University of Nevada, Reno


**Life History Patterns and Population Dynamics of Common Goldeneyes in the
Northern Boreal Forest**


A thesis submitted in partial fulfillment of the requirements for the degree of Master of

Science in Natural Resources and Environmental Science


by

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We recommend that the thesis
prepared under our supervision by

**ABIGAIL J. LAWSON**

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**ABSTRACT:** Alaska sea duck populations have experienced substantial declines in the last half-century (Hodges et al. 1996). Though environmental conditions and anthropogenic activities have been implicated in some declines (Dickson and Gilchrist 2002), other potential causes remain unknown (Henny et al. 1995). In recent years, population trajectories among sea duck species (tribe: *Mergini*) have differed markedly (U.S. Fish and Wildlife Service [USFWS] 1999, 2012). In particular, eider (*Somateria Polystitcta* spp.) and scoter (*Melanitta* spp.) populations have declined to historically low levels, whereas populations of cavity nesting species (e.g., *Bucephala*, *Mergus* spp.) have generally increased or stabilized.

Variation in population trajectories likely reflects a combination of proximate causes, such as differences in habitat quality (e.g., wetlands and tundra vs. forest), as well as variation in life history strategies, which influence how a population may respond to potential disturbance (Stearns 1992). My thesis research examined life history patterns and population dynamics of Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye*)* in the northern boreal forest of interior Alaska. Goldeneyes are a cavity nesting sea duck with a holarctic distribution (Eadie et al. 1995). Between 1977 and 1994, goldeneye breeding populations in Alaska declined by 45% (Hodges et al. 1996), though current trends indicate a stable or increasing population in both Alaska (USFWS 1999) and continent-wide (USFWS 2012).

I used capture-mark-recapture data from a long term (1997-2010) nest box study within the Chena River State Recreation Area, approximately 50 km. east of Fairbanks, Alaska. Goldeneyes are an ideal species for demographic study because they readily use artificial nest boxes and exhibit high rates of natal and breeding philopatry (Nilsson 1971,

Dow and Fredga 1983, Savard and Eadie 1989, Pöysä et al. 1997, Ludwichowski et al. 2002), which allows for ease in capture and the ability to encounter the same individual for many years, often with a known breeding history.

In chapter 1, my objective was to describe life history patterns of goldeneyes in relation to other sea duck species, which are typically described as long-lived, with delayed maturity, low and variable annual breeding probability, and invariant adult female survival. I used multistate capture-mark recapture models (Arnason 1972, 1973) in Program MARK (White and Burnham 1999) to estimate multiple demographic parameters, and used several explanatory variables to investigate the effects of climate on breeding and wintering areas, nesting density (as indexed by nest box occupancy), and individual variation (e.g., body condition) on my demographic parameters of interest. I detected substantial annual variation in adult survival ($\varphi^A = 0.66 \pm 0.10$ SE to $0.82 \pm 0.09$). In contrast, breeding probability remained relatively high and invariant ($\psi^{BB} = 0.98 \pm 0.13$) and was positively related to individual nest success the year prior. Nonbreeding individuals in year $t$ were more likely to remain a nonbreeder, than attempt to breed in year $t+1$. Probability of recruitment into the breeding population conditioned on survival to two-years of age was age invariant and followed a negative linear trend over time ($\psi^{PB} = 0.96 \pm 0.01$).

In chapter 2, I used Pradel capture-mark-recapture models (Pradel 1996) to evaluate variation in per-capita recruitment ($f$) and population growth ($\lambda$), and determine the extent to which emigration and immigration may influence study area population dynamics. I detected significant differences in demographic patterns among two groups within my study population: (1) *in-situ* (IS) individuals that were marked as ducklings on the study

area and later encountered as breeding adults; and (2) unknown recruitment origin (UN) individuals that were initially encountered as adults. *In-situ* per-capita recruitment was negatively related to the proportion of boxes occupied by goldeneyes in the year prior to recruitment ($\overline{f^{IS}} = 0.52 \pm 0.12$), whereas recruitment in the unknown group was positively related to the proportion of boxes occupied ($\overline{f^{UN}} = 0.30 \pm 0.03$). In the year prior to recruitment, yearlings typically prospect for potential nest sites (Eadie and Gauthier 1985), therefore, these results suggest that conditions during the prospecting year may facilitate density-dependent dispersal.

Population-level $\lambda$ varied substantially over time, and averaged $1.04 \pm 0.03$, the top two competitive models contained interactions between recruitment group and a linear temporal trend, and an effect of the proportion of ducklings marked two years prior. I investigated varying levels of marking effort on $\lambda$, and determined that even under maximum effort (100% hatched ducklings marked), $\lambda$ s for the *in-situ* and unknown groups were significantly $<1$ ($\lambda^{IS} = 0.69$, $\lambda^{UN} = 0.45$), suggesting the population would decline in the absence of immigration. Furthermore, the non-zero value of $\lambda^{UN}$ suggests that individuals produced outside nest boxes continue to contribute to $\lambda$, even when all potential *in-situ* recruits are marked.

The demographic patterns I detected in goldeneyes are most consistent with a bet-hedging life history strategy (Sæther et al. 1996), rather than a survivor species strategy, as observed in other sea duck species (Goudie et al. 1994). Bet-hedging species are thought to persist in high-quality breeding habitat that enables annual breeding attempts, contrasted with survivor species that breed in lower quality habitat that constrains annual breeding opportunities (Sæther et al. 1996). As such, the importance of suitable nest sites

to goldeneye demography is a recurring theme within my thesis research. High probability of breeding at the earliest age possible likely reflects both the necessity of obtaining a nest site, and the need to accumulate as many breeding attempts as possible over a lifetime, as expected of bet-hedging species— females that nest in the same nest site multiple years generally have earlier nest initiation dates and higher nest success than females that change nest sites (Dow and Fredga 1983). Furthermore, the negative relationship between *in-situ* per-capita recruitment and conspecific nesting density I detected, suggests that under certain conditions, a paucity of available nest sites may inhibit local recruitment patterns and mediate natal dispersal.

The contrast in life history patterns in goldeneyes and other sea ducks may be a contributing factor to observed differences in current population trajectories, therefore, understanding variation in life history strategies within the sea duck group should be of fundamental interest to managers. Furthermore, I detected substantial evidence for both emigration and immigration in our study area, which suggests that nest box populations may be porous, despite assertions of perceived benefits to breeding of natal philopatry (Dow and Fredga 1983). Finally, a lack of demographic parameter estimates for age and sex classes throughout the goldeneye's range has precluded the construction of a population model (Sea Duck Joint Venture 2008). The estimates presented here are among the first for goldeneyes within Alaska (Schmidt et al. 2006) and will contribute to a better understanding of goldeneyes throughout their North American range.

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[1] [1]This thesis is composed in accordance to the University Nevada, Reno's Alternative Formatting for Thesis or Dissertation, in which the following two chapters are being published concurrently with the submission of the thesis.

**Life history patterns of breeding common goldeneyes in the northern boreal forest**

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**ABSTRACT** – Life history patterns and their associated tradeoffs are known to influence population dynamics, as they determine how individuals allocate resources among competing demographic traits. Here we examined life history strategies in Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye), a cavity-nesting sea duck, in the northern boreal forest of interior Alaska. We used multistate capture-mark-recapture models to estimate adult survival, breeding probability, first-year survival, and recruitment probability using a long term nest box study (1997-2010). We detected substantial variation in adult survival, which varied from $0.66 \pm 0.10$ (SE) to $0.82 \pm 0.09$. In contrast, breeding probability remained relatively high and invariant ($0.98 \pm 0.13$) and was related to individual nest success the year prior. Nonbreeding individuals in one year were more likely to remain a nonbreeder, than attempt to breed the following year. We found evidence for stabilizing selection on duckling mass, as heavier ducklings had higher first-year survival, but were less likely to be recruited into the breeding population. First-year survival decreased with later relative hatch dates and larger brood sizes. Probability of recruitment into the breeding population conditioned on survival to two-years of age followed a negative linear trend over time ($\bar{x} = 0.96 \pm 0.01$), and did not vary among ages 2-5 years-old. Overall, goldeneyes exhibited relatively high, but variable, adult survival, as well as high breeding and recruitment probabilities, which is consistent with observed patterns in bet-hedging species that breed annually in high quality breeding environments, but whose reproductive output is often influenced by stochastic events. The demographic estimates from this study are among the first for goldeneyes within Alaska. Life history patterns are known to vary geographically,

therefore, we recommend further examination of life history patterns within the holarctic distribution of goldeneyes.

**INTRODUCTION**

Life history strategies generally form a continuum with long-lived species with delayed maturity at one extreme and fast-growing, short-lived species at the other (Sæther et al. 1996). Within avian species, three general categories are recognized that include high-reproductive species, characterized by high reproductive output and low survival, survivor species that exhibit high survival and low reproductive output, and bet-hedging species that also have high survival, but whose reproductive output is controlled by stochastic variation in breeding conditions (e.g., climate, predation rates; Sæther et al. 1996). Relative to survivor species, bet-hedging species have higher annual breeding probabilities as a mechanism to temporally distribute reproductive attempts in a variable environment; however, mean reproductive output across years is typically similar between these two groups (Sæther et al. 1996).

Life history strategies observed within a species may vary substantially due to environmental variation, population density, disturbance, or individual quality (Clutton-Brock 1988, Sandercock et al. 2005, Martin et al. 2009, Camfield et al. 2010). Furthermore, demographic response to environmental variation is largely driven by life history strategies (Sæther and Bakke 2000). For example, population growth in long-lived species (i.e. survivor and bet-hedging species; Sæther et al. 1996) is typically most sensitive to changes in adult survival (Stearns 1992), as such, population growth would be less affected by widespread reproductive failure than an adult mortality event of equal

magnitude. Traits to which population growth is most sensitive are typically conserved, therefore, other traits may have a greater effect on population dynamics (Cooch et al. 2001). Therefore, an understanding of life history patterns across species or populations can play a crucial role in predicting outcomes of a potential disturbance or proposed management action.

A central tenet of life history theory is the existence of tradeoffs, in which limited resources are divided among competing life history components, typically resulting in a negative covariation among demographic traits (Williams 1966, Stearns 1992). Of particular interest, is the balance between current reproductive effort and future breeding probability or survival. Heightened energetic demands associated with egg formation, incubation, and brood-rearing combined with an increased predation risk, may subject breeding females to increased costs to survival or future breeding, relative to non-breeding females (Sæther 1988, Stearns et al. 1992, Viallefont et al. 1995, Erikstad et al. 1998, Wiebe and Martin 2000, Nager et al. 2001, Milonoff et al. 2004).

The manner in which species allocate limited resources to reproduction is influenced by their life history strategy. In long-lived species that breed numerous times, longevity is key to maximizing lifetime fitness, therefore, individuals are expected to minimize costs to their own survival (Williams 1966, Newton 1989). Individuals may minimize costs by breeding only in favorable conditions or abandoning reproductive attempts. Such mechanisms will likely produce high and relatively invariant rates of annual survival coupled with low and variable annual reproduction.  In contrast, short-lived species with fewer opportunities to breed are predicted to maximize investment in current

reproduction as opposed to survival, resulting in relatively low and variable annual survival with more constant annual reproduction (Stearns 1992).

Reproductive costs can be influenced by numerous factors, including population density, environmental conditions, age, and age at first reproduction (Viallefont et al. 1995, Erikstad et al. 1998, Descamps et al. 2009). In life history theory, age at first breeding is viewed as the result of a tradeoff in which individuals balance the benefits of earlier maturation, which enable increased breeding opportunities, against delayed maturation and potentially greater reproduction at older ages (Stearns 1992, Viallefont et al. 1995, Oli et al. 2002). In short-lived species, such opposing forces are likely to generate stabilizing selection in favor of an invariant "optimal" breeding age, whereas more variation is typically observed in long-lived species, and is likely influenced by external factors; such as environmental conditions during early development, disease, parental effects, and population density (Christensen 1999, Reed et al. 2003, Sedinger et al. 2004, Aubry et al. 2009, Hario and Rintala 2009, Lee et al. 2012).

We examined life history patterns in female Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye), a cavity nesting sea duck (tribe *Mergini*), from a long-term study in the boreal forest of interior Alaska, near the northern limit of the species' breeding distribution (Bellrose 1980, Eadie et al. 1995). Goldeneyes spend most of their annual cycle in a marine environment, but come inland to breed for approximately four months each year (Eadie et al. 1995). Goldeneyes are an ideal species for examining life histories because they readily use artificial nest boxes and exhibit high rates of natal and breeding philopatry (Nilsson 1971, Dow and Fredga 1983, Savard and Eadie 1989, Pöysä

et al. 1997a, Ludwichowski et al. 2002), which allows for ease in capture and the ability to encounter the same individual for many years, often with a known breeding history.

As a group, sea ducks exhibit traits reflective of long-lived species, such as high adult survival and delayed maturity (Goudie et al. 1994, Krementz et al. 1997a), though substantial variation in these traits exists within the group. For example, most goldeneyes begin breeding as 2 or 3 year-olds (Eadie et al. 1995), whereas most Common Eiders (*Somateria molissima* spp.) delay breeding until at least 4 years of age (Baille and Milne 1982). Though goldeneyes are relatively well-studied among sea ducks, it remains unclear where goldeneyes fall on the life history continuum (Sæther et al. 1996). Demographic studies in which modern maximum-likelihood based methods were used to estimate life history parameters remain uncommon for this species (Ludwichowski et al. 2002, Schmidt et al. 2006). Most existing adult survival estimates are actually return rates (Nilsson 1971, Dow and Fredga 1984, Savard and Eadie 1989), which are typically biased low, as they do not separate apparent survival from detection probability.

Detection of reproductive costs in goldeneyes have been mixed. Multiple studies have reported no difference in survival rates among females that bred successfully compared to those that failed (Savard and Eadie 1989, Ludwichowski et al. 2002), whereas Milonoff et al. (2004) reported a negative effect of brood rearing on future reproductive output. Additionally, Dow and Fredga (1984) reported that first-time breeding females that laid larger clutches were less likely to be encountered again, which suggests that age-related costs of reproduction may exist that could potentially affect recruitment decisions, as detected in other avian species (Newton 1989, Viallefont et al. 1995).

Multiple studies in goldeneyes have reported a positive covariance among demographic traits (Dow and Fredga 1984, Milonoff et al. 2002), meaning that the longest lived females were the most productive (i.e., of higher quality). If higher quality individuals consistently attain greater breeding success and longer lifespan compared to lower-quality individuals, such patterns will likely lead to a positive covariation among demographic traits, that may mask reproductive costs (van Noordwijk and deJong 1986, Cam et al. 2002, Wilson and Nussey 2010). Such patterns could explain the lack of reproductive costs detected by other goldeneye studies (Savard and Eadie 1989, Ludwichowski et al. 2002).

Our objective was to understand variation in life histories of goldeneyes and the influence of such variation on population dynamics. We estimated first-year survival, adult survival, recruitment into the breeding population, and probability of breeding, using multistate models with unobservable states. We investigated the effects of environmental conditions in breeding and wintering areas, breeding population density, maternal quality, and individual heterogeneity on these life history traits. We hypothesized that goldeneyes, like other sea duck species, would exhibit life history patterns consistent with long lived species, specifically, relatively invariant adult female survival, with greater temporal variation in recruitment and breeding probabilities. We expected to find positive covariation between demographic traits, indicative of heterogeneity in individual quality (van Noordwijk and deJong 1986, Cam et al. 2002).We further predicted that heterogeneity in individual quality would influence recruitment probability and contribute to variation in age at first breeding, characteristic of long-lived species.

**STUDY AREA**

Our study focused on a nest-box population of goldeneyes in Interior Alaska, USA. The study area was located within the Chena River State Recreation Area and encompassed approximately 102-km$^2$ along the north and middle forks of the Chena River. Ice break-up generally occurs in April to early May, when portions of the study area may flood in years of rapid melt (E. Taylor, personal observation). During the winters of 1994-1997, nest-boxes ($n$ = 150) were installed on trees at heights of 3-7m above the ground near sloughs, oxbows, ponds, and portions of the Chena River. Nest box sites were dominated by mixed stands of balsam poplar (*Populus balsamifera*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). From April to May temperatures typically range between -1–16º C, with minimal precipitation, while during brood-rearing (June – early September; E. Taylor, personal observation) temperatures vary between 10–21 º C. Most annual precipitation occurs between June and August (approximately 20 cm), and can cause additional flooding of nest box sites in some years. We obtained precipitation and temperature data during the breeding and brood-rearing season (April – August, E. Taylor, personal observation) from the Two Rivers National Weather Service station (64°52'N, 146°57'W), located approximately 8 km from the study area's western boundary.

**METHODS**

*Field Methods* –Nest-boxes have been monitored annually since 1997, except during 2006 and 2007. We checked all nest-boxes weekly beginning May 1 to determine occupancy. Active nests were revisited every 1 to 3 days to determine egg-laying rates

and capture the adult nesting female in the nest by blocking the nest box entrance. All eggs were candled to determine incubation progress (Weller 1956) and numbered with a permanent marker to allow us to identify new or missing eggs. We revisited nests until the adult female was captured or the clutch neared completion. Upon initial capture we weighed each adult female using a Pesola spring scale (± 5g), measured head length, culmen length, and tarsus length using dial calipers (± 0.1mm) , and applied a USGS stainless steel leg band, if no band was present.

We revisited nests during late incubation to recapture incubating females and monitor incubation progress. For females that were previously captured during egg-laying, we recorded only body mass and verified the band number. We used egg-laying rate and candling observations to back-calculate a nest initiation date and estimate likely hatch dates for each nest, assuming an egg-laying rate of one egg per 48 hours, average clutch size of 8-10 eggs (adjusting for parasitic eggs), and an incubation period of 28 days (Bellrose 1980, Eadie et al. 1995). All hatched ducklings were marked in their natal box with web tags (1997, 2009-2010 field seasons), plasticine-filled metal leg bands (1998-2008; ARANEA, Lodz, Poland; Blums et al. 1994), or a combination of both (2009-2010). We weighed ducklings using a Pesola spring scale (± 0.5 g; 2000-2008) or an electronic scale (± 0.01g; 2009-2010). We did not determine sex of ducklings at hatch. All procedures were approved by the necessary Institutional Animal Care and Use Committees.

*Multistate Modeling Framework* – We constructed individual capture histories for all individuals in our study population, based on ducklings marked in their natal box at hatch and annual nest box captures of breeding adult females. We assigned individuals to 1 of 2

groups: known-age and unknown age. Known-age individuals were those marked as duckling in their natal box between 1997 and 2008, a subset of which were later encountered as breeding adult females. Ducklings hatched from eggs parasitically laid in the nests of other species were excluded. The unknown age group included females initially captured as unmarked adults from 1997-2010. Our study design only allowed for the capture of adult breeding females (i.e., those using a nest box), therefore, immature juveniles and nonbreeding adults were unavailable for capture. Previous studies have suggested that temporary emigration may exist in adult female goldeneyes, when an individual, following a breeding attempt in year $t$, may skip breeding in year $t+1$, and attempt to breed in year $t+2$ (Dow and Fredga 1984).

We used a multistate modeling framework (Arnason 1972, 1973) with unobservable states, to assess hypotheses and estimate demographic rates. Multistate models allow for state-specific variation in apparent survival ($\varphi$; hereafter survival) and detection probability ($p$), and estimate the probability of transitioning between states ($\psi$), conditioned on survival. Traditional multistate modeling approaches assume that all individuals within each state are available for capture (i.e., observable), whether they were actually captured or missed. These models derive detection probabilities that account for the possibility that missed individuals were in each of the possible observable states. Including an unobservable state allows researchers to account for temporary emigration (Fujiwara and Caswell 2002, Kendall and Nichols, 2002, Schaub et al. 2004).

Using the multistate recaptures-only module in Program MARK (White and Burnham 1999), we created a modeling framework (Fig. 1) with three reproductive states: prebreeding (P), breeding (B), and nonbreeding (N). Due to our inability to detect

juveniles before recruitment, as well as nonbreeding adults, we treated states P and N as unobservable states (Kendall and Nichols 2002), whereas state B was observable. Known-age individuals began in state P at hatch, where they were constrained to remain for both their first-year (i.e., hatch-year) and their second-year (Fig. 1), to reflect delayed maturity in goldeneyes. After second-year individuals, up to age five, could recruit to the breeding population (i.e. enter state B) with probability $\psi^{PB}$, or remain in state P ($\psi^{PP}$).

Here we defined $\psi^{PB}$ as the probability that an individual in state P in year $t$ transitions to state B in year $t+1$, given that they survived to year $t+1$ (hereafter recruitment probability) whereas $\psi^{PP}$ represented the probability that an individual in state P in year $t$ remains in state P in year $t+1$, given that they survived to $t+1$. We set $\psi^{PB}$ equal to zero for individuals six and older, which we believe was appropriate given that 95% of goldeneyes recruit at younger ages (Eadie et al. 1995), and that the oldest age of first breeding observed in our study population was four (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data). Unknown age individuals were first observed in state B, given that they were fully mature upon their initial nest box capture. All individuals in state B could remain in the state the following year with probability $\psi^{BB}$, or become a nonbreeder (i.e., enter state N; $\psi^{BN}$). From state N, individuals could either remain in state N with probability $\psi^{NN}$, or return to state B ($\psi^{NB}$). To constrain and apply covariates to parameters $\psi^{BB}$ and $\psi^{NB}$, we directly estimated $\psi^{BB}$ and $\psi^{NB}$, with $\psi^{BN}$ and $\psi^{NN}$ estimated by subtraction because transition probabilities from a given state must sum to 1 (Arnason 1972, 1973). Additionally, we fixed impossible transition probabilities to equal zero to reflect biological reality. For example, individuals in state P could not enter state N unless they had attempted to breed at least once, meaning that individuals could not

directly transition to state N from state P, therefore we fixed $\psi^{PN}$ to zero (Fig. 1).

Similarly, $\psi^{NP}$ and $\psi^{BP}$ were both fixed to zero because individuals could not return to the prebreeding state after they had become breeders.

Detection probabilities in the unobservable prebreeding ($p_P$) and nonbreeding ($p_N$) states were fixed to zero; hereafter detection probability refers to the breeding state only ($p_B = p$). Additionally, we removed state-specificity from our estimates of adult survival ($\varphi^A$); we constrained survival rates for those in state N to equal those for state B (Kendall and Nichols 2002). To estimate first-year survival in state P ($\varphi^J$; hereafter first-year survival), we constrained survival over the second-year (during which female goldeneyes remain unobservable) to equal adult survival, an assumption supported for other waterfowl species (Owen and Black 1989, Sedinger et al. 2007) and sea ducks in particular (Boyd et al. 2009, Schamber et al. 2009, Oppel and Powell 2010).

We recognize that our first-year survival estimate is biased low due to the inclusion of both sexes, despite only females being available for recruitment. Other studies in sea ducks estimated first-year survival based on returns of individuals marked near or post-fledging (Boyd et al. 2009, Oppel and Powell 2010). Therefore, to compare our estimates to existing studies, we assumed a primary sex ratio of 1:1 in our marked sample (Swennen et al. 1979, Blums and Mendis 1996), and multiplied our estimates of $\varphi^J$ by 2 to account for our inability to detect males; we then divided each estimate by Schmidt et al.'s estimate of duckling survival to 30 days on our study area (0.66) to derive an estimate of post-fledging survival ($\varphi^{J'}$).

Finally, we placed additional constraints on models to accommodate the gap in data collection (2006, 2007) during our study. Detection probabilities for all states during

these years were fixed to zero. For $\varphi^{J}$, the last estimable interval for this parameter before the gap was 2003-2004, because data were not collected when individuals were likely recruited ($t+2$ or $t+3$), therefore we constrained $\varphi^{J}$ for the 2004-2005 through the 2007-2008 intervals to be the same. For transition parameters, $\psi^{PB}$ and $\psi^{BB}$, the last estimable interval before the gap was 2004-2005. We, thus, constrained $\psi^{PB}$ and $\psi^{BB}$ for the 2005-2006 through the 2008-2009 intervals to be the same as the 2004-2005 interval. Further, though individuals may have appeared to be recruited during the 2007-2008 and 2008-2009 intervals, it is likely that these individuals were actually recruited during the gap in data collection (assuming recruitment at 2-3 years of age). For $\psi^{BB}$, we constrained the 2005-2006 to 2007-2008 intervals to be the same as 2004-2005. For $\varphi^{A}$ we treated the gap as a single time interval (2005-2008), with three subintervals.

