# BREEDING ECOLOGY AND FASTING TOLERANCE OF SCAUP AND OTHER DUCKS IN THE BOREAL FOREST OF ALASKA

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# BREEDING ECOLOGY AND FASTING TOLERANCE OF SCAUP AND OTHER DUCKS IN THE BOREAL FOREST OF ALASKA

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

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By

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# ABSTRACT

Information on the breeding ecology of boreal forest ducks is lacking, despite management concern for species such as the lesser scaup (*Aythya affinis*), whose population has declined markedly since the 1980s. The mechanisms impacting population growth of scaup, and which component of their population dynamics is most affected, are unknown. Previous investigators hypothesized that food deprivation in the spring may reduce breeding success. My objectives were to: 1) examine reproductive parameters of lesser scaup and other ducks on the Yukon Flats in interior Alaska, and 2) measure the tolerance of captive scaup to fasting, in comparison to sympatric Northern shovelers (*Anas clypeata*) and American wigeon (*Anas americana*). Although breeding probability of paired females was assumed to be 1.0, the breeding probability of paired female scaup was between 0.12 (SE = 0.05, n=67) to 0.68 (SE = 0.08, n=37), and was positively related to body mass. These results suggest that managers may overestimate the productivity of boreal ducks using traditional survey methods. In addition, captive female scaup completely recovered from a loss of 11% body mass in only four days, suggesting that mass loss can be rapidly reversed, and may be able to obtain the body condition required for reproduction, if food supplies are adequate.

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# INTRODUCTION

Population change is driven by four factors: births, deaths, immigration and emigration. These factors vary in the degree of their contribution to population change and can be heavily influenced by environmental conditions and life history strategies (Gotelli 1998). The effectiveness of population management in predicting population change relies on quality estimation of these four factors, and how each varies spatially and temporally within species.

Components of productivity and adult survival have been extensively studied in North American waterfowl. Productivity is a function of fecundity, nest survival, brood survival, and juvenile survival (Cowardin and Blohm 1992). Many of these factors have been studied extensively in the prairie-parkland regions of North America, particularly the nest survival and adult survival of mallards (*Anas platyrhynchos*). Managers couple productivity information with extensive population monitoring via spring breeding pair and winter aerial surveys, harvest surveys and banding efforts to set harvest regulations (Baldesarre and Bolen 2006).

Although the majority of waterfowl research has been concentrated in the prairie-parkland region, other regions are important to continental waterfowl production; for example, over 34% of duck pairs are counted in the northern boreal forest strata during annual spring surveys (Wilkins et al. 2006). Differences in adult breeding season survival and production rates between the boreal forest and other regions could exist because of a shorter breeding season in the boreal forest, as wells as differences in nesting habitat, food sources, and predator communities between regions (Calverly and

Boag 1977, Johnson et al. 1992). However, adequate information on survival and production rates of boreal ducks is lacking (Petrula 1994). Thus, many waterfowl management strategies are based on population status and components of productivity of mallards in the prairie-parkland, and the habitat conditions in that region, regardless of the species or population being managed (Baldasarre and Bolen 2006). Population models and subsequent management could be improved with more refined information on rates of survival and productivity of ducks in the boreal forest (Boomer and Johnson 2005).

Information needs are especially pressing for species that nest primarily in the boreal region and are currently declining, such as lesser scaup (*Aythya affinis*; Austin et al. 2000, Afton and Anderson 2001). The combined population of lesser and greater scaup has declined from 6.5 million birds in the early 1980s to 3.2 million birds in 2006 (Wilkins et al. 2006). Although lesser and greater scaup are not distinguished in population surveys, lesser scaup comprise nearly 90% of the continental population (Bellrose 1980). The majority of lesser scaup (70%) breed in the western boreal forest of Alaska and Canada, where scaup populations have seen the steepest declines (Afton and Anderson 2001).

It is unclear whether changes in adult female survival, productivity, or both, have ultimately caused the decline in the scaup population (Afton and Anderson 2001, Koons et al. 2006). Survival and productivity can be broken down into several components. For example, female survival likely varies between the breeding season and non-breeding season (Sargeant and Raveling 1992, Lake et al. 2006); and productivity is a product of breeding effort and the survival of eggs, ducklings, and juveniles (Johnson et al. 1992). Managers have limited time and resources; therefore, it is important to focus research on components of survival and recruitment that are most important to population change in scaup. Perturbation analyses on greater scaup (Flint et al. 2006) and lesser scaup (Koons et al. 2006) vital rates have suggested that changes in female survival, specifically during the breeding season, induce a greater population change than changes in recruitment parameters such as nest survival. However, these population models were based on limited data, particularly for female survival and breeding probability of scaup in the boreal forest.

In addition to obtaining improved estimates of population parameters, it is important to understand the mechanisms underlying a decline in female survival and/or productivity of scaup. Many hypotheses have been proposed, including increased contaminant loads, limiting food resources, and landscape-level changes in the boreal forest or wintering grounds (Austin et al. 2000). One prominent explanation, the spring condition hypothesis, asserts that food limitation during spring migration has affected female reproductive effort (Anteau and Afton 2004). However, the ability of scaup to recover from a loss of body mass, and how that affects their breeding effort, is unknown.

Most waterfowl face food restriction at some point throughout their annual cycle (Lovvorn 1994, Pease et al. 2005, Afton and Paulus 1992). Extensive literature documents the ability of birds to cope with fasting by using tissues to provide lipid and protein during the deficit, and then increasing both food intake and digestive function to restore body mass when food becomes available (Barboza and Jorde 2001 and 2002, McWilliams and Karasov 2001). For example, migration can be compared to a high energy fast (Battley et al. 2001), and many birds change digestive organs and pectoralis muscles (Hume and Biebach 1996, Piersma 1998, Lindstrom et al. 2000, Guglielmo and Williams 2003) in reaction to fluctuations in food intake before, during, and after migration. Therefore, hypertrophy (or atrophy) of digestive organs and large protein stores, such as the pectoralis and gizzard, are likely correlates to fasting or intermittent feeding. To examine how periods of low food intake may affect scaup reproductive effort, it is important to understand the body mass, body composition, and organ changes that occur in scaup subjected to intermittent periods of fasting and ad libitum feeding.

I had two main objectives for this study. First, I examined breeding season vital rates of scaup in the Alaskan boreal forest, specifically breeding probability, nest survival, and female survival (Chapter 1). Second, I tested the spring condition hypothesis, by examining the tolerance of scaup to intermittent feeding (Chapter 2). In both chapters, I used a multi-species approach by including Northern shovelers (*Anas clypeata*) and American wigeon (*Anas americana*) for comparison. These sympatrically breeding species are abundant both in the Alaska boreal forest and the prairie-parkland region, have relatively stable or increasing continental populations, and provide contrasts in terms of life history strategies and characteristics (Bellrose 1980, Wilkins et al 2006).

# CHAPTER 1. Comparative Demography of Lesser Scaup and Other Boreal Ducks on the Yukon Flats, Alaska[1]

**ABSTRACT** Information on the breeding ecology of boreal waterfowl is lacking, despite the boreal region's importance to the continental waterfowl population and to duck species that are currently declining, such as lesser scaup. We estimated breeding probability, nest survival, and female breeding season survival of lesser scaup, Northern shoveler, and American wigeon on the Yukon Flats National Wildlife Refuge, Alaska, in 2005 and 2006. We captured and marked 119 female ducks (93 lesser scaup) with radio transmitters during the pre-laying and nesting periods. Although all marked females were paired throughout the pre-laying and incubation periods, breeding probability over both years was estimated as 0.12 (SE = 0.05, n = 67) using radio telemetry. The proportion of females undergoing rapid follicle growth at capture in 2006 was 0.46 (SE = 0.11, n = 37), based on concentration of yolk precursors in the blood plasma. By combining multiple methods of characterizing reproductive status (radio telemetry, yolk precursors, and post-ovulatory follicles), we estimated the maximum lesser scaup breeding probability as 0.68 (SE = 0.08, n= 37) in 2006. Notably, breeding probability of scaup was positively related to female body mass. Nest survival probability was 0.08 (SE

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= 0.05) for lesser scaup, and 0.22 (SE = 0.03) for other ducks nesting during the same time period as scaup. Survival of adult female lesser scaup during the breeding season was 0.92 (SE =0.05) in 2005 and 0.86 (SE = 0.08) in 2006. Our results suggest that breeding probability is much lower than expected for boreal lesser scaup, and the assumption that all paired females attempt to breed should be re-evaluated. Recruitment estimates based on annual breeding pair surveys may overestimate the productivity of scaup pairs in the boreal region.

**KEY WORDS** breeding probability, boreal forest, female survival, lesser scaup, nest survival, shoveler, wigeon, Yukon Flats.

## INTRODUCTION

Extensive research has provided managers with information on the population dynamics of many waterfowl species nesting in the prairie and parkland regions of North America (e.g., Rohwer 1992, Johnson et al. 1992, Beauchamp et al. 1996). Conversely, data on ducks breeding in the boreal forest region are lacking even though the region is used by over 34% of the continental population (Wilkins et al. 2006). The breeding ecology of boreal ducks is poorly described, with only a few studies of nest survival (Petrula 1994, Grand 1995, Fournier and Hines 1998, Safine 2005, Walker et al. 2005, Corcoran et al. 2007) and female survival (Brook and Clark 2005).

Furthermore, the boreal forest is the most critical breeding area for some species that are currently declining, such as lesser scaup (*Aythya affinis*; Austin et al. 2000, Afton and Anderson 2001). In 2006, the combined populations of lesser and greater scaup were nearly 50% below the goal set by the North American Waterfowl Management Plan (Wilkins et al. 2006). The decline is likely most pronounced in lesser scaup, which comprise nearly 90% of the continental scaup population. The majority of lesser scaup (70%) breed in the western boreal forest of Alaska and Canada (Bellrose 1980), which is also where scaup populations have seen the steepest declines (Afton and Anderson 2001).

Waterfowl management in North America is largely based on spring surveys of breeding duck populations, and the untested assumptions that 1) all observed paired females attempt to nest, and 2) the proportion of non-breeders (unpaired females) in a population is the same across all regions of the continent (Cowardin and Blohm 1992, Nichols et al. 1995). However, for many species, the proportion of non-breeding females in the population and how these non-breeders are distributed across the continent is unknown. Because regional differences in breeding season length, nesting habitat, food sources, and predator communities may influence duck production rates (Calverly and Boag 1977, Johnson et al. 1992), it is likely that breeding probability differs among species and across the landscape. Information on the differences between vital rates in the boreal forest and other regions could improve population monitoring and the management of waterfowl.

Population models predict that changes in female survival will affect scaup population growth to a greater extent than proportional changes in productivity (Flint et al. 2006, Koons et al. 2006); however, these predictions are based on limited data for seasonal patterns in mortality and several other population parameters (e.g., breeding probability), particularly for lesser scaup in the boreal forest. Because a significant portion of female mortality in other duck species occurs during the breeding season (DeVries et al. 2003), the breeding portion of the annual cycle could be more crucial to population dynamics than the remainder of the year (Sargeant and Raveling 1992, Hoekman et al. 2002).

In this study, we were initially interested in female breeding season survival and nest survival of boreal waterfowl for species and regional comparisons. In addition to lesser scaup, we chose Northern shoveler (*Anas clypeata,* hereafter shoveler) and American wigeon (*Anas americana,* hereafter wigeon) as study species due to their abundance in the Alaskan boreal forest (USFWS 1987) and their widespread breeding distribution in both the boreal forest and prairie-parkland (Bellrose 1980). We predicted that the majority of females migrating to the boreal forest would attempt to breed, resulting in relatively low female survival during the breeding season due to increased risk of predation during incubation and brood rearing. However, data collected in our first field season led us to expand our objectives to include scaup breeding probability, defined as the probability that a female will lay ≥ 1 egg during the season. Although there are little data on breeding probability for most species of ducks, it is commonly assumed that females of relatively small-bodied, short-lived waterfowl species, such as scaup, attempt to nest every year (Bellrose 1980, Johnson et al. 1992), and that a large proportion of female mortality is associated with nesting activities (Sargeant and Raveling 1992). However, non-breeding or delayed breeding has been documented in large-bodied species such as canvasbacks (*Aythya valisineria,* Anderson et al. 2001), and low breeding probability has been suggested as the reason for the decline of black ducks (*Anas rubripes*) in eastern North America (Petrie et al. 2000). Thus, our objectives were to examine the factors affecting breeding probability, nest survival, and hen survival of scaup, shoveler, and wigeon on the Yukon Flats National Wildlife Refuge in interior Alaska.

## STUDY AREA

The Yukon Flats National Wildlife Refuge (Yukon Flats) encompasses approximately 9 million acres of boreal forest along the Yukon River floodplain, and comprises the largest interior wetland basin in Alaska (Heglund 1992). Over 48% of the Yukon Flats landscape is classified as wetland and riparian areas, with as many as 40,000 lakes occurring on the refuge (USFWS 1987). Most lakes on the Yukon Flats are closed basin lakes over discontinuous permafrost, which were once believed to have little annual variation in wetland size and abundance compared to other major waterfowl breeding areas in North America (USFWS 1987). However, Riordan et al. (2006) showed that some closed basin lakes on the Yukon Flats have lost 18% of their area over the past 50 years, possibly due to affects of global warming. The Yukon Flats supports about

800,000 duck pairs annually, the second largest concentration of ducks in Alaska (USFWS 1987), and is regarded as a principal area of production in the North American Waterfowl Management Plan (USFWS 1986). Scaup have the highest density of the waterfowl species on the refuge, with over 100,000 pairs surveyed per year (Conant and Groves 2005). Waterfowl nest in the refuge's forested areas and wet graminoid meadows (Heglund 1992), but the refuge includes a varied landscape that is heavily influenced by frequent fire disturbance and flooding (USFWS 1987).

Our study site was located on the Long Lake wetland complex (66° 20' N, 147° 58' W) 6 km north of Marten Island on the Yukon River and approximately 25 km west of the village of Beaver, Alaska (Fig. 1). The site is representative of the habitats on the Yukon Flats, as its many lakes are surrounded by emergent vegetation, wet meadows, black spruce bogs (*Picea mariana*) and mixed forest uplands characterized by stands of aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Previous waterfowl research has been conducted in this area (Grand 1995, Esler et al. 2001), and in other areas on the refuge (Heglund 1988 and 1992, Safine 2005, Corcoran et al. 2007).

## METHODS

### Data collection

Females were captured on the breeding grounds using decoy traps with live scaup, shoveler, and wigeon decoy hens (Anderson et al. 1980, Sharp and Lokemoen 1987). We used 10-14 decoy traps throughout the study area for 24 hours a day from May 20-June 10 in 2005, and May 12 – June 10 in 2006. Because shovelers and wigeon have earlier nest initiation dates than scaup (Bellrose 1980), shovelers and wigeon were targeted during the first two weeks of trapping, and scaup were targeted after the first week of trapping until June 10. Traps were checked at least once every 12 hours. We marked wild females with 9g transmitters (Advanced Telemetry Systems, Isanti, MN) using a prong and glue attachment method (Pietz et al. 1995) and a USFWS leg band. Each scaup was also marked with an individually coded nasal saddle. Transmitters were equipped with a mortality switch, which increased the signal speed after 12 hours of inactivity. We weighed each female and took measurements of size, including wing chord, culmen, tarsus, and head length. Age was determined by assessing wing plumage in shovelers and wigeon (Carney 1992). Scaup age was determined in 2005 by comparing eye color with charts from Trauger (1974). In 2006, we compared eye color with Munsell soil color charts (GretagMacbeth, New Windsor, NY; Trauger 1974) to examine eye color with more accuracy, which we then compared with age determinations in Trauger (1974).

In 2006, we also collected blood from each captured female for analysis of yolk precursors in the blood plasma. High levels of the yolk precursors vitilogenin (VTG) and very low density lipoprotein (VLDL) indicate rapid follicle growth (RFG, Gorman 2005). Yolk precursor concentration in the blood increases to detectable levels when the first follicle begins RFG, and it remains high throughout the laying period (Gorman 2005). We collected blood from the brachial vein into heparinzed vacutainers via blood collection kits (23 gauge needles with 30.5cm tubing, BD Vacutainer, Franklin Lakes, NJ), and kept it cool until it could be centrifuged, usually within two hours of collection. Plasma was extracted from the blood, frozen, and shipped to Simon Fraser University for analysis as described in Gorman (2005). Females undergoing RFG were classified as those with VLDL levels ≥ 5.3 mmol/L and VTG levels ≥ 1.4 ug/mL, from validation on greater scaup (Gorman 2005).

