery due to investigator disturbance; these nests were not included in the analysis. If at least 1 whole shell, egg membrane, or duckling was present in the nest bowl, we recorded the nest as successful.

## Data Analysis

We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the relative support for potential relationships between nest survival and the variables that we measured. We began by creating a set of candidate models that described competing hypotheses about nest survival of ducks at Minto Flats. Each model represented the Daily Survival Rate (DSR) of the nest as a function of some combination of species or tribe, year, habitat type, nest age, date, and distance to water. We considered additive and multiplicative relationships between DSR and these independent variables. We sought to create a set of models that were interpretable in an ecological and management context and systematically described most of the plausible patterns of variation in nest survival at our study site.

Each nest in the analysis was described by 3 categorical variables: year, species, and habitat type. Diving duck species included in the analysis were canvasbacks, redheads (*Aythya americana*), lesser scaup, and greater scaup. Dabbling ducks were American wigeon, gadwalls (*Anas strepera*), green-winged teal (*Anas crecca*), mallards (*Anas platyrhynchos*), northern pintails (*Anas acuta*), and northern shovelers (*Anas clypeata*). Not all species were encountered in all years. We considered 4 habitat types: meadow, floating vegetation, upland, and island. These habitat types reflected the range of structural diversity of vegetation and accessibility of nest habitats to predators on the study area.

Nests were further defined by their age, date of discovery, and distance to open water. We estimated the age of the nest when found as the sum of number of eggs and estimated incubation stage of eggs (Klett et al. 1986). Nest age and date are somewhat confounded (Dinsmore et al. 2002); however, during our study, nests were initiated throughout the nesting season so we considered these variables separately. Distance to water, in meters, was used as a continuous individual covariate. We included this covariate because mammalian predators may use shorelines as travel corridors and thus reduce survival of nests located near shorelines.

We used program MARK (White and Burnham 1999) to estimate parameters and evaluate the relative support for our candidate models. Program

MARK uses generalized linear models (McCullough and Nelder 1989) with user-specified link function and error distribution to generate maximum likelihood estimates of regression coefficients and their sampling variances and covariances. For our analysis of nest survival, we used the logit link function and binomial error distribution. This approach extends the survival models developed by Johnson (1979) by permitting direct evaluation of the impact of covariates, including daily covariates like nest age, on DSR (Dinsmore et al. 2002). We did not interpret logit-scale regression coefficients if their 95% confidence intervals overlapped zero (Neter et al. 1996).

To assure accurate estimation of DSR, this model required that 5 general assumptions were fulfilled: (1) nest ages were correctly determined on the initial visit, (2) nest fates were known with certainty, (3) investigator activity did not influence nest fate, (4) fates of nests were uncorrelated, and (5) there was no heterogeneity in survival among nests (Dinsmore et al. 2002). Our observations of successful nests indicated that field candling provided accurate estimates of nest age. We did not include nests with unknown fates in the analysis. We reduced the potential effect of our visits on nest survival by: (1) visiting nests in the late afternoon when the female was likely to be absent (Gloutney et al. 1993), (2) scheduling revisits at 5–7 day intervals, and (3) spending as little time at the nest as possible. Although we were confident that assumptions 1, 2, and 3 were satisfied, we thought that assumptions 4 and 5 were probably violated during our study and therefore required additional consideration.

Clustering of nests, particularly on islands, could have created some correlation of nest fates. Age and experience of the nesting females were unknown to us and could have led to heterogeneity among nest fates (Trauger 1971, Afton 1984). To correct for these infractions, we estimated a variance inflation factor ( $\hat{c}$ ) from the most highly parameterized model (McCullough and Nelder 1989:118) and applied it to all estimates of sampling variance and model selection criteria. Thus, differences in Akaike's Information Criterion, corrected for finite sample size and overdispersion, provided the basis for discrimination among competing models ( $\Delta QAIC_c$ ; Burnham and Anderson 1998). There were some limitations to this method of estimating overdispersion (Dinsmore et al. 2002). Specifically, these estimates of  $\hat{c}$  have been shown to be positively biased with ordinary sample sizes (McCullough and Nelder 1989:118); therefore,

Table 1. Total number, fate, and apparent causes of failure of duck nests found at Minto Flats, Alaska, USA, during 1989–1993 and 2002–2003.

