

# Survival of Ducks Banded in the Boreal Forest of Alaska

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## Abstract

<sup>†1</sup> *Limited information is available about the population dynamics of ducks in the boreal forest. We conducted an analysis of recovery data from 5 species of ducks banded in the boreal forest of Alaska, USA, during 1959–1966, and records of 3 species of ducks banded during 1989–2000, with the objective of examining sources of variation in survival and sampling probability and to complement recent studies of the breeding ecology of ducks in the boreal forest. Survival of ducks during 1959–1966 was species- and year-specific. During 1989–2000, survival of northern pintail (*Anas acuta*) was age-, sex-, and year-specific. Age-class by sex interaction, without year-specificity, however, best-described survival of mallard (*A. platyrhynchos*) and green-winged teal (*A. crecca*). Annual survival of male ducks from the Alaska boreal forest was generally similar to annual survival of the same species banded in the midcontinent. Survival probability of female ducks from the Alaska boreal forest, however, was generally higher than survival of female ducks from midcontinent regions. Sampling probability during 1989–2000 was lower for females than males, and increased after 1996, concurrent with the initiation of electronic band reporting. Our results suggest that patterns of duck survival differ between the boreal forest and the midcontinent, especially for after-hatch-year females. Regional variation in survival and reproduction and the factors affecting these parameters should continue to be monitored and considered in continental management plans. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):000–000; 2006)*

## Key words

*Alaska, boreal forest, capture–recapture, duck survival, population dynamics, sampling probability, survival probability.*

Estimates of annual survival and productivity are vital to understanding the population dynamics of waterfowl (Johnson et al. 1992). Northern regions, such as the boreal forest of Alaska and northern Canada, have long been considered less productive for breeding waterfowl than midcontinent regions, despite their large geographic area and relative lack of ecological disturbance (Calverley and Boag 1977, Johnson and Grier 1988). Aerial survey data suggest that approximately 10% of the continental duck population breeds in the boreal forest of Alaska (Conant and Groves 2002). Recent studies of nesting and brood ecology (Grand 1995, Walker and Lindberg 2005, Walker et al. 2005), and nutrient-reserve dynamics (Mann and Sedinger 1993, MacCluskie and Sedinger 2000) indicate that the boreal forest of Alaska may be a more important region for waterfowl production than previously thought.

Limited information exists about patterns of survival for ducks using the boreal forest (Trauger 1971, Fournier and Hines 1998). Survival of ducks may differ between the boreal forest and the midcontinent for several reasons. Ducks that breed at high latitudes undertake migrations that are expensive energetically (Alisauskas and Ankney 1992) and potentially experience prolonged annual periods of harvest mortality because they are exposed to harvest prior to migration, as well as during migration and winter (U.S. Fish and Wildlife Service 2003). During the breeding season, differences in degree of habitat alteration and types of predators between the boreal forest and the midcontinent may contribute to differences in survival of breeding females (Beauchamp et al. 1996, DeVries et al. 2003). Patterns of survival may also differ for individuals using the less temporally dynamic wetlands of the boreal forest (Johnson and Grier 1988).

Moreover, the abundance of species such as lesser scaup (*Aythya affinis*) and northern pintail, which nest extensively in the boreal

forest, are currently well below the goals set by The North American Waterfowl Management Plan (U.S. Fish and Wildlife Service 2003); thus, survival rates for these species are of distinct interest to waterfowl managers (Miller and Duncan 1999, Austin et al. 2000, Afton and Anderson 2001). Current management of North American duck populations is based primarily on demographic information derived for midcontinent mallard populations (U.S. Fish and Wildlife Service 2002). Management programs could be refined, however, if potential differences in vital rates between midcontinent and boreal forest duck populations are identified.

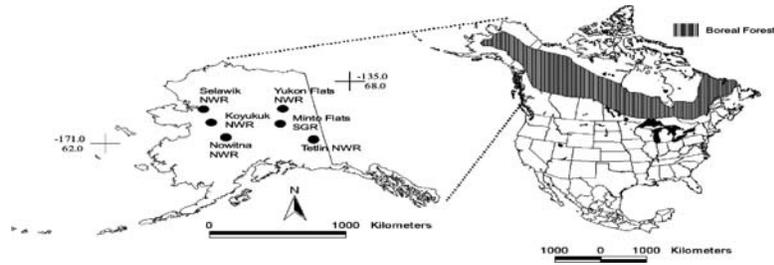
Additionally, the climate of the boreal forest is currently undergoing ecological change, characterized by warming and thawing of permafrost (Camill and Clark 1998, Osterkamp et al. 2000), which in turn affects the quality and stability of wetlands used by ducks. Boreal forest habitats are increasingly threatened by commercial forestry, mineral extraction, and agricultural development (Ducks Unlimited 2000, Hobson et al. 2002). Therefore, it is important to evaluate survival rates to understand what component of the demography of boreal forest species may be impacted by these large-scale changes.