*Life History Patterns and Tradeoffs* – To test hypotheses and describe life history patterns and tradeoffs in goldeneyes, we constructed all combinations of competing models in which survival, detection probability, and transition probabilities were held constant, allowed to vary across years, or constrained with trends, age effects, or covariates and their interactions. We allowed for potential age effects in adults for up to 6 age classes (2 to $\geq$7) for all parameters. In the known-age group, these classifications represented true age, whereas in unknown age individuals it represented minimum age. We determined the average age of first breeding (i.e. recruitment) for our study population to be approximately 2.26 ($\pm$ 0.01 SE) years (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data) based on observations of first-time breeding attempts of known-age females ($n = 64$). Therefore, we assigned unknown age individuals a minimum age of 2 during their initial capture (Eadie et al. 1995).

Our inability to observe nonbreeding individuals prevented us from directly modeling reproductive costs on survival by comparing annual survival rates of breeders vs. nonbreeders. As an alternative, we examined the effects of nest success in year $t$ on survival to year $t+1$. We assigned individuals a 1 if they successfully incubated a clutch in which at least one duckling hatched, or a 0 for an unsuccessful nesting attempt. Nest success and all other covariates, were standardized across years so that missing covariate values, for absent individuals or those whose nest fate was unknown, were assigned a 0. A negative effect of nest success on survival would support a reproductive cost of incubation or brood-rearing. Goldeneye broods were not followed after departure from the nest box, therefore, we could not separate the potential costs of successful incubation from those associated with brood-rearing.

We also included nest success as a covariate in models of detection probability and transition probabilities representing probability of breeding ($\psi^{BB}$ and $\psi^{NB}$). If the probability of breeding in year $t+1$ was greater for individuals that had not bred in year $t$ as opposed to those that had ($\psi^{NB} > \psi^{BB}$), that would suggest a cost was associated with current reproduction. A negative effect of nest success on $\psi^{BB}$ would suggest a cost of successful incubation or brood rearing for future probability of breeding.

To investigate if differences in individual quality induced a positive correlation among life history traits that could potentially mask reproductive costs, we investigated the effects of additional covariates thought to reflect individual quality. These included nest success, relative nest initiation date, and body condition. Relative nest initiation dates were included as an individual time-varying covariate; we defined relative nest initiation date as the number of days relative to the mode (peak) nest initiation date in a

given year. Modal nest initiation date was computed for all goldeneye nests encountered in a given year, excluding "dump nests" (nests with no signs of an incubation attempt, e.g. few eggs and no down deposited).

We obtained annual indices of female body condition using residuals from a mixed effects model using PROC MIXED in SAS (SAS Institute 2011).  Females were sometimes weighed multiple times within a nesting season, so we used mixed effects models, with female as the random effect, to account for multiple measurements of individual females. We constructed a set of candidate models that included the following explanatory variables: year (fixed effect); female (random effect); PC1 score (structural size; Freeman and Jackson 1990, Sedinger et al. 1995, Schmidt et al. 2006) and day of nesting (day 1= nest initiation), and day of nesting squared. PC1 scores were derived from a principle components analysis of morphological measurements (culmen, head, and tarsus lengths) using PROC PRINCOMP in SAS (SAS Institute 2011). Using our most parsimonious model (Burnham and Anderson 2002) for mass, which included all covariates, we averaged residuals within each year for each female to derive annual indices of body condition.

We incorporated measures of local population density (as indicated by nest box occupancy), productivity, and weather during the breeding and wintering seasons to examine if life-history tradeoffs in recruitment and breeding varied depending on environmental conditions. We assessed three different measures of box occupancy: the proportion of occupied nest boxes (all nest boxes containing at least one egg were considered occupied), the proportion of nest boxes occupied by goldeneyes, and the

proportion of nest boxes occupied by experienced female goldeneyes (see Table 1) for density covariates.

We also used apparent nest success, modal nest initiation and hatch dates, and average female mass during mid-incubation to index annual productivity. Apparent nest success was defined as the number of successful goldeneye nests in which one or more ducklings hatched, divided by the total number of goldeneye nests (excluding dump nests). Modal nest initiation and hatch dates were used as a measure of annual nesting phenology. Presumably, average hen mass during mid-incubation would reflect both food abundance (i.e., environmental conditions) in the breeding area and annual productivity. Years in which females weighed more were more productive and would potentially contribute to increased brood-rearing densities (Paasivaara and Pöysä 2007). All of our population density and productivity covariates, with the exception of apparent nest success, followed a significant trend over time. Therefore, to avoid multicollinearity in our covariates, we detrended the data by creating a linear regression with the covariate as a response variable and year as a predictor variable, and applied the residuals as covariates during modeling. Finally, we included average monthly temperature and total precipitation during the time period when goldeneyes were present on our study area (April – September), obtained from the National Climate Data Center (NCDC; http://www.ncdc.noaa.gov/oa/ncdc.html).

No adult band returns from our study have been reported to date (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data), making it difficult to determine a likely wintering area for our study population. We, therefore, included winter variables from both local and regional scales. For the local scale, we obtained barometric pressure

(PRES), sea surface (WTMP) and ambient temperature (ATMP) data from through the

National Oceanic and Atmospheric Administration's National Data Buoy Center (NDBC;

http://www.ndbc.noaa.gov/) using a buoy located in the Gulf of Alaska (NDBC station

46001; 56°17'59" N 148°1'16" W), a known goldeneye wintering area (Eadie et al. 1995).

Additionally, we obtained Pacific Decadal Oscillation (PDO) index data from the Joint

Institute for Study of the Atmosphere and Ocean at the University of Washington

(http://jisao.washington.edu/pdo/PDO.latest) to assess potential region wide patterns. In

the Pacific Northwest, negative values of PDO (cool phase) are associated with higher

precipitation and cooler temperatures, whereas positive values indicate lower rainfall and

higher temperatures. We averaged monthly values for our winter variables (ATMP,

WTMP, PRES, PDO; Table 1) over each winter, defined as October$_t$ to March$_{t+1}$. We

modeled our density, productivity, and environmental covariates with 1-2 year lag

effects.

   To investigate our hypotheses about life history patterns in goldeneyes, we used a

multi-step process for model construction and evaluation. We first developed a set of a

priori hypotheses regarding associations between each parameter and potential

constraints (e.g., age, time, linear or quadratic time trends). To identify the combination

of constraints and covariates that best explained variation in demographic parameters, we

modeled each parameter sequentially with varying effects, while all other parameters

were held constant (Appendix A). We began by modeling structures for $p$, while retaining

an additive state and time structure for survival, and state transition probabilities held

time-invariant (constant). Models of $p$ included combinations of time, age class, and

linear or quadratic trends over time and ages, and a set of covariates that we hypothesized influenced detection probabilities.

The order in which parameters were modeled could influence the structure of the resulting best-supported model. Therefore, using the best-supported for structure for $p$, we created two preliminary model sets that differed in sequence, with which we modeled $\varphi$ and $\psi$. In the "$\varphi$ first" model set, we placed varying constraints and covariate effects on the remaining parameters beginning with $\varphi^J$, followed by $\varphi^A$, $\psi^{PB}$, and $\psi^{BB}$ ($\psi^{NB}$ was set to zero, see Results; Appendix A, Table A1). Whereas, in the "$\psi$ first" model set we modeled the parameters in the reverse order from the "$\varphi$ first" model set, beginning with $\psi^{BB}$ (Appendix A, Table A2). In each step we retained the best-supported structure on the previously modeled parameter, and a structure of moderate complexity on parameters yet to be modeled (additive state and time structure on survival with time-invariant transition probabilities).

We used Akaike's Information Criterion adjusted for small sample size (AIC$_c$) to identify the most parsimonious model in each step, though we considered all models within 2 $\Delta$AIC$_c$ units of the most parsimonious model to be competitive (Burnham and Anderson 2002). To determine the best model overall, we created a final model set that included the top model from each of the model sets ("$\varphi$ first" and "$\psi$ first", hereafter $\varphi$ and $\psi$ model sets), and additional models that represented intermediates between the two top models, by omitting or including covariates that differed between the two models for a given parameter (Table 2). We then used all models within 2 $\Delta$AIC$_c$ units of the most parsimonious model to obtain model-averaged parameter estimates.

**RESULTS**

During the study, we captured and marked 276 unique adult females, which included 174 individuals of unknown age. Between 1997 and 2008, we marked 2799 day-old ducklings in their natal box, 102 of which were later recruited as breeding adults and recaptured in a nest box within the study area. The detection probability model set included 25 different structures, while the $\varphi$ and $\psi$ model sets each included 76 and 89 models, respectively, in which all parameters were estimated (Appendix A, Table A1, A2). We had difficulty estimating the transition parameter, $\psi^{NB}$, due to its close proximity to the 0 boundary on the logit scale, and the relatively small proportion of breeding females that returned to breed after entering the nonbreeding state (6%). Despite using a profile-likelihood to estimate $\psi^{NB}$ (Morgan and Freeman 1989), we were unable to estimate this parameter, so we fixed $\psi^{NB}$ to zero.

Next, we determined the best structure for $p$ consisted of two age classes, 2 year-olds and individuals 3 and older, with a positive effect of nest success the year prior (Appendix A, Table A1). We retained this structure in the preliminary $\varphi$ and $\psi$ model sets, as well as the final model set (Table 2). The effect of nest success was only applied to the ≥3 age class, because 2 year-olds were all first-time breeders that had no prior nesting history. Further, the effect of nest success in the overall best-supported model (Table 2), also the top model in the $\psi$ model set (Appendix A, Table A1) was relatively weak and the confidence intervals overlapped zero ($\beta = 0.41$; 95% CI -0.14, 0.95).  The model-averaged estimates of $p$ indicated the ≥3 age class had a higher detection probability ($\hat{p} = 0.96 \pm 0.01$ SE) than two year-old's ($\hat{p} = 0.69 \pm 0.07$).

The two preliminary model sets produced similar best-supported models, that differed only in support for specific covariates among $\varphi^J$, $\varphi^A$, and $\psi^{BB}$. The best-supported model from the $\psi$ model set was also the best-supported in the final model set (Table 2) and is hereafter referred to as the top model. The top model contained an additive effect of state and time for survival parameters ($\varphi^J$, $\varphi^A$). Adult survival ($\varphi^A$) was best described by annual variation with no covariates; survival ranged from 0.66 ($\pm$ 0.10) to 0.82 ($\pm$ 0.08; Fig. 2b). Though the top model did not contain any covariate effects for $\varphi^A$, several less parsimonious models, including the two other models used to derive model-averaged estimates, contained a positive additive effect of prior nest success ($\beta = 0.30$; 95% CI 0.01, 0.60; second model in Table 2). For breeding probability ($\psi^{BB}$), the top model included a positive effect of prior nest success ($\beta = 1.4$; 95% CI -4.4, 7.32), though the wide confidence intervals and large standard error ($\pm$ 2.99) suggest substantial uncertainty exists for this effect. Model-averaged estimates of $\psi^{BB}$ were essentially constant ($\psi^{BB} = 0.98 \pm 0.13$).

We detected annual variation in first-year survival ($\varphi^J$), with additive effects of duckling mass ($\beta = 0.55$; 95% CI 0.22, 0.88), brood size ($\beta = -0.18$; 95% CI -0.42, 0.05), and relative hatch date ($\beta = -0.53$; 95% CI -1.02, -0.03); all of which were contained in the models used to derive model-averaged estimates (Table 2). Model-averaged annual first-year survival ($\hat{\varphi}^J$) ranged from $0.05 \pm 0.01$ to $0.10 \pm 0.02$ (Fig. 2a). When we adjusted the $\varphi^J$ estimates for the inclusion of both sexes and to remove pre-fledging mortality (Schmidt et al. 2006), post-fledging survival ($\varphi^{J'}$) ranged from 0.13 to 0.31 ($\bar{x} = 0.19 \pm 0.03$; Fig. 2a). Recruitment probability ($\psi^{PB}$) included a significant negative linear trend over time ($\beta = -0.63$; 95% CI -1.03, -0.19) with a negative effect of duckling mass

($\beta$ = -1.58; 95% CI -2.85, -0.32). During the study, model-averaged $\psi^{PB}$ estimates varied

between 0.99 ($\pm$ 0.1; 1998) and 0.87 ($\pm$ 0.11; 2004; Fig. 3).

**DISCUSSION**

*Individual Heterogeneity* **–** Our results suggest that substantial heterogeneity in individual

quality exists in our study population, as indicated by extensive support for individual

covariate effects in juvenile demographic parameters ($\varphi^{J}$ and $\psi^{PB}$), and the positive

covariation among demographic components observed in adults (Cam et al. 2002).

Though the latter finding is consistent with other goldeneye studies (Dow and Fredga

1984, Milonoff et al. 2002), it may have reduced our ability to detect reproductive costs

(van Noordwijk and deJong 1986, Wilson and Nussey 2010).

We found consistent support that prior nest success (NS) positively influenced

breeding and detections probabilities, and moderate support for a positive effect of prior

nest success on survival for adult females. Detection probability, though typically

considered a nuisance parameter, is informative in our study because it implies both a

breeding status, and also reflects a measure of nest success– females that nest

successfully are more likely to be detected because they inhabit a nest box (i.e., are

available for capture) for a longer period of time than females whose nests fail during

egg-laying or incubation. The positive effect of NS on demographic parameters in this

study suggests that successful females have an advantage over unsuccessful females, as

they are not only more likely to survive and continue breeding, but they are also more

likely to be successful in their current nesting attempt. However, the significance NS

effect was relatively inconsistent for all the demographic parameters in which it was

included as a covariate, therefore, we acknowledge that some uncertainty exists regarding individual quality in goldeneyes.

The positive covariation among demographic traits we detected does not imply that reproductive costs in goldeneyes are unimportant. The relationship between current reproduction and survival remains unclear for several reasons. First, our sample consisted only of observations of breeding individuals, so we could not compare survival rates among breeders and nonbreeders. Nonbreeding by adult females could minimize costs to survival for years in which costs of reproduction are high, which has been documented in other sea duck species (Coulson 1984) and is consistent with life history patterns predicted for long-lived species (Newton 1989, Stearns et al. 1992). Our results, however, suggest that nearly all goldeneye females (98%) attempted to breed every year. The small proportion of breeding birds (2%) entering the nonbreeding state and the low probability with which these females return to the breeding state suggests that nonbreeding represents the typical state for a small segment of the population, rather than a strategy to reduce reproductive costs.

We acknowledge that uncertainty regarding the unobservable, "nonbreeding" state creates further difficulty in evaluation of both reproductive costs and life history patterns in goldeneyes. Ludwichowski et al. (2002) reported that very old female goldeneyes returned to the breeding area but did not breed, whereas Sedinger et al. (2008) attributed variation in breeding probability of Black Brant (*Branta bernicla nigricans*) to heterogeneity in individual quality, and described a permanent nonbreeding segment within the population. In our study, a small proportion of purported nonbreeders may have been breeding individuals that were missed, such as individuals engaged in

alternative nesting strategies. In the absence of intensive capture methods (e.g., Zicus traps; Zicus 1989), individuals that exclusively lay eggs in the nests of other females, are unlikely to be detected because they are only available for capture while laying an egg, which requires between 1.5 and 4 hours (Eadie et al. 1995 and references therein).

Individual heterogeneity also influenced observed life history patterns in juveniles. Earlier relative hatch date and smaller brood sizes were positively related to first-year survival. Individuals that hatch later have slower growth patterns (Sedinger and Flint 1991) and survive at lower rates (Dow and Fredga 1984, Dawson and Clark 2000, Traylor and Alisauskas 2006), potentially due to a seasonal deterioration in food resources (Daan et al. 1998). Female goldeneyes are more likely to abandon their broods if within-brood mortality is high (Pöysä et al. 1997b), which may disproportionately occur in larger broods more visible to predators (Eriksson 1979; but see Dow and Fredga 1984, Schmidt et al. 2006, Paasivaara and Pöysä 2007).

Duckling mass was positively related to first-year survival, and negatively associated with recruitment probability. Precocial goldeneye ducklings leave the nest with their mother between 12 − 48 hours following hatch (Eadie et al. 1995). Larger ducklings may have a survival advantage over smaller individuals due to increased thermoregulatory ability (Rhymer 1988). Within goldeneyes, duckling mass may have a greater influence on first-year survival for populations at northern latitudes subject to more variable weather patterns and shorter breeding seasons, relative to temperate latitude populations. On our study site, Schmidt et al. (2006) detected a consistent negative effect of precipitation on duckling survival to 30 days, whereas similar studies at temperate latitudes detected no such effect (Paasivaara and Pöysä 2007). Though our sample

included duckling masses from both males and females, we believe this did not significantly influence the effect of duckling mass in our results, as other studies of ducks have reported minimal difference in mass between sexes in earlier age classes (Austin and Serie 1994, Traylor and Alisauskas 2006).

Our study is consistent with others that indicate duckling mass (or body size) at or near hatch can positively influence duckling survival to 30 days (Guyn and Clark 1996) and over the hatch year (Sedinger et al. 1995, Sedinger and Chelgren 2007); but differs from those that also detected a positive effect of duckling mass on recruitment (Dawson and Clark 2000). Although we detected negative sampling covariance between first-year survival and recruitment, which could potentially produce a spurious negative correlation between the effect of duckling mass on recruitment and survival probabilities, sampling covariance was very small (-0.09 ± 0.01). Therefore, we suggest that the opposing effects of duckling mass on first-year survival and recruitment suggests stabilizing selection on offspring size: larger individuals are more likely to survive to recruitment age, while smaller individuals, if they survive, have a higher probability of recruitment.

Contrary to our predictions that heterogeneity in individual quality would contribute to age-related variation in recruitment probability, we found that individuals had a high probability of recruitment beginning at 2 years of age ($\bar{x} = 0.96 \pm 0.01$). We included age at first breeding as a covariate for both adult survival and breeding probability to investigate potential trade-offs with recruitment age. However, age of first breeding was not competitive in models of either survival or breeding probability, which does not support a trade-off scenario, or selection for an earlier age at first breeding (Appendix A, Table A1, A2). However, age-invariant recruitment probability, beginning at the

youngest age possible is consistent with duckling mass influence we described. Smaller individuals will reach reproductive maturity earlier than larger individuals, which may enable recruitment at a younger age. In goldeneyes, experienced breeders typically initiate nesting earlier than inexperienced breeders (Dow and Fredga 1984, Milonoff et al. 2002), and earlier nesting improves duckling survival (Guyn and Clark 1999). Therefore, gaining breeding experience as young as possible may provide an advantage to securing a nest box the following breeding season.

We detected substantial age-related differences in detection probability ($p_{\text{AGE }2} < p_{\text{AGE} \geq 3}$), which is likely attributed to age-related differences in reproductive success and nesting strategies. Inexperienced females typically have lower nest success and are more likely to engage in alternative nesting strategies (e.g., pure parasitism; Eadie 1989) than experienced females (Dow and Fredga 1984, Eadie 1989). Age-related variation in $p$ can likely account for the discrepancy between the high probability of recruitment beginning at 2 years of age reported here, and other goldeneye studies that reported average age at first breeding to be closer to 3 years-old (Eadie et al. 1995, Milonoff et al. 2002). These latter studies based their estimates of age at first breeding solely on observations of known-first time breeding attempts, which are likely to be biased high due to the lower detection probability of 2 year-olds.

*Density Dependence* – During the study, overall box occupancy increased by 11% and goldeneye occupancy increased by 22% (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data). We detected a significant negative trend in recruitment probability over time (Fig. 3), which is consistent with several studies that suggest the density-dependent availability of suitable nest sites may constrain breeding opportunities in

cavity-nesting species (Boyd et al. 2009). Such constraints may be especially true of inexperienced females that generally initiate nesting later than experienced females (Dow and Fredga 1984, Milonoff et al. 2002), and are therefore, more likely to be disproportionately affected by high nesting densities in their year of recruitment. As such, limited nest site availability is thought to have contributed to the evolution of alternative nesting strategies, in which inexperienced females more frequently engage compared to experienced females (Eadie et al. 1989).

Our results further suggest that within-cohort density dependence may also influence recruitment patterns. First-year survival model-averaged estimates were negatively correlated with the proportion of boxes occupied by goldeneyes (COGO occ; Table 1) in the cohort's year of recruitment (Pearson's r = -0.51). In the year prior to recruitment, one year-old nonbreeding goldeneyes return to their natal grounds to prospect for potential nest sites and thereby gain information about potential nest sites for the following breeding season (Eadie and Gauthier 1985). Higher first-year survival rates could create increased densities of returning one-year olds, which may encourage individuals to forego breeding or disperse, leading to reduced nest box occupancy rates the following year. Boyd et al. (2009) observed a similar pattern in first-year apparent survival rates of Barrow's goldeneyes, which were negatively correlated with subsequent within cohort survival rates.

Additionally, we found that apparent nest success (ANS; Table 1) and model-averaged estimates for subsequent first-year survival were negatively correlated (Pearson's r = -0.46). In Barrow's goldeneyes and other waterfowl species, duckling survival is lower in areas with higher brood-rearing densities (Savard et al. 1991,

Gunnarsson et al. 2006), an expected product of increased nest success. Goldeneyes are highly territorial towards conspecifics and other waterfowl species during nesting and brood-rearing (Savard 1984), which may contribute to duckling mortality at high densities, as more individuals compete for limited food resources (Newton 1998). Our results are consistent with other studies that suggest the availability of nest sites may constrain breeding opportunities for inexperienced individuals (Boyd et al. 2009), though other density dependent mechanisms may ultimately regulate population-level reproductive output (Pöysä and Pöysä 2002).

*Life History Patterns in Goldeneyes* – We predicted that goldeneyes, like other sea ducks, would exhibit life history patterns similar to other long-lived species (*sensu* "survivor species" in Sæther et al. 1996), specifically, delayed maturity, relatively high and invariant adult survival, contrasted with low and variable levels of reproduction (Stearns 1992). We found that goldeneyes exhibited relatively high, yet variable adult survival, high breeding and recruitment probabilities, and delayed maturity with most individuals breeding as early as possible. Though some of these traits were consistent with those of survivor species, we believed that two traits in particular, placed goldeneyes in the bet-hedging life history strategy category: (1) high annual breeding probability in adults; and (2) the high probability of recruitment, beginning at the earliest age possible.

Bet-hedging species are thought to persist in high quality breeding habitat that allows for annual reproductive attempts, whereas survivor species inhabit lower quality breeding habitat that may preclude consistent breeding (Sæther et al. 1996). For cavity-nesting species like goldeneyes, suitable nesting habitat is more likely to be consistently available, but may be severely limited, than suitable nesting habitat for ground-nesting

species, which is subject to floods or other climatic conditions that could preclude breeding. The patterns we observed in goldeneyes are consistent with those of a bet-hedging species in which high quality breeding habitat may be limited. Specifically, recruitment probability declined as nesting density increased, and consistent annual breeding attempts of adults may act as a mechanism to retain and protect nesting cavities from other females.

Like survivor species, reproductive output in bet-hedging species is controlled by stochastic variation in breeding conditions which produce greater variance in reproductive success than survival (Sæther et al. 1996). Though we did not evaluate reproductive output at the individual level, annual apparent nest success on our study area varied, between 0.56 and 0.91 ($\overline{x} = 0.79 \pm 0.02$ SE), and was strongly driven by variation in nest depredation rates by American pine martens (*Martes americanus*; E. Taylor, USFWS, Anchorage, AK, USA, unpublished data).

Somewhat consistent with our prediction of high adult female survival, this parameter averaged $0.74 \pm 0.02$ during our study, which is slightly lower than 0.83 reported by Ludwichowski et al. (2002) for goldeneyes in northern Germany, and higher than Boyd et al.'s (2009) 0.68 estimate for Barrow's goldeneyes in British Columbia, Canada. Ludwichowski et al. (2002) derived their estimate using Barker models that combine live resight data with band recovery data (Barker 1997, 1999); their survival estimates, thus, represented true survival. We were unable to account for permanent emigration and the estimates we report here may be biased low compared to those of Ludwichowski et al. (2002).

Our survival estimates are lower than those reported for females of other sea duck species, including Common Eiders on the Yukon-Kuskokwim Delta (0.89; Wilson et al. 2007), Steller's Eiders in western Alaska (*Polysticta stelleri*; 0.89; Flint et al. 2007), White-Winged Scoters at Redberry Lake in Saskatchewan (*Melanitta fusca*; 0.77; Krementz et al. 1997b). All of the aforementioned studies used maximum likelihood-based methods that differentiate between apparent survival and detection probabilities. Our survival estimate was lower than that of King Eiders (*Somateria spectabilis*; 0.94; Oppel and Powell 2010) from a satellite telemetry study on the north slope of Alaska that used known-fate models, in which detection probability is assumed to be equal to one, to estimate survival. Therefore, these studies are more appropriate for comparison to the results presented here than return rates reported in earlier goldeneye studies (e.g., Savard and Eadie 1989) in which detection probabilities are not accounted for.