After a female was marked with a radio transmitter, we located her once or twice a day until July 15 to determine her fate (alive or dead) and breeding status (e.g., nesting, renesting, or not apparently nesting) using ground telemetry. During this intensive search period, we also tracked females using a floatplane equipped with a telemetry receiver 1-2 times a week to ensure that all females on the study area were located. If we suspected that a female was on a nest during an aerial telemetry session, we would confirm her location by ground telemetry as soon as possible. After July 15, we located females every 3-5 days using both ground and aerial telemetry. When a mortality signal was detected, we visited the site of death to collect data (e.g., hair, track, disturbance level) to determine the apparent cause of mortality (Sargeant et al. 1998).

When a nest was found, we recorded the location with a GPS unit and placed a small piece of flagging 10m north of the nest. During the initial nest visit, we recorded clutch size, measured and marked each egg with permanent ink, and candled a subset of eggs to determine the start of incubation (Weller 1957). Active nests were visited every 5-7 days to determine success or failure of the nest. To minimize disturbance, we visited nests in the afternoon when females were more likely to be on an incubation break (Gloutney et al. 1993), and we remained at the nest for the shortest time possible. Nests of marked hens were monitored using telemetry and we attempted to visit the nest only when the female was absent. If a nest failed, we collected data on condition of nest bowl and surrounding area (e.g., scat, cached eggs) to determine the likely cause of failure (Sargeant et al. 1998).

We also used rope-dragging (Petrula 1994) to locate additional nests for estimates of nest survival. Although we opportunistically found nests during the trapping period, intensive nest searching began on June 10 in both years. This sampling regime was used primarily to gather information about scaup nest survival, and it likely excluded many nests of species that initiate prior to scaup (e.g., most dabbling ducks). Because there are also late nesting attempts by non-scaup species such as shoveler and green-winged teal (*Anas crecca*), it allowed a comparison between scaup and non-scaup during the same time frame.

In addition to capturing females during the pre-laying period, nest traps were used to capture a larger sample of breeding scaup on nests from 10 to 25 days of incubation (Weller 1957). Nest trapped females were marked with radio transmitters and processed in the same way as decoy trapped hens, except we lightly anesthetized the bird with methoxyflurane (Metofane, Schering-Plough Animal Health Corporation, Union, NJ) before placing her back on the nest to reduce the chance of nest abandonment (Rotella and Ratti 1990).

After 15 July 2006, we collected 10 marked females that had not apparently nested by shooting. We froze the carcasses immediately after collection and later extracted the ovaries, which we stored in 10% formalin. We macroscopically examined the ovaries for post-ovulatory follicles, using visual cues as described in Lindstrom et al. (2006) to determine reproductive status.

## Statistical analysis

We used an information-theoretic approach to select models, to estimate nest and female survival and breeding probability, and to evaluate hypotheses concerning the relative importance of explanatory variables to each of these parameters. For all analyses, we used general linear models in program MARK (White and Burnham 1999) to generate maximum likelihood estimates and associated sampling variances. We used the logit link function for all covariates to accommodate the binomial nature of survival and breeding probability data (Ramsey and Shafer 1997).

To estimate breeding probability, we used the known-fate module in program MARK, which allows probabilities to be modeled as a function of multiple covariates, such as time, age, and habitat characteristics (Dinsmore et al. 2002). To estimate both hen survival and nest survival, we used the nest survival module in program MARK, which is a form of known-fate model that allows for uncertainty in the exact date of female mortality or nest failure when irregular sampling intervals are used. The assumptions of known-fate and nest survival models are: 1) with nest survival data, nests are correctly aged during the first visit; 2) fate is determined correctly; 3) there is no observer effect on the fate; 4) individual fates are independent; and 5) there is no heterogeneity in survival probability (Dinsmore et al. 2002).

We began by developing a set of biologically relevant models prior to each analysis and used Akaike's Information Criterion ($AIC_c$) to select the best-approximating model (Burnham and Anderson 1998). There was likely some over-dispersion created by assumption violations; however, we chose not to use the currently available methods for correcting for over-dispersion because they tend to over-inflate the variance by an unknown amount (Dinsmore et al. 2002). We calculated estimates from the best-approximating model by back-transforming the logit link regression equation using the beta estimates and covariate values. Covariates were considered important when they were included in models within 7 $AIC_c$ of the best model (Burnham and Anderson 1998). For period-specific estimates of survival, we raised the daily survival probability to the number of days in the corresponding interval. For nest survival, we used 35 days as the combined laying and incubation period, assuming an average clutch size of 9 eggs and average incubation time of 26 days in scaup (Bellrose 1980, Austin et al. 1998). We estimated female survival over a period of 82 days. We estimated the sampling variance of products using the Delta method (Seber 1982).

**Breeding probability**

Due to a small sample size of shoveler and wigeon, we only estimated breeding probability for lesser scaup. Breeding probability is defined as the probability that a female will initiate a nest (lay ≥ 1 egg) during a breeding season. This information can only be obtained by directly observing that females initiated a nest via radio telemetry or by examining post-ovulatory follicles (Lindstrom et al. 2006). We used radio telemetry methods in both 2005 and 2006. However, telemetry methods often do not distinguish between birds that failed during the laying period and non-breeders. The probability of detecting a nest is extremely low during the laying period because females spend little time on the nest (Afton and Paulus 1992). To define the uncertainty associated with using telemetry to estimate breeding probability, McPherson et al. (2003) developed a method to estimate the number of missed nesting attempts. Because of a limited sample size, we used a similar ad hoc equation based on the Mayfield method (Miller and Johnson 1978, Johnson and Shaffer 1990) to estimate the number of nesting attempts we would expect from marked females ( $\hat{N}_{MJ}$ ) in both 2005 and 2006:

$$\hat{N}_{MJ} = \frac{x_J}{\hat{S}_1 \hat{S}_2 \cdots \hat{S}_J}$$

where J is the age of the oldest nest found, $x_J$ is the number of nests that survived to day J, and $\hat{S}_J$ is the DSR for each day up to day J. Nest age (J) included the laying period and was calculated as the sum of the clutch size (assuming that the female laid one egg per day) and the number of days incubated when the nest was found. Sampling variance of $\hat{N}_{MJ}$ was estimated as:

$$Var(\hat{N}_{MJ}) = \frac{(x_J)^2}{Var(\hat{S}_1 \hat{S}_2 \cdots \hat{S}_J)}$$

using the Delta method (Seber 1982).

In 2006, we also measured levels of plasma yolk precursors (YP) to identify females that were undergoing RFG at the time of capture. A confirmation that a female is developing eggs is not equivalent to determining that a female lays ≥ 1 egg because it is possible that a female could abort RFG, reabsorb the nutrients contributed to developing follicles, and never initiate a nest (Gilbert et al. 1983, Thomas 1988). However, the measurement of YP can indicate if a female was physiologically able to breed. Similar to telemetry methods, YP measurements are not without some error. Levels of YP are only elevated up to 12-16 days prior to laying (Gorman 2005, Safine 2005). Across the set of observed nests in our study areas, initiation dates differed more than 30 days; thus there is the possibility that some individuals were captured on the breeding area prior to initiation of RFG. However, we timed capture to minimize the time between capture and the mean nest initiation date of lesser scaup at our study site.

In summary, we estimated two parameters related to breeding effort, and examined sources of variation for both parameters in two separate analyses using the known-fate model: 1) breeding probability using telemetry data from 2005 and 2006 and 2) the probability that a female was undergoing RFG at the time of capture (RFG probability), determined from YP analysis in 2006. We hypothesized that the variables of age, body condition, and year (breeding probability only) could be used to predict both breeding probability and RFG probability. Older females and those with more body reserves may be more likely to nest (Johnson et al. 1992). In addition, annual variation in food resources or other environmental conditions could affect breeding probability. We considered both two-way additive and multiplicative models with age, body mass, and year. We included additive models that controlled for date of capture because body mass probably increases after arrival to the breeding area. To also control for potential effects of variation in structural size (Sedinger et al. 1997), we included models with an additive relationship between body mass and one or two of the following structural measurements: tarsus, culmen, wing chord, and head length. We also performed a principal components analysis (PCA, PROC FACTOR, SAS Institute version 9.1) on all four structural measurements. The first principal component (PC1), which accounted for 43% of the variation in the morphological measurements, was also included in additive models with body mass.

A main assumption of known-fate models is that the fate is known for certain. Here there is some uncertainty about the classification of females in non-nesting and non-RFG groups. We cannot be certain that females were correctly classified as non-nesters or non-RFG, so our statistical methods for estimating breeding probability using only telemetry data, or the probability that a female was undergoing RFG using only YP data, are conservative and likely represent the minimal probability of breeding or RFG.

We therefore calculated breeding probability of scaup in 2006 by combining all available methods: telemetry, YP, and the examination of post-ovulatory follicles (POF) of 10 collected females. However, it is important to note that this approach requires the assumption that all females characterized as undergoing RFG actually laid ≥ 1 egg. We used three incremental approaches: 1) combining telemetry data and YP data, 2) combining telemetry and YP data with POF data, and 3) combining telemetry, YP data and POF data, and inflating the number of RFG females to compensate for an unknown amount of detection error due to early capture. We estimated misclassification rates for combined telemetry and YP data by determining the proportion of females that were classified as non-breeders from one method, but were classified as a breeder with the other method (Bond et al., in prep). The total proportion of misclassified breeders is simply the product of the misclassification rates from YP and telemetry methods added to the total proportion of females classified as breeders with either method. We could not calculate a misclassification error for POF data because we examined only 10 of 37 females for POF's. Thus, when POF data were included (second and third approaches), we incorporated the misclassification rate for telemetry and YP data only. In the third approach, we also assumed that all females captured on or before May 31 had the same RFG probability as females captured after May 31. May 31 was the latest date that a female was classified as non-RFG but actually bred as indicated by POF methods.

### Covariates of nest survival

For the nest survival analysis, we included the covariates of year, group (lesser scaup vs. all other duck species combined), and the distance of the nest to open water. We hypothesized that daily survival rates (DSR) of nests vary by year because previous studies have found high annual variation in waterfowl nest survival (Walker et al. 2005, Flint et al. 2006), and summer temperatures and precipitation are variable on the Yukon Flats (Heglund 1992). We included a group covariate (lesser scaup vs. other duck species) because lesser scaup initiate nests later than other duck species (Bellrose 1980), when nest habitat quality or predator communities may differ, which could result in different nest survival probabilities. Additionally, low nest survival has been proposed as a reason for the scaup decline (Austin et al. 2000); thus DSR may be lower for lesser scaup than other species nesting at the same time. Nests that are close to the water's edge may have a lower survival probability because predators, such as black bears (*Ursus americanus*), red fox (*Vulpes vulpes*), and mink (*Mustela vison)*, may use lake margins for foraging (K. Martin, pers. obs). We also considered that DSR may demonstrate an increasing or decreasing linear or quadratic trend over the season (season day and season day$^2$) or with the age of the nest (nest age and nest age$^2$). DSR may be higher for nests initiated earlier or later in the nesting season because of changes in vegetation, hen condition, or predator communities as the season progresses (Klett and Johnson 1982). It is also likely that nests have lower survival during the laying period than during incubation because the nests at the most risk of predation probably get depredated early (Klett and Johnson 1982). We considered all covariates singly, and in two-way additive and multiplicative models.

### Covariates of female survival

We hypothesized that female survival would differ between genus (*Aythya sp.* vs. *Anas sp.*) because of different life history strategies and nesting habits; therefore we only considered models that included genus as a group covariate (Krementz et al. 1997, Blums et al. 2002). We then considered the following covariates in additive and multiplicative models with genus: year, trend across the breeding season (season day), nesting behavior (e.g. nesting or not nesting), and body mass at capture. We hypothesized that average female survival probability would differ by year because of variation in the environment (weather, food resources, predator abundance), and in breeding effort (Rotella et al.

2003). In addition, female survival probability could vary across the breeding season, as females may be at more risk of mortality during incubation or brood rearing periods than during the pre-laying period. Nesting behavior may put females at higher risk of predation than other activities (Sargeant and Raveling 1992). Thus, we considered nesters and non-nesters as separate groups, where nesters, defined as those birds observed on nests using radio telemetry. Likewise, we included body mass as a covariate because females with a larger body mass may expend more reproductive effort, which could result in lower survival probability (Rotella et al. 2003).

## RESULTS

### Breeding probability

All marked females remained paired after capture and throughout the nest initiation period at our study site. Yet in 2005 we identified only 7 out of 31 marked female scaup as nesters using radio telemetry, one of which initiated 2 nests. In 2006, we identified 4 out of 38 marked scaup as nesters with radio telemetry. In both years, one scaup left the study area directly after capture, and thus both were censored from the analysis of breeding probability. Of the 5 shovelers captured in 2005 and 2006, 4 were identified as nesters, 2 of which also re-nested in the same season. The remaining shoveler left the study area after capture; consequently its nesting status was unknown. Of 11 marked wigeon in 2005, two left the study area after capture, and 3 out of 9 remaining females were found on nests. In 2006, 1 wigeon left the study area after capture, and none of the 8 remaining wigeon were found on nests. Because of low sample sizes for shoveler and wigeon, we focused only on lesser scaup breeding probability for the remainder of the analysis, but addressed breeding probability of these two species in the discussion.

*Lesser Scaup breeding probability.*-- The best-approximating model suggested that yearly variation, female body mass, and capture date were important predictors of breeding probability (Table 1, Fig. 2). Breeding probability likely varied by year, with a higher probability in 2005 than 2006, but the logit estimate confidence interval bounded zero; hence the year effect was only weakly supported by the models ($\beta_{year} = 3.27$, SE = 1.75, 95% CI = -0.02 to 6.70). However, there was evidence of a positive effect of body mass ($\beta_{wt} = 0.02$, SE = 0.01, Fig. 2), and a negative effect of capture date ($\beta_{date} = -0.25$, SE = 0.10) on breeding probability in the top model. Capture date likely lessens the positive effect of body mass because females probably increased their body mass over time. Thus, females captured later were generally larger than those captured earlier during trapping. Head length was consistently included in the top models; thus, structural size was an important covariate when we included body mass as a predictor of breeding probability. Model selection did not lend strong support to female age as a predictor of breeding probability, as the first model that included age has a $\Delta AIC_c$ of 3.73 and $AIC_c$ weight of 0.04 (Table 1). Because of high model selection uncertainty (e.g. 31 models within 7 $AIC_c$ of the top model, Table 1), we chose to use model averaging to obtain estimates of breeding probability. Using radio telemetry methods alone, the probability that a lesser scaup female laid at least one egg is 0.12 (SE = 0.05).

*Number of nests initiated by Lesser Scaup.*-- Estimates of the number of nests initiated in 2005 and 2006 indicate that we missed only a small number of lesser scaup nesting attempts with radio telemetry methods; however, data were limited and uncertainty in estimates was high. In 2005, the oldest nest from a marked female lesser scaup was found 16 days after the first egg was laid, and the nest survival probability during days 1-16 was 0.27 (SE=0.08). Three out of these 8 nests survived to day 16, and 1 failed in a time interval that included day 16. When assuming that the fourth nest survived to day 16, the estimated number of nests initiated by marked lesser scaup was 15 (SE = 39). When we assumed that the fourth nest did not survive to day 16, the estimated number of nests initiated was 11 (SE = 52) in 2005. In 2006, the oldest nest of a marked female scaup was found at 13 days old, and the nest survival probability during that interval was 0.21 (SE = 0.07). We located 4 nests of marked females, one of which survived to 13 d. Based on these data, we would expect that 5 scaup nests (SE = 15) were initiated by marked females in 2006. Although these estimates have high imprecision, they suggest that we found approximately 0.75 of the nests initiated by marked scaup (12 out of 16 nests).

*Lesser Scaup RFG probability.* -- Yolk precursor analysis indicated that 17 out of 37 lesser scaup were undergoing RFG when captured. Seven of the females categorized as RFG had VLDL plasma levels below, but VTG plasma levels above, the respective cutoff values for RFG, though the converse did not occur. Because measures of VTG have a lower error rate when discriminating between reproductive states than measures of VLDL (10% vs. 26%, Gorman 2005), the VTG measurements were given precedence in these cases. Only VLDL was measured for four females due to a small blood sample; thus for these birds, VLDL was used as the definitive measure.

The best-approximating model of RFG probability included body mass and two structural covariates (Table 2, Fig. 3). Body mass had a positive effect on RFG probability ($\beta_{wt}$ = 0.04, SE = 0.01, Fig. 3), but the magnitude of this relationship was lessened with the inclusion of two structural covariates: head length and tarsal length, each of which had negative parameter estimates ($\beta_{head}$ = -0.94, SE = 0.40; $\beta_{tarsus}$ = -1.04, SE = 0.61). Similar to the structural covariates, capture date was included in many top models, the first of which had a $\Delta AIC_c$ of 0.43, and $AIC_c$ weight of 0.16. We chose to use a model averaged estimate because of high model selection uncertainty. Based on the top model, the probability that a lesser scaup female was undergoing RFG at capture in 2006 is 0.46 (SE = 0.11).