To estimate annual survival for ducks in the boreal forest of Alaska, we conducted a retrospective analysis using data from approximately 20 years (1959–1966, 1989–2000) of band recoveries. Our objectives were to estimate survival probability; investigate possible sources of variation resulting from species, tribe, sex, age, or year; and compare patterns of variation in survival estimates from the boreal forest with estimates from the midcontinent region.

## Study Area

We investigated the survival probability of ducks banded at Koyukuk National Wildlife Refuge (NWR), Nowitna NWR, Selawik NWR, Tetlin NWR, Yukon Flats NWR, and Minto

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**Figure 1.** Approximate extent of boreal forest in North America, and National Wildlife Refuge (NWR) and State Game Refuge (SGR) duck banding locations in Alaska, USA. During 1959–1966, lesser scaup, canvasback, Barrow’s goldeneye, American wigeon, and northern pintail were banded. During 1989–2000, northern pintail, green-winged teal, and mallard were banded.

Flats State Game Refuge; these refuges were located between 62°0′–68°0′N and 141°0′–160°0′W (Fig. 1). State and federal management agencies selected these banding locations for their high densities of ducks (King 1963, U.S. Fish and Wildlife Service 2003).

Boreal-forest habitat has been described as mixed-forest communities comprised primarily of white spruce (*Picea glauca*), black spruce (*P. mariana*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*; La Roi 1967). Upland shrub comprised of various species of willow (*Salix* spp.) and alder (*Alnus* spp.), as well as Labrador tea (*Ledum decumbens*; La Roi 1967) while low-lying sites were dominated by meadows of bluejoint grass (*Calamagrostis canadensis*), and in poorly drained soils, sedges (*Carex* spp.), and marsh five-finger (*Potentilla palustris*; Petrula 1994). Climate of the boreal forest has been described as continental subarctic with high seasonal variation in photoperiod and temperature as well as low annual precipitation (18–43 cm; Hare and Ritchie 1972).

Lowland basins, such as the banding areas, were drained by major rivers and tended to have even topography (<15 m total relief; Hooper 1952, Grand 1995), variable hydrology (Petrula 1994), and were interspersed with semipermanent waterbodies of varying size (<1 ha to >1,000 ha). These areas attracted high densities of breeding, molting, and migrating ducks (Rowinski 1958, U.S. Fish and Wildlife Service 2003).

## Methods

### Data Collection

We acquired records of all ducks banded during 1959–2000 between 62°0′N–68°0′N and 141°0′W–160°0′W from the U.S. Geological Survey Bird Banding Laboratory. We obtained records of American wigeon (*Anas americana*), canvasback (*Aythya valisineria*), lesser scaup, northern pintail, and Barrow’s goldeneye (*Bucephala islandica*) banded from 1959 to 1966 and records of mallard, green-winged teal, and northern pintail banded from 1989 to 2000. These species and years were included because they comprised all the available data for ducks banded in the boreal forest of Alaska. In our analysis, all bands reported were included if the reported information indicated the bird was shot or found dead between 1959 and 1966 and 1989 and 2000. All banding occurred during late July and August. During 1959–1966, molting ducks were captured using drive traps (King 1963), and during 1989–2000, ducks were captured with baited live traps. Only wild, nonexperimental birds marked with federal metal leg bands were included.

### Data Analysis

We conducted a separate analysis for each period (1959–1966, 1989–2000), and separated the records into categories based on species, sex, and age (hatch year [HY] or after hatch year [AHY]). We used program MARK (White and Burnham 1999) to estimate survival probability and sampling probability (Seber 1970). Survival probability ( $S$ ) is the probability that a bird alive during banding in year  $i$  will survive to the banding period in year  $i + 1$ . Sampling probability ( $r$ ) is the conditional probability that a banded bird is found in year  $i$ , and its band number reported, given that it is dead. We used the Seber (1970) parameterization of the band-recovery model to avoid potential problems of modeling  $S$  with covariates under the Brownie et al. (1985) parameterization of the band-recovery model (Otis and White 2002). Sampling probability—the joint probability of recovering and reporting a band from a dead bird—should not be confused with true reporting rate ( $\lambda$ ), which is traditionally estimated with reward band studies (Henny and Burnham 1976).