Contrary to expected patterns for bet-hedging species, we detected substantial temporal variation in adult survival (Fig. 2b), compared to patterns observed in the longest-lived sea duck species (Flint et al. 2000, Wilson et al. 2007, Oppel and Powell 2010). Additionally, adult survival exhibited greater temporal variation than recruitment probability (Fig. 2b, 3), the opposite of predictions for long-lived species (Stearns 1992). We were unable to detect a relationship between survival and time varying covariates. Uncertainty about the wintering and migration areas used by our study population prevented us from using climate or oceanographic variables specific to these areas, which hampered our ability to model annual survival.

Our results strongly suggest that goldeneyes, unlike other sea duck species, do not intermittently breed (Coulson 1984). Therefore, the assumption of no temporary

emigration may be met for studies that rely solely on nest box encounters to evaluate

adult female survival, if sufficiently intensive encounter methods are used. Females must

be encountered during egg-laying rather than late incubation, however, to ensure

detection of females whose nests fail early.

Our estimates of first-year survival required several assumptions, including equal

survival of 1 year-olds (i.e., survival over the second year) and adults, as well as equal

survival between sexes. However, to the extent that our estimates of apparent survival

$(\varphi^A)$ underestimated true survival in adults, we may have overestimated first-year survival

because we could only observe individuals following their second year. The probability

we encountered a 2 year-old represented the product of: $\varphi_t^J * \varphi_{t+1}^A * \psi_{t+2}^{PB} * p_{\text{AGE 2}}$.

Therefore, to the extent that we underestimated $\varphi^A$ we must have overestimated $\varphi^J$. Our

average post-fledging survival estimate $(\varphi^{J'}; \bar{x} = .20 \pm 0.03)$ is significantly lower than

existing estimates for female Barrow's goldeneyes (0.68; Boyd et al. 2009). However, we

were unable to further adjust for potential sex differences in survival because detection

probability for males was zero in our study.

The lower post-fledging survival estimates reported here may reflect potential

differences in mortality or dispersal patterns compared to Boyd et al.'s (2009) study. Our

study population is near the northern distributional limit of the goldeneye's breeding

range (Eadie et al. 1995), and may be subject to harsher wintering conditions, longer

migration, and a more constrained nesting phenology, all of which may create different

mortality patterns, relative to temperate latitude populations (e.g., Boyd et al. 2009).

Alternatively, nest sites may have been more limited in our study population compared to

Boyd et al.'s (2009), leading to higher natal dispersal that lowered our estimates of post-

fledging survival. Though an assessment of differential box occupancy between our study and Boyd et al.'s would allow us to determine relative nest site limitation between the two sites, our current study design does not allow us to distinguish mortality from permanent emigration (i.e. dispersal).

Similarly, permanent emigration to an unobservable state in adult females also remains unclear. A study in northern Germany estimated breeding site fidelity to be 91% among adult females based on resights of marked individuals (Ludwichowski et al. 2002). While this estimate is relatively high, it is lower than previously thought (Savard and Eadie 1989) and suggests that a small proportion of females may disperse outside the study area, although it remains unclear as to whether dispersers engage in breeding. Given that suitable nesting sites are likely limited (Savard 1988, Boyd et al. 2009), females that dispersed away from a breeding location seem unlikely to breed at the new location. Therefore, permanent emigration likely represents transition to a relatively permanent nonbreeding state. Use of external markers that allow for resighting would improve our ability to disentangle dispersers from local nonbreeders.

Though goldeneyes are traditionally grouped with other sea duck species for management purposes, we have identified several key differences in life history traits between goldeneyes and other long-lived sea duck species that should be considered when evaluating proposed management actions. As such, differences in life history strategies may have contributed to observed differences in population trajectory between goldeneyes, in which populations are considered stable or increasing, and other species that continue to decline (United States Fish and Wildlife Service 1999, 2012, Dickson and Gilchrist 2002). Similar to other sea duck species, we found that demography in

goldeneyes in largely influenced by heterogeneity in individual quality, which may have reduced our ability to detect reproductive costs. Most notably, we found that goldeneyes breed every year rather than intermittently, though a small proportion enter a permanent unobservable nonbreeding state each year. The permanent emigration patterns observed in adults requires further investigation, as dispersal patterns in goldeneyes, especially females, remain poorly understood. Furthermore, life history traits are known to vary geographically, therefore, future research should investigate if variation in the patterns we described exist throughout the goldeneye's holarctic breeding range. The demographic estimates presented here are among the first from their Alaska breeding range and will fill a void in our understanding of goldeneye population dynamics.

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Table 1. Summary of the covariates used to estimate first-year survival ($\varphi^J$), adult female survival ($\varphi^A$), recruitment probability ($\psi^{PB}$), and breeding probability ($\psi^{BB}$) of goldeneyes in the northern boreal forest of Alaska from 1997-2010. All individual time-varying covariates (e.g., NS, bc, oc) were standardized across years.

| Variable | Description |
| --- | --- |
| Individual Covariates | |
| *Ducklings* | |
| brood | Brood size - the number of ducklings (all species) leaving the nest box |
| dmass | Duckling mass- Mass recorded at hatch, only available for individuals hatched after 2002 |
| henage | Minimum age of maternal hen |
| rhatch | Relative hatch date - the number days relative to peak (mode) hatch date for year *t* |
| *Adults* | |
| brdage | Age at first breeding, applied to known-age individuals only |
| NS | Nest success - The nesting outcome of an individual in *t-1* for interval *t-1* to *t*, nesting outcome coded as: 1 = successful (nests in which $1 \leq$ ducklings hatched), 0 = unsuccessful |
| bc | Average annual body condition (year adjusted) - Residuals from a mixed effects model with mass as a response variable and structural size, day of nesting$^2$, individual (random effect), and year (fixed effect) as explanatory variables; model residuals were averaged for each hen within each year |
| oc | Overall body condition - Residuals from a mixed effects model with mass as a response variable and structural size, day of nesting$^2$, and individual (random effect) as explanatory variables; model residuals were averaged for each hen within each year |
| Population-level Covariates | |
| *Density and Productivity* | |
| hen mass | Annual average hen mass during mid-incubation, derived using mixed models used for body condition covariates described above |
| box occ | Annual proportion of occupied nest boxes |
| COGO occ | Annual proportion of total nest boxes occupied by goldeneyes |
| exp occ | Annual proportion of total nest boxes occupied by goldeneyes with prior breeding experience |

| | |
|---|---|
| ANS | Annual apparent nest success - the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests) |
| pNID | Annual peak (mode) goldeneye nest initiation date |
| phatch | Annual peak (mode) goldeneye nest hatch date |

*Weather and Climate*

| | |
|---|---|
| temp | Average of monthly mean temperatures on the study area from April to September (i.e. breeding and brood-rearing) |
| precip | Total precipitation on the study area from April to September |
| PRES | Sea level pressure (hPa) from October$_{t-1}$ to March$_t$ in purported wintering region |
| ATMP | Air temperature (Celsius) from October$_{t-1}$ to March$_t$ in purported wintering region |
| WTMP | Sea surface temperature (Celsius) from October$_{t-1}$ to April$_t$ in purported wintering region |
| PDO | Annual Pacific Decadal Oscillation index, averaged monthly mean values from May$_{t-1}$ to April$_t$ |

Table 2. Models representing hypotheses about life history patterns in Common Goldeneyes in interior Alaska. This table contains the top models from each of the preliminary model sets ($\varphi$ and $\psi$; denoted by footnotes b and c, respectively; Appendix A, Table A1, A2), and additional models that represent intermediates between the top two models, to determine the best supported model overall. In the preliminary model sets, each parameter was modeled sequentially, beginning with $\varphi^J$, followed by $\varphi^A$, $\psi^{PB}$, and $\psi^{PB}$ for the $\varphi$ model set, and the reverse sequence for the $\psi$ model set. In each step of the sequential modeling process, the best-supported structure for each previously modeled parameter was retained when modeling subsequent parameters; the results are contained in Appendix A (Table A1, A2). The additional models are intermediate structures between the two top models identified by the preliminary model sets that were not considered during the preliminary modeling process, due to the sequential modeling approach. The most parsimonious detection probability ($p$) structure was determined in the first step of the $\varphi$ modeling process and was retained for all subsequent models. Model-averaged estimates reported in the main text include all models within 2 $\Delta AIC_C$ units of the top model.

| Model[a] | k | Dev. | AICc | ΔAICc | $w_i$ | Likel-ihood |
|---|---|---|---|---|---|---|
| $\varphi^J$ (t + brood + rhatch + dmass), $\varphi^A$(t), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (NS)[b] | 23 | 1754.73 | 1801.05 | 0.00 | 0.39 | 1.00 |
| $\varphi^J$ (t + brood + rhatch + dmass), $\varphi^A$ (t + NS), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (.) | 23 | 1756.08 | 1802.40 | 1.35 | 0.20 | 0.51 |
| $\varphi^J$ (t + brood + rhatch + dmass), $\varphi^A$ (t + NS), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (NS) | 24 | 1754.69 | 1803.04 | 1.99 | 0.15 | 0.37 |
| $\varphi^J$ (t + brood + dmass), $\varphi^A$ (t), $\psi^{PB}$ (T + dmass), $\psi^{BB}$(NS) | 22 | 1759.06 | 1803.36 | 2.31 | 0.12 | 0.32 |
| $\varphi^J$ (t + brood + dmass), $\varphi^A$ (t + NS), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (.)[c] | 22 | 1760.53 | 1804.83 | 3.78 | 0.06 | 0.15 |

| Model | K | Deviance | AICc | ΔAICc | w | Likelihood |
|---|---|---|---|---|---|---|
| $\varphi^J$ (t + brood + dmass), $\varphi^A$ (t + NS), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (NS) | 23 | 1759.04 | 1805.37 | 4.31 | 0.05 | 0.12 |
| $\varphi^J$ (t + brood + rhatch + dmass), $\varphi^A$ (t), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (.) | 21 | 1765.23 | 1807.50 | 6.45 | 0.02 | 0.04 |
| $\varphi^J$ (t + brood + rhatch + dmass), $\varphi^A$ (t + NS), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (NS) | 23 | 1762.21 | 1808.54 | 7.48 | 0.01 | 0.02 |
| $\varphi^J$ (t + brood + dmass), $\varphi^A$(t), $\psi^{PB}$ (T + dmass), $\psi^{BB}$ (.) | 20 | 1769.66 | 1809.91 | 8.85 | 0.00 | 0.01 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes time variation, (T) denotes a linear trend effect, (.) means that a parameter was held constant, and a + sign indicates an additive effect between two variables, whereas a * denotes an interaction. Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval $t$-$1$ to $t$. For example, a $t$-$1$ subscript denotes conditions at the beginning of the interval. For all models, the probability of returning to breeding ($\psi^{NB}$) was set to zero, and detection probability ($p$) followed the structure (Age 2, $\geq$3 + NS), representing two age classes of 2 year-olds and individuals 3 and older, with individual nesting outcome the previous year (NS) applied to individuals three and older only. NS = nesting outcome of an individual in year $t$-$1$, in which the outcome was coded as 1 = successful (nests in which 1$\leq$ ducklings hatched) and 0 = unsuccessful; dmass = individual duckling mass recorded at hatch, standardized across years, and only available for individuals hatched after 2002; brood = the number of ducklings (all species) leaving the nest box; rhatch = individual relative hatch date, the number of days relative to peak (modal) hatch date each year. All covariates were z-standardized across years (mean = 0.0, SD = 1.0), with missing values assigned a 0.

[b]Top model from the $\psi$ model set

[c]Top model from the φ model set

Figure 1. Visual representation of our multistate modeling framework, including all parameters associated with each reproductive state, and important constraints implemented within our framework. Individuals of both sexes marked as ducklings (i.e., known-age individuals) entered the Prebreeding state (P) at hatch, where they remained for at least 2 years to reflect delayed maturity in goldeneyes. First-year survival is denoted by $\varphi^J$, whereas second-year survival was constrained to equal that of adult females in the breeding population ($\varphi^A$). We estimated post-fledging survival ($\varphi^{J'}$) by multiplying $\varphi^J$ by 2 to adjust for the inclusion of both sexes, and then dividing the product by 0.655, the average estimate of duckling survival to 30 days on our study area (Schmidt et al. 2006). After 2 years, juveniles could recruit into the breeding population (state B) with probability $\psi^{PB}$, or remain in state P ($\psi^{PP}$). All individuals (known and unknown age) in the breeding population could continue to breed the following year ($\psi^{BB}$), or enter the Nonbreeding state (N; $\psi^{BN}$), where they could remain ($\psi^{NN}$) or return to breeding ($\psi^{BN}$). Several movements between states were impossible and were set to zero: $\psi^{PN}$, $\psi^{NP}$, and $\psi^{BP}$. Individual encounter histories used only nest box observations (i.e., hatched ducklings and breeding individuals). Immature juveniles in state P and nonbreeding adults in state N were not available for encounter, so detection probabilities for these states ($p_P$ and $p_N$, respectively) were equal to zero, and survival in state N was constrained to equal survival of adults ($\varphi^A$) in the breeding population (i.e, state B; Kendall and Nichols 2002).

Figure 2. Model-averaged annual estimates from year $t$ to year $t+1$ for (a.) first-year survival ($\varphi^J$, $n = 8$) and (b.) adult female survival ($\varphi^A$; $n = 11$). The 2005 annual survival

estimate represents the average annual survival for each interval over the three intervals
(2005 – 2008) affected by the gap in collection of data during the 2006 and 2007 field
seasons. In b. the post-fledging survival estimates ($\varphi^{J'}$) were derived by multiplying raw
estimates of $\varphi^{J}$ by 2 to adjust for the inclusion of both sexes, and then dividing the
product by 0.655, the average estimate of duckling survival to 30 days on our study area
(Schmidt et al. 2006). The breaks on the x-axes in both figures represent years in which
data was not collected and associated parameters could not be estimated. Error bars
represent standard errors (SE) of model-averaged parameter estimates generated using
multistate recaptures-only models in Program MARK.

Figure 3. Model-averaged recruitment probability ($\psi^{PB}$) estimates for year *t* to *t+1*.
Recruitment probability estimates are only shown prior to the gap in data collection
(2006, 2007), as the only post-gap interval in which $\psi^{PB}$ was estimable (2008-2009) is
biased low because only individuals hatched in 2008 were available for recruitment.
Though individuals that hatched during the gap in data collection (2006, 2007) may have
recruited over this interval, these individuals would not be considered recruits (i.e.
known-age individuals) because they were not marked at hatch. Error bars represent
standard errors (SE) of model-averaged parameter estimates generated using multistate
recaptures-only models in Program MARK.
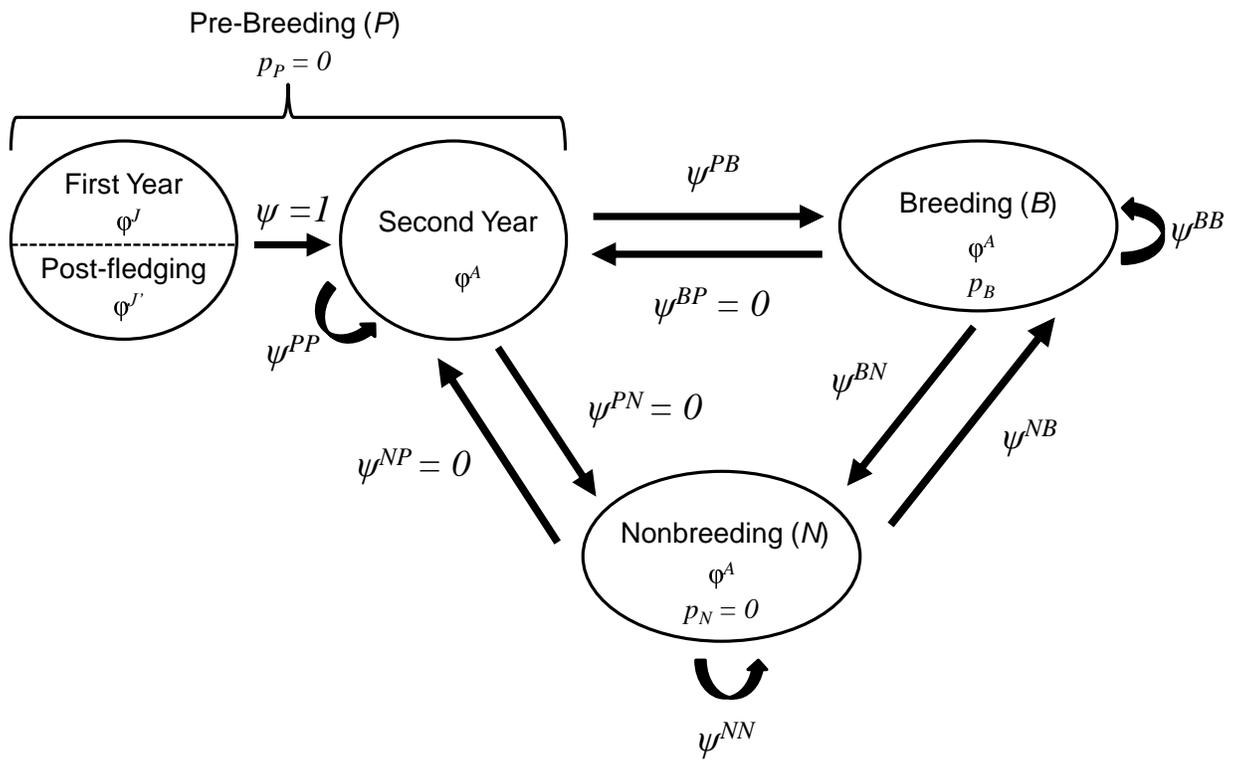
Figure 1.
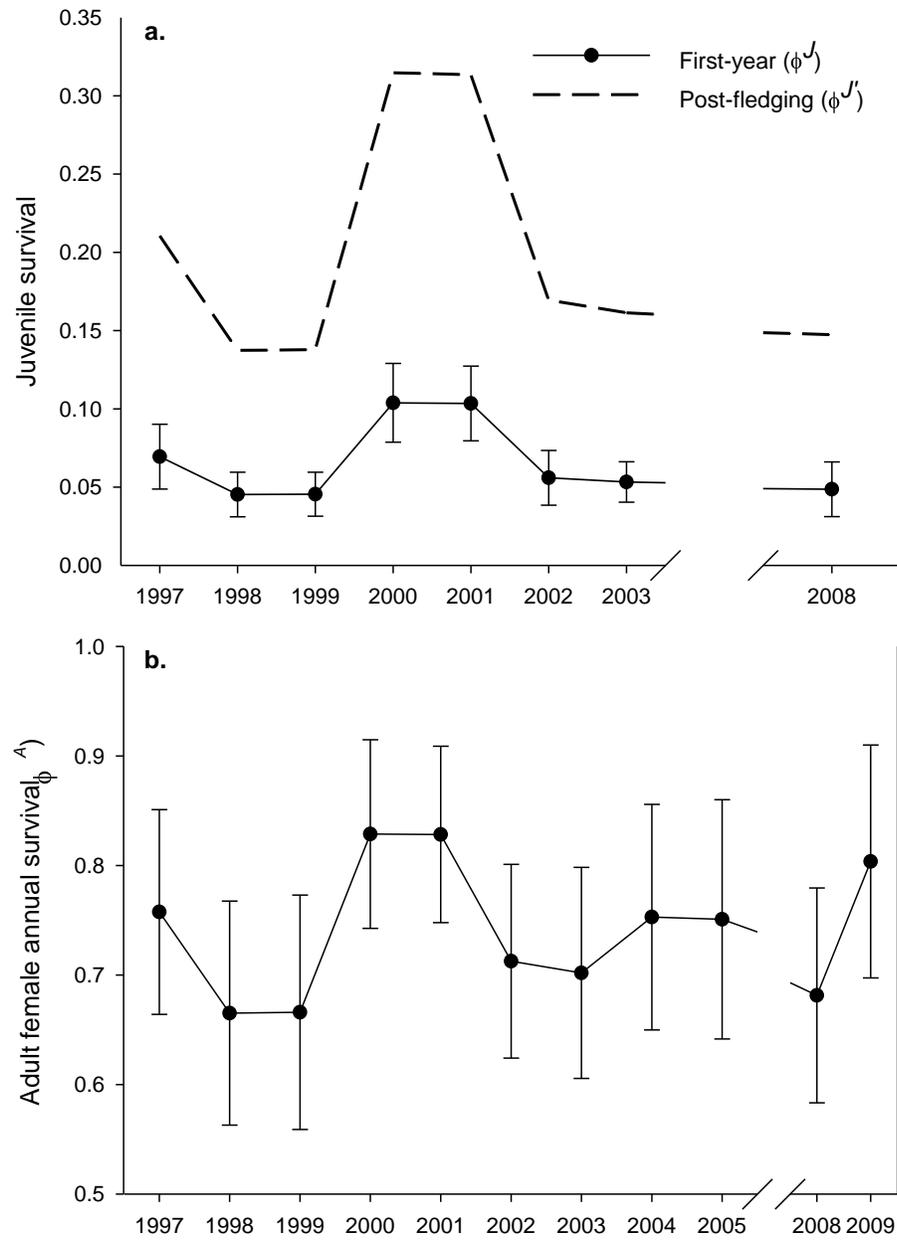
Figure 2.
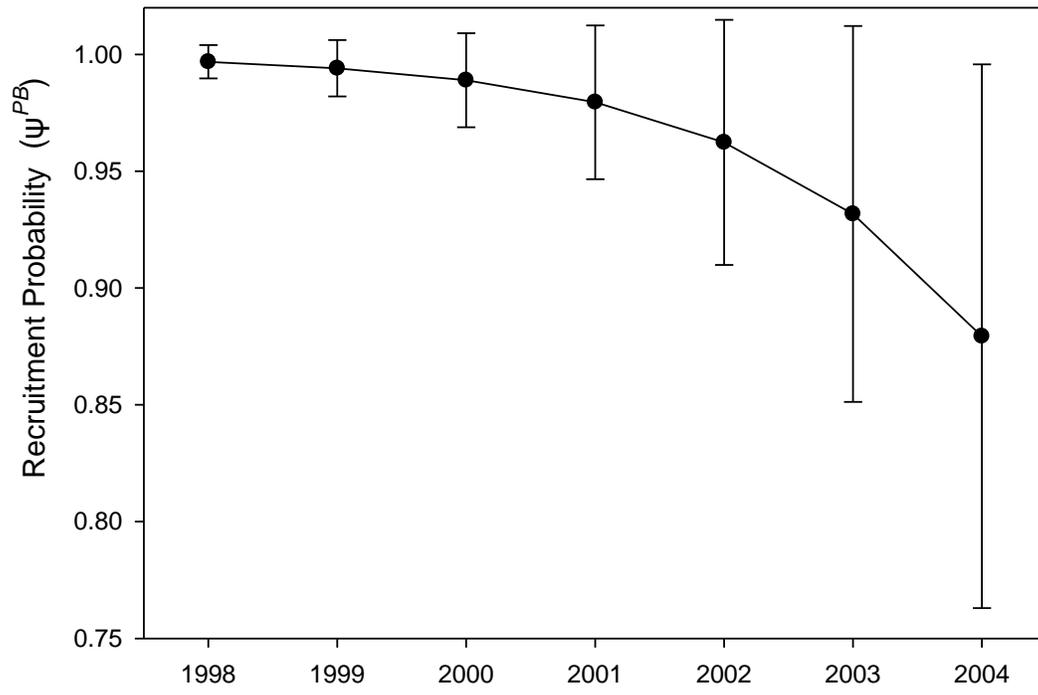
Figure 3.