*Lesser Scaup Post-ovulatory Follicles.--* Based on macroscopic examination of ovaries, 4 of the 10 collected female lesser scaup had visible evidence of post-ovulatory follicles. None of these females were classified as nesters using telemetry methods. Two were classified as non-egg producers via YP methods; however, both of these were captured relatively early during the breeding season (May 21 and May 25).

*Lesser Scaup breeding probability from combined methods.--* First, we estimated the breeding probability using both telemetry and YP data. In 2006, only one female lesser scaup was classified as both a RFG bird and a nester. Three scaup classified as nesters with telemetry were classified as non-RFG with YP methods. All three misclassified females were captured early in the season, one 16 days before nest initiation, and two 23 days before nest initiation, when we were targeting shovelers and wigeon for capture. The proportion of female lesser scaup classified as RFG using YP methods was 0.46, and the proportion of female lesser scaup classified as breeders from telemetry methods was 0.12. The misclassification rates were 0.08 and 0.43, respectively, and their product (the overall misclassification rate) was 0.04. Twenty out of 37 lesser scaup were classified as potential breeders using telemetry and YP data combined, resulting in a breeding probability estimate of 0.57 (SE = 0.08) when the misclassification rate was applied.

Second, we incorporated POF data from 10 collected females. Twenty-two out of 37 lesser scaup were classified as potential breeders from telemetry, YP or POF methods. Using the same misclassification rate as above, these methods resulted in a probability estimate of 0.63 (SE = 0.08).

Finally, we combined telemetry, YP data, and POF data, and inflated the number of birds undergoing RFG to compensate for error due to early capture. Thirteen of 20 females caught after May 31 were classified as RFG by YP methods, representing a RFG probability of 0.65 during that period. We applied this probability to the 17 birds caught on or before May 31, resulting in 11 birds classified as RFG. Because nine of these birds were already classified as breeders by YP, telemetry, or POFs, this method resulted in inflating the number of breeding females from 22 to 24 out of 37. Using the misclassification rate of 0.04, the breeding probability of scaup using all methods is 0.68 (SE = 0.08).

**Nest survival**

We monitored 250 duck nests during 2005 and 2006, 122 of which were scaup nests. Notably, we located fewer nests in 2006 (115) than in 2005 (135), despite a greater search effort during the 2006 field season. We censored 19 scaup nests and 14 non-scaup nests because of abandonment after the first visit to eliminate bias caused by possible observer effects, resulting in a total of 217 total duck nests used in the analysis. Non-scaup nests belonged to shoveler, wigeon, green-winged teal, canvasback, mallard (*Anas platyrhynchos*), Northern pintail (*Anas acuta*), ring-necked duck (*Aythya collaris*), redhead (*Aythya americana*), and white-winged scoter (*Melanitta fusca*). Shoveler nests constituted the majority of non-scaup nests (66 %). After censoring for nests that failed during the laying period, mean clutch size of scaup over both years was 7.6 (n = 107, SE = 0.14). Mean nest initiation date of scaup was 8 June in 2005 (range = 21 May – 21 June, n = 63, SE = 0.94) and 7 June in 2006 (range = 23 May – 27 June, n = 57, SE = 0.91).

The main cause of nest failure was predation, as it accounted for 98% (2005) and 88% (2006) of failed nests in our analysis. We directly observed a black bear depredating nests, and we suspect that bears search for duck nests around the edges of ponds and lakes during the early breeding season. Other likely mammalian nest predators include red fox, mink, marten (*Martes americana*), wolf (*Canis lupus*), lynx (*Lynx canadensis*), ermine (*Mustela erminea*), and squirrel (*Tamiasciurus hudsonicus* and *Spermophilus parryii*). Avian predators, such as Northern harriers (*Circus cyaneaus*), short-eared owls (*Asio flammeus*), red-tailed hawks (*Buteo jamaicensis*), and mew gulls

(*Larus canus*) also frequent the area during the nesting period. The other cause of nest mortality was abandonment, probably because of cold weather or inadequate body condition of incubating females.

The best-approximating model of nest survival, DSR (group*season day$^2$), indicates that DSR is lower for scaup than for other ducks nesting during the same time period ($\beta_{scaup}$ = 0.34 SE = 1.77; $\beta_{other\ ducks}$ = 3.10, SE = 0.73; Table 3). This model also includes a quadratic increase in DSR with season day at a different rate for scaup than for other ducks (Fig. 4). Overall nest survival estimated from the best approximating model was 0.08 (SE = 0.05) for scaup and 0.22 (SE = 0.03) for other ducks.

The year covariate is included in many of the models within 7 AICc of the best approximating model (Table 3), indicating some annual variation in DSR. In the second best model, DSR (year*season day), DSR for all duck species combined was higher in 2005 (0.20, SE = 0.04) than in 2006 (0.08, SE = 0.03). Model selection lends little support to the effects of nest age on DSR at this study area, as the first model that includes this covariate has a $\Delta AIC_c$ of 5.64 and $AIC_c$ weight of 0.03 (Table 3). Likewise, a relationship between distance of the nest to open water and DSR was not well supported, as the first model that includes this covariate has a $\Delta AIC_c$ of 6.01 and $AIC_c$ weight of 0.03 (Table 3).

**Female survival**

Over the course of the study, 119 females were captured and marked with radio transmitters. In 2005, we captured 31 scaup, 11 wigeon, and one shoveler early in the breeding season, and 14 scaup during nesting. In 2006, we captured 38 scaup, 10 wigeon, and 4 shovelers early in the season, and 10 scaup during nesting. Two scaup, one from each year, were censored from the analysis because they left the study area directly after capture. We also censored data from females that left the study area for more than 14 days, because their fate could not be determined during that time. There were 10 mortalities during the study: in 2005, 2 scaup and 1 wigeon died, and in 2006 7 scaup died. The cause of mortality for females was largely unknown; however, 2 scaup were found partially consumed by predators in the vicinity of their previously active nests, and 1 wigeon radio transmitter was found in an active red fox den.

The best approximating model indicated that female survival during the breeding season varied by genus and year ($\beta_{aythya\ 2005}$ = 6.89, SE = 0.71; $\beta_{anas2005}$ = 6.27, SE = 1.00; $\beta_{aythya\ 2006}$ = 5.69, SE = 0.38; Table 4). From this model, we estimated female scaup survival in 2005 as 0.92 (SE = 0.05) and female scaup survival in 2006 as 0.76 (SE = 0.08). Survival of shoveler and wigeon combined in 2005 was 0.86 (SE = 0.13), and 1.0 in 2006 because there were no female shoveler or wigeon mortalities in that year. An effect of nesting behavior on survival was not well supported by our data, as the first model that included this covariate had a $\Delta AIC_c$ of 2.25 and AICc weight of 0.13 (Table 4). Likewise, a body mass effect was not well supported, as the first model including body mass as a covariate had $\Delta AIC_c$ of 3.92 and AICc weight of 0.06 (Table 4).

In each year, five females lost transmitters before the last day of monitoring. These transmitters probably fell off during preening, as all were located in the water, but none could be retrieved. We believe that this was not a result of mortality because all occurred in the last month of monitoring, when the attachment was likely less secure.

# DISCUSSION

## Breeding probability

We used multiple methods to examine the breeding probability of scaup, which resulted in a large range of estimates; however, breeding probability is < 1.0 and may vary between years. Notably, all marked scaup females, even those that showed no evidence of breeding, remained paired after capture and throughout the nest incubation period.

We used multiple methods to estimate breeding probability of scaup resulting in a range of estimates. We contend that true scaup breeding probability at the Long Lake complex lies between 0.12 and 0.68. First, the radio telemetry estimate of breeding probability (0.12 in this study) is likely an underestimate. Detection probability can be low during the egg laying period, when females spend little time incubating (Afton and Paulus 1992), and daily survival rates are generally lower than that of older nests (Klett and Johnson 1982). However, we believe that the apparent breeding probability estimate was not driven by poor nest detection probability, because our radio-telemetry methods are equally (or more) rigorous than those in previous studies, which assumed a large proportion of nests were detected (Cowardin et al. 1985, Flint and Grand 1996, DeVries et al. 2003, McPherson et al. 2003). In addition, our calculation of nests initiated by marked scaup suggest that we found 0.75 of nests initiated, similar to the rate estimated by McPherson et al. (2003).

Conversely, the estimate of breeding probability using all methods combined (0.68) is probably positively biased. If true breeding probability was 0.68, our nest detection probability was only 0.16, which is unlikely considering our methodology. Additionally, in combining methods we assumed that once a female initiated RFG, she always laid at least one egg. However, follicular atresia and subsequent re-absorption of nutrients from developed follicles has been documented in arctic nesting geese (Barry 1962) and other birds (Gilbert et al. 1983, Thomas 1988). For species that occasionally forego breeding in a given year, females should continually assess environmental cues that affect their chances of reproductive success and survival because egg development and incubation have high energetic costs (Alisauskas and Ankney 1992, Afton and Paulus 1992) and incubation incurs high predation risk (Sargeant and Raveling 1992). If conditions become unfavorable (e.g., poor food availability, adverse weather, high predator abundance), the ability to abort egg development at any stage and retain the lipid and protein in follicles would be advantageous to females (Barry 1962). Thus, some of the disparity between breeding probability estimates using radio telemetry and yolk precursor data could be explained by follicular atresia. In addition, some non-breeders may not migrate to the breeding grounds; therefore, our study site may have a higher proportion of breeders than the continental scaup population, causing us to overestimate breeding probability.

Although there are no available estimates of scaup breeding probability in the boreal region, breeding probability of lesser scaup in Manitoba was between 0.72 and 0.98 over four years (Afton 1984). This estimate is considerably higher than the scaup breeding probability at the Long Lake complex in 2005 and 2006, but it is still suggests that the a proportion of female scaup do not breed each year.

While we did not thoroughly examine breeding probability of shovelers and wigeon due to low samples sizes, shovelers and wigeon probably have a higher breeding probability than scaup. Although our results indicate low breeding probability for wigeon, it is likely that some nesting attempts were undetected with telemetry methods (McPherson et al. 2003), and the observed lack of nesting may be due to the timing of capture. The mean initiation date of wigeon on the Yukon Flats was May 29 (n = 9, SE = 3.0) during our study. Many female wigeon were unintentionally caught in traps with scaup decoys after June 1 (48% over both years), and they may have already attempted to nest. Even though yolk precursor dynamics have not been validated for wigeon, we collected blood samples from 8 wigeon in 2006. Only 1 out of 5 wigeon captured after June 1 had elevated YP levels in the blood plasma, whereas all 3 females caught before June 1 had elevated YP levels. We suspect that the females captured late were transitioning between the failure of the first nest and a possible re-nesting attempt, prompting their territorial behavior towards decoy hens. Conversely, all shovelers were captured early during trapping (May 15- May 24), and all 4 that remained on the study area attempted to nest. It is possible that the higher observed breeding probability of shovelers, relative to scaup, was due to higher nest survival of shovelers, which resulted in a higher detection probability of shoveler nests.

We found no apparent evidence that transmitters and/or capture and handling affected the breeding effort of female ducks. Both Paquette et al. (1997) and Rotella et al. (1993) compared sutured back-mounted transmitters and implanted transmitters on mallards and found no difference in the number of females that nested. However, the effect of handling and transmitters has not been directly measured because of the difficulty of including a true control group. We have anecdotal evidence that transmitters had little effect on the behavior of birds; for instance, one marked female successfully nested and was harvested in Mississippi by hunters the following January with the transmitter intact and uninfected. In addition, if transmitters or handling affected the breeding probability of scaup, we would also expect to see transmitter or handling effects on shovelers. Shovelers have the smallest body mass of the species that we captured, and they seem to be most sensitive to environmental changes based on the difficulties we had with maintaining a healthy flock of wild-stock shoveler decoy hens. However, all marked wild female shovelers attempted to nest at least once.

Low breeding probability of lesser scaup at the Long Lake complex may not be related to age. Although young female scaup typically delay breeding more often than older females (Afton 1984, Rotella et al. 2003), our model results indicate that older birds have the same breeding probability as young birds, at least for the birds in our study area. Our short term study may have failed to detect delayed breeding by younger birds. Age is difficult to determine for scaup when comparing eye color to charts (Trauger 1974), and inaccurate aging may have induced sampling error that obscured an age effect.

Our results also suggest that lesser scaup females with higher body mass are more likely to initiate RFG or to nest. However, structural size covariates were negatively related to RFG probability, indicating that there may be a limit to the advantages of a large body size. Perhaps because structurally larger females need a larger absolute amount of food than structurally smaller females, they cannot gain enough nutrients to maintain body tissues and reproduce when food supplies are low. This suggests that food availability may limit breeding effort of scaup at the Long Lake complex.

Anteau and Afton (2004) have asserted that food limitation on migratory routes has led to a reduction of female body mass and lipid reserves, which has reduced reproductive success and contributed to the scaup population decline. They found that females migrating through the upper Mississippi flyway were 58.5g smaller in 2000 and 2001 than females in the 1980s, when food resources were thought to be more abundant (Anteau and Afton 2004). Similarly, the mean body mass of female scaup captured by decoy trapping during the pre-laying period in 2005 and 2006 at the Long Lake complex was 700g (n = 71, SE = 7.1), approximately 68g less than the mean body mass of pre-nesting females collected by D. Esler (unpub. data) in 1991 on the Yukon Flats (mean = 768g, n = 34, SE = 13.7). Although decoy trapping may provides a sample that is biased towards birds in poorer condition, this has not been tested formally. Therefore, the lower body mass of pre-breeding female scaup on our study area, and their low breeding probability, lend support to the portion of the spring condition hypothesis that suggests that body condition of female scaup at arrival influences reproductive effort.

In a related study, Martin et al. (Chapter 2) found that captive scaup can completely restore body mass losses of 65g (11% of body mass) in less than 4 days, with no observed changes in body composition. Further, the rates at which modeled body mass is regained is dependent on the quantity and quality of food available to scaup. Because lesser scaup spend 3-4 weeks on the breeding grounds before initiating a nest (Afton 1984), they presumably have adequate time to make up for any mass lost en route if food resources in the boreal forest are sufficient. In addition, Barboza and Jorde (2002) found that the regularity with which food resources are available during the breeding season affects whether black ducks initiate egg laying. Because females can regain mass losses when food is available, we suggest that food- related cues after arrival to the breeding grounds are important in activating the physiological process leading to reproduction. This seems especially likely for scaup, since they depend in part on exogenous resources for the energy to support reproduction (Esler et al. 2001). Thus, the low breeding probability of scaup at the Long Lake complex may be due to inadequate food availability on the breeding grounds, inhibiting them from regaining mass lost on the migratory route. However, direct data on food availability for scaup in the boreal forest are lacking and should be a priority for future research.

### Nest survival

The low overall estimate of scaup nest survival probability at the Long Lake complex (0.08) is consistent with recent studies of nest survival in other Alaskan boreal forest areas. For example, Corcoran et al. (2007) estimated lesser scaup nest survival probability at 0.13 over three years on a similar study area on the Yukon Flats. If nest survival probabilities are now consistently below 0.15- 0.20, and scaup exhibit similar life-histories as prairie nesting dabbling ducks (Cowardin 1985), then nest survival may be a limiting factor to scaup population growth in this region. However, because there is annual variation in scaup nest survival probability, low nest survival may not be consistent over a long time period. Walker et al. (2005) found high annual variation in scaup nest survival at Minto Flats, Alaska, with years of extremely low (0.01) and relatively high nest survival probability (0.61). Studies of nest survival of waterfowl in the boreal forest should span a longer time frame to assess how the variation in nest survival affects scaup population growth. Furthermore, annual survival probability of adult scaup is higher than for most prairie nesting dabbling ducks (Lake et al. 2006, Koons et al. 2006); consequently, nest survival has less effect on the population dynamics of diving ducks with more K-selected life history strategies (e.g., greater scaup, Flint et al. 2006) than prairie nesting dabbling ducks that are more r-selected (Hoekman et al. 2002).

Although early nesters are generally thought to have higher productivity (Johnson et al. 1992), we found that nest success of lesser scaup on the Yukon Flats increased over the nesting season. This could be due to decreases in predation rates or an increase in nesting cover over time, consistent with previous studies of nest survival in the boreal forest (Grand 1995, Walker et al. 2005).