Year	Total nests	Exposure days	Successful	Failed	Apparent cause of failure			
					Predator	Abandoned	Flooded	Undetermined
1989	178	1,802	68	110	65	10	20	15
1990	317	2,778	97	220	206	9	0	5
1991	323	2,896	102	221	147	13	55	6
1992	119	958	20	99	22	9	68	0
1993	262	3,739	165	99	63	27	9	0
2002	332	3,645	149	183	139	12	5	27
2003	290	2,133	67	223	201	22	0	0

we probably over-inflated our sampling error by an unknown amount. Nevertheless, we used this method as there was no viable alternative (Din-smore et al. 2002).

We used back-transformed estimates of DSR from our best-approximating model:

$$DSR_i = 1 / 1 + \exp(-(\hat{\beta}_0 + \hat{\beta}_1 X_{1i}, \dots, \hat{\beta}_i X_{ni}))$$

where the  $\hat{\beta}_i$  are the estimated regression coefficients from the model and the  $X_i$  are the date-specific values of the independent variables, to generate estimates of nest survival, assuming nesting periods of standard length (35 days for both species of scaup; Bellrose 1980, Klett et al. 1986). These estimates were the product of all of the daily survival probabilities predicted by the model, evaluated at the median, minimum, and maximum covariate values. We used the median and the extremes because covariates such as date and distance to water tended to have highly asymmetric (right-skewed) distributions, and we wanted to accurately display the full range of variation in nest survival probability for a given species. Sampling variances of nest survival were estimated with the Delta Method (Seber 1982:7).

We estimated average DSR of all species (average of the year-specific estimates weighted by the inverse of their sampling variances; Schmutz and Morse 2000) among the 7 years of data. We estimated temporal process variation (total variance – sampling variance; Burnham et al. 1987:260) in DSR of all species using an intercept-only model (Burnham and White 2002).

**RESULTS**

We analyzed encounter histories of 1,821 duck nests (Table 1), of which 554 were scaup nests (127 greater scaup and 427 lesser scaup). Of all nests, 37% survived and 63% failed. The main apparent cause of nest failure for all species over all years was destruction by predators

(73%), followed by flooding (14%), abandonment (8%), and unknown causes (5%). In some years, however, flooding of nests was a more important apparent cause of nest failure than predation (Table 1). For scaup nests, we observed similar apparent causes of nest mortality. Thirty-five percent of scaup nests survived and 65% failed. Apparent causes of nest failure for scaup were destruction by predators (76%), flooding (12%), abandonment (8%), and unknown causes (4%).

**Model Selection**

The variance inflation factor ( $\hat{c}$ ) estimated from the following model, DSR = Species + Habitat + (Species \* Year) + (Habitat \* Year), was 1.94. We adjusted AIC<sub>c</sub> values to quasi-AIC<sub>c</sub> (QAIC<sub>c</sub>) values (Table 2) and inflated the estimates of sampling error by a factor of  $\sqrt{1.94} = 1.39$ .

Table 2. Models of Daily Survival Rate (DSR) of duck nests found at Minto Flats, Alaska, USA, during 1989–1993 and 2002–2003. Models are ranked by differences in Quasi-AIC values ( $\Delta QAIC_c$ ).

DSR model <sup>a</sup>	K <sup>b</sup>	-2logL	$\Delta QAIC_c$
DW <sup>c</sup> + habitat + year * T <sup>d</sup>	18	3,500.77	0.00
Habitat + year * T	17	3,507.17	1.27
Year + DW + habitat	13	3,538.00	9.07
Year + habitat + TT <sup>e</sup>	13	3,546.06	13.23
Year + T + DW + habitat	12	3,551.85	14.19
Species + year * T	22	3,520.66	18.37
DW + habitat + year * nest age	18	3,536.57	18.45
Year + nest age	8	3,588.01	24.77
Year + tribe + habitat	11	3,579.25	26.30
Year	7	3,624.51	41.57
Species + habitat + (species * year) + (habitat * year)	81	3,391.61	74.44
Constant	1	3,808.60	124.42
Other species + scaup	2	3,808.55	126.40

<sup>a</sup> The + between variables indicates an additive effect; the \* denotes interaction.