# APPENDIX A. COMPLETE MODEL LIST FOR MULTISTATE CAPTURE-MARK-RECAPTURE ANALYSES IN PROGRAM MARK

**Table A1.** These models represent hypotheses regarding life history patterns in Common Goldeneyes in interior Alaska. We modeled detection probability ($p$) first, followed by first-year survival ($\varphi^J$), adult survival ($\varphi^A$), recruitment probability ($\psi^{PB}$), and probability of continuing to breed ($\psi^{BB}$); and are referred to as the "Phi models" in the main article. The most parsimonious structure for each parameter was retained when modeling the subsequent parameter. Refer to Table 1 in the main article for covariate descriptions. Only models in which all parameters were estimated are included in these tables.

| | | | WITHIN-SET | | | OVERALL | |
|---|---|---|---|---|---|---|---|
| **Model**[a] | **$k$** | **Dev.** | **$\Delta AIC_c$** | **$w_i$** | **Likel-ihood** | **$\Delta AIC_c$** | **$w_i$** |
| *Detection probability $(p)$[b]* | | | | | | | |
| **$p$(Age 2, 3≤ + NS)** | **17** | **1795.57** | **0.00** | **0.28** | **1.00** | **24.92** | **0.00** |
| $p$(Age 2, 3≤ + NS + PDO$_{t-1}$) | 18 | 1794.72 | 1.17 | 0.15 | 0.56 | 26.08 | 0.00 |
| $p$(Age 2, 3, 4≤ * NS) | 19 | 1793.41 | 1.88 | 0.11 | 0.39 | 26.80 | 0.00 |
| $p$(Age 2, 3, 4, 5≤ + NS) | 19 | 1793.77 | 2.25 | 0.09 | 0.32 | 27.17 | 0.00 |
| $p$(Age 2, 3, 4, 5≤ * NS) | 21 | 1790.10 | 2.62 | 0.07 | 0.27 | 27.54 | 0.00 |
| $p$(NS) | 16 | 1800.32 | 2.73 | 0.07 | 0.26 | 27.65 | 0.00 |
| $p$(Age 2, 3≤) | 16 | 1801.87 | 4.28 | 0.03 | 0.12 | 29.19 | 0.00 |
| $p$(Age 2, 3, 4, 5≤) | 18 | 1797.86 | 4.31 | 0.03 | 0.12 | 29.22 | 0.00 |
| $p$(Age 2, 3≤ + PDO$_{t-1}$) | 17 | 1800.83 | 5.26 | 0.02 | 0.07 | 30.18 | 0.00 |
| $p$(Age 2, 3, 4≤) | 17 | 1801.09 | 5.52 | 0.02 | 0.06 | 30.43 | 0.00 |
| $p$(PDO$_{t-1}$) | 16 | 1803.50 | 5.91 | 0.01 | 0.05 | 30.83 | 0.00 |
| $p$(Age 2, 3, 4, 5≤ + ANS$_t$) | 19 | 1797.54 | 6.01 | 0.01 | 0.05 | 30.93 | 0.00 |
| $p$(Age 2, 3≤ + ANS$_t$) | 17 | 1801.71 | 6.14 | 0.01 | 0.05 | 31.06 | 0.00 |
| $p$(Age 2, 3, 4, 5, 6≤) | 19 | 1797.79 | 6.26 | 0.01 | 0.04 | 31.18 | 0.00 |
| $p$(exp occ$_t$) | 16 | 1803.97 | 6.38 | 0.01 | 0.04 | 31.30 | 0.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $p(\text{pNID}_t)$ | 16 | 1804.30 | 6.71 | 0.01 | 0.04 | 31.62 | 0.00 |
| $p(T)$ | 16 | 1804.49 | 6.90 | 0.01 | 0.03 | 31.82 | 0.00 |
| $p(.)$ | 15 | 1806.64 | 7.03 | 0.01 | 0.03 | 31.95 | 0.00 |
| $p(\text{ANS}_t)$ | 16 | 1804.98 | 7.39 | 0.01 | 0.02 | 32.31 | 0.00 |
| $p(\text{Age 2, 3, 4} \leq + \text{ANS}_t)$ | 18 | 1800.99 | 7.44 | 0.01 | 0.02 | 32.35 | 0.00 |
| $p(\text{Age 2, 3, 4, 5, 6} \leq + \text{ANS}_t)$ | 20 | 1797.50 | 8.00 | 0.01 | 0.02 | 32.91 | 0.00 |
| $p(\text{hen mass}_t)$ | 16 | 1806.01 | 8.42 | 0.00 | 0.01 | 33.34 | 0.00 |
| $p(\text{box occ}_t)$ | 16 | 1806.40 | 8.81 | 0.00 | 0.01 | 33.73 | 0.00 |
| $p(\text{COGO occ}_t)$ | 16 | 1806.45 | 8.86 | 0.00 | 0.01 | 33.78 | 0.00 |
| $p(g)$ | 16 | 1806.51 | 8.92 | 0.00 | 0.01 | 33.83 | 0.00 |

*First-year survival $(\varphi^J)^c$*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\varphi^J(t + brood + dmass)$** | **19** | **1784.25** | **0.00** | **0.22** | **1.00** | **17.64** | **0.00** |
| $\varphi^J(t + dmass)$ | 18 | 1786.31 | 0.04 | 0.21 | 0.98 | 17.68 | 0.00 |
| $\varphi^J(t + brood + dmass + rhatch)$ | 20 | 1782.38 | 0.16 | 0.20 | 0.93 | 17.80 | 0.00 |
| $\varphi^J(t + dmass + rhatch)$ | 19 | 1785.09 | 0.84 | 0.14 | 0.66 | 18.49 | 0.00 |
| $\varphi^J(t + dmass + henage)$ | 19 | 1785.58 | 1.33 | 0.11 | 0.52 | 18.97 | 0.00 |
| $\varphi^J(t + dmass * rhatch)$ | 20 | 1784.21 | 1.98 | 0.08 | 0.37 | 19.62 | 0.00 |
| $\varphi^J(t + brood + rhatch)$ | 19 | 1790.44 | 6.19 | 0.01 | 0.05 | 23.83 | 0.00 |
| $\varphi^J(t + brood)$ | 18 | 1793.26 | 6.99 | 0.01 | 0.03 | 24.63 | 0.00 |
| $\varphi^J(t)$ | 17 | 1795.57 | 7.27 | 0.01 | 0.03 | 24.92 | 0.00 |
| $\varphi^J(t + rhatch)$ | 18 | 1793.57 | 7.29 | 0.01 | 0.03 | 24.94 | 0.00 |
| $\varphi^J(t + henage)$ | 18 | 1793.76 | 7.49 | 0.01 | 0.02 | 25.13 | 0.00 |
| $\varphi^J(T^2)$ | 19 | 1793.37 | 9.12 | 0.00 | 0.01 | 26.76 | 0.00 |
| $\varphi^J(t * rhatch)$ | 26 | 1784.23 | 14.17 | 0.00 | 0.00 | 31.83 | 0.00 |
| $\varphi^J(T)$ | 18 | 1802.39 | 16.11 | 0.00 | 0.00 | 33.76 | 0.00 |
| $\varphi^J(\text{PRES}_{t-1})$ | 18 | 1805.05 | 18.78 | 0.00 | 0.00 | 36.42 | 0.00 |
| $\varphi^J(\text{pNID}_{t-1})$ | 18 | 1806.05 | 19.78 | 0.00 | 0.00 | 37.42 | 0.00 |
| $\varphi^J(\text{hen mass}_{t-1})$ | 18 | 1806.48 | 20.21 | 0.00 | 0.00 | 37.85 | 0.00 |
| $\varphi^J(\text{box occ}_{t-1})$ | 18 | 1806.74 | 20.46 | 0.00 | 0.00 | 38.10 | 0.00 |
| $\varphi^J(\text{exp occ}_{t-1})$ | 18 | 1807.21 | 20.93 | 0.00 | 0.00 | 38.57 | 0.00 |

*Adult survival $(\varphi^A)^d$*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\varphi^A(t + NS)$** | **20** | **1774.45** | **0.00** | **0.63** | **1.00** | **9.86** | **0.00** |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $\varphi^A(PDO_{t-1} + NS)$ | 18 | 1779.80 | 1.31 | 0.33 | 0.52 | 11.17 | 0.00 |
| $\varphi^A(t)$ | 19 | 1784.25 | 7.78 | 0.01 | 0.02 | 17.64 | 0.00 |
| $\varphi^A(t + brdage)$ | 20 | 1783.74 | 9.29 | 0.01 | 0.01 | 19.16 | 0.00 |
| $\varphi^A(PDO_{t-1})$ | 18 | 1787.88 | 9.38 | 0.01 | 0.01 | 19.243 | 0.00 |
| $\varphi^A(bc_{t-1})$ | 20 | 1783.96 | 9.51 | 0.01 | 0.01 | 19.37 | 0.00 |
| $\varphi^A(t + rhatch)$ | 20 | 1783.98 | 9.53 | 0.01 | 0.01 | 19.40 | 0.00 |
| $\varphi^A(t + oc_{t-1})$ | 20 | 1784.09 | 9.64 | 0.01 | 0.01 | 19.51 | 0.00 |
| $\varphi^A(Age\ 2, 3\leq + t)$ | 20 | 1784.25 | 9.80 | 0.00 | 0.01 | 19.66 | 0.00 |
| $\varphi^A(Age\ 2, 3, 4\leq + t)$ | 21 | 1783.78 | 11.36 | 0.00 | 0.00 | 21.22 | 0.00 |
| $\varphi^A(box\ occ_{t-1})$ | 18 | 1790.99 | 12.50 | 0.00 | 0.00 | 22.36 | 0.00 |
| $\varphi^A(Age\ 2, 3, 4, 5\leq + t)$ | 22 | 1783.71 | 13.31 | 0.00 | 0.00 | 23.17 | 0.00 |

*Probability of recruitment ($\psi^{PB}$)[e]*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\psi^{PB}(T + dmass)$** | **22** | **1760.53** | **0.00** | **0.47** | **1.00** | **0.00** | **0.14** |
| $\psi^{PB}(phatch_{t-2} + dmass)$ | 22 | 1762.17 | 1.64 | 0.21 | 0.44 | 1.64 | 0.06 |
| $\psi^{PB}(dmass)$ | 21 | 1765.06 | 2.50 | 0.14 | 0.29 | 2.50 | 0.04 |
| $\psi^{PB}(COGO\ occ_{t-1} + dmass)$ | 22 | 1763.54 | 3.01 | 0.10 | 0.22 | 3.01 | 0.03 |
| $\psi^{PB}(T)$ | 21 | 1770.32 | 7.76 | 0.01 | 0.02 | 7.76 | 0.00 |
| $\psi^{PB}(phatch_{t-2})$ | 21 | 1771.18 | 8.62 | 0.01 | 0.01 | 8.62 | 0.00 |
| $\psi^{PB}(T^2)$ | 22 | 1769.39 | 8.85 | 0.01 | 0.01 | 8.85 | 0.00 |
| $\psi^{PB}(hen\ mass_{t-1})$ | 21 | 1771.53 | 8.97 | 0.01 | 0.01 | 8.97 | 0.00 |
| $\psi^{PB}(PRES_{t-1})$ | 21 | 1771.62 | 9.06 | 0.01 | 0.01 | 9.06 | 0.00 |
| $\psi^{PB}(COGO\ occ_{t-1})$ | 21 | 1771.67 | 9.11 | 0.00 | 0.01 | 9.11 | 0.00 |
| $\psi^{PB}(WTMP_{t-2})$ | 21 | 1771.91 | 9.35 | 0.00 | 0.01 | 9.35 | 0.00 |
| $\psi^{PB}(precip_{t-2})$ | 21 | 1772.10 | 9.54 | 0.00 | 0.01 | 9.54 | 0.00 |
| $\psi^{PB}(.)$ | 20 | 1774.45 | 9.86 | 0.00 | 0.01 | 9.86 | 0.00 |
| $\psi^{PB}(pNID_t)$ | 21 | 1772.70 | 10.14 | 0.00 | 0.01 | 10.14 | 0.00 |
| $\psi^{PB}(exp\ occ_t)$ | 21 | 1773.31 | 10.75 | 0.00 | 0.00 | 10.75 | 0.00 |
| $\psi^{PB}(PDO_{t-1})$ | 21 | 1773.35 | 10.79 | 0.00 | 0.00 | 10.79 | 0.00 |
| $\psi^{PB}(box\ occ_t)$ | 21 | 1773.45 | 10.89 | 0.00 | 0.00 | 10.89 | 0.00 |
| $\psi^{PB}(COGO\ occ_t)$ | 21 | 1773.47 | 10.91 | 0.00 | 0.00 | 10.91 | 0.00 |
| $\psi^{PB}(temp_{t-1})$ | 21 | 1773.60 | 11.04 | 0.00 | 0.00 | 11.04 | 0.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $\psi^{PB}$(hen mass$_{t-1}$) | 21 | 1773.71 | 11.15 | 0.00 | 0.00 | 11.15 | 0.00 |
| $\psi^{PB}$(box occ$_{t-2}$) | 21 | 1773.91 | 11.35 | 0.00 | 0.00 | 11.35 | 0.00 |
| $\psi^{PB}$(rhatch) | 21 | 1774.00 | 11.44 | 0.00 | 0.00 | 11.44 | 0.00 |
| $\psi^{PB}$(brood) | 21 | 1774.00 | 11.44 | 0.00 | 0.00 | 11.44 | 0.00 |
| $\psi^{PB}$(WTMP$_{t-1}$) | 21 | 1774.06 | 11.50 | 0.00 | 0.00 | 11.50 | 0.00 |
| $\psi^{PB}$(ATMP$_{t-1}$) | 21 | 1774.06 | 11.50 | 0.00 | 0.00 | 11.50 | 0.00 |
| $\psi^{PB}$(pNID$_{t-2}$) | 21 | 1774.09 | 11.53 | 0.00 | 0.00 | 11.53 | 0.00 |
| $\psi^{PB}$(box occ$_{t-1}$) | 21 | 1774.14 | 11.58 | 0.00 | 0.00 | 11.58 | 0.00 |
| $\psi^{PB}$(PRES$_{t-2}$) | 21 | 1774.40 | 11.84 | 0.00 | 0.00 | 11.84 | 0.00 |
| $\psi^{PB}$(exp occ$_{t-2}$) | 21 | 1774.42 | 11.86 | 0.00 | 0.00 | 11.86 | 0.00 |
| $\psi^{PB}$(pNID$_{t-1}$) | 21 | 1774.45 | 11.88 | 0.00 | 0.00 | 11.88 | 0.00 |
| $\psi^{PB}$(COGO occ$_{t-2}$) | 21 | 1774.45 | 11.89 | 0.00 | 0.00 | 11.89 | 0.00 |
| $\psi^{PB}$(exp occ$_{t-1}$) | 21 | 1774.45 | 11.89 | 0.00 | 0.00 | 11.89 | 0.00 |
| *Probability of breeding ($\psi^{BB}$)$^{f}$* | | | | | | | |
| **$\psi^{BB}$(.)** | **22** | **1760.53** | **0.00** | **0.17** | **1.00** | **0.00** | **0.14** |
| $\psi^{BB}$(NS) | 23 | 1759.04 | 0.53 | 0.13 | 0.77 | 0.53 | 0.11 |
| $\psi^{BB}$(temp$_{t-1}$) | 23 | 1760.34 | 1.84 | 0.07 | 0.40 | 1.84 | 0.06 |
| $\psi^{BB}$(pNID$_{t-1}$) | 23 | 1760.41 | 1.90 | 0.07 | 0.39 | 1.90 | 0.06 |
| $\psi^{BB}$(ATMP$_{t-1}$) | 23 | 1760.48 | 1.97 | 0.06 | 0.37 | 1.97 | 0.05 |
| $\psi^{BB}$(PDO$_{t-1}$) | 23 | 1760.50 | 1.99 | 0.06 | 0.37 | 1.99 | 0.05 |
| $\psi^{BB}$(WTMP$_{t-1}$) | 23 | 1760.50 | 1.99 | 0.06 | 0.37 | 1.99 | 0.05 |
| $\psi^{BB}$(PRES$_{t-1}$) | 23 | 1760.51 | 2.00 | 0.06 | 0.37 | 2.00 | 0.05 |
| $\psi^{BB}$(precip$_{t-1}$) | 23 | 1760.52 | 2.01 | 0.06 | 0.37 | 2.01 | 0.05 |
| $\psi^{BB}$(hen mass$_{t-1}$) | 23 | 1760.52 | 2.01 | 0.06 | 0.37 | 2.01 | 0.05 |
| $\psi^{BB}$(COGO occ$_{t-1}$) | 23 | 1760.52 | 2.02 | 0.06 | 0.37 | 2.02 | 0.05 |
| $\psi^{BB}$(ANS$_{t-1}$) | 23 | 1760.53 | 2.03 | 0.06 | 0.36 | 2.03 | 0.05 |
| $\psi^{BB}$(box occ$_{t-1}$) | 23 | 1760.53 | 2.03 | 0.06 | 0.36 | 2.03 | 0.05 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes

time variation, (T) denotes a linear trend effect, (.) means that a parameter was held

constant, and a + sign indicates an additive effect between two variables, whereas a *

denotes an interaction. Time-varying covariates were applied to parameters with multiple

lag effects, in relation to interval *t-1* to *t*. For example, a *t-1* subscript denotes conditions

at the beginning of the interval. dmass = individual duckling mass recorded at hatch,

standardized across years, and only available for individuals hatched after 2002; henage =

minimum age of maternal hen; rhatch = individual relative hatch date, the number of

days relative to peak (modal) hatch date each year; brdage = age at first breeding, applied

to known-age individuals only; NS = nesting outcome of an individual in year *t-1*, in

which the outcome was coded as 1 = successful (nests in which 1≤ ducklings hatched)

and 0 = unsuccessful; brood = the number of ducklings (all species) leaving the nest box;

bc = Average annual body condition (year adjusted) , residuals from a mixed effects

model with mass as a response variable and structural size, day of nesting$^2$, individual

(random effect), and year (fixed effect) as explanatory variables; model residuals were

averaged for each hen within each year; oc = overall body condition, residuals from a

mixed effects model with mass as a response variable and structural size, day of nesting$^2$,

and individual (random effect) as explanatory variables; model residuals were averaged

for each hen within each year; hen mass = annual average hen mass during mid-

incubation, derived using mixed models used for body condition covariates described

above; box occ= annual proportion of occupied nest boxes; COGO occ = annual

proportion of nest boxes occupied by goldeneyes with prior breeding experience; ANS =

annual apparent nest success, the number of goldeneye nests in which at least one

duckling hatched, divided by the total number of goldeneye nests (excluding "dump"

nests); pNID = annual peak (mode) goldeneye nest initiation date; phatch = annual peak

(mode) goldeneye nest hatch date; temp = average of monthly mean temperatures on the study area from April to September (i.e. breeding and brood-rearing); precip = total precipitation on the study area from April to September; PRES = sea level pressure (hPa) from October$_{t-1}$ to March$_t$ in purported wintering region; ATMP = air temperature (Celsius) from October$_{t-1}$ to March$_t$ in purported wintering region; WTMP = sea surface temperature (Celsius) from October$_{t-1}$ to April$_t$ in purported wintering region; PDO = Annual Pacific Decadal Oscillation index, averaged monthly mean values from May$_{t-1}$ to April$_t$.

[b]Other parameters held constant with structure: $\varphi^J$(t), $\varphi^A$(t), **$p$(xx)**, $\psi^{PB}$(.), $\psi^{BB}$(.), $\psi^{OB}$(0)

[c]— **$\varphi^J$(xx)**, $\varphi^A$(t), $p$(Age 2, 3≤ + NS), $\psi^{PB}$(.), $\psi^{BB}$(.), $\psi^{OB}$(0)

[d]— $\varphi^J$(t + brood + dmass), **$\varphi^A$(xx)**, $p$(Age 2, 3≤ + NS), $\psi^{PB}$(.), $\psi^{BB}$(.), $\psi^{OB}$(0)

[e]— $\varphi^J$(t + brood + dmass), $\varphi^A$(t + NS), $p$(Age 2, 3≤ + NS), **$\psi^{PB}$(xx)**, $\psi^{BB}$(NS), $\psi^{OB}$(0)

[f]— $\varphi^J$(t + brood + dmass), $\varphi^A$(t + NS), $p$(Age 2, 3≤ + NS), $\psi^{PB}$(T + dmass), **$\psi^{BB}$(xx)**, $\psi^{OB}$(0)

**Table A2.** These models represent hypotheses regarding life history patterns in Common Goldeneyes in interior Alaska. The most parsimonious detection probability (*p*) structure listed in Table A1 was used for all models in this table. Results are shown from modeling probability of continuing to breed ($\psi^{BB}$) first, followed by recruitment probability ($\psi^{PB}$), adult survival ($\varphi^B$), and duckling survival ($\varphi^P$); and are referred to as the "Psi models" in the main article. The most parsimonious structure for each parameter was retained when modeling the subsequent parameter. Refer to Table 1 in the main article for covariate descriptions. Only models in which all parameters were estimated are included in these tables.

| Model[a] | $k$ | Dev. | WITHIN-SET | | | OVERALL | |
| | | | $\Delta AIC_c$ | $w_i$ | Likel-ihood | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|---|---|
| *Probability of breeding ($\psi^{BB}$)[b]* | | | | | | | |
| $\psi^{BB}$(NS) | 18 | 1784.83 | 0.00 | 0.92 | 1.00 | 19.98 | 0.00 |
| $\psi^{BB}$(.) | 17 | 1795.57 | 8.72 | 0.01 | 0.01 | 28.70 | 0.00 |
| $\psi^{BB}$(pNID$_{t-1}$) | 18 | 1793.97 | 9.15 | 0.01 | 0.01 | 29.12 | 0.00 |
| $\psi^{BB}$(hen mass$_{t-1}$) | 18 | 1794.85 | 10.03 | 0.01 | 0.01 | 30.00 | 0.00 |
| $\psi^{BB}$(exp occ$_{t-1}$) | 18 | 1795.06 | 10.24 | 0.01 | 0.01 | 30.21 | 0.00 |
| $\psi^{BB}$(box occ$_{t-1}$) | 18 | 1795.26 | 10.43 | 0.00 | 0.01 | 30.41 | 0.00 |
| $\psi^{BB}$(bc$_{t-1}$) | 18 | 1795.41 | 10.58 | 0.00 | 0.01 | 30.56 | 0.00 |
| $\psi^{BB}$(temp$_{t-1}$) | 18 | 1795.45 | 10.62 | 0.00 | 0.00 | 30.60 | 0.00 |
| $\psi^{BB}$(COGO occ$_{t-1}$) | 18 | 1795.47 | 10.64 | 0.00 | 0.00 | 30.62 | 0.00 |
| $\psi^{BB}$(oc$_{t-1}$) | 18 | 1795.49 | 10.66 | 0.00 | 0.00 | 30.63 | 0.00 |
| $\psi^{BB}$(precip$_{t-1}$) | 18 | 1795.51 | 10.68 | 0.00 | 0.00 | 30.66 | 0.00 |
| $\psi^{BB}$(ANS$_{t-1}$) | 18 | 1795.52 | 10.69 | 0.00 | 0.00 | 30.66 | 0.00 |
| $\psi^{BB}$(ATMP$_{t-1}$) | 18 | 1795.56 | 10.73 | 0.00 | 0.00 | 30.71 | 0.00 |
| $\psi^{BB}$(PDO) | 18 | 1795.57 | 10.74 | 0.00 | 0.00 | 30.71 | 0.00 |
| $\psi^{BB}$(WTMP$_{t-1}$) | 18 | 1795.57 | 10.74 | 0.00 | 0.00 | 30.72 | 0.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $\psi^{BB}(PRES_{t-1})$ | 18 | 1795.57 | 10.74 | 0.00 | 0.00 | 30.72 | 0.00 |