Nest survival probability of lesser scaup was more than two times lower than the nest survival probability of other duck species nesting during the same time period at the Long Lake complex. The species difference that we detected may be attributed to the composition of the sample of non-scaup nests, which included only late-nesting attempts for most species. Because nest survival increases over the season, our sample does not account for early nesting attempt by wigeon and shovelers that could have lowered the overall nest survival estimate for these species.

## Female survival

Breeding season survival rates of female lesser scaup at the Long Lake complex were variable between years (0.92 and 0.76). In 2005 both scaup mortalities were due to predation while females were nesting. However, in 2006 three of the seven mortalities occurred after July 23, when the scaup nesting period was over, and none of the three females were rearing broods. Previous studies have shown that most female mortality during the breeding season occurs while the female is incubating or rearing broods (Cowardin et al. 1985, Kirby and Cowardin 1986, Devries et al. 2003, Richkus et al. 2005); therefore these mortalities may represent mortalities unrelated to the breeding season. The cause of mortality was unknown, but necropsies performed on two of the birds revealed that the mortalities were not attributed to effects of transmitters (K. Converse, USGS National Wildlife Health Center, pers. comm.). Exclusion of these mortalities results in a higher female survival probability of 0.86 (SE = 0.07), which is probably more consistent with lesser scaup female survival during the breeding season.

Although our sample size of shovelers and wigeon was limited, our results indicate that their combined female survival probability was slightly lower than that of scaup in 2005 (0.86), and higher than scaup survival probability in 2006 (1.0). Previous research has also detected species or tribal variation in annual survival of waterfowl (Krementz 1997), and Blums et al. (2002) found that diving duck species had higher annual survival than dabbling ducks. The lower survival of wigeon and shovelers in 2005 may have been driven by increased nesting effort, which increased their predation risk. The overall nesting effort of ducks at the Long Lake complex was probably higher in 2005 than in

2006 because fewer nests were found in 2006 despite an increased search effort. However, because nest survival was higher in 2005 than 2006, it is difficult to discern if this is a consequence of higher nesting effort, higher nest survival, or both.

Although three studies have estimated the breeding season survival of boreal ducks to date (Brook and Clark 2005, Safine 2005, Walker and Lindberg 2005), their direct comparability to this study is limited due to inferences based on differing time frames, methods, and study species. However, all suggest that mortality during the breeding season of boreal waterfowl is substantially higher during the breeding season than at other times of the year, and constitutes nearly 0.50 of total annual mortality. In contrast, breeding season survival of scaup at the Long Lake complex was 0.89 (mean of 0.92 and 0.86). If true annual survival of boreal scaup was 0.58 (apparent annual survival of scaup in the parkland region, Rotella et al. 2003), then the proportion of mortality that occurred during the breeding season of scaup from our study area was only 0.26 (0.11/0.42) of annual mortality. This suggests that either annual survival of boreal scaup is higher than that of prairie-parkland scaup, which is consistent with band-recovery survival estimates of female boreal ducks by Lake et al. (2006), or that a substantial portion of mortality occurs during non-breeding portions of the annual cycle of boreal scaup.

Either sample size or individual heterogeneity could have restricted our ability to detect a relationship between nesting effort and female survival of scaup at the Long Lake complex. Yet, the low breeding probability of scaup suggests that the relatively high breeding season survival probability of scaup could be a result of low breeding effort. Life history theory predicts trade-offs between components of fitness; namely, that the cost of reproduction in one year may impair survival and reproduction in subsequent years (Cam et al. 1998, Stearns 1989). Some evidence supports this idea of a tradeoff for lesser scaup (Rotella et al. 2003), and for prairie-nesting dabbling duck species (Arnold and Clark 1996, Dufour and Clark 2002). Duck species may exhibit this tradeoff to varying degrees along a continuum from r-selected to K-selected life history strategies (Johnson and Grier 1988). A strongly r-selected species attempts to reproduce each year, and consequently has a low survival probability. If the survival cost of breeding varies by age or environmental conditions, a K-selected species may defer breeding when conditions are unfavorable, which could increase their probability of survival and reproduction in following years. Although lesser scaup have been regarded as more K-selected than some dabbling ducks (Vickery and Nudds 1984, Johnson and Grier 1988), our results suggest that boreal forest scaup are closer to the K-selected extreme than previously thought, or that their life history has been artificially altered, leading to their decline.

## MANAGEMENT IMPLICATIONS

All marked lesser scaup females at the Long Lake complex were paired throughout the period of nest initiation and incubation, even those who showed no evidence of breeding. Spring breeding pair surveys assume that all pairs attempt to breed (Cowardin and Blohm 1992, Nichols et al. 1995); however, we found that some pairs on breeding areas are not breeding. Recruitment estimates based on annual breeding pair surveys may be overestimating the productivity of scaup pairs in the boreal, which in turn may have implications for harvest management of these birds. Managers should re-evaluate the definition of a breeding pair and the assumption that all scaup pairs, no matter where they are counted during annual spring surveys, have equal potential productivity.

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Table 1. Selected models of breeding probability (BP) of lesser scaup measured by radio telemetry at the Long Lake complex, Yukon Flats NWR, Alaska, USA in 2005-2006. Models were ranked by their Akaike's Information Criterion scores (AICc) in ascending order. Models contained one or more of the effects of year, age, and body mass (wt). We also included the date of capture (date), structural covariates (tarsus length, culmen length, head length and wing chord length), and a principal components score of structural measurements (PC1) with body mass as effects in some models. Additive effects are denoted with (+).

| Model | k[a] | -2log (l) | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight[b] |
|---|---|---|---|---|---|
| BP (year + wt + date) | 4 | 1.00 | 56.35 | 0.00 | 0.23 |
| BP (wt + date) | 3 | 0.43 | 58.05 | 1.70 | 0.10 |
| BP (wt + date + tarsus) | 4 | 0.36 | 58.41 | 2.06 | 0.08 |
| BP (wt + date + wing) | 4 | 0.29 | 58.81 | 2.46 | 0.07 |
| BP (wt + date + culmen) | 4 | 0.24 | 59.17 | 2.82 | 0.06 |
| BP (wt + date + head) | 4 | 0.19 | 59.65 | 3.30 | 0.04 |
| BP (age + wt + date) | 4 | 0.16 | 60.08 | 3.73 | 0.04 |
| BP (wt + date + PC1) | 4 | 0.15 | 60.12 | 3.77 | 0.03 |
| BP (wt) | 2 | 0.10 | 60.90 | 4.55 | 0.02 |
| BP (wt + tarsus) | 3 | 0.10 | 60.90 | 4.55 | 0.02 |
| BP (wt + wing + tarsus) | 4 | 0.09 | 61.07 | 4.73 | 0.02 |
| BP (age + wt + tarsus) | 4 | 0.09 | 61.09 | 4.74 | 0.02 |
| BP (age + wt) | 3 | 0.08 | 61.45 | 5.10 | 0.02 |
| BP (wt + PC1) | 3 | 0.04 | 62.59 | 6.24 | 0.01 |

[a] Number of parameters

[b] Relative likelihood of the model given the data (Burnham and Anderson 1998)

Table 2. Selected models of the probability of undergoing rapid follicle growth by lesser scaup at Long Lake complex, Yukon Flats NWR, Alaska, USA in 2006. Models were ranked by their Akaike's Information Criterion scores (AICc) in ascending order. Models contained one or more of the effects of age and body mass (wt). We also included the date of capture (date), structural covariates (tarsus length, culmen length, head length and wing chord length), and a principal components score of the structural measurements (PC1) with body mass as effects in some models. Additive effects are denoted with (+).

| Model | k[a] | -2log (l) | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight[b] |
|---|---|---|---|---|---|
| BP (wt + tarsus + head) | 4 | 1.00 | 42.28 | 0.00 | 0.18 |
| BP (wt + date + tarsus) | 4 | 0.81 | 42.71 | 0.43 | 0.15 |
| BP (wt + date + head) | 4 | 0.77 | 42.79 | 0.51 | 0.14 |
| BP (wt + head) | 3 | 0.61 | 43.27 | 0.99 | 0.11 |
| BP (wt + date) | 3 | 0.41 | 44.05 | 1.77 | 0.07 |
| BP (wt + date + PC1) | 4 | 0.41 | 44.09 | 1.81 | 0.07 |
| BP (wt + wing + head) | 4 | 0.33 | 44.47 | 2.19 | 0.06 |
| BP (age + wt + head) | 4 | 0.19 | 45.63 | 3.35 | 0.03 |

[a] Number of parameters

[b] Relative likelihood of the model given the data (Burnham and Anderson 1998)

Table 3. Selected models of daily survival rate (DSR) of duck nests at Long Lake complex, Yukon Flats NWR, Alaska, USA in 2005-2006. Models were ranked by their AIC$_c$ scores in ascending order. Models contained one or more of the effects of group (scaup vs. other duck species), year, season day (linear trend across the season), nest age (linear trend with nest age), and DW (distance of the nest to water). Quadratic trends in season day and nest age (season day$^2$ and nest age$^2$) were also considered. Additive effects are denoted with (+) and interactions denoted with (*).

| Model | k[a] | -2log (l) | AIC$_c$ | ΔAIC$_c$ | AIC$_c$ weight[b] |
|---|---|---|---|---|---|
| DSR (group * season day$^2$) | 6 | 495.31 | 507.35 | 0.00 | 0.53 |
| DSR (year * season day) | 4 | 502.22 | 510.24 | 2.89 | 0.12 |
| DSR (group + season day) | 3 | 505.43 | 511.45 | 4.10 | 0.07 |
| DSR (year * season day$^2$) | 6 | 499.64 | 511.68 | 4.33 | 0.06 |
| DSR (group * season day) | 4 | 503.99 | 512.01 | 4.66 | 0.05 |
| DSR (year * nest age$^2$) | 6 | 500.94 | 512.99 | 5.64 | 0.03 |
| DSR (group + season day$^2$) | 4 | 505.17 | 513.20 | 5.85 | 0.03 |
| DSR (season day * DW) | 4 | 505.34 | 513.36 | 6.01 | 0.03 |
| DSR (year + season day) | 3 | 508.00 | 514.01 | 6.66 | 0.02 |

[a] Number of parameters

[b] Relative likelihood of the model given the data (Burnham and Anderson 1998)

Table 4. Selected models of daily survival rate (DSR) of female ducks at Long Lake wetland, Yukon Flats NWR, Alaska, USA in 2005-2006. Models were ranked by their AICc scores in ascending order. Models contained one or more of the effects of genus (*Aythya affinis* vs. *Anas clypeata* and *Anas americana*), year, season day (linear trend across the season), body mass, and whether the female was nesting or not nesting (nest). Additive effects are denoted with (+) and interactions denoted with (*).

| Model | $k^a$ | -2log(l) | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ Weight$^b$ |
|---|---|---|---|---|---|
| DSR (genus * year) | 3 | 120.85 | 126.86 | 0.00 | 0.40 |
| DSR (genus) | 2 | 124.94 | 128.95 | 2.09 | 0.14 |
| DSR (genus + nest) | 3 | 123.11 | 129.11 | 2.25 | 0.13 |
| DSR (genus + year) | 3 | 123.50 | 129.51 | 2.65 | 0.11 |
| DSR (genus * nest) | 4 | 122.57 | 130.57 | 3.72 | 0.06 |
| DSR (genus + body mass) | 3 | 124.77 | 130.78 | 3.92 | 0.06 |
| DSR (genus + season day) | 3 | 124.79 | 130.79 | 3.93 | 0.06 |
| DSR (genus * season day) | 4 | 124.16 | 132.17 | 5.31 | 0.03 |
| DSR (genus * body mass) | 4 | 124.77 | 132.78 | 5.92 | 0.02 |

[a] Number of parameters

[b] Relative likelihood of the model given the data (Burnham and Anderson 1998)

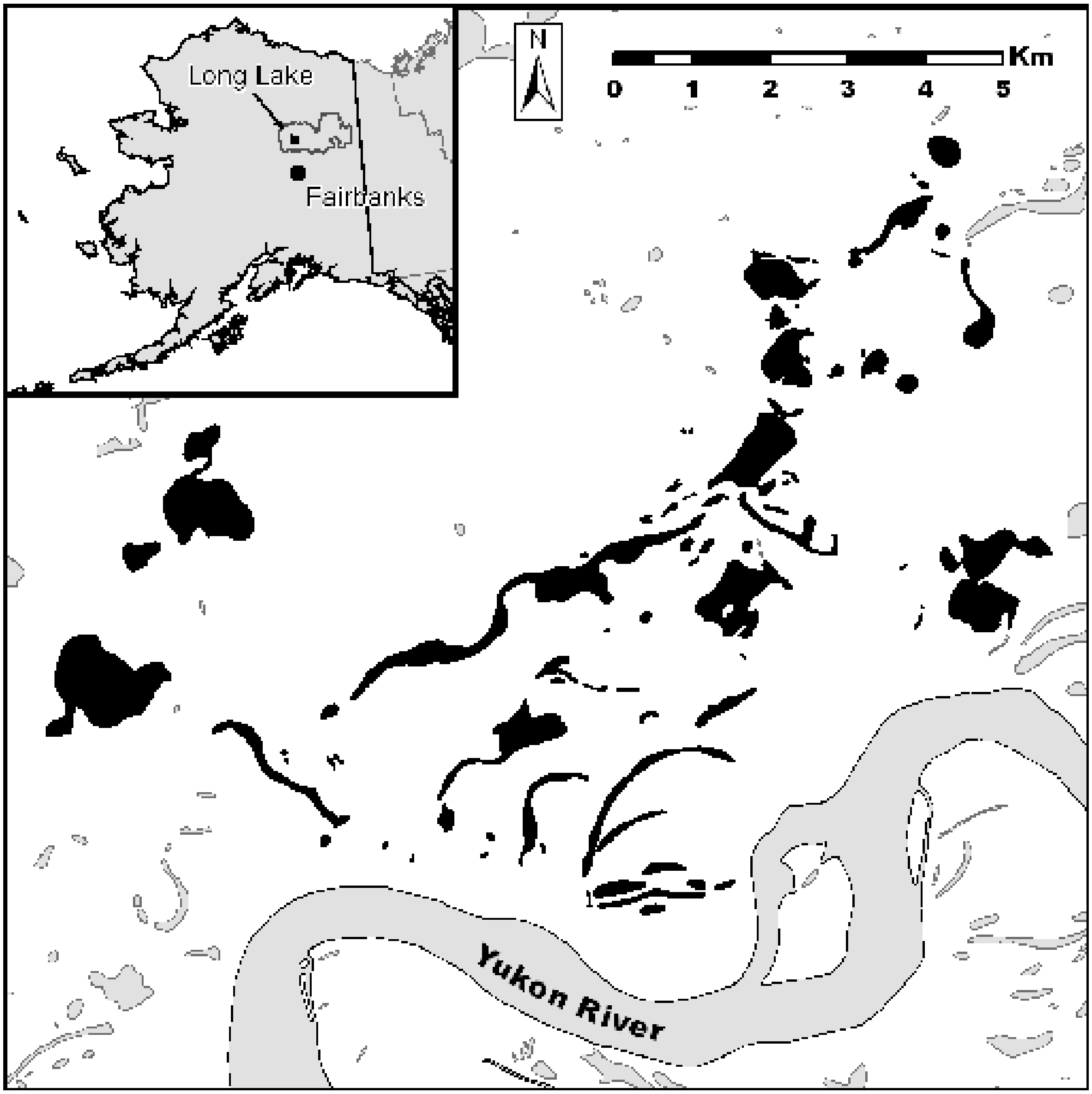

Figure 1. Long Lake complex on the Yukon Flats National Wildlife Refuge, Alaska, USA. The study area lakes are in black, with the inset showing the location of the study area in the state.