For each period, we developed a candidate model set that represented different sources of variation in annual survival and sampling probability. In our models, we considered all additive relationships as well as all 2- and 3-way interactions. For each period, we discriminated among competing models and selected the best-approximating model using Akaike’s Information Criterion, corrected for finite sample size and lack of fit (QAIC<sub>c</sub>; Burnham and Anderson 1998). We used normalized QAIC<sub>c</sub> weights to quantify the relative support for a model (Burnham and Anderson 1998). We estimated annual survival and sampling probability from the best-approximating model, and whenever possible we calculated average annual survival and average annual sampling probability. We calculated average annual survival and sampling probabilities by weighting estimates by their estimated sampling variance–covariance matrix (White et al. 2001).

We assessed the goodness-of-fit of each dataset to Model 1 (time-specific variation in survival and recovery rate) in program ESTIMATE (Brownie et al. 1985). The 1959–1966 dataset showed evidence of lack of fit ( $\chi^2 = 63.3$ ,  $df = 21$ ,  $P < 0.001$ ), as did the 1989–2000 dataset ( $\chi^2 = 35.9$ ,  $df = 47$ ,  $P = 0.88$ ). We therefore estimated the variance inflation factor ( $\hat{c}$ ) for each dataset by comparing the deviance of the global model with a bootstrap estimate of the deviance (White and Burnham 1999). We used the bootstrap to estimate  $\hat{c}$  because it did not require us to assume that the deviance for the model was  $\chi^2$  distributed. We applied a  $\hat{c}$  of 2.43 to the 1959–1966 dataset and 1.23 to the 1989–2000 dataset, and adjusted the model selection criterion and

**Table 1.** Numbers of ducks banded in the boreal forest of Alaska, USA, and recovered by period, species, age (after hatch year [AHY] or hatch year [HY]), and sex.

Period	Species	Age	Sex	No. banded	No. recovered
1959–1966	Lesser scaup	AHY	Female	3,572	138
	Lesser scaup	AHY	Male	26,882	1015
	Canvasback	AHY	Female	645	53
	Canvasback	AHY	Male	1,504	126
	Barrow's goldeneye	AHY	Female	1,537	27
	Barrow's goldeneye	AHY	Male	2,645	59
	American wigeon	AHY	Male	4,688	579
	Northern pintail	AHY	Female	787	24
	Northern pintail	AHY	Male	876	28
	1989–2000	Northern pintail	AHY	Female	3,609
Northern pintail		AHY	Male	919	74
Northern pintail		HY	Female	4,319	142
Northern pintail		HY	Male	2,738	203
Green-winged teal		AHY	Female	1,265	52
Green-winged teal		AHY	Male	1,579	110
Green-winged teal		HY	Female	1,295	39
Green-winged teal		HY	Male	1,229	70
Mallard		AHY	Female	1,001	53
Mallard		AHY	Male	1,317	114
Mallard		HY	Female and male	985	68

estimates of sampling variance accordingly (Burnham and Anderson 1998).

Our candidate model set for the early period (1959–1966) described annual survival as a function of tribe, species, sex, and year and sampling probability as a function of year or tribe. Data for Barrow's goldeneye were limited to 1959–1962, and data for northern pintail were limited to 1959–1961. We were unable to consider age in these models because all records were of AHY birds, and we were unable to examine sex-specificity in American wigeon because no females were banded. We could only estimate tribal variation in sampling probability because models including annual variation in sampling probability would not converge to an estimate. Additionally, we were unable to estimate average annual survival for Barrow's goldeneye or northern pintail during this period because there were insufficient years of data to estimate variances and covariances appropriately.

Our candidate model set for the late period (1989–2000) described annual survival as a function of species, sex, age, and year and sampling probability as a function of year and sex. Despite past evidence for sex-specific survival of mallard (Johnson et al. 1992), we combined HY male and female records because there were too few recoveries to consider sexes separately.