*Probability of recruitment ($\psi^{PB}$)[c]*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\psi^{PB}(T + dmass)$** | **20** | **1774.74** | **0.00** | **0.34** | **1.00** | 13.94 | 0.00 |
| $\psi^{PB}(dmass)$ | 19 | 1777.71 | 0.94 | 0.22 | 0.62 | 14.88 | 0.00 |
| $\psi^{PB}(T)$ | 19 | 1779.76 | 2.99 | 0.08 | 0.22 | 16.93 | 0.00 |
| $\psi^{PB}(hen\ mass_{t-1})$ | 19 | 1781.11 | 4.34 | 0.04 | 0.11 | 18.28 | 0.00 |
| $\psi^{PB}(phatch_{t-2})$ | 19 | 1781.62 | 4.85 | 0.03 | 0.09 | 18.79 | 0.00 |
| $\psi^{PB}(COGO\ occ_{t-1})$ | 19 | 1781.65 | 4.88 | 0.03 | 0.09 | 18.82 | 0.00 |
| $\psi^{PB}(PRES_{t-1})$ | 19 | 1781.77 | 5.00 | 0.03 | 0.08 | 18.94 | 0.00 |
| $\psi^{PB}(WTMP_{t-2})$ | 19 | 1782.35 | 5.58 | 0.02 | 0.06 | 19.52 | 0.00 |
| $\psi^{PB}(precip_{t-2})$ | 19 | 1782.50 | 5.73 | 0.02 | 0.06 | 19.67 | 0.00 |
| $\psi^{PB}(.)$ | 18 | 1784.83 | 6.04 | 0.02 | 0.05 | 19.97 | 0.00 |
| $\psi^{PB}(pNID_t)$ | 19 | 1782.94 | 6.17 | 0.02 | 0.05 | 20.11 | 0.00 |
| $\psi^{PB}(exp\ occ_t)$ | 19 | 1783.30 | 6.53 | 0.01 | 0.04 | 20.47 | 0.00 |
| $\psi^{PB}(COGO\ occ_t)$ | 19 | 1783.43 | 6.66 | 0.01 | 0.04 | 20.60 | 0.00 |
| $\psi^{PB}(PDO_{t-1})$ | 19 | 1783.61 | 6.84 | 0.01 | 0.03 | 20.78 | 0.00 |
| $\psi^{PB}(temp_{t-1})$ | 19 | 1783.61 | 6.84 | 0.01 | 0.03 | 20.78 | 0.00 |
| $\psi^{PB}(box\ occ_t)$ | 19 | 1783.63 | 6.86 | 0.01 | 0.03 | 20.80 | 0.00 |
| $\psi^{PB}(rhatch)$ | 19 | 1783.87 | 7.10 | 0.01 | 0.03 | 21.04 | 0.00 |
| $\psi^{PB}(hen\ mass_t)$ | 19 | 1783.92 | 7.15 | 0.01 | 0.03 | 21.09 | 0.00 |
| $\psi^{PB}(brood)$ | 19 | 1783.98 | 7.22 | 0.01 | 0.03 | 21.15 | 0.00 |
| $\psi^{PB}(box\ occ_{t-2})$ | 19 | 1784.27 | 7.50 | 0.01 | 0.02 | 21.44 | 0.00 |
| $\psi^{PB}(WTMP_{t-1})$ | 19 | 1784.45 | 7.68 | 0.01 | 0.02 | 21.62 | 0.00 |
| $\psi^{PB}(ATMP_{t-1})$ | 19 | 1784.46 | 7.69 | 0.01 | 0.02 | 21.63 | 0.00 |
| $\psi^{PB}(pNID_{t-2})$ | 19 | 1784.53 | 7.76 | 0.01 | 0.02 | 21.70 | 0.00 |
| $\psi^{PB}(box\ occ_{t-1})$ | 19 | 1784.62 | 7.85 | 0.01 | 0.02 | 21.79 | 0.00 |
| $\psi^{PB}(PRES_{t-2})$ | 19 | 1784.71 | 7.94 | 0.01 | 0.02 | 21.88 | 0.00 |
| $\psi^{PB}(precip_{t-1})$ | 19 | 1784.79 | 8.02 | 0.01 | 0.02 | 21.96 | 0.00 |
| $\psi^{PB}(exp\ occ_{t-2})$ | 19 | 1784.81 | 8.04 | 0.01 | 0.02 | 21.98 | 0.00 |
| $\psi^{PB}(exp\ occ_{t-1})$ | 19 | 1784.83 | 8.06 | 0.01 | 0.02 | 22.00 | 0.00 |
| $\psi^{PB}(COGO\ occ_{t-2})$ | 19 | 1784.83 | 8.06 | 0.01 | 0.02 | 22.00 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $\psi^{PB}(pNID_{t-1})$ | 19 | 1784.83 | 8.06 | 0.01 | 0.02 | 22.00 | 0.00 |

*Adult survival ($\varphi^A$)[d]*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\varphi^A(t)$** | **20** | **1774.74** | **0.00** | **0.21** | **1.00** | **13.94** | **0.00** |
| $\varphi^A(t + bc_{t-1})$ | 21 | 1774.29 | 1.57 | 0.10 | 0.46 | 15.50 | 0.00 |
| $\varphi^A(t + oc_{t-1})$ | 21 | 1774.31 | 1.59 | 0.10 | 0.45 | 15.53 | 0.00 |
| $\varphi^A(t + rhatch)$ | 21 | 1774.37 | 1.65 | 0.09 | 0.44 | 15.59 | 0.00 |
| $\varphi^A(t + brdage)$ | 21 | 1774.43 | 1.71 | 0.09 | 0.43 | 15.65 | 0.00 |
| $\varphi^A(PDO_{t-1} + NS_{t-1})$ | 19 | 1778.68 | 1.91 | 0.08 | 0.38 | 15.85 | 0.00 |
| $\varphi^A(Age\ 2, \geq 3 + t)$ | 21 | 1774.68 | 1.96 | 0.08 | 0.38 | 15.90 | 0.00 |
| $\varphi^A(t + NS)$ | 21 | 1774.70 | 1.98 | 0.08 | 0.37 | 15.92 | 0.00 |
| $\varphi^A(PDO_{t-1})$ | 19 | 1779.10 | 2.33 | 0.07 | 0.31 | 16.27 | 0.00 |
| $\varphi^A(Age\ 2, 3, \geq 4 + t)$ | 22 | 1773.80 | 3.11 | 0.04 | 0.21 | 17.05 | 0.00 |
| $\varphi^A(precip_{t-1})$ | 19 | 1781.37 | 4.60 | 0.02 | 0.10 | 18.54 | 0.00 |
| $\varphi^A(box\ occ_{t-1})$ | 19 | 1781.58 | 4.81 | 0.02 | 0.09 | 18.75 | 0.00 |
| $\varphi^A(Age\ 2, 3, 4, \geq 5 + t)$ | 23 | 1773.73 | 5.06 | 0.02 | 0.08 | 19.00 | 0.00 |
| $\varphi^A(Age\ 2, \geq 3 * t)$ | 31 | 1767.02 | 14.62 | 0.00 | 0.00 | 28.56 | 0.00 |

*First-year survival ($\varphi^J$)[c]*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **$\varphi^J(t + brood + dmass + rhatch)$** | **23** | **1754.73** | **0.00** | **0.40** | **1.00** | **0.00** | **0.40** |
| $\varphi^J(t + dmass + rhatch)$ | 22 | 1757.11 | 0.36 | 0.33 | 0.84 | 0.36 | 0.33 |
| $\varphi^J(t + dmass)$ | 21 | 1760.80 | 2.02 | 0.14 | 0.36 | 2.02 | 0.14 |
| $\varphi^J(t + brood + dmass)$ | 22 | 1759.06 | 2.31 | 0.12 | 0.32 | 2.31 | 0.12 |
| $\varphi^J(t + rhatch)$ | 21 | 1768.99 | 10.21 | 0.00 | 0.01 | 10.21 | 0.00 |
| $\varphi^J(t + henage)$ | 21 | 1772.56 | 13.78 | 0.00 | 0.00 | 13.78 | 0.00 |
| $\varphi^J(t + brood)$ | 21 | 1772.66 | 13.88 | 0.00 | 0.00 | 13.88 | 0.00 |
| $\varphi^J(t)$ | 20 | 1774.74 | 13.94 | 0.00 | 0.00 | 13.94 | 0.00 |
| $\varphi^J(T^2)$ | 22 | 1774.62 | 17.86 | 0.00 | 0.00 | 17.86 | 0.00 |
| $\varphi^J(.)$ | 19 | 1780.91 | 18.08 | 0.00 | 0.00 | 18.08 | 0.00 |
| $\varphi^J(exp\ occ_{t-1})$ | 20 | 1779.78 | 18.97 | 0.00 | 0.00 | 18.97 | 0.00 |
| $\varphi^J(temp)$ | 21 | 1779.11 | 20.33 | 0.00 | 0.00 | 20.33 | 0.00 |
| $\varphi^J(PRES_{t-1})$ | 21 | 1780.22 | 21.44 | 0.00 | 0.00 | 21.44 | 0.00 |
| $\varphi^J(COGO\ occ_{t-1})$ | 21 | 1780.53 | 21.75 | 0.00 | 0.00 | 21.75 | 0.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $\varphi^J$(box occ$_{t-1}$) | 21 | 1780.71 | 21.93 | 0.00 | 0.00 | 21.93 | 0.00 |
| $\varphi^J$(T) | 21 | 1780.76 | 21.98 | 0.00 | 0.00 | 21.98 | 0.00 |
| $\varphi^J$(WTMP$_{t-1}$) | 21 | 1780.79 | 22.01 | 0.00 | 0.00 | 21.01 | 0.00 |
| $\varphi^J$(pNID) | 21 | 1780.86 | 22.08 | 0.00 | 0.00 | 22.08 | 0.00 |
| $\varphi^J$(phatch) | 21 | 1780.87 | 22.09 | 0.00 | 0.00 | 22.09 | 0.00 |
| $\varphi^J$(hen mass$_{t-1}$) | 21 | 1780.91 | 22.13 | 0.00 | 0.00 | 22.126 | 0.00 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes time variation, (T) denotes a linear trend effect, (.) means that a parameter was held constant, and a + sign indicates an additive effect between two variables, whereas a * denotes an interaction. Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval $t$-$1$ to $t$. For example, a $t$-$1$ subscript denotes conditions at the beginning of the interval. dmass = individual duckling mass recorded at hatch, standardized across years, and only available for individuals hatched after 2002; henage = minimum age of maternal hen; rhatch = individual relative hatch date, the number of days relative to peak (modal) hatch date each year; brdage = age at first breeding, applied to known-age individuals only; NS = nesting outcome of an individual in year $t$-$1$, in which the outcome was coded as 1 = successful (nests in which $1 \leq$ ducklings hatched) and 0 = unsuccessful; brood = the number of ducklings (all species) leaving the nest box; bc = Average annual body condition (year adjusted) , residuals from a mixed effects model with mass as a response variable and structural size, day of nesting$^2$, individual (random effect), and year (fixed effect) as explanatory variables; model residuals were averaged for each hen within each year; oc = overall body condition, residuals from a mixed effects model with mass as a response variable and structural size, day of nesting$^2$,

and individual (random effect) as explanatory variables; model residuals were averaged for each hen within each year; hen mass = annual average hen mass during mid-incubation, derived using mixed models used for body condition covariates described above; box occ= annual proportion of occupied nest boxes; COGO occ = annual proportion of nest boxes occupied by goldeneyes with prior breeding experience; ANS = annual apparent nest success, the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests); pNID = annual peak (mode) goldeneye nest initiation date; phatch = annual peak (mode) goldeneye nest hatch date; temp = average of monthly mean temperatures on the study area from April to September (i.e. breeding and brood-rearing); precip = total precipitation on the study area from April to September; PRES = sea level pressure (hPa) from $October_{t-1}$ to $March_t$ in purported wintering region; ATMP = air temperature (Celsius) from $October_{t-1}$ to $March_t$ in purported wintering region; WTMP = sea surface temperature (Celsius) from $October_{t-1}$ to $April_t$ in purported wintering region; PDO = Annual Pacific Decadal Oscillation index, averaged monthly mean values from $May_{t-1}$ to $April_t$.

[b]Other parameters held constant with structure: $\varphi^A(t)$, $\varphi^J(t)$, $p$(Age 2, 3≤ + NS), $\psi^{PB}(.)$, $\boldsymbol{\psi^{BB}(xx)}$, $\psi^{0B}(0)$

[c]— $\varphi^J(t)$, $\varphi^A(t)$, $p$(Age 2, 3≤ + NS), $\boldsymbol{\psi^{PB}(xx)}$, $\psi^{BB}(NS)$, $\psi^{0B}(0)$

[d]— $\varphi^J(t)$, $\varphi^A(\boldsymbol{xx})$, $p$(Age 2, 3≤ + NS), $\psi^{PB}(T + dmass)$, $\psi^{BB}(NS)$, $\psi^{0B}(0)$

[e]— $\boldsymbol{\varphi^J(xx)}$, $\varphi^A(t)$, $p$(Age 2, 3≤ + NS), $\psi^{PB}(T + dmass)$, $\psi^{BB}(NS)$, $\psi^{0B}(0)$

**Recruitment Patterns and Population Dynamics of Breeding Common Goldeneyes in the Northern Boreal Forest**

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**ABSTRACT** Traits with the greatest proportional effects on fitness are typically conserved (Stearns 1992), therefore, traits with larger temporal variation frequently play a dominant role in population dynamics (Cooch et al. 2001). We examined recruitment patterns and population growth in Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye), using Pradel capture-mark-recapture models to estimate per-capita-recruitment (*f*) and population growth ($\lambda$) from a long-term nest box study (1997-2010). Our objectives were to estimate recruitment and population growth in relation to recruitment origin (*in-situ* or unknown), evaluate environmental and density dependent effects on these parameters, and quantify potential immigration into the study population. We detected group-specific (*in situ* or unknown) differences for *f* (*in-situ*: $\bar{x} = 0.47 \pm 0.13$ SE, unknown: $\bar{x} = 0.31 \pm 0.04$), and the proportion of boxes occupied by goldeneyes the year prior to recruitment had a significant negative effect on recruitment for the *in-situ* group ($\beta = -1.04$; 95% CI: -1.38–-0.70), and a positive effect for the unknown group ($\beta = 0.45$; 95% CI: 0.24–0.67). For the *in-situ* group, the negative effect of box occupancy the year prior to recruitment, when yearling goldeneyes prospect for potential nest sites, suggests that local nesting densities may inhibit recruitment of locally produced females. We identified two competitive models for $\lambda$, which included interactions between recruitment group and a linear temporal trend, and an effect of the proportion of ducklings marked two years prior. Population-level $\lambda$ varied substantially over time, and averaged $1.04 \pm 0.03$ (SE). We evaluated varying levels of the proportion of ducklings marked on $\lambda$, and determined that even if all hatched ducklings were marked in a given year, the resulting *in-situ* $\lambda$ is consistently lower than the population $\lambda$, indicating that individuals produced outside nest boxes continue to contribute to $\lambda$, even when all

potential *in-situ* recruits  are marked.  Female goldeneyes are considered highly

philopatric to their natal and breeding areas, though our results suggest that female natal

and breeding dispersal may be more important than previously thought.

**KEY WORDS** *Bucephala clangula*, common goldeneye, density dependence, lambda,

nest-boxes, Pradel models, recruitment, sea ducks

An understanding of the mechanisms by which populations respond to environmental

change or disturbance is of fundamental interest. In wild populations, variation in

demographic traits with the greatest proportional effects on potential population growth

are typically conserved (Caswell 1989), while more variable demographic traits often

have a greater influence on realized population growth (Caswell 1989). For long-lived

waterfowl, in particular, adult female survival has the greatest proportional effects on

fitness (Schmutz et al. 1997, Tombre et al. 1998, Schamber et al. 2009, Bentzen and

Powell 2012), though frequently, annual recruitment has the greatest contribution to

observed variation in population growth (Cooch et al. 2001, Gauthier et al. 2001, Flint et

al. 2006).  Recruitment into a breeding population is likely to vary considerably because

it is the end-product of multiple sequential events, including incubation, pre-fledging

survival, post-fledging-survival to recruitment age, and breeding (Flint et al. 2006).

In long-lived waterfowl species, females are thought to annually adjust reproductive

effort to minimize costs to survival (Stearns 1992).  Accordingly, recruitment, the final

product of a successful reproductive effort, is thought to be more reflective of

environmental conditions, compared to more conserved traits. Therefore, identifying

sources of variation in annual recruitment, and its associated components (e.g., pre-fledging survival), may elucidate potential environmental and ecological factors that drive population dynamics. For example in arctic breeding lesser snow geese (*Chen caerulescens caerulescens*), large-scale reduction in per-capita food availability driven by density-dependence and habitat destruction effects caused a decline in gosling growth rates (Cooch et al. 1991), an important determinant of first-year survival in geese (Francis et al. 1992, Sedinger et al. 1995). As a result, recruitment had a greater influence on local population growth than adult survival (Cooch et al. 2001).

The rate of change of a population ($\lambda$) is determined by the relative number of additions (e.g., births, immigration) versus subtractions (e.g., deaths, emigration). Adult females in our study population consisted of two groups: *in-situ* recruited individuals that were originally marked as ducklings and later encountered as breeding adults, and unknown individuals that were originally encountered as unmarked adults. An unknown proportion of these unmarked adults were immigrants from outside the study area. The relative contributions of *in-situ* recruitment versus immigration to total recruitment is generally unknown because of the difficulty of separating the two sources of new individuals in a population. Evaluating the potential sources of recruitment may be important for isolated populations of waterfowl, or those in which suitable nests sites are likely limited (e.g., cavity nesting or highly territorial species), though very few studies have examined such effects.

We estimated per-capita recruitment (hereafter recruitment) and population growth in female Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye), a cavity-nesting sea duck (tribe *Mergini*), from a long-term study in the boreal forest of interior Alaska.

Goldeneyes begin breeding between 2-5 years of age (Eadie et al. 1995), though yearling females return to their natal grounds to prospect for nest sites to be used the following year (Eadie and Gauthier 1985). Goldeneyes are an ideal species for demographic studies because they readily use artificial nest boxes and exhibit high rates of natal and breeding philopatry (Dow and Fredga 1983, Savard and Eadie 1989, Pöysä et al. 1997, Ludwichowski et al. 2002), which allows for ease in capture and the ability to encounter the same individual for many years. Though goldeneyes are relatively well-studied among sea ducks, demographic studies that used modern maximum-likelihood based approaches remain uncommon for this species (Ludwichowski et al. 2002, Schmidt et al. 2006, Lawson et al. 2012).

Our objectives were to examine environmental and density dependent effects on recruitment patterns and population growth in goldeneyes, as well as the manner and the extent to which immigration to the study area may have influenced these parameters. Furthermore, we were interested in characterizing the relative importance of recruitment to population growth in relation to expected patterns for long-lived species. We hypothesized that recruitment and population growth rates would exhibit negative density dependence. We predicted that productive nesting years would create increased within-cohort competition for access to limited resources (e.g., quality brood rearing areas, nest sites), potentially through immediate effects over the first year or lagged effects during the recruitment year or the year prior. Similarly, we also predicted that high nesting densities of experienced breeders could potentially facilitate dispersal or alternative nesting strategies among potential recruits, leading to lower observed *in-situ* recruitment and population growth as a product of among-cohort negative density-dependence.

We further hypothesized that if density dependent effects could facilitate dispersal of potential recruits, we would likely detect immigration into our study population. Given the philopatry patterns observed in goldeneye females (Dow and Fredga 1983, Savard and Eadie 1989, Pöysä et al. 1997, Ludwichowski et al. 2002), we predicted population-level estimates of recruitment and population growth would primarily reflect variation in *in-situ* recruitment, but that *in-situ* recruitment alone would not explain population-level patterns. We further predicted that, if unknown individuals were truly immigrants, rather than individuals that hatched on the study area but were not marked, they would not be influenced by within-cohort competition on our study area and would not have prior knowledge of nesting densities, resulting in less annual variation in recruitment and population growth for this group. Like other long-lived waterfowl species, we predicted that annual variation in recruitment, rather than adult survival, would have a greater influence on population growth.

**STUDY AREA**

The study area was located within the Chena River State Recreation Area, encompassing approximately 102-km$^2$ along the north and middle forks of the Chena River. Ice break-up generally occurs in April to early May, when portions of the study area may flood in years of rapid melt (E. Taylor, personal observation). During the winters of 1994-1997, nest boxes ($n = 150$) were installed on trees at heights of 3-7m above the ground near sloughs, oxbows, ponds, and portions of the Chena River. Nest box sites were dominated by mixed stands of balsam poplar (*Populus balsamifera*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). From April to May

temperatures typically range between -1–16º C, with minimal precipitation, while during

brood-rearing (June – early September; E. Taylor, personal observation) temperatures

vary between 10–21 º C. Most annual precipitation occurs between June and August

(approximately 20 cm), and can cause additional flooding of nest box sites in some years.

We obtained precipitation and temperature data during the breeding and brood-rearing

season (April – August, E. Taylor, personal observation) from the Two Rivers National

Weather Service station (64°52'N, 146°57'W), located approximately 8 km from the

study area's western boundary.

**METHODS**

**Field Methods**

Nest boxes were monitored annually 1997-2010, except during 2006 and 2007. We

checked all nest boxes weekly beginning May 1 to determine occupancy. Active nests

were revisited every 1 to 3 days to determine egg-laying rates and capture the nesting

female in the nest by blocking the nest box entrance. We candled all eggs to determine

incubation progress (Weller 1956) and numbered eggs with a permanent marker to allow

us to identify new or missing eggs. We revisited nests until the adult female was captured

or the clutch neared completion. Upon initial capture we weighed each adult female using

a Pesola spring scale (± 5g), measured head length, culmen length, and tarsus length

using dial calipers (± 0.1mm) , and applied a USGS stainless steel leg band, if no band

was present.

    We revisited nests during late incubation to recapture incubating females and monitor

incubation progress. For females that were previously captured during egg-laying, we

recorded only body mass and verified the band number. We used egg-laying rate and

candling observations to back-calculate a nest initiation date and estimate likely hatch

dates for each nest, assuming an egg-laying rate of one egg per 48 hours, average clutch

size of 8-10 eggs (adjusting for parasitic eggs), and an incubation period of 28 days

(Bellrose 1980, Eadie et al. 1995). All hatched ducklings were marked in their natal box

with web tags (1997), plasticine-filled metal leg bands (1998-2008; ARANEA, Lodz,

Poland; Blums et al. 1994), or a combination of both (2009-2010). We weighed ducklings

using a Pesola spring scale (± 0.5 g; 2000-2008) or an electronic scale (± 0.01g; 2009-

2010). We did not determine sex of ducklings at hatch. All procedures were approved by

the necessary Institutional Animal Care and Use Committees.


**Statistical Methods**

We constructed individual capture histories based on annual captures of breeding adult

females in nest boxes. We then assigned individuals to 1 of 2 groups that described an

individual's recruitment origin: *in-situ* versus unknown. *In-situ* individuals were marked

as ducklings in their natal boxes between 1997 and 2008, and encountered later as

breeding adults, whereas the unknown group included females initially captured as

unmarked adults. We used Pradel models (Pradel 1996) in Program MARK (White and

Burnham 1999) to estimate adult female apparent survival ($\varphi$; hereafter survival),

detection probability ($p$), annual per-capita recruitment ($f$), and per-capita population

growth ($\lambda$). Nest box studies provide an ideal study system for Pradel models because the

assumption of constant study area size (Franklin 2001) is generally met. In our study, the

number of nest boxes remained constant ($n = 150$), and nest boxes that required

relocation were placed on the nearest tree of the same species, at a similar height and orientation.

To describe recruitment and population growth patterns in goldeneyes, we constructed a set of models in which $f$ and $\lambda$ were allowed to vary among years, and allowed for group effects, linear and quadratic temporal trends, time-varying covariates, and their interactions. This required two separate analyses, as Program MARK does not allow for simultaneous direct estimation of these two parameters, because they can be derived from one another using the equation: $\lambda_t = f_t + \varphi_t$.

To evaluate our hypotheses related to recruitment and population growth in goldeneyes, we included two general classes of covariates in our models: (1) density and (2) environmental. Density covariates were subdivided into two classes, the first being those that represented three direct measures of local nesting density, as indicated by box occupancy: (1) the proportion of occupied nest boxes, in which all nest boxes containing at least one egg were considered occupied); (2) the proportion of nest boxes occupied by goldeneyes; (3) and the proportion of nest boxes occupied by experienced female goldeneyes.

The second subclass of density covariates represented indirect measures of study area wetland productivity, intended to provide an index of potential within-cohort density. Presumably, productive years with greater food availability for nesting females would lead to greater reproductive success, and would likely produce a larger cohort of potential recruits. We used apparent nest success, modal nest initiation and hatch dates to index annual reproductive success. Apparent nest success was defined as the number of successful goldeneye nests in which one or more ducklings hatched, divided by the total

number of goldeneye nests (excluding dump nests). Nests with no signs of an incubation attempt (e.g., few eggs and no down deposited), were classified as "dump nests", and were only used for the density covariates. Modal nest initiation and hatch dates were used as measures of annual nesting phenology. Earlier nesting years may enable breeding attempts by lower-quality females that would otherwise skip breeding or resort to alternative nesting strategies, potentially leading to greater duckling production. Earlier hatched ducklings survive at higher rates (Dow and Fredga 1984), therefore, earlier hatch years may increase overall duckling survival, especially for broods that hatched late relative to the peak hatch date.

We included average female mass during mid-incubation as an index of wetland productivity; presumably, when females weighed more wetlands were more productive and would potentially contribute to increased brood-rearing densities (Paasivaara and Pöysä 2007). We used observations of female mass during egg-laying, incubation, and at hatch to derive an annual index of population-level female body condition from a mixed effects model created using PROC MIXED in SAS (SAS Institute 2011). Females were sometimes weighed multiple times within a nesting season, so we used mixed effects models, with female as the random effect, to account for multiple measurements of individual females. We constructed a set of candidate models of female mass that included the following explanatory variables: year (fixed effect); female (random effect); PC1 score (structural size; Freeman and Jackson 1990, Sedinger et al. 1995, Schmidt et al. 2006) and day of nesting (day 1= nest initiation), and day of nesting squared. PC1 scores were derived from a principle components analysis of morphological measurements (culmen, head, and tarsus lengths) using PROC PRINCOMP in SAS (SAS

Institute 2011). Using our most parsimonious model (Burnham and Anderson 2002) for mass, which included all covariates, we evaluated the potential relationship between productivity, as influenced by body condition, and subsequent recruitment or population growth.