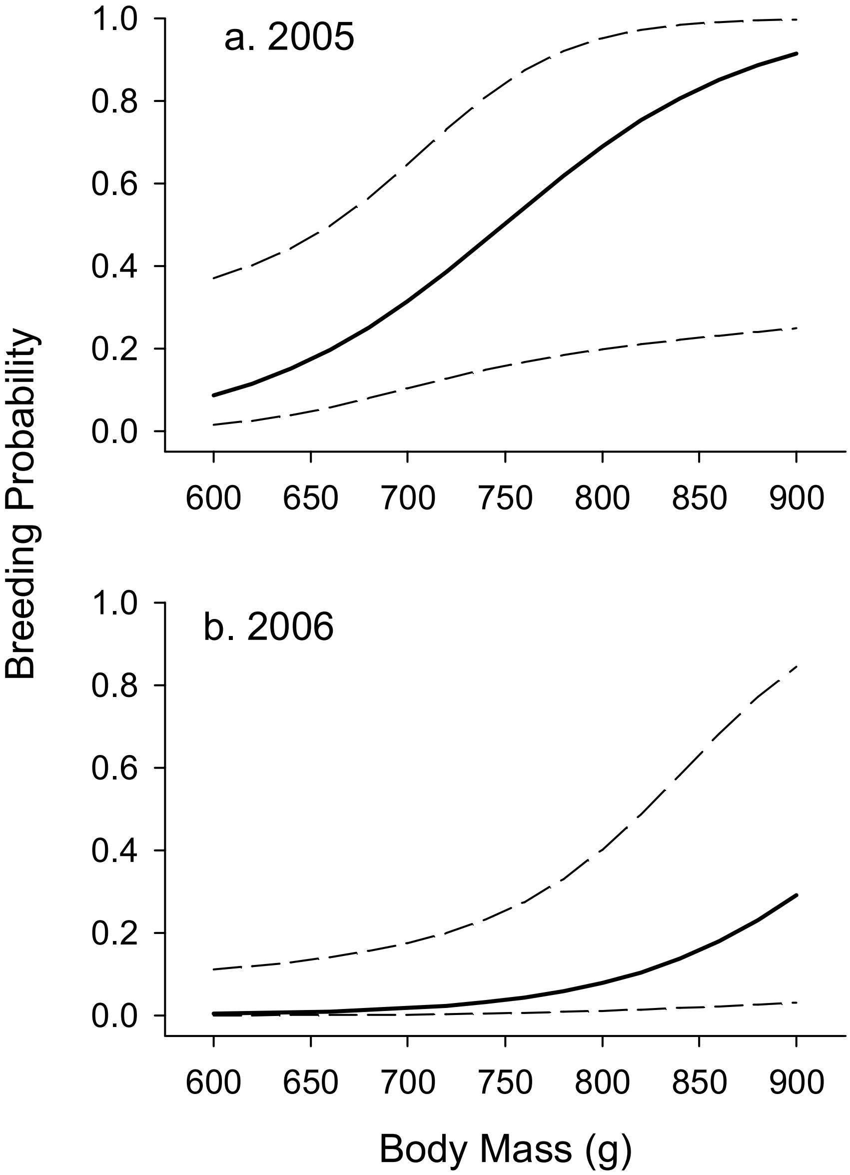

Figure 2. Breeding probability from radio-telemetry methods versus body mass (solid line) of lesser scaup in 2005 (a) and 2006 (b) at Long Lake complex, Yukon Flats NWR, USA. Estimates were derived from the best-approximating model, BP (yr + wt + date), with the capture date held constant at its mean value. Dashed lines indicate the 95% confidence interval.

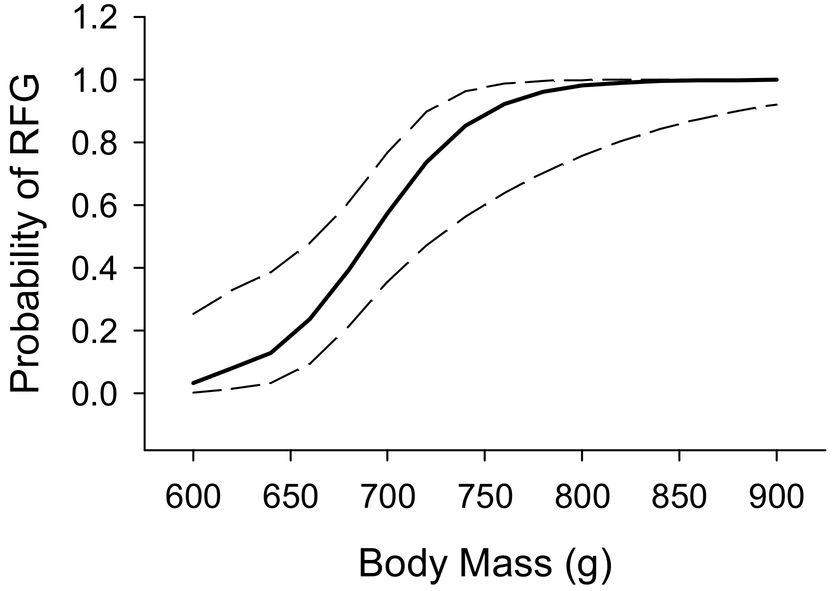

Figure 3. The probability of undergoing rapid follicle growth (RFG) versus body mass (solid line) of lesser scaup at Long Lake complex, Yukon Flats NWR, USA in 2006. Estimates were derived from the best-approximating model, BP (wt + tarsus + head), where both tarsus length and head length were held constant at their respective means. Dashed lines indicate the 95% confidence interval.

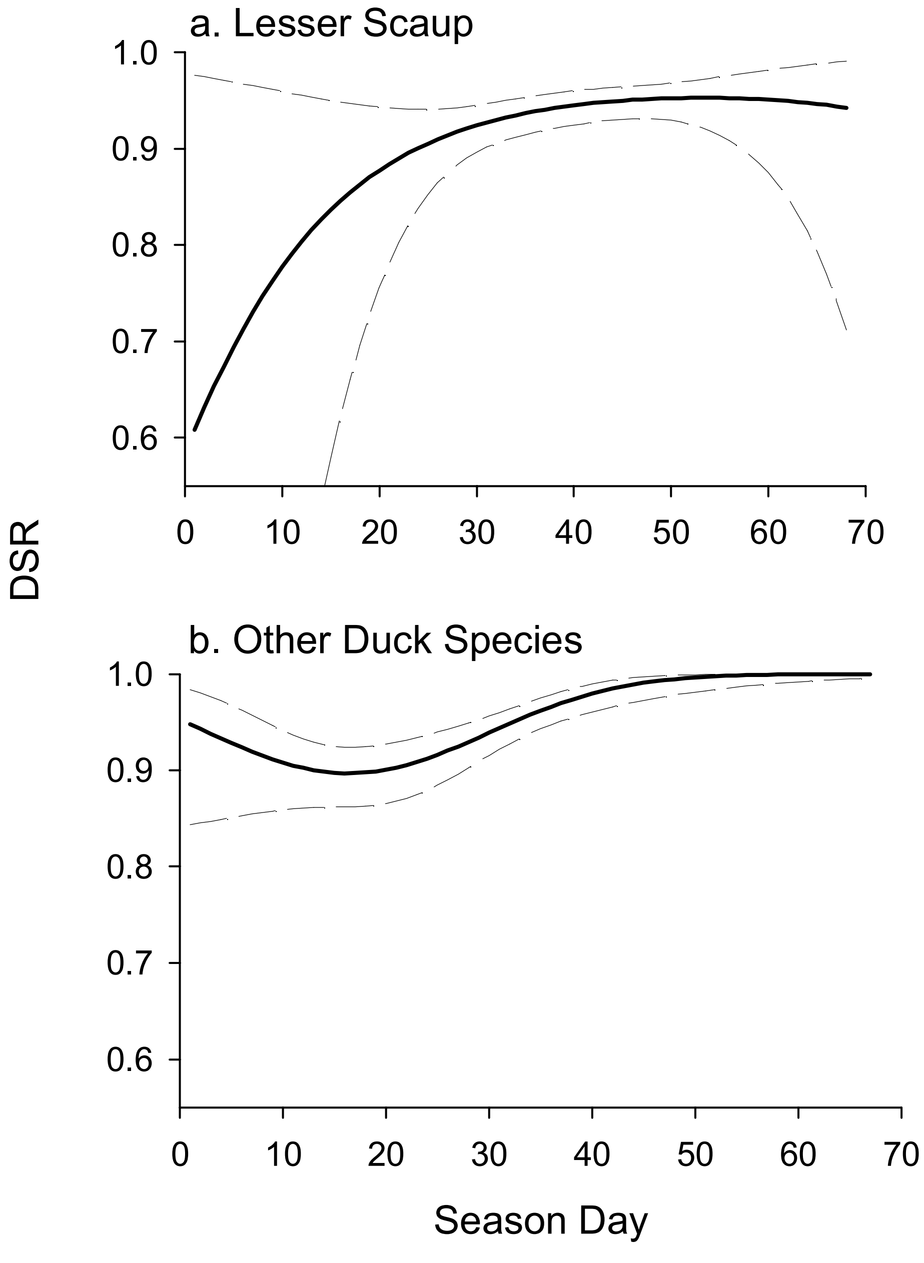

Figure 4. Daily nest survival rate (DSR) of lesser scaup (a) and other duck species (b) versus season day (May 20 = day 1) at Long Lake, Yukon Flats NWR, Alaska in 2005 and 2006. Dashed lines represent 95% confidence intervals.

# Chapter 2. Fasting Tolerance of Scaup and Other Ducks: Testing the Spring Condition Hypothesis[2]

**ABSTRACT** Previous studies have hypothesized that food limitation on migratory routes has reduced the reproductive output of scaup, contributing to the decline of the population. We compared scaup with sympatric shovelers and wigeon by measuring changes in the whole body and organs during intermittent fasting and feeding. Scaup were as tolerant of fasting as other species of waterfowl whose populations are not declining. Captive scaup lost 11 ± 2 % body mass in three days of fasting, but fully recovered that loss in four days of ad libitum feeding without significant changes in body composition. Intermittent feeding increased the mass of digestive organs such as the pancreas (all species), liver (shoveler and wigeon) and gizzard (scaup). We estimated the time required to recover 11% body mass for wild scaup that consume invertebrates. Scaup could recover lost energy and protein within four days on soft-bodied prey such as amphipods and chironomids with dry matter intakes at 9% of body mass. Birds consuming shelled prey such as gastropods and bivalves would require more than 10 days at dry matter intakes of over 70% of body mass to recover lost body energy. Scaup rely on the abundance and quality of food on the breeding grounds to recover from migration and to initiate reproduction in the boreal forest.

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**KEY WORDS** body composition, fasting, intermittent feeding, scaup, northern shoveler, spring condition hypothesis, wigeon

## INTRODUCTION

The combined North American population of Lesser Scaup (*Aythya affinis*) and Greater Scaup (*Aythya marila*) has declined from 6.5 million birds in the early 1980s to 3.2 million birds in 2006. Scaup are 48% below the North American Waterfowl Management Plan (NAWMP) population target, a management goal derived from average scaup breeding population levels when environmental conditions were apparently more favorable (Wilkins et al. 2006, NAWMP Plan Committee 2004). The decline is likely most pronounced in Lesser Scaup, which comprise nearly 90% of the continental scaup population. The majority of Lesser Scaup (70%) breed in the western boreal forest of Alaska and Canada (Bellrose 1980).

Whether changes in components of adult female survival, productivity, or both, have ultimately caused the decline in the scaup population is unclear (Afton and Anderson 2001, Koons et al. 2006). Many hypotheses have been developed to explain mechanisms affecting specific components of scaup population dynamics (Austin et al. 2000, 2006). One prominent explanation, coined the Spring Condition Hypothesis (SCH), asserts that food limitation on migratory routes has reduced female reproductive success (Anteau and Afton 2004). A large percentage (40%) of Lesser Scaup use the Mississippi Flyway during spring migration (Bellrose 1980, Afton and Anderson 2001), where foods such as aquatic invertebrates have declined in abundance (Anteau and Afton 2006). Anteau and Afton (2004) found that body masses and lipid reserves of females along the Mississippi Flyway, specifically those collected in the upper Midwestern United States, were smaller in 2000 and 2001 than in the mid-1980s.

Anteau and Afton (2004) speculated that the lower body condition of females at spring staging areas would lead to reduced reproductive performance during the summer.

Female breeding success has been correlated with high body mass in waterfowl (Gloutney and Clark 1991, Arnold et al. 1995, Blums and Clark 1997). Previous work suggests that females must exceed a threshold of nutrient reserves before initiating rapid follicle growth (Ankney et al. 1991, Esler et al. 2001). Thus, if food is limiting on the migratory routes, the ability of scaup to regain body mass and nutrient reserves after arrival on the breeding grounds likely affects their ability to reproduce successfully. Additionally, recent research suggests that breeding probability of scaup in the Alaska boreal forest is lower than previously thought (Martin et al. in prep., Chapter 1).

Not all boreal nesting waterfowl populations are experiencing as sharp a decline as scaup. Populations of both Northern Shovelers (*Anas clypeata*, hereafter shovelers) and American Wigeon (*Anas americana*, hereafter wigeon) have not declined significantly even though they share the same breeding areas as scaup (Wilkins et al. 2006). Although we do not know if shovelers and wigeon face similar food deficits as scaup, some species are more vulnerable than others to fasting because of differences between species in feeding behavior or digestive function (Barboza and Hume 2006). Thus, we used a multi-species approach to determine if scaup were inherently less tolerant of fasting than other species of ducks with breeding distributions in the boreal forest and the prairie-parkland regions.

Birds cope with food restriction by using tissues to provide lipid and protein during the deficit, and then increase both food intake and digestive function to restore body mass when food becomes available (Barboza and Jorde 2001, McWilliams and Karasov 2001, Barboza and Jorde 2002). We tested the responses of scaup to intermittent feeding in three experiments: 1) on adult female scaup, 2) on juvenile scaup, shoveler, and wigeon females, and 3) on juvenile scaup, shoveler, and wigeon males. We used an intermittent supply of food to replicate uncertain feeding conditions. Birds were fed ad libitum throughout the experiment (control) or subjected to fasting days followed by ad libitum feeding (treatment). This situation of famine and feast emulates the most extreme response of ducks to an inadequate food supply. We tested the responses of female ducks during the spring, when those in the wild are migrating and not yet using large amounts of energy or protein for reproduction. This response should be relevant to pre-breeding females on arrival to the breeding grounds before the initiation of rapid follicle growth. Male experiments were included to determine the physiological mechanisms involved with intermittent feeding in these species, such as tissue and organ changes, that may be useful indicators of inadequate food supplies in wild populations. Females could not be euthanized for tissue analysis because they were used in another study. The objectives of this study were three-fold: 1) determine if adult female scaup can tolerate fasting by measuring changes in both body mass and composition; 2) compare fasting tolerance of female scaup, shovelers and wigeon; and 3) describe changes in organ mass and composition of scaup, shoveler and wigeon exposed to intermittent feeding. Finally, we developed a model of time for scaup to recover from body mass lost during a period of fasting.

## METHODS

### Capture and maintenance of birds

Ducks used in this study were part of a captive flock founded with eggs and ducklings collected from areas in interior Alaska, predominantly Minto Flats State Game Refuge (65°00'N, 149°31'W), in June and August of 2004 and 2005. Birds of the same sex and species were housed at the University of Alaska Fairbanks in indoor concrete pens in groups of either 4-5 birds (1.1 m wide x 1.3 m long x 2.5 m tall) or 5-10 birds (1.9 m wide x 1.7 m long x 2.5 m tall). Each pen was cleaned daily and included running water, a swimming tub, and a heated roosting pad at all times. Light cycles were gradually changed in accordance with the amount of light available to wild waterfowl seasonally. We held light cycles constant during experiments and acclimation periods in fall and spring at 10 hr light: 14 hr dark. Temperature in pens ranged from 15 -23° C (mean = 21° C) and were within the thermoneutral zone for all three species (Baldassarre and Bolen 1994).

Ducklings were fed a crumbled diet for growing waterfowl (Mazuri Waterfowl Starter #5641, Purina Mills, St. Louis, MO) until they were approximately five months old. We then used two pelleted feeds that were both formulated for maintenance and reproduction of waterfowl: Mazuri Waterfowl Maintenance # 5642 (Purina Mills, St. Louis, Missouri) or Duck and Goose Maintenance Ration (Alaska Pet and Garden, Anchorage AK). Guaranteed composition (% air dry) of all feeds included adequate crude protein (14-20 %) and crude fat (3.0 %) for all stages of domestic waterfowl. Crude fiber (4.0-6.5 %) and ash (6.0-7.5 %) were below the maximum suggested for domestic waterfowl (National Resource Council 1994).

### Experimental design

We defined hatch year birds (HY) as those birds in the same calendar year as their hatch, second year birds (SY) as those in the calendar year after their year of hatch, and adult birds (ASY) as those in the second calendar year after their year of hatch.

We conducted two sets of experiments: one with SY and ASY females and a second experiment with HY males. The female experiment was conducted on 2 February – 24 March. The comparison between scaup and wigeon males was conducted 24 September – 21 October, and the comparison between scaup and shoveler males was conducted 16 October – 12 November. We used a non-lethal method for measuring body composition of females, whereas males were euthanized at the end of the experiment for tissue sampling (Fig.1).