<sup>b</sup> Number of parameters.

<sup>c</sup> Distance to water.

<sup>d</sup> Logit-linear trend with date.

<sup>e</sup> Quadratic trend with date.

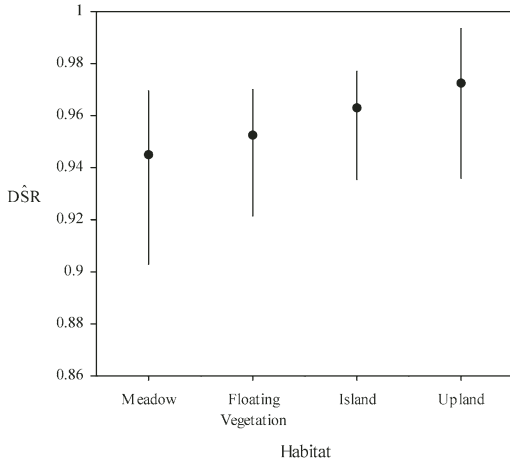


Fig. 2. Daily Survival Rate (DSR) of duck nests in different habitats at Minto Flats, Alaska, USA, during 1989–1993 and 2002–2003. Error bars represent 95% confidence limits.

The best-approximating model indicated that DSR of nests varied among years, within seasons among years (date), among habitat types, and with distance to water (Table 2). DSR was highest in upland habitat, intermediate on islands, and

lowest in meadows (Fig. 2); floating vegetation was indistinguishable from meadow in terms of DSR (logit-scale difference = 0.157, SE = 0.407). A positive relationship between distance to water and DSR was estimated in the best-approximating model, but the 95% confidence interval overlapped zero ( $\hat{\beta} = 0.150$ , SE = 0.09). Within years, unique slope coefficients for date were estimated; in 1993 and 2002 these trends were positive (Fig. 3). Date coefficients had 95% confidence intervals that overlapped zero in all other years; in most years these coefficients were positive. Models with a common date coefficient for all years or quadratic date terms were not supported ( $\Delta QAIC_c > 13$ ).

Daily survival rate did not vary among species, between tribes, or with nest age under the set of candidate models. Parameterizations including species or tribe affiliations were not selected ( $\Delta QAIC_c > 18$ ; Table 2). We also examined a model describing different DSR for scaup than other species ( $\Delta QAIC_c = 126.40$ ); this model received less support than a model of constant DSR across all variables (Table 2). Models depicting a relationship between nest age and DSR, whether unique to each year or common to all years, also received little relative support (Table 2). Taxonomic affiliation, however, remained

important to us because species have been the practical units of management. Thus, when calculating nest survival, we returned to the specific values of covariates for scaup.

### Nest Survival

*Scaup*.—Because the model selection results indicated that variation among species was not related to nest survival, we combined observed covariate values for greater and lesser scaup and generated 3 estimates of nest survival for scaup in each year. These estimates represented the lowest, median, and highest nest survival possible for the nesting scaup that we observed. For instance,