Finally, we used environmental covariates during the breeding and winter seasons to assess their influence on recruitment and population growth. For the breeding season, we included average monthly temperature and total precipitation during the period when goldeneyes were present on our study area (April – September), obtained from the National Climate Data Center (NCDC; http://www.ncdc.noaa.gov/oa/ncdc.html). No adult band returns from our study have been reported to date (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data), making it difficult to determine a likely wintering area for our study population. We, therefore, included winter variables from both local and regional scales. For the local scale, we obtained barometric pressure (PRES), sea surface (WTMP) and ambient temperature (ATMP) data from through the National Oceanic and Atmospheric Administration's National Data Buoy Center (NDBC; http://www.ndbc.noaa.gov/) using a buoy located in the Gulf of Alaska (NDBC station 46001; 56°17'59" N 148°1'16" W), a known goldeneye wintering area (Eadie et al. 1995). Additionally, we obtained Pacific Decadal Oscillation (PDO) index data from the Joint Institute for Study of the Atmosphere and Ocean at the University of Washington (http://jisao.washington.edu/pdo/PDO.latest) to assess potential region wide patterns. In the Pacific Northwest, negative values of PDO (cool phase) are associated with higher precipitation and cooler temperatures, whereas positive values indicate lower rainfall and higher temperatures. We averaged monthly values for our winter variables (ATMP,

WTMP, PRES, PDO; Table 1) over each winter, defined as October$_t$ to March$_{t+1}$. We modeled the effects of density, productivity, and environmental covariates to reflect conditions at three stages of the recruitment process: (1) during an individual's year of hatch; (2) during the second year, when females return to prospect for potential nest sites (Eadie and Gauthier 1985); and (3) at recruitment (assuming recruitment at 2 years-old). See Table 1 for additional covariate descriptions and abbreviations.

For both the $f$ and $\lambda$ analyses, we began with a fully time varying model for $\varphi$ and $p$, with $\lambda$ or $f$ held constant (Franklin 2001). To determine the best structure for $p$, we constructed additional models that included group + year, and group * year. Only temporally varying structures for $p$ were considered, to account for potential variation attributed to observer variability or other conditions that might have influenced detection (e.g., nest success rates– successful individuals remain in the nest box longer and are more likely to be detected). Furthermore, we did not investigate other model structures for $\varphi$, because previous modeling had determined simple annual-variation to be the most appropriate structure (Lawson et al. 2012).

We applied additional modeling constraints to address parameter confounding and the gap in data collection (2006-2007). The last $\varphi$, $p$, $f$, and $\lambda$ parameters were confounded in a fully time-dependent model (Lebreton et al. 1992), therefore, we constrained these parameters to be equal for the penultimate and final intervals. To accommodate the missing years of data, we treated the gap as a single three-year time interval (2005-2008) for $\varphi$, $f$, and $\lambda$. Covariates in which the values were known over the gap in data collection (e.g., precipitation) were assigned the average of these years (2005-2007), whereas, those

in which the value was unknown (e.g., box occupancy) were assigned a zero, the mean after z-standardization.

We retained the best-supported structure for $p$ and applied the structures for $f$ and $\lambda$ described earlier. All covariates were z-standardized (mean = 0.0, S.D = 1.0). We used Akaike's Information Criterion adjusted for small sample size ($AIC_c$) to identify the most parsimonious model in each step. All models within 4 $\Delta AIC_c$ units were used to derive model-averaged parameter estimates (Burnham and Anderson 2002).

We were also interested in a population-level estimate of $\lambda$ ($\lambda^{POP}$), in addition to group specific estimates. To do this, we determined the annual proportions of captured individuals that belonged to each group, and then multiplied the model-averaged annual group specific estimates of $\lambda$ ($\lambda^{IS}$ and $\lambda^{UK}$) by their respective annual proportions and added the products together. Finally, to assess the relative importance of survival and recruitment to population growth, we used $\lambda^{POP}$ and $\varphi$ estimates from the population growth analysis to derive annual seniority parameter ($\gamma$) estimates using the following formula: $\lambda_t = \varphi_t / \gamma_{t+1}$. Seniority is defined as the probability that individual present in year $t$ was also present in year $t-1$ (Pradel 1996, Nichols 2000), thus, $\gamma$ represents the proportion of the population that is not new recruits. We followed the retrospective approach used in Nichols et al. (2000); if $\gamma < 0.50$, then recruitment had a greater proportional effect on $\lambda$, whereas, if $\gamma > 0.50$ then adult survival had a greater proportional effect on $\lambda$ (Sandercock 2006).

**RESULTS**

Between 1997 and 2010, we captured and marked 276 unique adult females, which included 102 *in-situ* recruits and 174 individuals of unknown recruitment origin. We investigated group, time, trend, covariate effects, and their interactions for $f$ and $\lambda$. Each model set included 102 models (Appendix A; Table A1, A2), in which all parameters were estimated. Estimates of detection probabilities for some (1997, 1998, 2000, 2001, and 2005) years equaled 1, which was confirmed by examining capture histories; during these years, no previously marked individual was missed but encountered later on in the study. We fixed $p$ to equal 1 for these years, and then implemented more complex structures for $p$ that included, group + time and group * time, though simple time variation remained the most competitive structure, and was retained for all subsequent modeling of $f$ and $\lambda$.

The best-supported model for $f$ included an interaction between group and the proportion of boxes occupied by goldeneyes in year prior to recruitment (COGO $occ_{t-1}$; Table 1, 2), and was the only competitive structure within the model set ($AIC_c$ weight = 0.79). The second best-supported model within the set contained a group by temporal trend interaction. COGO $occ_{t-1}$ had a strong negative effect on $f$ for the *in-situ* group ($\beta$ = -1.04, 95% CI: -1.38–-0.70) and a positive, though weaker, effect on $f$ for the unknown group ($\beta$ = 0.46, 95% CI: 0.24–0.67). Model-averaged *in-situ* per-capita recruitment ($f^{IS}$) rates ranged from 0.06 (95% CI: 0.03–0.14) in 2009 to 1.47 (95% CI: 0.68–2.28) in 1999. Conversely, variation in recruitment of unknown individuals ($f^{UN}$) was substantially smaller (Fig. 1), and ranged between 0.15 (95% CI: 0.09–0.24) in 1999, and 0.59 (95% CI: 0.38–0.77) in 2009.

The λ model set included 4 models, which differed only in support for specific covariates (Table 2). The best-supported model ($AIC_c$ weight = 0.54) contained a group interaction with a linear temporal trend; which was negative for the *in-situ* group (β = -0.07, 95% CI: -0.10–-0.05), and positive for the unknown group (β = 0.03, 95% CI: 0.02–0.05). Lambda was greater for the *in-situ* group (β = 0.94, 95% CI: 0.71–1.17). The second most parsimonious model ($AIC_c$ weight = 0.34) contained a group interaction with the proportion of goldeneye ducklings marked two years prior to recruitment ($dband_{t-2}$; Table 1); which was positive for the *in-situ* group (β = 0.49, 95% CI: 0.35–0.62) and negative for the unknown group (β = -0.13, 95% CI: -0.21–-0.07). The model-averaged population growth estimates indicated that population growth was greater, though more variable for the *in-situ* group than the unknown group (Fig. 2); as λ averaged 1.22 (95% CI: 1.04–1.38) and 1.01 (95% CI: 0.94–1.08) for each group, respectively.

Overall, λ adjusted for the proportion of individuals present in each group at the beginning of each interval, averaged 1.04 ± 0.02 during the study (Fig. 2). We used $\lambda^{POP}$ and the adult survival estimates from the population growth analysis to derive the seniority parameter, which averaged 0.68 ± 0.01 (Fig. 4). Estimates of adult survival and detection probabilities from the recruitment and population growth analyses are located in Appendix B.

**DISCUSSION**

Density dependent effects can influence multiple demographic parameters within a population through a number of mechanisms. Our results suggest that natal area

conditions during an individual's second year, strongly influence *in-situ* recruitment rates the following year (assuming recruitment at 2 years of age; Lawson 2012), as evidenced by general support for covariates that described second-year conditions (*t-1* covariates in Table 2), as opposed to duckling (*t-2*) or recruitment year (*t*) conditions (Table 2). The best-supported model suggested that the proportion of nest boxes occupied by goldeneyes on the study site in year *t-1* (COGO occ$_{t-1}$; Table 1) had a significant negative effect on *in-situ* recruitment the following year.

Our results are consistent with other studies that suggest competition for suitable nest sites may limit breeding opportunities for cavity nesting waterfowl (Savard 1988, Lawson et al. 2012). Female goldeneyes typically return to their natal area during their second year (i.e., as yearlings) to prospect for potential nest sites to be used the following breeding season (Eadie and Gauthier 1985, Zicus and Hennes 1989). Though both yearlings and experienced breeders prospect for nest sites (Eadie and Gauthier 1985), visitation patterns differ between the two groups; experienced females visit successful nest sites more frequently than failed or unoccupied nest sites, whereas yearling females visit nest sites at random (Zicus and Hennes 1989). Variation in visitation patterns may reflect differences in how nest prospecting information is being used. For example, experienced females may assess potential nest sites for their suitability (previously successful vs. not), whereas inexperienced females may assess overall nest site availability (occupied vs. unoccupied), which may then influence their reproductive decisions, and therefore recruitment, for the following breeding season.

Though natal and breeding philopatry is assumed to be high in goldeneyes (Dow and Fredga 1983, Savard and Eadie 1989, Pöysä et al. 1997, Ludwichowski et al. 2002), a

recent study of the closely related Barrow's goldeneye (*Bucephala islandica*) in British

Columbia, Canada reported that only a small proportion of yearling females that returned

to their natal grounds for nest prospecting were actually recruited into the breeding

population (Boyd et al. 2009). The authors detected a negative correlation between first-

year apparent survival and subsequent within-cohort apparent survival, and suggested

that within-cohort density dependence, rather than nest site availability, which was not

examined, may reduce local recruitment (Boyd et al. 2009). However, we evaluated the

effect of first-year survival on subsequent recruitment rates for cohorts and the term as

not supported (Model 17 in Appendix A, Table A1). Furthermore, we believe that the

negative linear temporal trend in *in-situ* recruitment ($\beta$ = -0.25, 95% CI: -0.33--0.17)

included in the second best-supported recruitment model (Table 2) represents the effect

of nest box occupancy, which increased by 11% overall, and 22% for goldeneyes during

the study (E. Taylor, USFWS, Anchorage, AK, USA, unpublished data)**.** Our best-

supported model for population growth also included a trend by group interaction with

the same effects (positive vs. negative) reflected in each group, which we suspect also

reflects box occupancy.

We believe that the mechanism by which density-dependent nest site availability

reduces subsequent recruitment rates is through natal dispersal. Adult survival, which is

assumed to be similar to second-year survival rates in sea ducks (Boyd et al. 2009,

Schamber et al. 2009), in our study population is relatively high (0.74 ± 0.01, Lawson et

al. 2012), as is probability of recruitment for individuals that survived to two years of age

(0.96 ± 0.01, Lawson et al. 2012). Therefore, we contend that the density dependent

reduction in recruitment rate is due to permanent emigration from the study area (i.e.,

dispersal), rather than individuals foregoing breeding as 2 year-olds and attempting to breed at an older age, or a density-dependent reduction in survival rates over the second-year.

Natal dispersal remains relatively unexamined in female goldeneyes, as it is difficult to study, and is assumed to occur at low levels (Dow and Fredga 1983, Savard and Eadie 1989, Pöysä et al. 1997, Ludwichowski et al. 2002). However, natal dispersal does not necessarily require moving a large geographic distance between an individual's recruitment origin and a new breeding site. In nest box studies, for example, an individual hatched on the study may use a natural cavity within the study area instead of a next box, and remain undetected if external markers visible from a distance are not used. Conversely, an individual hatched in a natural cavity within the study area may eventually switch to a nest box, and be classified as an individual of unknown recruitment origin (i.e., an immigrant).

If density-dependent natal dispersal is prevalent in goldeneyes, then a proportion of the unknown recruitment origin group likely consisted of immigrants from other populations, in addition to individuals that were hatched on the study area but not marked as ducklings. If the unknown group consisted of mostly "missed" *in-situ* individuals, then covariates would be expected to influence both groups in similar ways and models that contained group by covariate interactions would likely have received less support. In both the recruitment and population growth analyses, however, we found consistent support for models that contained group by covariate interactions (Tables 1, 2). In the top recruitment model, for example, conspecific box occupancy prior to recruitment had a positive effect on recruitment of unknown individuals, in sharp contrast with the negative

effect for the *in-situ* group. One possible explanation is that unknown individuals may be a product of breeding dispersal, meaning that they emigrated from outside the study area and were not present on the study area in the year prior to recruitment, and were, thus, unaware of local nest site availability. Alternatively, the unknown individuals could be composed of older individuals that originated within or near the study area, hatched either in natural cavities or nest boxes (i.e., missed *in-situ*s).

We used the covariate dband$_{t-2}$ (Table 1) to directly determine if demographic patterns in the purported unknown recruitment origin group were simply a function of the proportion of ducklings marked two years prior to recruitment. Controlling for the proportion of each cohort marked allowed us to evaluate if potential differences between recruitment groups was an artifact of variation in marking effort, or if they reflected possible endogenous differences between the two groups (e.g., recruitment origin, age). Overall, models that contained dband$_{t-2}$ performed relatively well compared to other covariates (Appendix A, Table A1, A2), though the term was only considered competitive in the population growth model set, as a group by covariate interaction (Table 2). As expected, dband$_{t-2}$ positively influenced *in-situ* population growth, and negatively influenced population growth of unknown individuals.

We used the beta estimates from the second best-supported population growth model, which contained a group by dband$_{t-2}$ interaction and was considered competitive (Table 2), to derive group specific estimates of population growth at varying levels of dband$_{t-2}$. We determined that even if all hatched ducklings (i.e., potential *in-situ* recruits) were marked in a given year, population growth rate for the unknown group was equal to 0.45, and 0.69 for the *in-situ* group (Fig. 3b). Population growth rates 1> denote a population

decrease, whereas values >1 denote an increase. Therefore, our results suggest that the study population would decline if *in-situ* recruitment was the only source of population growth (i.e., no immigration), and alternatively, population decline would also occur if immigration were the only source (i.e., no *in-situ* recruitment). Population-level growth rate during the study averaged 1.04 ($\pm$ 0.02), which suggests that in most years, both *in-situ* recruitment and immigration were contributing to population growth. Additionally, we compared group specific population growth estimates under maximum marking effort (dband$_{t-2}$ = 100%) to observed variation in population-level growth ($\lambda^{POP}$, see Methods). The *in-situ* population growth rate under maximum marking effort equaled 0.69, which is lower than all observed $\lambda^{POP}$ estimates (Fig. 2) and suggests that unknown individuals likely entered the population on a consistent annual basis.

Group specific differences in observed patterns of population growth and recruitment between the two groups partially reflect artifacts of study design. For example, no ducklings were marked during 2006 and 2007 when no data were collected. Consequently, during the intervals when individuals that hatched during the gap in data collection were potentially recruited (2005-2008 and 2008-2009), recruitment and population growth for the unknown group were significantly higher than the *in-situ* group's estimates.

In general, both recruitment and population growth for the unknown group exhibited smaller annual variation than the *in-situ* group (Fig. 1, 2). The relatively invariant recruitment and population growth rates in the unknown group may reflect a relatively constant influx of immigrants from outside the study area. A potential explanation for such a pattern is that these immigrants originated from existing natural cavities near the

study area, rather than immigration from more distant breeding populations. However, additional information using external markers visible from a distance, intensive capture methods, genetic or stable isotope data would be required to effectively evaluate competing explanations or mechanisms for the observed patterns.

Adult survival had a greater proportional influence on population growth than recruitment, as all seniority parameter estimates were >0.50 (Sandercock 2006), which is consistent with other demographic studies of long-lived waterfowl species (Cooch et al. 2001, Gauthier et al. 2001, Schamber et al. 2009, Bentzen and Powell 2012). Furthermore, we detected substantial variation in recruitment when compared to adult survival (Fig. 4, Appendix B) which is consistent with expected patterns for long-lived species (Stearns 1992). Despite similarities between demographic patterns reported here and those observed in other sea ducks, adult survival in female goldeneyes is lower and more variable compared to other sea duck species (Lawson 2012). Annual variation in population growth is thought to be more reflective of recruitment patterns (due to its variability relative to adult survival), as reported in other long-lived waterfowl studies (Cooch et al. 2001, Gauthier et al. 2001, Flint et al. 2006). However, we believe that, due to its relative variability, annual adult survival likely influences annual variation in population growth to a greater extent, when compared to other sea duck species.

We presented substantial evidence for immigration into our study population, and a density-dependent dispersal mechanism for immature juveniles from our study population. Furthermore, it is likely that the patterns we detected may differ depending on nesting density, nest site availability, or the degree of geographic isolation from other breeding habitats. We believe that these findings will provide future research

opportunities to further elucidate immigration and emigration patterns, and will inform on-going breeding studies that may have relied on assumptions of female natal and breeding philopatry. Though our findings highlight the importance of recruitment to population dynamics in long-lived waterfowl species, it is likely that such patterns differ markedly in cavity-nesting species given nest site limitations. Therefore, continuing to investigate demographic differences among goldeneyes and other sea ducks will improve our understanding of variation in these key demographic parameters.

## MANAGEMENT IMPLICATIONS

We determined that variation in per-capita-recruitment had a greater contribution to observed variation in goldeneye population growth than adult female survival. Given the complexity of recruitment and its importance to population growth, we recommend further study to identify the most important components of this parameter. The negative density-dependence in recruitment we detected has important implications for goldeneye management at multiple scales. Though our results suggest that nest site availability may limit breeding opportunities in immature waterfowl, other studies have suggested that installation of additional nest sites does not increase overall reproductive output (Pöysä and Pöysä 2002). Therefore, we encourage local nest box program managers to recognize the potential demographic constraints that density-dependence may impose in relation to project objectives. Additionally, we suggest that management efforts should examine large-scale movement and dispersal patterns, as they may influence recruitment. We believe that such large-scale investigations are necessary because the majority of goldeneyes and other cavity nesting species use natural cavities (Eadie et al. 1995), the

abundance of which are largely influenced by anthropogenic activities (e.g., logging), and may vary substantially within the goldeneye's breeding range (Denton et al. 2012).

Goldeneyes are among the most heavily studied sea ducks species, yet a lack of demographic estimates throughout their range has precluded the construction of a population model (Sea Duck Joint Venture 2008). Few demographic parameters for Alaska goldeneye populations exist (Eadie et al. 1995, Schmidt et al. 2005, Lawson et al. 2012), where breeding populations declined by 45% between 1977 and 1994 (Hodges et al. 1996). However, we estimated a population growth rate of $1.04 \pm 0.02$ for our study population, which is consistent with continent-wide patterns of stable or increasing goldeneye populations over the same time period (United States Fish and Wildlife Service 2012). We hope these estimates will be used for future population modeling purposes and that the demographic patterns described here may aide our understanding of the underlying mechanisms that contribute to population change in goldeneyes.

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Table 1. Summary of covariates in models of per-capita recruitment ($f$) and population growth ($\lambda$) of goldeneyes in the northern boreal forest of Alaska from 1997-2010. All covariates were z-standardized across years (mean = 0.0, S.D. = 1.0), with missing values assigned a 0.

| Variable | Description |
| --- | --- |
| *Density* | |
| Direct | |
| hen mass | Annual average hen mass during mid-incubation, derived using mixed models used for body condition covariates described above |
| box occ | Annual proportion of occupied nest boxes |
| COGO occ | Annual proportion of total nest boxes occupied by goldeneyes |
| exp occ | Annual proportion of total nest boxes occupied by goldeneyes with prior breeding experience |
| Indirect | |
| pNID | Annual peak (mode) goldeneye nest initiation date |
| phatch | Annual peak (mode) goldeneye nest hatch date |
| dphi | First-year survival, estimated iusing multistate models *in* Lawson et al. (2012) |
| dband | Annual proportion of hatched goldeneye ducklings marked by the study |
| ANS | Annual apparent nest success - the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests) |
| *Environmental* | |
| temp | Average of monthly mean temperatures on the study area from April to September (i.e. breeding and brood-rearing) |
| precip | Total precipitation on the study area from April to September |
| PRES | Sea level pressure (hPa) from October$_{t-1}$ to March$_t$ in purported wintering region |
| ATMP | Air temperature (Celsius) from October$_{t-1}$ to March$_t$ in purported wintering region |
| WTMP | Sea surface temperature (Celsius) from October$_{t-1}$ to April$_t$ in purported wintering region |
| PDO | Annual Pacific Decadal Oscillation index, averaged monthly mean values from May$_{t-1}$ to April$_t$ |

Table 2. Performance of Pradel capture-mark-recapture models for per-capita recruitment

(*f*) of female Common Goldeneye (*Bucephala clangula*) in interior Alaska, from 1997-

2010.  Structure for survival ($\varphi$) and detection probability (*p*) were held constant across

models as: $\varphi$ = Year; *p* = Year. Model-averaged estimates reported in the main text

include all models within 4 $\Delta AIC_C$ units of the top model. This table contains a selection

of the most competitive models from the model selection process and other models that

contained alternative constraints. A complete list of models can be found in Appendix A,

Table A1.

| Model[a] | $\Delta AIC_c$[b] | $w_i$[c] | No. of Parameters | Deviance |
|---|---|---|---|---|
| *f* (g * COGO occ$_{t-1}$) | 0.00 | 0.79 | 20 | 186.94 |
| *f* (g * T) | 2.62 | 0.21 | 20 | 189.56 |
| *f* (g * box occ$_{t-1}$) | 15.28 | 0.00 | 20 | 202.21 |
| *f* (g * dmass$_{t-1}$) | 23.17 | 0.00 | 20 | 210.11 |
| *f* (g * dband$_{t-2}$) | 24.00 | 0.00 | 20 | 210.94 |
| *f* (g * hen mass$_{t-1}$) | 32.02 | 0.00 | 20 | 218.95 |
| *f* (g * PRES$_{t-2}$) | 38.38 | 0.00 | 20 | 225.32 |
| *f* (g * box occ$_{t-2}$) | 38.65 | 0.00 | 20 | 225.58 |
| *f* (g * dphi$_{t-1}$) | 40.09 | 0.00 | 20 | 227.03 |
| *f* (g * COGO occ$_{t-2}$) | 43.41 | 0.00 | 20 | 230.34 |
| *f* (g * hen mass$_{t-2}$) | 44.34 | 0.00 | 20 | 231.28 |
| *f* (g * phatch$_{t-1}$) | 45.59 | 0.00 | 20 | 232.53 |
| *f* (g * ANS$_{t-2}$) | 47.48 | 0.00 | 20 | 234.42 |
| *f* (.) | 60.13 | 0.00 | 17 | 253.42 |
| *f* (g) | 62.13 | 0.00 | 18 | 253.31 |
| *f* (t) | 67.67 | 0.00 | 25 | 243.88 |
| *f* (g + t) | 69.73 | 0.00 | 26 | 243.78 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes

time variation, (T) denotes a linear trend effect, (g) denotes a group effect (*in-situ* vs.

unknown recruitment origin), (.) indicates that a parameter was held constant, and a +

sign indicates an additive effect between two variables, whereas a * denotes an interaction. All covariates were z-standardized across years (mean = 0.0, S.D. = 1.0), with missing values assigned a 0. Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval *t-1* to *t*. For example, a *t-1* subscript denotes conditions at the beginning of the interval. COGO occ = annual proportion of nest boxes occupied by goldeneyes with prior breeding experience; box occ= annual proportion of occupied nest boxes; dmass = individual duckling mass recorded at hatch, standardized across years; dband = annual proportion of hatched goldeneye ducklings marked by the study; hen mass = annual average hen mass during mid-incubation adjusted for structural size and day of incubation, and year; PRES = sea level pressure (hPa) from October$_{t-1}$ to March$_t$ in purported wintering region; dphi = first-year survival, estimated using multistate models in Lawson et al. (2012); phatch = annual peak (mode) goldeneye nest hatch date; ANS = annual apparent nest success,  the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests).