Ducks were grouped by species. Each animal was weighed to the nearest gram on a platform balance, and assigned to one of two groups (*n* = 5) so groups would have a similar mean and variance in body mass. Because sibling relationships were unknown, we could not randomly allocate siblings to groups. Each group was randomly assigned to either control or treatment. Mass of all experimental birds was within the range of each species in the wild (Bellrose 1980, DuBowy 1996, Austin et al. 1998, Morbray 1999). All groups were housed in adjacent, randomly selected pens to provide similar temperature and light conditions. Two scaup in both the fasted and control groups of female SY scaup were Greater Scaup, as determined by measurements of culmen and tarsus length. All other scaup used in this study were Lesser Scaup. Each group was acclimated with ad libitum food until they maintained or increased body mass at a steady state (Fig.1).

We realize that this design can be viewed as pseudoreplication, with groups, not individuals, as the true experimental units (Hurlbert 1984). Replicate groups of birds or isolation of individual birds would have constituted a more rigorous design, but this was impractical because of space limitations. We were also concerned that isolation of a social species would change their typical behavior and feeding patterns. For the statistical analysis, we considered individuals as the experimental units. We do not think our experimental design was subject to any systematic differences in groups or pens that may have caused the results we observed.

The control group was given ad libitum food at all times. Treatment groups were fasted for three days, then fed ad libitum for four days in two cycles (Fig. 1) in a similar manner to experiments on Black Ducks (*Anas rubripes*; Barboza and Jorde 2001). All birds were weighed before and after each interval of the experiment.

**Body composition analyses**

Indirect measures of body composition were made by isotope dilution (following the procedure of Barboza and Jorde 2001) in all females at the beginning and end of the experiment. Ducks were given a single intragastric dose of deuterium oxide (3 g $kg^{-1}$ body mass; 99% $^2$D, Cat# 43,576-7, Sigma-Aldrich, St. Louis, MO) measured to the nearest 0.0001g. Doses were administered with an infant feeding tube (8 French x 54 cm) and rinsed with 3 mL of tap water. We began dilutions in the morning after removing food from all pens to minimize variation associated with digesta fill. We also removed water tubs from each pen to avoid dilution of the dose with drinking water during equilibration. Water space was determined from blood sampled at 90 min after dosing. We collected approximately 1.5 mL of blood from the tarsal vein into a heparinzed tube using a blood collection set (23 gauge needles with 30.5 cm tubing, Cat # 36-7253, BD Vacutainer, Franklin Lakes, NJ). Plasma was separated from cells by centrifugation at 3000 x *g* and stored at -20°C. Plasma was diluted with distilled water (1:200) for isotope ratio mass spectrometry using a Europa GEO 20-20 mass spectrometer. Deuterium concentrations were expressed as δD ‰ against Vienna Standard Mean Ocean Water and converted to $gD_2O{\cdot}g^{-1}$ plasma. Each sample was assayed in triplicate for a mean coefficient of variance of 0.7%. Deuterium concentrations were corrected for background to calculate water space, lean mass, and lipid mass from relationships validated against direct measures of body composition of Black Ducks (Barboza and Jorde 2001).

**Organ mass and composition analyses**

We euthanized males directly after the last refeeding period by overdose with isoflurane (Halocarbon, River Edge, NJ). Carcasses were cooled, double-wrapped in plastic and stored at -20° C for dissection. We removed the following organs: pectoralis, supracoracoideus, visceral adipose (abdominal fat and fat surrounding the intestines), heart, liver, esophagus, gizzard, pancreas, small intestine, colon and cecae. Organs were weighed to the nearest 0.1g. We removed gut contents from the esophagus, gizzard, small intestine, colon and cecae, and then re-weighed each tissue to estimate digesta content by difference. All tissues were then frozen separately at -20°C. We homogenized the pectoralis and liver in a hand blender for further analysis. Pectoralis, liver, gizzard and pancreas were freeze dried to a constant mass to determine dry matter (DM). Lipid was extracted from pectoralis and liver with petroleum ether in a modified Soxhlet procedure (Model HT6 Soxtec, Tecator, Foss North 50 America, Silver Spring, MD). Nitrogen content in the pectoralis and liver was determined using an elemental analyzer (Model no. CNS 2000, Leco, St. Joseph, MI), and protein was calculated by multiplying the nitrogen content by 6.25 (Robbins 1993).

### Statistical analyses

We used ANOVA to test for the effect of treatment, species, and interactions between treatment and species on the percent body mass change from the beginning to the end of the experiment. Because the percentages were small, we used an arcsine transformation to meet the assumption of normality for ANOVA (Zar 1996). We also used ANOVA to test for the effect of treatment and species on absolute lean mass change and absolute lipid mass change over the experimental period. Tarsus length, used as a structural size covariate, was not significant in analyses of body mass and composition change; therefore we did not include tarsus in these tests. The lack of an effect of structural size in the analysis was probably a result of controlling for structural size (body mass) in the assignment of groups. To test the effect of treatment on organ size and composition (pectoralis, liver, gizzard, and pancreas) in the male experiment, we used ANCOVA with the covariate of net body mass (ingesta free body mass – fresh mass of the organ; Christians 1999). SYSTAT version 10.2 (Systat Software 2002) was used for all analyses, and significance accepted at $\alpha = 0.05$. All means are expressed with one standard error.

**Recovery model**

Our tests reflect the most conservative scenario because we provided high quality foods with relatively low energetic demands, illustrating the most efficient response of scaup to intermittent feeding. Wild birds likely face more demanding conditions; thus we constructed a model to evaluate the limits to regaining body mass under varying intake and food quality. We were particularly interested in whether female scaup could regain their original mass by consuming foods available in the wild over 21 days, which we assumed was the minimum time female scaup spend on the breeding grounds before nest initiation (Bellrose 1980, Afton 1984, Austin et al. 1998).

To construct the model, we first calculated the energy and protein lost from the whole body in scaup during a 3d fast. Based on the results of our body composition analyses, we assumed that lost body mass contained the same proportions of protein and lipid as the whole body. We used the gross energy content of muscle protein (23.7 kJ $g^{-1}$) and adipose lipid (39.3 kJ $g^{-1}$; Blaxter 1989) to calculate total energy lost as protein and lipid from the body.

We estimated the energy demands for maintenance in wild scaup as 2.4 times the basal metabolic rate (BMR) for non-passerine birds at 308 $kJ \cdot kg^{0.734} \cdot d^{-1}$ (Aschoff 1981). The multiple of BMR is a weighted average of 12 hr rest (1.5·BMR) and 12 hr flying or diving for waterfowl (3.3·BMR, Afton and Paulus 1992). Sugden and Harris (1972) measured similar energy expenditures for juvenile scaup. The maintenance requirement for protein was calculated from a relationship for several omnivorous birds at 3.5 gCP $\cdot kg^{0.58} \cdot d^{-1}$ (Klasing 1998).

The model used the available metabolizable energy and protein of four foods commonly used by wild scaup, as well as the commercial formulation used in this study (Table 1). Concentrations of crude protein, lipid, ash and fiber of each food were derived from published data (Table 1). Total non-structural carbohydrate was estimated by difference as the nitrogen free extract (NFE = DM - (Lipid + Protein + Fiber + Ash)). We calculated the available energy in each food (kJ $g^{-1}$) with the fuel values for lipid (37.66 kJ $g^{-1}$), protein (16.74 kJ $g^{-1}$) and non-structural carbohydrate (16.74 kJ $g^{-1}$) from each diet (Atwater and Bryant 1900). Metabolizable energy (kJ $g^{-1}$) and protein (gCP $g^{-1}$) contents of foods were calculated as the product of available energy or protein and the corresponding metabolizability (Table 1). We assumed that the metabolizability of protein was 63% (Barboza and Jorde 2001) and that metabolizability of energy was 80% for all foods (Barboza and Jorde 2001) except bivalves, which were 45% metabolizable for energy because of the low digestibility of the shell (Richman and Lovvorn 2004).

The model assumed that daily intake of metabolizable energy and protein in excess of maintenance was available to restore body mass. We used daily dry matter intakes ranging from 1.5% to 100% of body mass in the model. Fasted captive ducks regain body mass with daily dry matter intakes ranging from 9.5% of body mass on formulated diets (Black Ducks, Barboza and Jorde 2001) to 181% on clams (Canvasbacks, Jorde et al 1995), but maximum intakes of wild ducks could be higher. The number of days required to recover the lost body mass was the total loss of energy and protein divided by the daily excess of energy and protein from the food.

## RESULTS

### Body mass and composition

Fasting reduced body mass by 9.5 ± 0.3 % to 20.2 ± 1.7 % in all experiments. Even with these considerable losses, body masses were restored by re-feeding for four days in all age groups of all three species (Fig. 2, Tables 2 and 3). Lost body mass included both the contents of the digestive tract as well as body tissues. Mean ingesta mass of dissected males was only 1.6 ± < 0.1 % of body mass, indicating that birds lost between 7.9% and 18.6% of ingesta-free body mass during the fasting period.

Adult female scaup (ASY) lost an average of 9.5 ± 0.3 % of their body mass in the first fast, and 10.6 ± 0.4 % in the second fast, while the control group maintained body mass during the same periods ($F_{1,8} = 231.3$; $P < 0.001$, Fig. 2). However, control and fasted groups did not differ in their overall mass change from the beginning to the end of the experiment (Table 2). Younger female scaup (SY) also lost mass during each fast, and showed the same response to intermittent feeding as adult birds (Table 2).

Young females gained more mass than ASY females over the experiment (45.7 ± 20.2 g vs. 10.9 ± 6.6; $F_{1,16} = 3.9$; $P = 0.04$) because young birds regained more mass during each re-feeding period (group*age; $F_{1,16} = 5.87$; $P = 0.03$, Table 2).

Scaup (treatment and control groups combined) gained more mass over the entire experiment than shovelers and wigeon ($F_{2,23} = 3.5$; $P = 0.049$, Table 2). Shoveler and wigeon treatment groups lost up to 11% of their body mass in three days of fasting, and then completely recovered body mass during re-feeding (Table 2). Treatment groups of SY females gained or maintained mass over the experiment, whereas controls lost (shovelers) or maintained body mass (group*species; $F_{2,23} = 3.6$; $P = 0.045$, Table 2). Lean and lipid components of body mass of females did not change significantly over the length of the experiment in either control or treatment groups of all three species (Fig. 2b and Table 2).

Young (HY) males of all three species also maintained or gained body mass over the entire experiment in both control and treatment groups (Table 3). In the first male experiment, both HY scaup and shoveler treatment groups completely regained lost body mass during re-feeding. Scaup and shoveler control groups gained more mass during the experiment than the treatment groups (group; $F_{1,16} = 6.4$; $P = 0.02$). In the second experiment, there was no difference between body mass changes in scaup and wigeon treatment over the length of the experiment ($F_{1,8} = 3.8$, $P = 0.08$).

## Organ mass and composition

Intermittent feeding caused changes in organ size and composition of scaup, shoveler and wigeon. However, the three species utilized tissues differently (Fig. 3 and

4). Intermittent fasting reduced pectoral mass in scaup (25.3 ± 2.6g vs. 33.1 ± 3.0g; $F_{1,,7} = 43.0$, $P = 0.03$), but not in shovelers or wigeon. The percent lipid in the pectoralis was smaller in the scaup treatment group compared to the scaup control group (6.6 ± 0.9% vs. 11.7 ± 1.6%, $F_{1,7} = 5.8$, $P < 0.05$), but the percent protein was similar between groups (79.1 ± < 0.1% vs. 77.3 ± < 0.1%, $F_{1,7} = 6.9$, $P = 0.12$). Liver mass increased in the shoveler treatment group (6.8 ± 0.6 g vs. 4.2 ± 0.2 g; $F_{1,7} = 54.9$, $P < 0.001$) and in the wigeon treatment group (7.2 ± 0.3 g vs. 6.7 ± 0.6 g; $F_{1,7} = 7.2$, $P = 0.03$), but not in the scaup treatment group. In both shovelers and wigeon, the concentrations of lipid and protein in the liver increased proportionally with dry mass. Pancreas DM was greater in treatment than in control groups for all species (scaup: 1.7 ± 0.1 g vs. 1.4 ± 0.1 g, $F_{1,7} = 5.8$, $P = 0.047$; shoveler: 1.3 ± 0.3 g vs. 0.8 ± 0.1 g, $F_{1,7} = 7.8$, $P = 0.03$; wigeon: 1.5 ± 0.3 g vs. 1.3 ± 0.1 g, $F_{1,7} = 7.7$, $P = 0.03$). Treatment groups gained gizzard mass in scaup (4.5 ± 0.7 g vs. 3.5 ± 0.2 g, $F_{1,7} = 15.8$, $P=0.005$) lost gizzard mass in wigeon (5.2 ± 0.2 g vs. 6.1 ± 0.2 g; $F_{1,7} = 6.1$, $P = 0.04$) and maintained gizzard mass in shovelers (2.8 ± 0.3 g vs. 2.6 ± 0.1 g; $F_{1,7} = 1.3$, $P = 0.28$).

**Recovery model**

Our model predicted that scaup could recover the energy lost in 11% body mass within 21d on all 5 foods (Fig. 5a). Although intakes were not measured directly during our experiments, our model indicates that daily dry matter intake at 9% body mass (BM) of the commercial diet would have allowed scaup to recover lost mass in 3.4 d. Daily dry matter intake of 9% BM of chironomids also allows recovery in 3.4 d, whereas the lower metabolizable content of energy in amphipods would require a higher intake (12% BM) to recover lost mass in 5 d. Poor quality diets such as gastropods and bivalves do not allow full compensation of energy stores at low intakes, and therefore require more time and higher intakes to recover lost mass. We predicted that scaup would require intakes above 70% BM of gastropods and above 90% BM of bivalves to recover lost mass within 21d.

Scaup could regain protein faster than energy stores when consuming the five foods in our model (Fig. 5b). Daily dry matter intakes at 9% BM would allow body protein to be restored in 2.9 d on the commercial diet, 0.7 d on chironomids and 1.0 d on amphipods. Lower concentrations of metabolizable protein in mollusks would require intakes at 18 % BM to recover lost body protein in 3.6 d on gastropods and in 13.5 days on bivalves.

## DISCUSSION

### Body mass and composition

The SCH suggests that food limitation during spring migration causes lower productivity of female scaup. One prediction of the SCH is that scaup cannot compensate for body mass lost during fasting in the spring. Fasting of scaup in our study caused mass losses (mean = 65.5 g) that are similar to the average declines in body mass of wild scaup in the Mississippi Flyway from the 1980s to 2000 and 2001 (mean = 58.5 g, Anteau and Afton 2004). Our data show that scaup can quickly compensate for a body mass loss of this magnitude without significant changes in body composition. Notably, young (SY) female scaup can compensate for the mass lost in fasting and also continue to grow even when subjected to intermittent feeding. Scaup are as tolerant of fasting as other species of waterfowl whose populations are not declining. Therefore, our data do not support the component of the SCH which suggests that scaup mass deficits would necessarily persist after arrival on the breeding grounds. Our results indicate that scaup and other ducks can quickly recover from food deficits of this magnitude if adequate food resources are available.

Female breeding success is related to high body mass in waterfowl (Gloutney and Clark 1991, Arnold et al. 1995, Blums and Clark 1997), where females likely must exceed a threshold of nutrient reserves before initiating rapid follicle growth (Ankney et al. 1991, Esler et al. 2001). Although females may have an advantage if the threshold is met earlier in the nesting season (Rohwer 1992), scaup are a late-nesting species that spend long periods of time on the breeding grounds before laying eggs. Scaup arrive four to six weeks before nest initiation in southern breeding areas (Afton 1984), and an average of four weeks before nest initiation in northern breeding areas of the Northwest Territories and interior Alaska (Bellrose 1980, Austin 1998). During the pre-laying period, female scaup have adequate time to gain protein, lipid, and mineral reserves required for reproduction (Afton and Ankney 1991) and compensate for lost energy or protein stores incurred along the migratory route.

Although mass deficits during spring migration alone may not alter breeding effort, other components of the SCH may be plausible. Breeding probability of Lesser Scaup in the Alaskan boreal forest is low compared to other duck species (Martin et al. in prep., Chapter 1), and is related to female pre-laying body mass. Intermittent feeding has been shown to delay breeding in Black Ducks until food is regularly available (Barboza and Jorde 2002), and it is possible that long periods of intermittent feeding in scaup may halt the process leading to rapid follicle growth, resulting in a lower number of breeding females.