## Results

### Banding and Reporting

A total of 63,392 ducks were banded across all years and sites (Table 1). Of these, 68% were banded during 1959–1966. The 1959–1966 group was composed entirely of AHY birds, mostly (85%) males. Of these ducks, 2,049 individuals were reported dead between 1959 and 1966. Between 1989 and 2000, banding crews marked 20,256 ducks, both HY (52%) and AHY birds. Within this group, 495 AHY birds and 522 HY birds were reported dead between 1989 and 2000.

### Survival Probability and Sampling Probability

**1959–1966.**—The best-approximating model indicated that survival varied among species by year, and sampling probability varied by tribe. The QAIC<sub>c</sub> weight was 1.0, indicating that this was the most well-supported model (Table 2). Lesser scaup and canvasback had higher annual survival than American wigeon or northern pintail, with the exception of 1959 (Table 3). Survival probability of northern pintail was poorly estimated with coefficients of variation approaching 50%. During most years, survival of Barrow's goldeneye was similar to survival of lesser scaup and canvasback. In 1962, however, survival of Barrow's goldeneye was substantially lower than any other species-year

**Table 2.** Best-approximating models of duck survival (*S*) and sampling probability (*r*) for ducks banded in the boreal forest of Alaska, USA, 1959–1966 with lowest Akaike's Information Criterion (QAIC<sub>c</sub>). Species include lesser scaup, canvasback, Barrow's goldeneye, American wigeon, and northern pintail.

Model <sup>a</sup>	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	Model weight	K <sup>b</sup>	–2*log likelihood
S(sp*t), r(tr)	9,076.92	0.00	1.00	35	21,886.67
S(sp*s*t), r(tr)	9,108.77	31.85	0.00	59	21,847.18
S(sp+t), r(tr)	9,132.80	55.88	0.00	15	22,119.78
S(sp+s+t), r(tr)	9,136.65	59.73	0.00	19	22,109.67
S(tr*t), r(tr)	9,137.04	60.12	0.00	24	22,086.30

<sup>a</sup> sp = species, s = sex, t = year, tr = tribe (*Anatini*, *Aythiini*, *Mergini*), + = additive relationship, \* = interaction.

<sup>b</sup> K = number of parameters.

**Table 3.** Yearly and average ( $\bar{x}$ ) survival for five species of ducks banded in the boreal forest of Alaska, USA, 1959–1966. Blank entries indicate inestimable parameters or years when data were not available.

Year	Lesser scaup		Canvasback		Barrow's goldeneye		American wigeon		Northern pintail	
	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE
1959	0.58	0.11	0.63	0.15	0.78	0.21	0.70	0.09	0.44	0.19
1960	0.90	0.03	0.79	0.12	0.77	0.09	0.66	0.04	0.40	0.15
1961	0.78	0.03	0.88	0.05	0.66	0.09	0.68	0.03		
1962	0.86	0.02	0.89	0.05	0.26	0.10	0.65	0.04		
1963	0.78	0.03	0.91	0.05			0.58	0.06		
1964	0.77	0.04	0.67	0.06			0.48	0.08		
1965	0.85	0.03	0.52	0.08			0.55	0.13		
$\bar{x}$	0.81	0.03	0.77	0.06			0.65	0.02		

**Table 4.** Best-approximating models of duck survival ( $S$ ) and sampling probability ( $r$ ) for ducks banded in the boreal forest of Alaska, USA, 1989–2000 with lowest Akaike's Information Criterion (QAIC<sub>c</sub>). Species include northern pintail, green-winged teal, and mallard.

Model <sup>a</sup>	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	Model weight	$K^b$	-2*log likelihood
$S(a2^*s^*t), r(t^*s)^c$	9,292.95	0.00	1.00	92	11,202.96
$S(a2^*s^*t), r(t)^c$	9,304.89	11.94	0.00	68	11,277.16
$S(a2^*s^*t), r(t)$	9,333.99	41.04	0.00	83	11,275.78
$S(s^*t), r(t)$	9,340.82	47.87	0.00	48	11,370.84
$S(a2), r(t)$	9,345.14	52.19	0.00	14	11,460.06

<sup>a</sup>  $a2$  = HY/AHY age classes,  $s$  = sex (specific to all but hatch year mallard),  $t$  = year, + = additive relationship, \* = interaction.

<sup>b</sup>  $K$  = number of parameters.