[b]Difference in AIC$_c$, relative to minimum AIC$_c$

[c]Akaike weight (Burnham and Anderson 2002)

Table 3. Performance of Pradel capture-mark-recapture models of population growth ($\lambda$) for female Common Goldeneye in interior Alaska, from 1997-2010. Structure for survival ($\varphi$) and detection probability ($p$) were held constant across models as: $\varphi$ = Year; $p$ = Year. Model-averaged estimates reported in the main text include all models within 4 $\Delta AIC_C$ units of the top model. This table contains a selection of the most competitive models from the model selection process and other models that contained alternative constraints. A complete list of models can be found in Appendix A, Table A2.

| Model[a] | $\Delta AIC_c$[b] | $w_i$[c] | No. of Parameters | Deviance |
|---|---|---|---|---|
| $\lambda$ (g * T) | 0.00 | 0.54 | 20 | 188.05 |
| $\lambda$ (g * dband$_{t-2}$) | 0.92 | 0.34 | 20 | 188.97 |
| $\lambda$ (g * COGO occ$_{t-1}$) | 3.12 | 0.11 | 20 | 191.17 |
| $\lambda$ (g * box occ$_{t-1}$) | 10.15 | 0.00 | 20 | 198.21 |
| $\lambda$ (g * dmass$_{t-1}$) | 14.73 | 0.00 | 20 | 202.78 |
| $\lambda$ (g * hen mass$_{t-1}$) | 24.75 | 0.00 | 20 | 212.80 |
| $\lambda$ (g * PRES$_{t-2}$) | 36.20 | 0.00 | 20 | 224.25 |
| $\lambda$ (g * dphi$_{t-1}$) | 42.15 | 0.00 | 20 | 230.20 |
| $\lambda$ (g * box occ$_{t-2}$) | 44.08 | 0.00 | 20 | 232.13 |
| $\lambda$ (g * hen mass$_{t-2)}$ | 44.96 | 0.00 | 20 | 233.01 |
| $\lambda$ (g * COGO occ$_{t-2}$) | 45.38 | 0.00 | 20 | 233.43 |
| $\lambda$ (g * ANS$_{t-2}$) | 52.05 | 0.00 | 20 | 240.11 |
| $\lambda$ (g * dphi$_{t-2}$) | 62.36 | 0.00 | 20 | 250.41 |
| $\lambda$ (.) | 67.44 | 0.00 | 17 | 261.85 |
| $\lambda$ (t) | 67.56 | 0.00 | 25 | 244.89 |
| $\lambda$ (g + T) | 68.12 | 0.00 | 19 | 258.30 |
| $\lambda$ (g) | 68.34 | 0.00 | 18 | 260.64 |
| $\lambda$ (g + t) | 69.64 | 0.00 | 26 | 244.81 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes time variation, (T) denotes a linear trend effect, (g) denotes a group effect (*in-situ* vs. unknown recruitment origin), (.) means that a parameter was held constant, and a + sign

indicates an additive effect between two variables, whereas a * denotes an interaction. All covariates were z-standardized across years (mean = 0.0, S.D. = 1.0), with missing values assigned a 0.Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval *t-1* to *t*. For example, a *t-1* subscript denotes conditions at the beginning of the interval. dband = annual proportion of hatched goldeneye ducklings marked by the study; COGO occ = annual proportion of nest boxes occupied by goldeneyes with prior breeding experience; box occ= annual proportion of occupied nest boxes; dmass = average annual goldeneye duckling mass; hen mass = annual average hen mass during mid-incubation adjusted for structural size and day of incubation, and year; PRES = sea level pressure (hPa) from $October_{t-1}$ to $March_t$ in purported wintering region; dphi = first-year survival, estimated using multistate models in Lawson et al. (2012); ANS = annual apparent nest success,  the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests).

[b]Difference in $AIC_c$, relative to minimum $AIC_c$

[c]Akaike weight (Burnham and Anderson 2002)

Figure 1. Annual per-capita recruitment (*f*) estimates for Common Goldeneye females in interior Alaska, from 1997-2009. No data were collected during 2006 and 2007, therefore, 2005-2008 was treated as a single three-year interval. Per-capita recruitment was estimated from year *t* to *t+1* using the best supported model: $\varphi$ = Year; *p* = Year; *f* = Group * COGO occ$_{t-1}$. The closed circles and solid line represent *f* for the *in-situ* group ($f^{IS}$; i.e., individuals originally marked as ducklings), whereas open circles and dashed line denote the unknown group ($f^{UN}$; i.e., individuals originally marked as breeding adults). Error bars represent standard errors (SE) of parameter estimates, generated using Pradel capture-mark-recapture models in Program MARK.

Figure 2. Annual population growth ($\lambda$) estimates of Common Goldeneye females in interior Alaska, from 1997-2010. No data were collected during 2006 and 2007, therefore, 2005-2008 was treated as a single three-year interval. Per-capita recruitment was estimated from year *t* to *t+1* using model-averaged estimates from the two best-supported models in which $\varphi$ and *p* contained annual variation for both models, and the following structures for $\lambda$: Group * Trend, and Group * dband$_{t-2}$. The closed circles and solid line represent $\lambda$ for the *in-situ* group ($\lambda^{IS}$; i.e., individuals originally marked as ducklings), whereas open circles and dashed line denote the unknown group ($\lambda^{UN}$; i.e., individuals originally marked as breeding adults), and the dashed line represents overall population growth ($\lambda^{POP}$). To derive $\lambda^{POP}$, we determined the annual proportions of captured individuals that belonged to each group, then multiplied the model-averaged annual group specific estimates of $\lambda$ ($\lambda^{IS}$ and $\lambda^{UK}$) by their respective annual proportions

and added the products together. Error bars represent standard errors (SE) of parameter estimates, generated using Pradel capture-mark-recapture models in Program MARK.

Figure 3. Group specific covariate effects of (a) COGO $occ_{t-1}$ on per-capita recruitment ($f$) and (b) $dband_{t-2}$ on population growth ($\lambda$) for Common Goldeneyes in interior Alaska, from 1997-2010. Both covariates are in relation to interval $t-1$ to $t$ for $f$ and $\lambda$. For a. and b., the solid line represents the covariate effect for the *in-situ* group (individuals originally marked as ducklings), and the dashed line for the unknown group (individuals initially encountered as breeding adults).

Figure 4. Retrospective contributions of apparent survival ($\varphi$) and per-capita recruitment ($f$) to overall annual rate of population change ($\lambda^{POP}$) in female Common Goldeneyes in interior Alaska, 1997-2010. For our $\lambda$ analysis, the best supported models supported a group by covariate interaction, which provided group-specific estimates of $\lambda$. To derive $\lambda^{POP}$, a population-level estimate of population change, we determined the annual proportions of captured individuals that belonged to each group, and then multiplied the model-averaged annual group specific estimates of $\lambda$ ($\lambda^{IS}$ and $\lambda^{UK}$) by their respective annual proportions and added the products together. With the formula $\lambda_t = f_t + \varphi_t$, we used the model-averaged $\varphi$ estimates from the $\lambda$ analysis, and the $\lambda^{POP}$ to determine annual contributions of $f$ to $\lambda$.
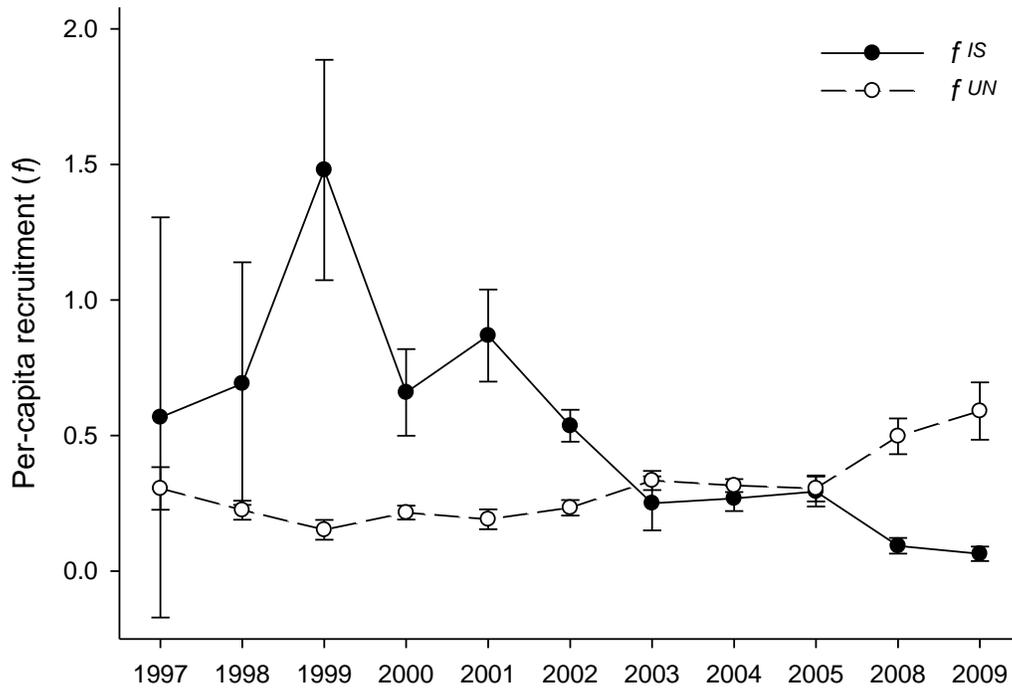
Figure 1.
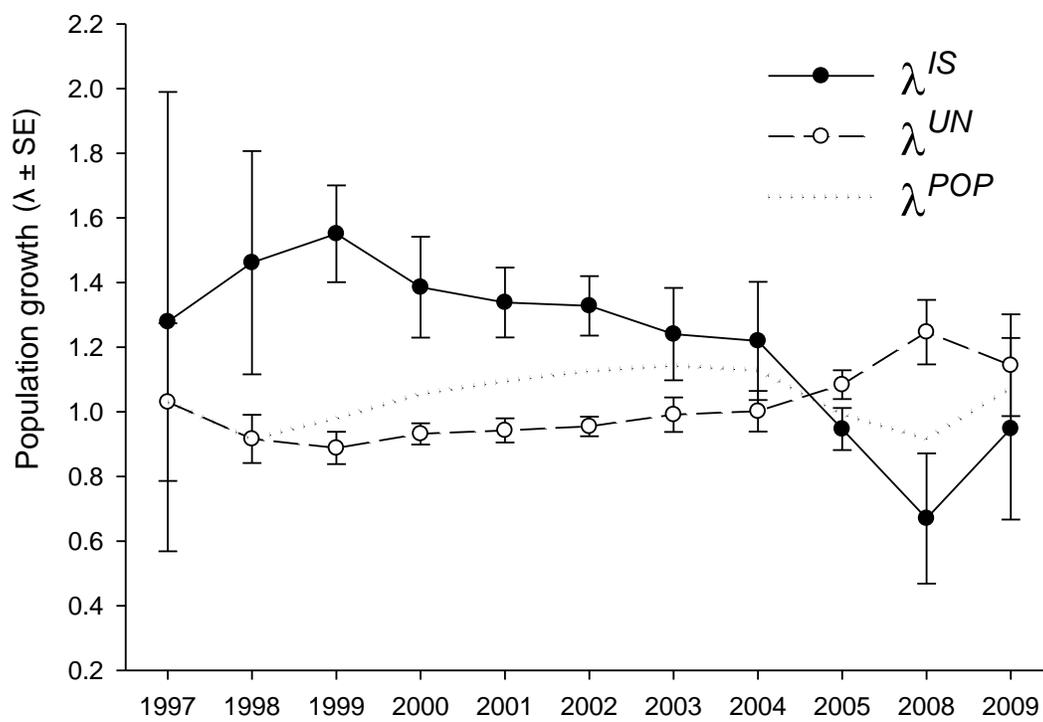
Figure 2.
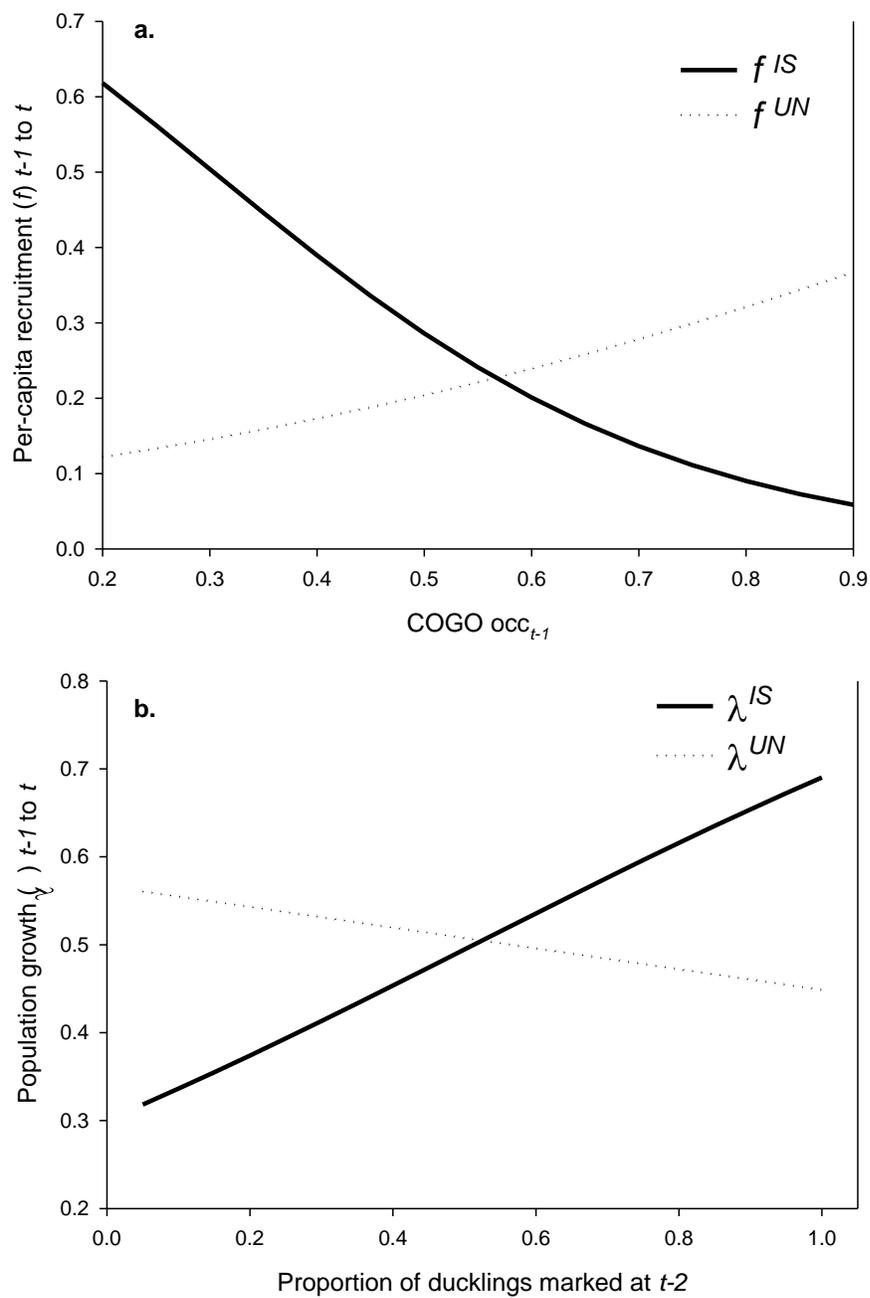
Figure 3.
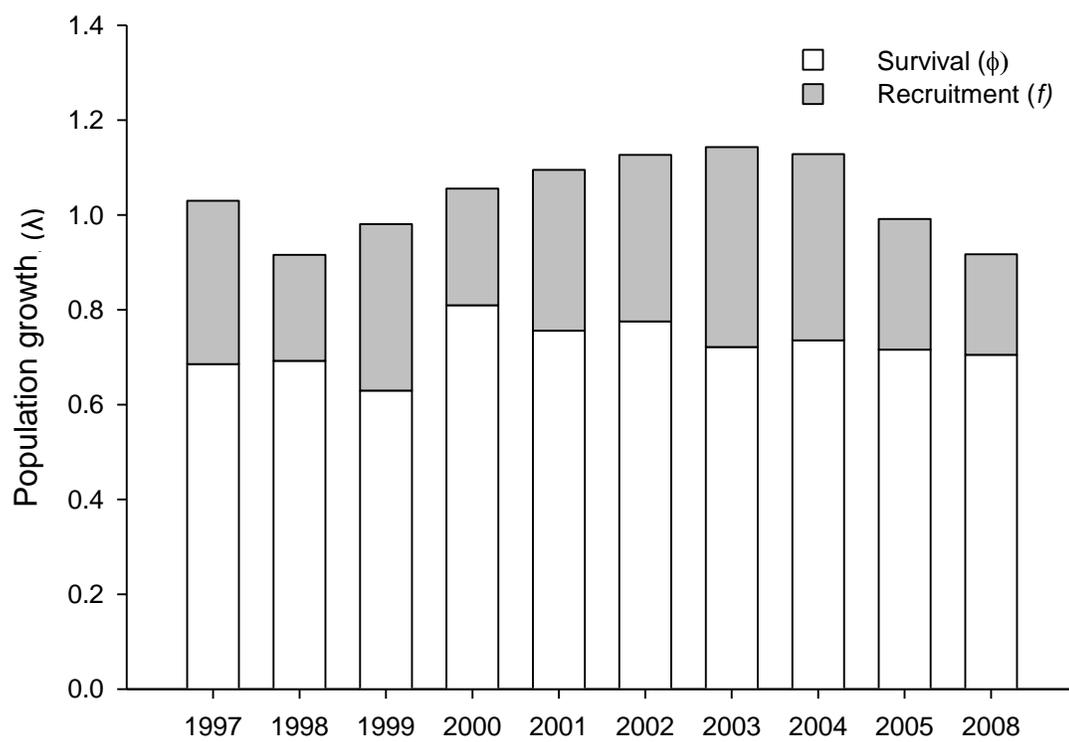
Figure 4.

**APPENDIX A. COMPLETE MODEL LIST FOR RECRUITMENT AND**

**POPULAITON GROWTH ANALYSES IN PROGRAM MARK**

Table A1. Performance of Pradel capture-mark-recapture models for per-capita recruitment (*f*) of female Common Goldeneye (*Bucephala clangula*) in interior Alaska, from 1997-2010.  Structure for survival ($\varphi$) and detection probability (*p*) were held constant across models as: $\varphi$ = Year; *p* = Year. Model-averaged estimates reported in the main text include all models within 4 $\Delta AIC_c$ units of the top model.

| Model[a] | $\Delta AIC_c$[b] | $w_i$[c] | *k* | Dev. |
|---|---|---|---|---|
| *f* (g * COGO occ $_{t-1}$) | 0.00 | 0.79 | 20 | 186.94 |
| *f* (g * T) | 2.62 | 0.21 | 20 | 189.56 |
| *f* (g * box occ $_{t-1}$) | 15.28 | 0.00 | 20 | 202.21 |
| *f* (g * dmass $_{t-1}$) | 23.17 | 0.00 | 20 | 210.11 |
| *f* (g * dband$_{t-2}$) | 24.00 | 0.00 | 20 | 210.94 |
| *f* (g * hen mass $_{t-1}$) | 32.02 | 0.00 | 20 | 218.95 |
| *f* (g * PRES $_{t-2}$) | 38.38 | 0.00 | 20 | 225.32 |
| *f* (g * box occ $_{t-2}$) | 38.65 | 0.00 | 20 | 225.58 |
| *f* (g * dphi $_{t-1}$) | 40.09 | 0.00 | 20 | 227.03 |
| *f* (g * COGO occ $_{t-2}$) | 43.41 | 0.00 | 20 | 230.34 |
| *f* (g * hen mass $_{t-2}$) | 44.34 | 0.00 | 20 | 231.28 |
| *f* (g * phatch $_{t-1}$) | 45.59 | 0.00 | 20 | 232.53 |
| *f* (g * ANS $_{t-2}$) | 47.48 | 0.00 | 20 | 234.42 |
| *f* (g * ATMP $_{t-1}$) | 52.56 | 0.00 | 20 | 239.50 |
| *f* (g * dband $_{t-1}$) | 52.87 | 0.00 | 20 | 239.80 |
| *f* (g * PRES $_{t-1}$) | 53.38 | 0.00 | 20 | 240.32 |
| *f* (g * dphi $_{t-2}$) | 55.25 | 0.00 | 20 | 242.19 |
| *f* (ANS $_{t-2}$) | 55.46 | 0.00 | 18 | 246.64 |
| *f* (g + ANS $_{t-2}$) | 57.55 | 0.00 | 19 | 246.61 |

| | | | | |
|---|---|---|---|---|
| $f$ (g * dmass $_{t-2}$) | 57.92 | 0.00 | 20 | 244.86 |
| $f$ (PRES $_{t-2}$) | 58.66 | 0.00 | 18 | 249.84 |
| $f$ (g * temp $_{t-2}$) | 58.82 | 0.00 | 20 | 245.75 |
| $f$ (g * temp $_{t-1}$) | 59.29 | 0.00 | 20 | 246.23 |
| $f$ (.) | 60.13 | 0.00 | 17 | 253.42 |
| $f$ (dphi $_{t-2}$) | 60.23 | 0.00 | 18 | 251.41 |
| $f$ (precip $_{t-2}$) | 60.29 | 0.00 | 18 | 251.47 |
| $f$ (dphi $_{t-1}$) | 60.59 | 0.00 | 18 | 251.77 |
| $f$ (g * precip $_{t-1}$) | 60.74 | 0.00 | 20 | 247.67 |
| $f$ (g + PRES $_{t-2}$) | 60.77 | 0.00 | 19 | 249.84 |
| $f$ (box occ $_{t-1}$) | 60.93 | 0.00 | 18 | 252.11 |
| $f$ (pNID $_{t-2}$) | 60.95 | 0.00 | 18 | 252.12 |
| $f$ (phatch $_{t-1}$) | 60.96 | 0.00 | 18 | 252.14 |
| $f$ (box occ $_{t-2}$) | 61.00 | 0.00 | 18 | 252.18 |
| $f$ (hen mass $_{t-2}$) | 61.01 | 0.00 | 18 | 252.19 |
| $f$ (g * pNID $_{t-1}$) | 61.04 | 0.00 | 20 | 247.98 |
| $f$ (dband $_{t-1}$) | 61.11 | 0.00 | 18 | 252.29 |
| $f$ (hen mass $_{t-1}$) | 61.14 | 0.00 | 18 | 252.32 |
| $f$ (g * precip $_{t-2}$) | 61.14 | 0.00 | 20 | 248.08 |
| $f$ (g * ATMP $_{t-2}$) | 61.28 | 0.00 | 20 | 248.21 |
| $f$ (PDO $_{t-2}$) | 61.32 | 0.00 | 18 | 252.50 |
| $f$ (PRES $_{t-1}$) | 61.33 | 0.00 | 18 | 252.50 |
| $f$ (temp $_{t-2}$) | 61.40 | 0.00 | 18 | 252.58 |
| $f$ (exp occ $_{t-2}$) | 61.73 | 0.00 | 18 | 252.91 |
| $f$ (temp $_{t-1}$) | 61.76 | 0.00 | 18 | 252.94 |
| $f$ (g * PDO $_{t-1}$) | 61.78 | 0.00 | 20 | 248.72 |
| $f$ (WTMP $_{t-1}$) | 61.89 | 0.00 | 18 | 253.07 |
| $f$ (ATMP $_{t-2}$) | 61.93 | 0.00 | 18 | 253.11 |
| $f$ (pNID $_{t-1}$) | 61.96 | 0.00 | 18 | 253.14 |
| $f$ (g * pNID $_{t-2}$) | 62.03 | 0.00 | 20 | 248.96 |
| $f$ (ATMP $_{t-1}$) | 62.10 | 0.00 | 18 | 253.28 |
| $f$ (COGO occ $_{t-2}$) | 62.11 | 0.00 | 18 | 253.29 |
| $f$ (WTMP $_{t-2}$) | 62.11 | 0.00 | 18 | 253.29 |