Our conclusions depend on food availability on the breeding grounds because recovery from mass losses could be compromised by poor quality or abundance of food (Jorde et al. 1995, Richman and Lovvorn 2004). Unfortunately, data quantifying food availability for scaup in the boreal region are lacking. However, invertebrate communities of wetlands may be changing in phenology and abundance in the boreal forest (Corcoran 2005). Historically, amphipods are the most favored food of scaup during spring migration and breeding (Afton and Hier 1991). If wetland changes occur, scaup may be forced to switch from amphipods, a high energy and high protein food, to smaller foods such as chironomids, or lower quality foods such as bivalves or gastropods (Corcoran 2005, Anteau and Afton 2006). Chironomids are similar to amphipods in concentrations of metabolizable energy and protein (Table 1), but chironomids are much smaller than amphipods, and wild scaup may use more energy to find and consume the smaller prey. Foraging costs may therefore affect the profitability and mass gain of scaup as prey size and abundance decline. In addition, available foraging time could also be compromised by predator disturbance or courting behaviors during migration or pre-breeding periods. Even if populations of bivalves and gastropods are easily accessible and individuals are large, concentrations of metabolizable energy and protein are much lower in shelled mollusks than either amphipods or chironomids. For example, Canvasbacks (*Aythya valisineria*) take more days to recover lost body mass while feeding on bivalves than while feeding on plant foods with a higher metabolizable content of dry matter (Jorde et al. 1995). It is unlikely that daily dry matter intakes could reach levels necessary for scaup to regain lost energy and protein when consuming bivalves and gastropods (above 70% and 90% of body mass, respectively). For example, if we assume bivalves have a moisture content of 80% (Jorde et al. 1995), a 700 g scaup would require 2450 g of bivalves, equivalent to 3.5 times its body mass, to satisfy a daily dry matter intake of 70% body mass.

### Organ mass and composition

Intermittent feeding did not change the composition of the whole body, but did affect the size and composition of organs as birds used reserves during a fast and restored those tissues during re-feeding. Because body mass can be restored quickly, tissue measurements may be more indicative of past food limitation than measures of body mass. Scaup, shovelers and wigeon likely use different behavioral and physiological mechanisms to tolerate intermittent feeding depending on the size and metabolic activity of their organs. Although they have overlapping diets, each species exhibits different feeding behaviors that may dictate how they utilize body stores and digestive organs. Shovelers are carnivores that sieve small aquatic invertebrates from the water's surface (DuBowy 1996). Wigeon are herbivores that consume mainly high-protein emergent aquatic vegetation. Aquatic invertebrates may however constitute up to 40% of the diet of wigeon during the breeding season (Krapu and Reinecke 1992, Morbray 1999). Scaup are divers that feed mainly on larger aquatic invertebrates throughout the water column, the most important of which are amphipods, bivalves, and chironomids (Afton and Hier 1991, Austin et al. 1998).

An increase in food intake during re-feeding is often associated with an increase in digestive organs such as the pancreas and liver (Piersma 1998, McWilliams and Karasov 2001). Scaup, shovelers, and wigeon all increased the mass of the pancreas during intermittent feeding (Fig. 4a). Gains in liver mass of shovelers and wigeon were associated with both the lipid and protein fractions of the tissue, both of which could reflect increased secretory capacity of bile and enzymes, as well as intermediary metabolism of absorbed nutrients (Klasing 1998). Scaup may have a high reserve capacity for liver metabolism because intermittent feeding did not increase liver mass (Fig. 3b), though this suggestion requires confirmation from direct measures of liver activity (Pinchasov et al. 1988, Karasov and Pinshow 1998, Sartori et al. 2000). In addition, both the pectoralis and gizzard represent large reserves of energy and protein in muscle that can change in response to increased or decreased food intakes (Lindstrom et al. 2000, Starck 1999), and energetic costs associated with migration and predator evasion (Dietz et al. 2007). Scaup, which often rely on diving to find food or evade predators, may utilize the protein and lipid in flight muscles during fasting, whereas shovelers and wigeon may retain pectoralis tissue because they rely more heavily on flight. Birds that typically have tough diets (e.g. bivalves and gastropods for scaup) may retain the gizzard for grinding, whereas the gizzard mass of wigeon was reduced by intermittent feeding (Fig. 3a). Thus, changes in pancreas, pectoralis, and gizzard mass may indicate that scaup are compensating for previously intermittent food supplies, whereas liver and gizzard mass may indicate intermittent feeding in dabbling ducks, such as shoveler and wigeon.

### Conservation

Waterfowl and other birds routinely face periods of food deprivation during their annual cycle; therefore, fluctuations of body mass occur on a regular basis and over a short time span (King and Murphy 1985). One measure of body mass or body composition may not be the best indicator of overall individual and population health. Changes in the mass and composition of organs may indicate intermittent food availability for wild birds. Thus, in addition to body mass and composition measurements, we suggest that measurements of digestive organs and metabolites may provide a more complete picture of nutritional resources for a population at a migratory stopover site or on the breeding grounds (Guglielmo et al. 2005).

Our results suggest that scaup have the capability of regaining the energy and protein lost during fasting if food quality and abundance are not limiting; however, data regarding food availability for scaup in the boreal forest are lacking. Mass loss alone does not indicate that the food or foraging conditions on migratory routes are inadequate for scaup. Nonetheless, body mass and nutrient reserves must be restored before birds can complete reproduction. If food resources are inadequate during the pre-laying period on the breeding grounds, scaup may be unable to rapidly compensate for mass loss, which could delay nest initiation, or cause females to forego breeding altogether. Because breeding probability may be low in the boreal forest (Martin et al. in prep, Chapter 1), food availability for scaup should be a concern in the boreal forest breeding grounds, where macroinvertebrate communities may have shifted due to climate change (Corcoran 2005). High quality and abundant food resources at northern stopover sites and breeding grounds in the boreal forest are crucial to scaup population recovery, and further research regarding food availability for scaup in the boreal forest is needed. Managers should devise strategies to monitor and maintain these resources for breeding waterfowl.

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Table 1. Metabolizable content (% dry matter) of energy and protein in foods used in the model of mass recovery in scaup.

| Diet | Available Energy (kJ $g^{-1}$) | Available ME (kJ $g^{-1}$)[f] | Crude Protein (%) | M Protein (gCP $g^{-1}$)[g] |
|---|---|---|---|---|
| Commercial Maintenance[a] | 15.84 | 12.67 | 21.84 | 0.14 |
| Amphipods[b] | 10.90 | 8.72 | 47.00 | 0.30 |
| Chironomids[c] | 15.76 | 12.61 | 66.40 | 0.42 |
| Gastropods[d] | 1.80 | 1.44 | 94.00 | 0.06 |
| Bivalves[e] | 1.54 | 0.78 | 31.49 | 0.02 |

[a] Duck and Goose Maintenance, Alaska Pet and Garden, Anchorage, AK
[b] *Gammarus sp*. from Ballard et al 2004
[c] Krapu and Swanson 1974
[d] Ballard et al 2004
[e] *M.balthica*, Richman and Lovvorn 2004
[f] Available metabolizable energy
[g] Available metabolizable protein

Table 2. Mass ± SE (g) of whole body (a) and lean and lipid components (b) of SY females fed intermittently (treatment) and ad libitum (control) throughout the experiment. Lean and lipid mass were measured at the beginning and end of the experiment.

a. Body Mass

| Species | Group | Fed 1 | Fast 1 | Fed 2 | Fast 2 | Fed Final |
|---|---|---|---|---|---|---|
| Scaup | Control | 665 ± 30 | 663 ± 31 | 690 ± 34 | 691 ± 37 | 686 ± 34 |
| Scaup | Treatment | 639 ± 26 | 566 ± 22 | 670 ± 35 | 587 ± 28 | 709 ± 45 |
| Shoveler | Control | 565 ± 19 | 541 ± 20 | 541 ± 19 | 546 ± 17 | 549 ± 19 |
| Shoveler | Treatment | 591 ± 17 | 531 ± 17 | 585 ± 11 | 522 ± 13 | 600 ± 12 |
| Wigeon | Control | 634 ± 75 | 645 ± 69 | 633 ± 64 | 625 ± 68 | 639 ± 69 |
| Wigeon | Treatment | 648 ± 45 | 581 ± 36 | 647 ± 45 | 579 ± 38 | 657 ± 47 |

b. Lean and Lipid Mass

| Species | Group | Fed 1 Lean | Fed 1 Lipid | Fed Final Lean | Fed Final Lipid |
|---|---|---|---|---|---|
| Scaup | Control | 562 ± 43 | 66 ± 17 | 564 ± 25 | 83 ± 23 |
| Scaup | Treatment | 539 ± 41 | 65 ± 26 | 604 ± 40 | 64 ± 42 |
| Shoveler | Control | 427 ± 17 | 102 ± 13 | 420 ± 20 | 89 ± 7 |
| Shoveler | Treatment | 392 ± 4 | 156 ± 13 | 417 ± 24 | 135 ± 18 |
| Wigeon | Control | 471 ± 31 | 128 ± 50 | 493 ± 31 | 101 ± 31 |
| Wigeon | Treatment | 499 ± 29 | 100 ± 12 | 513 ± 34 | 93 ± 11 |

Table 3. Whole body mass ± SE (g) of HY males throughout experiment 1 (a) and experiment 2 (b).

a. Experiment 1

| Species | Group | Fed 1 | Fast 1 | Fed 2 | Fast 2 | Fed Final |
|---|---|---|---|---|---|---|
| Scaup | Control | 536 ± 35 | 557 ± 37 | 563 ± 43 | 577 ± 37 | 570 ± 42 |
| Scaup | Treatment | 492 ± 24 | 425 ± 25 | 502 ± 29 | 418 ± 30 | 512 ± 34 |
| Shoveler | Control | 624 ± 18 | 638 ± 20 | 656 ± 16 | 669 ± 17 | 679 ± 15 |
| Shoveler | Treatment | 647 ± 44 | 580 ± 50 | 668 ± 43 | 590 ± 47 | 668 ± 41 |

b. Experiment 2

| Species | Group | Fed 1 | Fast 1 | Fed 2 | Fast 2 | Fed Final |
|---|---|---|---|---|---|---|
| Scaup | Treatment | 621 ± 36 | 522 ± 29 | 626 ± 41 | 521 ± 31 | 623 ± 39 |
| Wigeon | Control | 625 ± 17 | 640 ± 20 | 641 ± 16 | 659 ± 17 | 663 ± 18 |
| Wigeon | Treatment | 593 ± 30 | 527 ± 30 | 595 ± 34 | 528 ± 32 | 613 ± 28 |

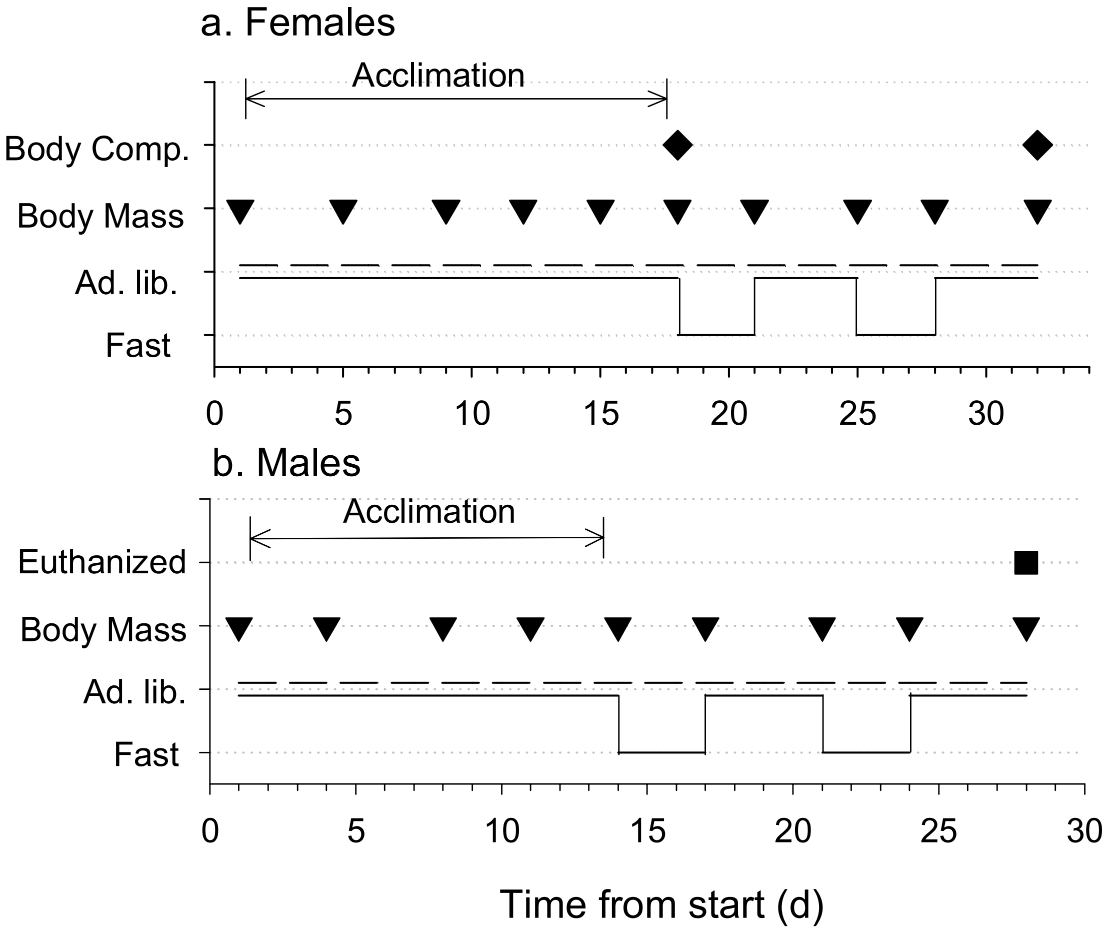

Figure 1. Timeline for experiments on control (broken line) and treatment (solid line) groups of female (a) and male (b) ducks. Body mass was measured at each interval of fasting and re-feeding (triangles). Body composition of females (diamonds) was measured by deuterium dilution (Barboza and Jorde 2001) before the first fasting period and at the end of the experiment. All males were euthanized for measures of tissue mass and composition (square) at the end of the experiment.

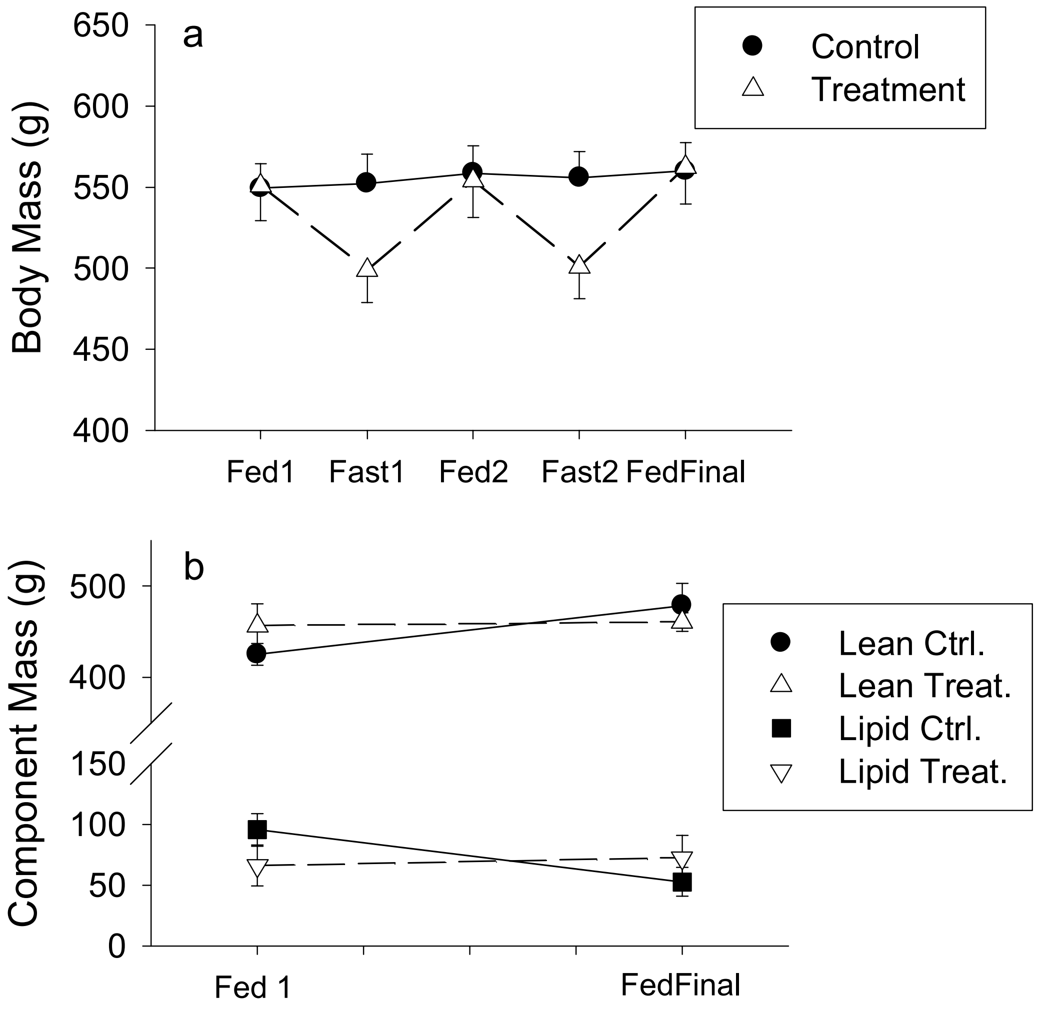

Figure 2. Mass (g) ± SE of whole body (a), lean and lipid components (b) of ASY female scaup fed ad libitum (control; circles and squares, solid line) and intermittently (treatment; triangles, broken line). Lean and lipid components were measured at the beginning and end of the experiment. Fed 1 corresponds to day 1 of the experiment, Fast 1 is directly after the first fast, Fed 2 is after the first re-feed, Fast 2 is after the second fast, and Fed Final is after the second and final re-feed.