<sup>c</sup> Mallard and green-winged teal survival held constant across years.

estimate ( $\hat{S} \pm SE_{\hat{S}}$ ;  $0.26 \pm 0.10$ ). Sampling probability varied by tribe (Table 2); *Anatini* had the highest sampling probability ( $\hat{r} \pm SE_{\hat{r}}$ ;  $0.100 \pm 0.006$ ), followed by *Aythini* ( $0.068 \pm 0.007$ ) then *Mergini* ( $0.021 \pm 0.003$ ).

**1989–2000.**—Our best-approximating model included annual estimates of survival for northern pintail, but estimates for green-winged teal and mallard were held constant across years in this model. Survival probability varied between sexes and age classes, and sampling probability varied by year and sex (Table 4). This was a constrained form of the original model, which included an estimate of survival for each species and year, and was necessary because of a lack of data in some years for green-winged teal and mallard. The best-approximating model received full support (QAIC<sub>c</sub> weight = 1.0, Table 4)

Survival of AHY green-winged teal during 1989–2000 ( $\hat{S} \pm SE_{\hat{S}}$ ) was  $0.64 \pm 0.06$  and  $0.66 \pm 0.04$  for males and females, respectively. Survival of HY green-winged teal was  $0.61 \pm 0.09$  for females and  $0.50 \pm 0.07$  for males. Mallard survival rate was  $0.49 \pm 0.06$  for AHY females,  $0.67 \pm 0.04$  for AHY males, and  $0.29 \pm 0.07$  for HY males and females combined.

Survival of northern pintail varied annually (Table 5). Average annual survival of AHY northern pintail ( $\hat{S} \pm SE_{\hat{S}}$ ) was  $0.70 \pm 0.04$  and  $0.76 \pm 0.03$  for females and males, respectively (Table 5). Average annual survival was  $0.42 \pm 0.04$  for HY females and  $0.65 \pm 0.04$  for HY males.

Average annual sampling probability from 1989 to 2000 was lower for females than males, but increased appreciably for both sexes in 1996 and doubled over the average by 1999 (Table 5).

## Discussion

### Species-specific Variation

We observed species-specific survival probabilities in both analyses. Kremetz et al. (1997) reported higher survival for female ducks in the tribe *Mergini* than ducks in the tribes *Aythini* and *Anatini*, and also observed a positive relationship between annual survival probability and body mass among species. They suggested that body mass and tribe were related to differences in life-history strategies among the species in their analysis. Our analysis did not support a relationship between survival probability and tribe, or reveal a pattern of increasing survival probability for larger species. In all but one year of the 1959–1966 period, Barrow's goldeneye (*Mergini*) had lower survival than members of the tribes *Aythini* and *Anatini*. Estimated survival probabilities were higher for larger species in some years, but this trend was inconsistent. For example, survival of Barrow's goldeneye (the largest species in the 1959–1966 sample) dropped to the lowest observed value of any species during this period. The Alaska population of Barrow's goldeneye winters almost exclusively in Prince William Sound and along the Kenai and Alaska peninsulas (Eadie et al. 2000). Perhaps unfavorable conditions at these wintering sites during 1962 had a population-wide effect.

Our data did not span the range of species, body masses, or years considered by Kremetz et al. (1997), and we were unable to make extensive within-tribe comparisons. Perhaps the individuals in this study were influenced by regional and temporal patterns of hunting and nonhunting mortality or environmental conditions that masked the patterns described by Kremetz et al. (1997). Furthermore, we cannot dismiss the alternative possibility that the

**Table 5.** Estimates of yearly and average ( $\bar{x}$ ) survival for AHY (after hatch year) and HY (hatch year) male (*M*) and female (*F*) northern pintail, and sex-specific yearly and average sampling probability for northern pintail, green-winged teal, and mallard combined. Data are from ducks banded in the boreal forest of Alaska, USA, 1989–2000.