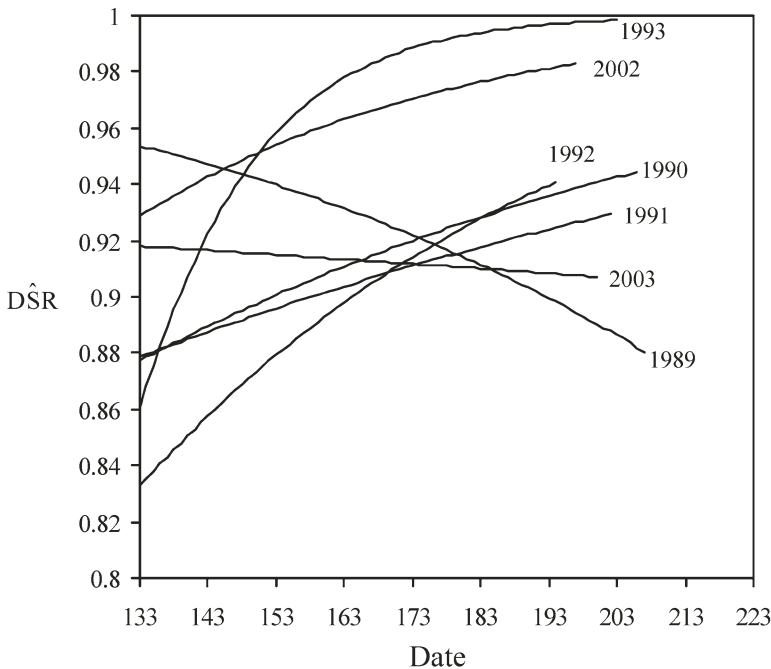


Fig. 3. Within-season trends in Daily Survival Rate (DSR) of duck nests at Minto Flats during 1989–1993 and 2002–2003. Trends for 1993 and 2002 were estimated with confidence intervals that did not overlap zero. Variation in intercepts represents among-year variation in DSR. Date is the number of days since 1 Jan.

in a given year, the lowest nest survival estimate for scaup represented the scaup nest found in meadow habitat that is initiated earliest and closest to water. The highest nest survival estimate in any year represented the scaup nest found on an island that was initiated latest and was farthest from water.

Nest survival of scaup was variable within and among years (Table 3). Minimum values of covariates resulted in nest survival estimates from 0.01 (95% CI: 0.00 to 0.03) in 1992 to 0.21 (95% CI: 0.13 to 0.30) in 2002. Estimates generated from median covariate values ranged from 0.01 (95% CI: 0.00 to 0.06) in 1992 to 0.61 (95% CI: 0.50 to 0.74) in 1993 (Fig 4). When maximum covariate values were incorporated, estimates ranged from 0.11 (95% CI: 0.02 to 0.47) in 1992 to 0.86 (95% CI: 0.77 to 0.96) in 1993.

*Temporal Variation in Nest Survival of All Species.*—Average year-specific DSR for all species of ducks at Minto Flats was 0.938 (95% CI: 0.919 to 0.957). Average year-specific nest survival (DSR<sup>35</sup>; Johnson 1979) was 0.11 (95% CI: 0.05 to 0.22). Estimated year-specific process variation ( $\hat{\sigma}$ ) in DSR was 0.02 (95% CI: 0.01 to 0.06). Adding 2 standard deviations ( $2\hat{\sigma} = 0.04$ ) to average DSR (0.938) and raising the resulting DSRs to the 35th power indicated a range of year-specific nest survival from 0.02 to 0.46.

## DISCUSSION

### Variation in Nest Survival

Patterns of variation in nest survival at Minto Flats were generally similar to those observed in other regions of North America. Predators have been the predominant cause of nest failure in the prairie pothole region and the Canadian parklands (Johnson et al. 1992, Sargeant and Raveling 1992). Similarly, destruction by predators was the most common apparent cause of nest failure at Minto Flats. Flooding of nests was also the cause of many nest failures on our study site but was probably of secondary importance.

The relationship between survival and nest habitat reflected a gradient of risk in terms of flooding and predation. Nests in meadow and floating vegetation habitat were accessible to all species of

Table 3. Estimated nest survival of greater and lesser scaup ( $\hat{S}$ ) and standard error (SE) during 1989–1993 and 2002–2003. Each estimate represents the combination of habitat, date, and distance to water that would lead to the minimum (Min), median, and maximum (Max) observed nest survival probability for that year.