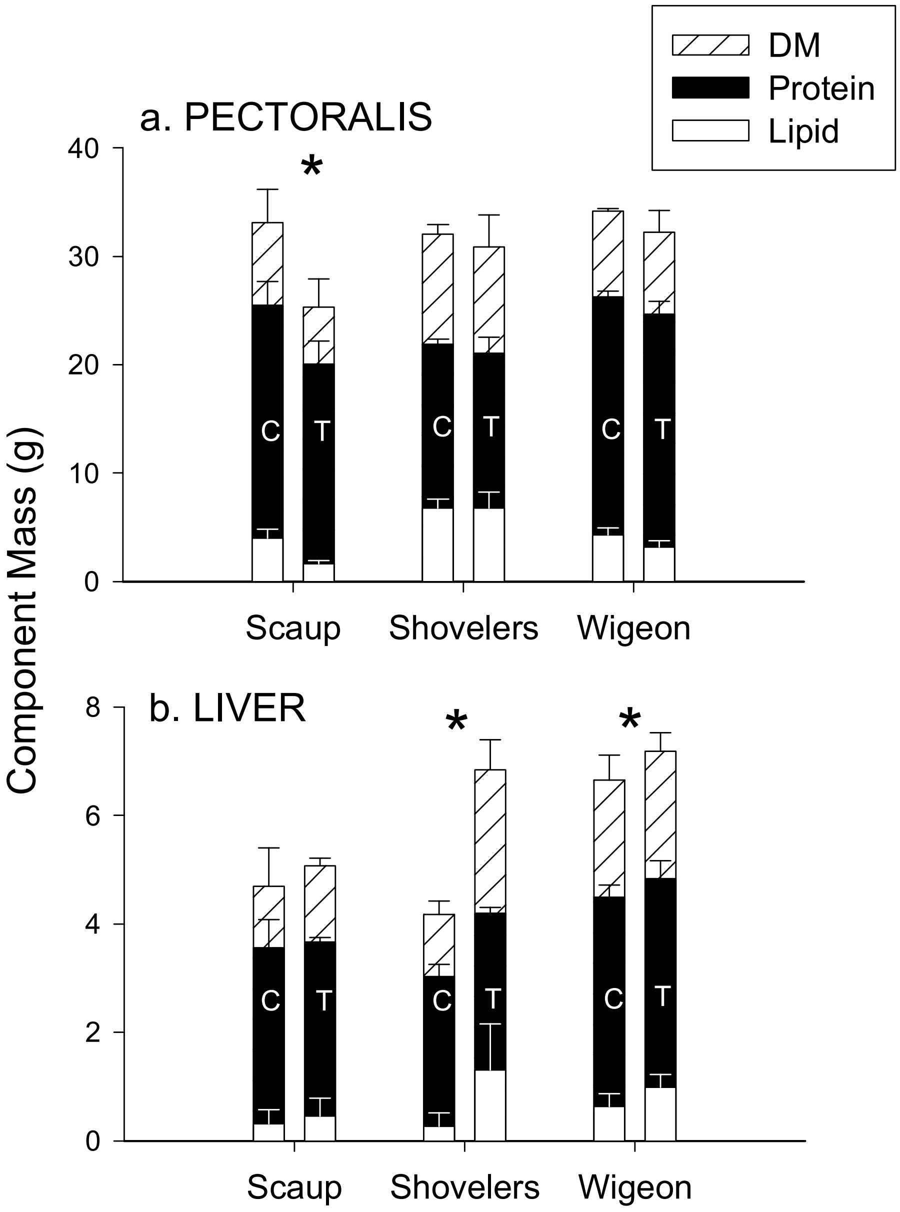

Figure 3. Dry mass (DM) ± SE (g) of tissues in HY males fed intermittently (treatment, T) and ad libitum (control, C), including pectoralis dry mass, lipid mass, and protein (a) and liver dry mass, lipid mass and lean mass (b). An asterisk (*) denotes a significant difference between DM in control and treatment groups (ANCOVA: $P < 0.05$).

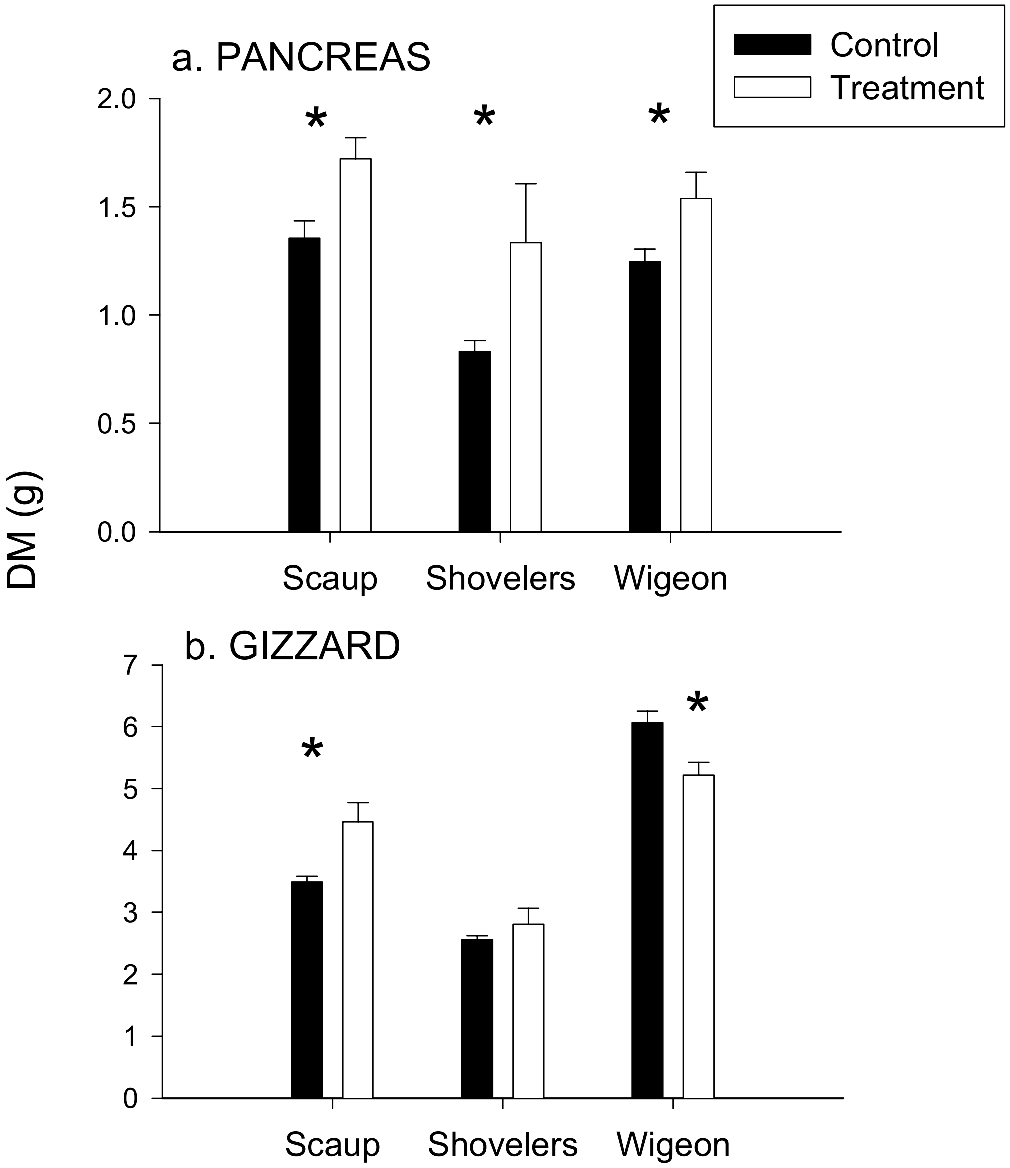

Figure 4. Dry mass (DM) ± SE (g) of pancreas (a) and gizzard (b) in HY males fed intermittently (treatment) and ad libitum (control). An asterisk (*) denotes a significant difference between tissue DM of control and treatment groups (ANCOVA: $P < 0.05$).

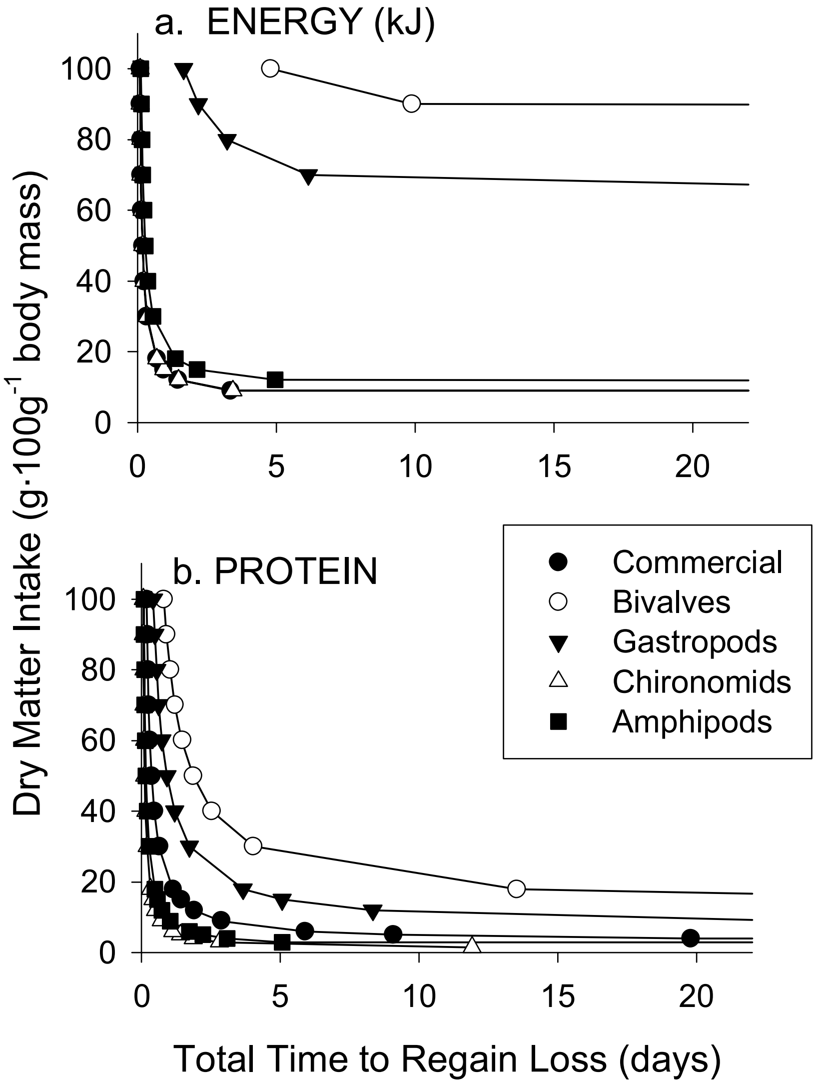

Figure 5. Model of energy and protein recovery in scaup after losing 11% body mass in a 3d fast. The model assumed that daily intake of metabolizable energy and protein in excess of maintenance (739 kJ·kg$^{-0.734}$ and 3.49 gProtein·kg$^{-0.58}$) was available to restore body mass. Each point represents the minimum time required to regain mass for daily dry matter intakes of 1.5% to 100% of body mass. Lines connect the set of minima for each diet.

# CONCLUSION

Few studies have examined breeding season parameters of waterfowl in the boreal forest, though some species depend on this region for reproduction. Although the boreal forest is regarded as relatively pristine compared to other ecosystems in North America, information needs are pressing because climate change and resource development (e.g. logging, oil and natural gas extraction) may cause detrimental changes to wetland communities (USFWS 2006, Zolkewich 1999). Furthermore, some boreal species, such as lesser scaup, are experiencing population declines of concern to managers. Although numerous hypotheses regarding the scaup population decline have been developed, many have not been tested. Here I presented the results of a study examining breeding season parameters of lesser scaup and other boreal ducks (Chapter 1), which have rarely (female survival, nest survival) or never (breeding probability) been estimated for populations using the boreal forest. I also tested the tolerance of scaup and other ducks to fasting, which has been proposed to affect these breeding parameters (Chapter 2).

My original intent was to estimate breeding season survival of female ducks at a boreal forest site because female survival affects population growth rate to a large degree in scaup and other species (Hoekman et al. 2002, Flint et al. 2006, Koons et al. 2006), and most mortality of female ducks occurs during the nesting season (Sargeant and Raveling 1992). I expected that a large majority of marked females of all species would attempt to nest, and that mortality rates would be high due to predation risk during incubation (Johnson et al. 1992).

Contrary to my predictions, the breeding probability of scaup at our study site was < 1.0, and probably lies between 0.12 to 0.68, whereas the breeding probability of wigeon and shovelers was higher than that of scaup (Chapter 1). The applicability of these estimates to other populations is uncertain, for at present there are no other available estimates of breeding probability of ducks in the boreal region. Scaup females with a higher body mass are more likely to begin rapid follicle growth and to lay eggs than smaller females at the Long Lake complex. Both the low breeding probability of scaup and the small body mass of pre-breeding female scaup captured at the Long Lake complex, partially supports of the spring condition hypothesis.

However, captive scaup can tolerate periods of intermittent feeding by quickly regaining mass when food is available (Chapter 2). In the wild, mass gains in scaup are likely dependent on nutrient availability: a combination of food quantity, food quality, and the amount of foraging time available to females. Lesser scaup have been shown to use exogenous resources for a significant fraction of their energy needs for reproduction (Esler et al. 2001), and they historically arrive 3-4 weeks before the mean initiation date on the Yukon Flats (Bellrose 1980, K.M., pers. obs.). Thus, female body mass on arrival may not be as important as the availability of food resources on the breeding grounds for use in regaining the energy and protein reserves lost during migration. The capability of scaup to recover from mass loss, yet the low breeding probability of scaup at the Long Lake complex, suggests that food availability in the boreal forest may not be adequate for reproduction in a portion of the scaup population. Unfortunately, data on food availability in this region, and its direct influence on breeding probability, are lacking, although recent studies suggest that aquatic communities have shifted due to climate change (Corcoran 2005).

Future research should focus on estimates of and factors influencing breeding probability of scaup in the boreal forest; however, there are challenges in obtaining an interpretable estimate of this parameter. Radio-telemetry can underestimate breeding effort if nest detection probability is low, which is usually the case during the egg laying stage. Measures of yolk precursors, which must be timed appropriately, indicate if a female is developing follicles but do not indicate if an egg is actually laid. Lethally collecting females after the nest initiation period for the examination of post-ovulatory follicles allows reliable classification as a breeder or non-breeder (Lindstrom et al. 2006), yet it is difficult to determine the focal population because individuals could have recently arrived from other areas. A combination of methods will give a more representative estimate of breeding probability than the use of any one method presently available.

Boreal ducks may use a different life history strategy than ducks in other regions of North America. For example, breeding season female survival of scaup at the Long Lake complex during the periods of high predation risk, egg laying and incubation, was higher than in the few previous studies that examined this parameter (Chapter 1; Brook and Clark 2005, Koons et al. 2006). Along with the low breeding probability of scaup at the Long Lake complex, this suggests that boreal scaup may trade reproductive effort for female survival if conditions are not ideal. Validation of this idea requires further research on breeding season parameters of multiple duck species that use the boreal region over longer spatial and temporal scales. This may have implications for harvest management, as female mortality may have a large effect on population growth of K-selected species.

In addition, all marked female ducks at the Long Lake complex were paired during the nest initiation and incubation periods, even those that showed no evidence of breeding. Therefore the dogma that all paired females attempt to breed may not be valid, and a re-evaluation of the assumptions associated with recruitment estimates based on survey data may be necessary. Further refinement of vital rate estimates at the regional level, particularly of boreal forest duck species, could improve continental waterfowl management.

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