Year	Northern pintail survival								Sampling probability			
	AHY <i>F</i>		AHY <i>M</i>		HY <i>F</i>		HY <i>M</i>		<i>F</i>		<i>M</i>	
	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{r}$	SE	$\hat{r}$	SE
1989	0.46	0.27	0.42	0.31	0.54	0.33	0.47	0.25	0.03	0.02	0.02	0.01
1990	0.71	0.23	0.47	0.24	0.53	0.23	0.68	0.15	0.03	0.02	0.06	0.02
1991	0.42	0.16	0.78	0.11	0.26	0.20	0.78	0.13	0.02	0.01	0.08	0.02
1992	0.76	0.15	0.75	0.08	0.12	0.13	0.68	0.15	0.04	0.01	0.06	0.02
1993	0.45	0.18	0.77	0.08	0.57	0.14	0.64	0.13	0.03	0.01	0.06	0.02
1994	0.67	0.12	0.77	0.07	0.43	0.12	0.77	0.10	0.03	0.01	0.05	0.01
1995	0.69	0.08	0.80	0.06	0.41	0.10	0.60	0.12	0.04	0.01	0.06	0.01
1996	0.76	0.08	0.73	0.07	0.35	0.17	0.65	0.13	0.05	0.01	0.09	0.02
1997	0.86	0.05	0.71	0.07	0.45	0.09	0.47	0.12	0.07	0.01	0.10	0.02
1998	0.79	0.07	0.80	0.06	0.61	0.14	0.58	0.11	0.07	0.02	0.12	0.02
1999	0.77	0.07	0.74	0.07	0.44	0.17	0.58	0.21	0.07	0.01	0.13	0.02
$\bar{x}$	0.70	0.04	0.76	0.03	0.42	0.04	0.65	0.04	0.04	0.01	0.07	0.01

**Table 6.** Sex-specific estimates of annual survival from ducks banded prior to hunting season and during winter (adapted from Franklin et al. 2002).

Species	Banding location	Years	Males		Females	
			$\hat{S}$	SE	$\hat{S}$	SE
Mallard	Alberta	1955–1996	0.681	0.006	0.550	0.018
Mallard	Manitoba	1955–1996	0.667	0.007	0.554	0.016
Mallard	North Dakota	1959–1996	0.675	0.009	0.555	0.012
Mallard	Saskatchewan	1955–1996	0.692	0.007	0.581	0.100
Canvasback <sup>a</sup>	New York	1955–1982	0.667	0.055	0.526	0.034
Greater scaup <sup>a</sup>	New York	1955–1990	0.727	0.010	0.599	0.028
Northern pintail	Alberta	1955–1996	0.677	0.010	0.550	0.019
Northern pintail	Manitoba	1967–1996	0.589	0.045	0.364	0.036
Northern pintail	North Dakota	1973–1996	0.686	0.023	0.570	0.036
Northern pintail	Saskatchewan	1955–1996	0.704	0.014	0.556	0.014
Northern pintail	California	1955–1980	0.708	0.014	0.562	0.021
American wigeon <sup>a</sup>	California	1955–1978	0.628	0.020	—	—

<sup>a</sup> Banded during winter.

relationship between body mass, life-history strategy, and survival probability varies geographically or temporally (Laurilla 1988, Johnson et al. 1992). Our analyses indicated that patterns of temporal variation in survival were not consistent among species; model structures proposing an additive relationship between species and time received little support.

### Sex- and Age-specific Variation

We did not consistently observe higher annual survival for AHY males than females. Other researchers, however, have reported higher survival for male than female ducks (Johnson et al. 1992, Franklin et al. 2002). The generally accepted explanation for this pattern is that females experience reduced survival as a result of the energetic costs and mortality risks of nesting and brood rearing (Johnson et al. 1992). Female ducks breeding in midcontinent regions are subject to high rates of mortality during the breeding season (Cowardin et al. 1985), accounting for as much as 57% of the annual mortality of females (DeVries et al. 2003). We hypothesize that mortality of female ducks during the breeding season could be lower in the boreal forest because human influence

on the landscape and predator communities has not increased the risk of predation (Sargeant and Raveling 1992), and females may have reduced exposure to predators because of a shorter nesting season. Nevertheless, we are unaware of any published estimates of breeding season mortality for this region. Studies that examine processes of breeding season mortality in boreal habitats could improve our understanding of the role of female mortality in the population dynamics of boreal-forest waterfowl and aid our interpretation of the relative importance of predation in midcontinent ducks (Garrettson et al. 1996, DeVries et al. 2003).