Year	$\hat{S}$					
	Min	SE	Median	SE	Max	SE
1989	0.02	0.02	0.07	0.03	0.30	0.11
1990	0.02	0.01	0.05	0.02	0.33	0.13
1991	0.02	0.01	0.10	0.04	0.20	0.11
1992	0.01	0.01	0.01	0.01	0.11	0.09
1993	0.13	0.06	0.61	0.06	0.86	0.05
2002	0.21	0.04	0.27	0.06	0.69	0.10
2003	0.03	0.04	0.04	0.02	0.18	0.04

avian and mammalian nest predators, and, in some years, were completely inundated by water after many nests had been initiated (Petrula 1994). Islands were likely less accessible to red foxes than were mainland sites but had little protection from flooding relative to upland habitats. Upland sites were probably least accessible to predators and least vulnerable to flooding, as these habitats were associated with the greatest amount of structural complexity and topographic relief. Furthermore, there was prior evidence that species that primarily nested in upland habitats (e.g., green-winged teal, American wigeon) had slightly higher nest survival (Petrula 1994). Our observations of higher nest survival on islands and in forested habitats were consistent with results of other studies of nest survival of ducks conducted in the mid-continent (Sugden and Beyersbergen 1987, Loken and Woodward 1992) and in the boreal forest (Trauger 1971, Fournier and Hines 2001).

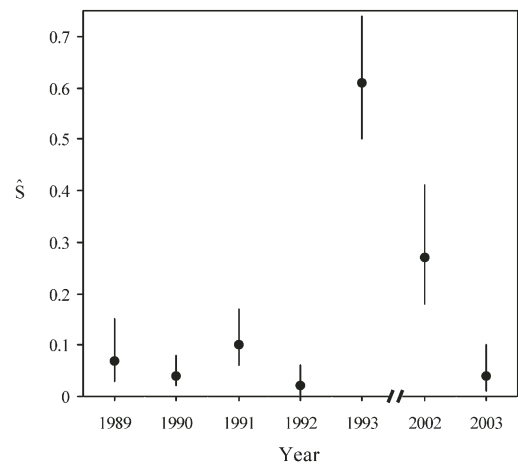


Fig. 4. Nest survival of scaup (greater and lesser combined) at Minto Flats, Alaska, USA, during 1989–1993 and 2002–2003. Error bars represent 95% confidence limits.

Increasing survival of duck nests through the season is commonly attributed to increasing abundance of alternative prey and to the phenology of nesting cover (Grand 1995, Greenwood et al. 1995). Relationships between date and nest survival were variable among years at Minto Flats but were positive in 5 of the 7 years.

Generally, species of duck has not been a strong predictor of nest survival (Higgins et al. 1992, Fournier and Hines 2001). Predators most likely do not differentially prey upon the nests of different species nesting in similar habitats at similar times of the season, regardless of differences in nesting behavior (Johnson et al. 1992). Similarly, at Minto Flats, nest survival did not vary among species or between tribes during our study.

Nest age was not predictive of nest survival during our study. Nest ages in our sample were not distributed uniformly across the season and were confounded with date only early and late in the season (Dinsmore et al. 2002). Perhaps daily variation in nest survival was not related to nest age because some older nests ( $\geq 17$  days) became vulnerable to predators or flooding as a result of within-season dynamics. For instance, rising water levels or melting of the ice pavements under mats of floating vegetation sometimes caused nest flooding (Petrula 1994). Low water levels later in the season probably made islands more accessible to predators (Petrula 1994). These events could have resulted in lower survival probability independent of nest age.

### Duck Production and Nest Survival

*Duck Production in the Boreal Forest.*—Considerable year-specific variation in nest survival of ducks has been observed in mid-continent regions (e.g., Higgins et al. 1992). This variation has been attributed to human-induced changes in predator communities and habitat conditions (Beauchamp et al. 1996), as well as periodic cycles of drought (Karl et al. 1990). Conversely, the boreal forest has been characterized by relatively stable wetland conditions (Jessen 1981) and fewer human-induced changes in landscape composition and predator communities (Sargeant and Raveling 1992). Therefore, the boreal forest might be expected to exhibit consistent, albeit comparably lower (due to increased energetic cost of migration), production of ducks through time and across space (Pospahala et al. 1974, Johnson and Grier 1988).