Sampling probability ( $r$ ) contains information about harvest, crippling loss, and reporting probability. Assuming no mortality between release and the hunting season and a sample comprised of hunter-killed birds only,  $r = K/(1 - S)(1 - c)\lambda$ , where  $K$  is the probability of kill by harvest,  $c$  is the probability that an individual is lost because it is crippled, and  $\lambda$  is the probability that a band is reported. We considered 3 alternative explanations for the sex-specific sampling probabilities that we observed, and we based our explanations on the components of sampling probability: 1) the retrieval process may be biased toward one sex; 2) there may be a

proclivity to report individuals of one sex but not the other; or 3) rates of natural mortality may be higher for one sex such that when an individual dies, its band is unlikely to be found, preventing it from being reported. However, little evidence exists to support a retrieval bias, or that there is a predisposition to report individuals of only one sex (Nichols et al. 1995). We observed consistently lower annual sampling probabilities for females than for males banded in the boreal forest, and we hypothesize that natural mortality may be the most important source of mortality for females in the boreal forest. If rates of natural mortality in the boreal forest are lower than in midcontinent regions, it could explain the lack of sex-specific variation in survival we observed. Furthermore, if bands are reported most commonly when hunters harvest banded birds, then the disparity between male and female sampling probabilities could be the result of relatively higher hunting mortality for males than females. Regardless of sex, sampling probabilities began to increase in 1996 and continued to increase through the end of the study. This pattern is consistent with a band solicitation program initiated by the U.S. Fish and Wildlife Service in 1996, whereby bands could be reported via a toll-free telephone number.

With respect to age-related variation, our results are generally consistent with the predictions of Johnson et al. (1992), and indicate that HY individuals were more vulnerable to mortality than AHY individuals, regardless of sex or species. A similar survival probability between HY and AHY female green-winged teal was the one exception to this pattern.

### **Regional Variation**

A regional comparison of survival rates was challenging because many studies of similar species estimated apparent survival (i.e., survival probability  $\times$  fidelity probability), or were conducted during different time periods. Comparison during different periods seemed reasonable, however, because recent studies of annual survival showed little temporal (process) variation in annual survival probabilities (Gould and Nichols 1998, Franklin et al. 2002).

Estimated annual survival for AHY female ducks was generally greater in the boreal forest of Alaska than in midcontinent regions. Female northern pintail and green-winged teal had higher survival than published estimates for northern pintail in the midcontinent (Table 6). After-hatch-year male ducks in the boreal forest had similar survival probability to those in midcontinent regions. These results were also consistent with estimates of survival from ducks banded in other regions of North America. Survival of AHY female northern pintail was greater in the boreal forest than California, but AHY male survival was similar (Table 6). Female and male lesser scaup and canvasback from the boreal forest of Alaska had higher survival probability than greater scaup (*Aythya marila*) or canvasback banded during winter in New York (Table 6). After-hatch-year male American wigeon from the boreal forest had similar survival probability to males banded during winter in California.

Overall, our results suggest that survival may be similar or higher for certain segments of the population using the boreal forest. Harvest is generally accepted as the primary source of mortality for male ducks (Johnson et al. 1992), and our results indicate that

prolonged exposure to harvest for some male boreal forest ducks may not negatively affect survival. We previously attributed the differences in AHY female survival between the boreal forest and the midcontinent to potential variation in the risk of mortality during the breeding season.

Furthermore, higher survival probability for some boreal forest ducks relative to midcontinent ducks may indicate a potential difference in life-history characteristics. Increases in survival may be explained by reduced investment in reproduction. Because of the relatively unaltered nature of boreal forest habitats, ducks breeding there may already be maximizing reproductive output, and management efforts may be best directed towards monitoring survival and the potential effects that emerging threats may have on both reproduction and survival.

### **Management Implications**

Information on annual survival from this study, and reproduction, from past research (Grand 1995, Walker et al. 2005, Walker and Lindberg 2005), collectively indicate that the boreal forest could be more productive than historically thought. Although our analysis included sites from most of the Alaska boreal forest and species representative of all tribes of ducks that occur in the boreal forest, additional analysis of population dynamics of ducks in the Canadian boreal forest would provide valuable insights about the consistency of the patterns that we observed. Nonetheless, we believe our results combined with past studies of breeding ecology indicate sufficient regional variation in population dynamics to justify continued monitoring of demographic rates and possibly development of management plans specific to populations of ducks in the boreal forest. We urge managers to continue surveys and consider expanding banding programs and research focused on demographics of ducks in the boreal forest. Population modeling should be used to guide regional management plans, particularly in the face of increased threats from development activities in the boreal forest.

Our study provided some indirect evidence that electronic band reporting is an effective way to increase sampling probability, and thus, the precision of survival estimates from band-recovery data. Large increases in sampling probability during the later years of this study indicate that continuation of this service is warranted.

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