Should North American waterfowl be managed under the assumption that a breeding pair has the same potential for reproduction regardless of

where that pair occurs? Our study and other recent studies of clutch size and nest survival of ducks have indicated that the boreal forest has been more productive and dynamic than previously thought, and support a revised view of duck production in this region (Petrula 1994, Grand 1995, Fournier and Hines 2001). Average clutch size of ducks nesting in boreal forest does not differ from clutch sizes of the same species of ducks nesting in the mid-continent (Bellrose 1980, Petrula 1994, Fournier and Hines 2001). Average nest survival probability of ducks in the boreal forest of Alaska and Canada has been similar to mid-continent observations (Higgins et al. 1992, Grand 1995, Greenwood et al. 1995, Fournier and Hines 2001, Reynolds et al. 2001). Therefore, expected production of breeding pairs may be equivalent across regions based on the parameters that have been studied to date.

Two factors require further consideration. Process variation in nest survival may influence the expectation for production in a given year for a given breeding area, and our data are the first to indicate that process variation in nest survival is extensive (range in nest survival: 0.02 to 0.46) in boreal forest and may not be related to the same factors (e.g., drought cycles) that appear to influence process variation in waterfowl breeding in the mid-continent. Second, we cannot yet consider all the parameters that may influence production. Notably, estimates of renesting probability and hen mortality during breeding, and variation in these rates, are not available for waterfowl in the boreal forest. Therefore, management of North American waterfowl may still be refined by considering differences in the reproductive potential of waterfowl across breeding areas.

*Nest Survival of Scaup.*—Nest survival in the range of 15% to 20% has been indicated as necessary to maintain stable or increasing populations of mallards (Cowardin et al. 1985). Scaup most likely require higher nest survival than mallards for population growth because of the differences in life history between these species (Johnson and Grier 1988). For example, scaup generally have lower renesting probabilities and may have lower average breeding probability (Afton 1984, Koons 2001, Kessel et al. 2002) than mallards (Hoekman et al. 2002). Estimates of median nest survival of scaup exceeded 20% only in 1993 and 2002; low nest survival could have limited the production of scaup during most years of our study.

This evidence is somewhat consistent with concurrent declines in scaup abundance in interior

Alaska (Hodges et al. 1996) and across the boreal forest (Wilkins and Otto 2003). Our study and other multi-year studies have revealed that nest survival of scaup has been highly variable among years at several study areas in the boreal forest (Petrula 1994, Grand 1995, Fournier and Hines 2001). Thus, occasional years when recruitment of scaup exceeds threshold levels for population maintenance or growth could be highly influential to the persistence of these populations. Observed variability in nest survival of scaup indicates that understanding the relationship between recruitment and population dynamics in these species will probably require estimation of recruitment parameters over multiple seasons across the entire boreal forest.

### MANAGEMENT IMPLICATIONS

The relative importance of boreal forest habitats for breeding waterfowl has increased as habitat conversion and loss has occurred in the central prairies of the U.S. and Canada. Minto Flats is an important area for breeding ducks, particularly lesser and greater scaup, in the boreal forest of interior Alaska (Hodges et al. 1996). Variation in nest survival of scaup and other common duck species indicates that Minto Flats has similar annual potential to produce ducklings as mid-continent regions (Hoekman et al. 2002). Management activities directed towards maintaining existing habitat would probably be the most effective strategy to support scaup populations at Minto Flats.

However, resource development and associated loss of nesting habitat are likely to occur at Minto Flats. The Alaska Department of Natural Resources has approved oil and gas exploration throughout most of the Minto Flats State Game Refuge (Alaska Department of Natural Resources, 2002. Nenana Basin exploration license: final finding of the director. Alaska Department of Natural Resources, Division of Oil and Gas, Anchorage, Alaska, USA). The effect of this exploration on nest survival of scaup at Minto Flats is likely to be related to the extent that exploration activity affects seasonal patterns of flooding (Petrula 1994) as well as disturbance to nesting habitat. Potential effects of resource development could be identified by research designed to measure and compare duck production among explored and unexplored areas.

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