| | | | | |
|---|---|---|---|---|
| $f$ (g) | 62.13 | 0.00 | 18 | 253.31 |
| $f$ (temp $_{t-1}$) | 62.13 | 0.00 | 18 | 253.31 |
| $f$ (PDO $_{t-1}$) | 62.14 | 0.00 | 18 | 253.32 |
| $f$ (dmass $_{t-2}$) | 62.14 | 0.00 | 18 | 253.32 |
| $f$ (exp occ $_{t-1}$) | 62.20 | 0.00 | 18 | 253.38 |
| $f$ (dmass $_{t-1}$) | 62.21 | 0.00 | 18 | 253.39 |
| $f$ (phatch $_{t-2}$) | 62.22 | 0.00 | 18 | 253.40 |
| $f$ (COGO occ $_{t-1}$) | 62.23 | 0.00 | 18 | 253.41 |
| $f$ (ANS $_{t-1}$) | 62.24 | 0.00 | 18 | 253.42 |
| $f$ (g + dphi $_{t-2}$) | 62.25 | 0.00 | 19 | 251.31 |
| $f$ (g * WTMP $_{t-1}$) | 62.37 | 0.00 | 20 | 249.31 |
| $f$ (g + precip $_{t-2}$) | 62.39 | 0.00 | 19 | 251.45 |
| $f$ (g + dphi $_{t-1}$) | 62.58 | 0.00 | 19 | 251.64 |
| $f$ (g + box occ $_{t-2}$) | 62.93 | 0.00 | 19 | 252.00 |
| $f$ (g + phatch $_{t-1}$) | 62.98 | 0.00 | 19 | 252.04 |
| $f$ (g + pNID $_{t-2}$) | 63.00 | 0.00 | 19 | 252.06 |
| $f$ (g + box occ $_{t-1}$) | 63.04 | 0.00 | 19 | 252.10 |
| $f$ (g + hen mass $_{t-2}$) | 63.12 | 0.00 | 19 | 252.19 |
| $f$ (g + T) | 63.14 | 0.00 | 19 | 252.20 |
| $f$ (g + dband $_{t-1}$) | 63.21 | 0.00 | 19 | 252.27 |
| $f$ (g + hen mass $_{t-1}$) | 63.26 | 0.00 | 19 | 252.32 |
| $f$ (g + PDO $_{t-2}$) | 63.38 | 0.00 | 19 | 252.44 |
| $f$ (g + temp $_{t-2}$) | 63.42 | 0.00 | 19 | 252.48 |
| $f$ (g + PRES $_{t-1}$) | 63.43 | 0.00 | 19 | 252.50 |
| $f$ (g + precip $_{t-1}$) | 63.67 | 0.00 | 19 | 252.73 |
| $f$ (g + exp occ $_{t-2}$) | 63.76 | 0.00 | 19 | 252.83 |
| $f$ (g + WTMP $_{t-1}$) | 63.86 | 0.00 | 19 | 252.93 |
| $f$ (g + pNID $_{t-1}$) | 63.94 | 0.00 | 19 | 253.00 |
| $f$ (g + ATMP $_{t-2}$) | 63.96 | 0.00 | 19 | 253.02 |
| $f$ (g + ATMP $_{t-1}$) | 64.10 | 0.00 | 19 | 253.16 |
| $f$ (g + COGO occ $_{t-2}$) | 64.10 | 0.00 | 19 | 253.16 |
| $f$ (g + WTMP $_{t-2}$) | 64.14 | 0.00 | 19 | 253.20 |
| $f$ (g + dband $_{t-2}$) | 64.14 | 0.00 | 19 | 253.20 |

| | | | | |
|---|---|---|---|---|
| $f$ (g + temp $_{t-1}$) | 64.14 | 0.00 | 19 | 253.21 |
| $f$ (g + dmass $_{t-2}$) | 64.15 | 0.00 | 19 | 253.21 |
| $f$ (g + PDO $_{t-1}$) | 64.15 | 0.00 | 19 | 253.22 |
| $f$ (g * exp occ $_{t-2}$) | 64.18 | 0.00 | 20 | 251.11 |
| $f$ (g + exp occ $_{t-1}$) | 64.20 | 0.00 | 19 | 253.26 |
| $f$ (g + phatch $_{t-2}$) | 64.21 | 0.00 | 19 | 253.27 |
| $f$ (g + COGO occ $_{t-1}$) | 64.21 | 0.00 | 19 | 253.28 |
| $f$ (g + dmass $_{t-1}$) | 64.22 | 0.00 | 19 | 253.28 |
| $f$ (g + ANS $_{t-1}$) | 64.24 | 0.00 | 19 | 253.31 |
| $f$ (g * PDO $_{t-2}$) | 64.25 | 0.00 | 20 | 251.19 |
| $f$ (g * ANS $_{t-1}$) | 64.72 | 0.00 | 20 | 251.66 |
| $f$ (g * phatch $_{t-2}$) | 64.79 | 0.00 | 20 | 251.73 |
| $f$ (g * WTMP $_{t-2}$) | 66.08 | 0.00 | 20 | 253.02 |
| $f$ (g * exp occ $_{t-1}$) | 66.29 | 0.00 | 20 | 253.23 |
| $f$ (t) | 67.67 | 0.00 | 25 | 243.88 |
| $f$ (g + t) | 69.73 | 0.00 | 26 | 243.78 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes time variation, (T) denotes a linear trend effect, (g) denotes a group effect (*in-situ* vs. unknown recruitment origin), (.) indicates that a parameter was held constant, and a + sign indicates an additive effect between two variables, whereas a * denotes an interaction. All covariates were z-standardized across years (mean = 0.0, S.D. = 1.0), with missing values assigned a 0.Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval *t-1* to *t*. For example, a *t-1* subscript denotes conditions at the beginning of the interval. hen mass = annual average hen mass during mid-incubation adjusted for structural size and day of incubation, and year; box occ= annual proportion of occupied nest boxes; COGO occ = annual proportion of nest boxes occupied by goldeneyes with prior breeding experience; exp occ = annual

proportion of total nest boxes occupied by goldeneyes with prior breeding experience;

pNID = Annual peak (mode) goldeneye nest initiation date; phatch = annual peak (mode)

goldeneye nest hatch date; dphi = first-year survival, estimated using multistate models in

Lawson et al. (2012); dmass = individual duckling mass recorded at hatch, standardized

across years; dband = annual proportion of hatched goldeneye ducklings marked by the

study; ANS = annual apparent nest success, the number of goldeneye nests in which at

least one duckling hatched, divided by the total number of goldeneye nests (excluding

"dump" nests); temp = average of monthly mean temperatures on the study area from

April to September (i.e. breeding and brood-rearing); precip = total precipitation on the

study area from April to September; PRES = sea level pressure (hPa) from $October_{t-1}$ to

$March_t$ in purported wintering region; ATMP = air temperature (Celsius) from $October_{t-1}$

to $March_t$ in purported wintering region; WTMP = sea surface temperature (Celsius) from

$October_{t-1}$ to $April_t$ in purported wintering region; PDO = Annual Pacific Decadal

Oscillation index, averaged monthly mean values from $May_{t-1}$ to $April_t$.

[b]Difference in $AIC_c$, relative to minimum $AIC_c$

[c]Akaike weight (Burnham and Anderson 2002)

Table A2. Performance of Pradel capture-mark-recapture models for population growth ($\lambda$) of female Common Goldeneye (*Bucephala clangula*) in interior Alaska, from 1997-2010.  Structure for survival ($\varphi$) and detection probability (*p*) were held constant across models as: $\varphi$ = Year; *p* = Year. Model-averaged estimates reported in the main text include all models within 4 $\Delta AIC_C$ units of the top model.

| Model[a] | $\Delta AIC_c$[b] | $w_i$[c] | k | Dev. |
|---|---|---|---|---|
| $\lambda$ (g * T) | 0.00 | 0.54 | 20 | 188.05 |
| $\lambda$ (g * dband $_{t-2}$) | 0.92 | 0.34 | 20 | 188.97 |
| $\lambda$ (g * COGO occ $_{t-1}$) | 3.12 | 0.11 | 20 | 191.17 |
| $\lambda$ (g * box occ $_{t-1}$) | 10.15 | 0.00 | 20 | 198.21 |
| $\lambda$ (g * dmass $_{t-1}$) | 14.73 | 0.00 | 20 | 202.78 |
| $\lambda$ (g * hen mass $_{t-1}$) | 24.75 | 0.00 | 20 | 212.80 |
| $\lambda$ (g * PRES $_{t-2}$) | 36.20 | 0.00 | 20 | 224.25 |
| $\lambda$ (g * dphi $_{t-1}$) | 42.15 | 0.00 | 20 | 230.20 |
| $\lambda$ (g * box occ $_{t-2}$) | 44.08 | 0.00 | 20 | 232.13 |
| $\lambda$ (g * PRES $_{t-1}$) | 44.79 | 0.00 | 20 | 232.85 |
| $\lambda$ (g * hen mass $_{t-2}$) | 44.96 | 0.00 | 20 | 233.01 |
| $\lambda$ (g * COGO occ $_{t-2}$) | 45.38 | 0.00 | 20 | 233.43 |
| $\lambda$ (g * phatch $_{t-1}$) | 46.30 | 0.00 | 20 | 234.35 |
| $\lambda$ (g * ANS $_{t-2}$) | 52.05 | 0.00 | 20 | 240.11 |
| $\lambda$ (g * dband $_{t-1}$) | 55.63 | 0.00 | 20 | 243.68 |
| $\lambda$ (g * ATMP $_{t-1}$) | 56.34 | 0.00 | 20 | 244.40 |
| $\lambda$ (g + ANS $_{t-2}$) | 57.49 | 0.00 | 19 | 247.67 |
| $\lambda$ (g * dphi $_{t-2}$) | 62.36 | 0.00 | 20 | 250.41 |
| $\lambda$ (g * temp $_{t-1}$) | 62.38 | 0.00 | 20 | 250.44 |
| $\lambda$ (g * dmass $_{t-2}$) | 62.81 | 0.00 | 20 | 250.87 |
| $\lambda$ (g * temp $_{t-2}$) | 63.28 | 0.00 | 20 | 251.33 |
| $\lambda$ (PRES $_{t-2}$) | 63.64 | 0.00 | 18 | 255.93 |
| $\lambda$ (g * precip $_{t-2}$) | 65.21 | 0.00 | 20 | 253.26 |
| $\lambda$ (g + PRES $_{t-2}$) | 65.30 | 0.00 | 19 | 255.48 |

| | | | | |
|---|---|---|---|---|
| $\lambda$ (dphi $_{t-2}$) | 65.62 | 0.00 | 18 | 257.91 |
| $\lambda$ (g * PDO $_{t-1}$) | 65.66 | 0.00 | 20 | 253.71 |
| $\lambda$ (dphi $_{t-1}$) | 66.26 | 0.00 | 18 | 258.55 |
| $\lambda$ (T) | 66.50 | 0.00 | 18 | 258.80 |
| $\lambda$ (dband $_{t-1}$) | 66.78 | 0.00 | 18 | 259.08 |
| $\lambda$ (g + dphi $_{t-2}$) | 66.80 | 0.00 | 19 | 256.97 |
| $\lambda$ (hen mass $_{t-1}$) | 66.89 | 0.00 | 18 | 259.19 |
| $\lambda$ (PRES $_{t-1}$) | 67.00 | 0.00 | 18 | 259.29 |
| $\lambda$ (hen mass $_{t-2}$) | 67.03 | 0.00 | 18 | 259.32 |
| $\lambda$ (.) | 67.44 | 0.00 | 17 | 261.85 |
| $\lambda$ (PDO $_{t-2}$) | 67.46 | 0.00 | 18 | 259.76 |
| $\lambda$ (g + dphi $_{t-1}$) | 67.51 | 0.00 | 19 | 257.68 |
| $\lambda$ (t) | 67.56 | 0.00 | 25 | 244.89 |
| $\lambda$ (box occ $_{t-2}$) | 67.73 | 0.00 | 18 | 260.02 |
| $\lambda$ (box occ $_{t-1}$) | 67.76 | 0.00 | 18 | 260.06 |
| $\lambda$ (precip $_{t-2}$) | 67.84 | 0.00 | 18 | 260.14 |
| $\lambda$ (phatch $_{t-1}$) | 67.94 | 0.00 | 18 | 260.24 |
| $\lambda$ (g + dband $_{t-1}$) | 68.10 | 0.00 | 19 | 258.28 |
| $\lambda$ (exp occ $_{t-2}$) | 68.12 | 0.00 | 18 | 260.42 |
| $\lambda$ (g + T) | 68.12 | 0.00 | 19 | 258.30 |
| $\lambda$ (g) | 68.34 | 0.00 | 18 | 260.64 |
| $\lambda$ (pNID $_{t-2}$) | 68.50 | 0.00 | 18 | 260.79 |
| $\lambda$ (g + PRES $_{t-1}$) | 68.54 | 0.00 | 19 | 258.72 |
| $\lambda$ (g + hen mass $_{t-1}$) | 68.56 | 0.00 | 19 | 258.74 |
| $\lambda$ (g + box occ $_{t-2}$) | 68.58 | 0.00 | 19 | 258.76 |
| $\lambda$ (g + hen mass $_{t-2}$) | 68.58 | 0.00 | 19 | 258.76 |
| $\lambda$ (g * WTMP $_{t-1}$) | 68.59 | 0.00 | 20 | 256.64 |
| $\lambda$ (g + PDO $_{t-2}$) | 68.69 | 0.00 | 19 | 258.87 |
| $\lambda$ (temp $_{t-2}$) | 68.83 | 0.00 | 18 | 261.13 |
| $\lambda$ (COGO occ $_{t-2}$) | 68.88 | 0.00 | 18 | 261.18 |
| $\lambda$ (g + box occ $_{t-1}$) | 68.92 | 0.00 | 19 | 259.09 |
| $\lambda$ (g * ATMP $_{t-2}$) | 68.92 | 0.00 | 20 | 256.97 |
| $\lambda$ (g * pNID $_{t-1}$) | 68.96 | 0.00 | 20 | 257.01 |

| | | | |
|---|---|---|---|
| $\lambda$ (phatch $_{t-2}$) | 69.01 | 0.00 | 18 | 261.30 |
| $\lambda$ (pNID $_{t-1}$) | 69.01 | 0.00 | 18 | 261.30 |
| $\lambda$ (ATMP $_{t-2}$) | 69.06 | 0.00 | 18 | 261.35 |
| $\lambda$ (g + precip $_{t-2}$) | 69.09 | 0.00 | 19 | 259.27 |
| $\lambda$ (g + phatch $_{t-1}$) | 69.13 | 0.00 | 19 | 259.31 |
| $\lambda$ (g * precip $_{t-1}$) | 69.14 | 0.00 | 20 | 257.19 |
| $\lambda$ (g + exp occ $_{t-2}$) | 69.14 | 0.00 | 19 | 259.32 |
| $\lambda$ (exp occ $_{t-1}$) | 69.23 | 0.00 | 18 | 261.53 |
| $\lambda$ (dband $_{t-2}$) | 69.38 | 0.00 | 18 | 261.67 |
| $\lambda$ (ANS $_{t-1}$) | 69.38 | 0.00 | 18 | 261.68 |
| $\lambda$ (WTMP $_{t-2}$) | 69.41 | 0.00 | 18 | 261.71 |
| $\lambda$ (dmass $_{t-2}$) | 69.42 | 0.00 | 18 | 261.71 |
| $\lambda$ (precip $_{t-1}$) | 69.50 | 0.00 | 18 | 261.80 |
| $\lambda$ (COGO occ $_{t-1}$) | 69.53 | 0.00 | 18 | 261.83 |
| $\lambda$ (temp $_{t-1}$) | 69.54 | 0.00 | 18 | 261.83 |
| $\lambda$ (dmass $_{t-1}$) | 69.54 | 0.00 | 18 | 261.83 |
| $\lambda$ (ATMP $_{t-1}$) | 69.55 | 0.00 | 18 | 261.85 |
| $\lambda$ (WTMP $_{t-1}$) | 69.55 | 0.00 | 18 | 261.85 |
| $\lambda$ (g + pNID $_{t-2}$) | 69.63 | 0.00 | 19 | 259.81 |
| $\lambda$ (g + t) | 69.64 | 0.00 | 26 | 244.81 |
| $\lambda$ (g + pNID $_{t-1}$) | 69.74 | 0.00 | 19 | 259.92 |
| $\lambda$ (g * phatch $_{t-2}$) | 69.79 | 0.00 | 20 | 257.85 |
| $\lambda$ (g + temp $_{t-2}$) | 69.82 | 0.00 | 19 | 259.99 |
| $\lambda$ (g + COGO occ $_{t-2}$) | 69.86 | 0.00 | 19 | 260.04 |
| $\lambda$ (g * pNID $_{t-2}$) | 70.07 | 0.00 | 20 | 258.12 |
| $\lambda$ (g + ATMP $_{t-2}$) | 70.09 | 0.00 | 19 | 260.27 |
| $\lambda$ (g + exp occ $_{t-1}$) | 70.10 | 0.00 | 19 | 260.28 |
| $\lambda$ (g + dband $_{t-2}$) | 70.12 | 0.00 | 19 | 260.30 |
| $\lambda$ (g + phatch $_{t-2}$) | 70.16 | 0.00 | 19 | 260.34 |
| $\lambda$ (g + dmass $_{t-2}$) | 70.36 | 0.00 | 19 | 260.54 |
| $\lambda$ (g + PDO $_{t-1}$) | 70.38 | 0.00 | 19 | 260.56 |
| $\lambda$ (g + ANS $_{t-1}$) | 70.39 | 0.00 | 19 | 260.56 |
| $\lambda$ (g + WTMP $_{t-2}$) | 70.40 | 0.00 | 19 | 260.57 |

| | | | | |
|---|---|---|---|---|
| $\lambda$ (g + WTMP $_{t-1}$) | 70.40 | 0.00 | 19 | 260.58 |
| $\lambda$ (g + dmass $_{t-1}$) | 70.41 | 0.00 | 19 | 260.58 |
| $\lambda$ (g * exp occ $_{t-2}$) | 70.42 | 0.00 | 20 | 258.47 |
| $\lambda$ (g + temp $_{t-1}$) | 70.45 | 0.00 | 19 | 260.63 |
| $\lambda$ (g + COGO occ $_{t-1}$) | 70.45 | 0.00 | 19 | 260.63 |
| $\lambda$ (g + ATMP $_{t-1}$) | 70.45 | 0.00 | 19 | 260.63 |
| $\lambda$ (g + precip $_{t-1}$) | 70.46 | 0.00 | 19 | 260.64 |
| $\lambda$ (g * PDO $_{t-2}$) | 70.51 | 0.00 | 20 | 258.56 |
| $\lambda$ (g * exp occ $_{t-1}$) | 71.31 | 0.00 | 20 | 259.36 |
| $\lambda$ (g * ANS $_{t-1}$) | 71.36 | 0.00 | 20 | 259.41 |
| $\lambda$ (g * WTMP $_{t-2}$) | 72.46 | 0.00 | 20 | 260.52 |

[a]Model selection notation follows Burnham and Anderson (2002), in which (t) denotes time variation, (T) denotes a linear trend effect, (g) denotes a group effect (*in-situ* vs. unknown recruitment origin), (.) indicates that a parameter was held constant, and a + sign indicates an additive effect between two variables, whereas a * denotes an interaction. All covariates were z-standardized across years (mean = 0.0, S.D. = 1.0), with missing values assigned a 0.Time-varying covariates were applied to parameters with multiple lag effects, in relation to interval *t-1* to *t*. For example, a *t-1* subscript denotes conditions at the beginning of the interval. hen mass = annual average hen mass during mid-incubation adjusted for structural size and day of incubation, and year, individual (random effect), and year (fixed effect) as explanatory variables; box occ= annual proportion of occupied nest boxes; COGO occ = annual proportion of nest boxes occupied by goldeneyes with prior breeding experience; exp occ = annual proportion of total nest boxes occupied by goldeneyes with prior breeding experience; pNID = Annual peak (mode) goldeneye nest initiation date; phatch = annual peak (mode) goldeneye nest

hatch date; dphi = first-year survival, estimated using multistate models in Lawson et al. (2012); dmass = individual duckling mass recorded at hatch, standardized across years; dband = annual proportion of hatched goldeneye ducklings marked by the study; ANS = annual apparent nest success,  the number of goldeneye nests in which at least one duckling hatched, divided by the total number of goldeneye nests (excluding "dump" nests);  temp = average of monthly mean temperatures on the study area from April to September (i.e. breeding and brood-rearing); precip = total precipitation on the study area from April to September; PRES = sea level pressure (hPa) from $October_{t-1}$ to $March_t$ in purported wintering region; ATMP = air temperature (Celsius) from $October_{t-1}$ to $March_t$ in purported wintering region; WTMP = sea surface temperature (Celsius) from $October_{t-1}$ to $April_t$ in purported wintering region; PDO = Annual Pacific Decadal Oscillation index, averaged monthly mean values from $May_{t-1}$ to $April_t$.

[b]Difference in $AIC_c$, relative to minimum $AIC_c$

[c]Akaike weight (Burnham and Anderson 2002)

**APPENDIX B. APPARENT SURVIVAL AND DETECTION PROBABILITY**

**ESTIMATES FROM RECRUITMENT AND POPULATION GROWTH**

**ANALYSES**


Table B1. Model averaged apparent survival ($\varphi$) estimates ($\pm$ SE) for adult female

Common Goldeneyes (*Bucephala clangula*) in interior Alaska from 1997-2010, from two

separate Pradel capture-mark-recapture analyses, in which per-capita recruitment (*f*) and

population growth ($\lambda$) were also estimated.  We considered a set of models in which *f* and

$\lambda$ were allowed to vary among years, and allowed for group effects, linear and quadratic

temporal trends, time-varying covariates, and their interactions. Alternatively, structures

for survival ($\varphi$) and detection probability (*p*) were held constant across models as: $\varphi$ =

Year; *p* = Year. In fully time-dependent capture-mark recapture models $\varphi$ and *p* are

confounded in the final interval (Lebreton 1992), therefore, we constrained $\varphi$ to be equal

for the penultimate and final intervals. As such, the final interval (2009-2010) is not

shown. Model-averaged estimates for each analysis were derived using all models within

4 $\Delta AIC_C$ units of the top model (Table 2 in the main text).


|      | *f* Models $\varphi \pm$ SE | $\lambda$ Models $\varphi \pm$ SE |
|------|-----------------|-----------------|
| 1997 | $0.73 \pm 0.07$ | $0.69 \pm 0.09$ |
| 1998 | $0.63 \pm 0.07$ | $0.69 \pm 0.06$ |
| 1999 | $0.57 \pm 0.08$ | $0.63 \pm 0.06$ |
| 2000 | $0.77 \pm 0.06$ | $0.81 \pm 0.05$ |
| 2001 | $0.81 \pm 0.06$ | $0.76 \pm 0.05$ |
| 2002 | $0.75 \pm 0.06$ | $0.78 \pm 0.05$ |
| 2003 | $0.69 \pm 0.06$ | $0.72 \pm 0.05$ |
| 2004 | $0.72 \pm 0.06$ | $0.74 \pm 0.05$ |

2005    0.75 ± 0.04    0.72 ± 0.04
2008    0.69 ± 0.04    0.71 ± 0.04

Table B2. Model averaged detection probability (*p*) estimates (± SE) for adult female

Common Goldeneyes (*Bucephala clangula*) in interior Alaska from 1997-2010, from two

separate Pradel capture-mark-recapture analyses, in which per-capita recruitment (*f*) and

population growth (λ) were also estimated.  We considered a set of models in which *f* and

λ were allowed to vary among years, and allowed for group effects, linear and quadratic

temporal trends, time-varying covariates, and their interactions. Alternatively, structures

for survival (φ) and detection probability (*p*) were held constant across models as: φ =

Year; *p* = Year. In fully time-dependent capture-mark recapture models φ and *p* are

confounded in the final interval (Lebreton 1992), therefore, we constrained *p* to be equal

for the penultimate and final intervals. As such, *p* for the final occasion (2010) is not

shown. We fixed detection probability estimates for multiple years. For 1997, 1998,

2000, 2001, and 2005 detection probability equaled 1, which was confirmed by

examining capture histories; during these years, no previously marked individual was

missed but encountered later on in the study. However, we fixed *p* to equal 0 for 1997

and 1998 for the *in-situ* (IS) group, as no individuals were available for capture during

these two intervals. However, all other detection probability estimates between the two

groups are the same. Model-averaged estimates for each analysis were derived using all

models within 4 $\Delta\text{AIC}_\text{C}$ units of the top model (Table 3 in the main text).

| | *f* Models | | λ Models | |
| --- | --- | --- | --- | --- |
| | $p^{IS}$ ± SE | $p^{UN}$ ± SE | $p^{IS}$ ± SE | $p^{UN}$ |
| 1997 | 0 | 1 | 0 | 1 |
| 1998 | 0 | 1 | 0 | 1 |
| 1999 | 0.93 ± 0.06 | 0.93 ± 0.06 | 0.92 ± 0.07 | 0.92 ± 0.07 |
| 2000 | 1 | 1 | 1 | 1 |

| | | | | |
|------|-----------------|-----------------|-----------------|-----------------|
| 2001 | 1 | 1 | 1 | 1 |
| 2002 | $0.88 \pm 0.05$ | $0.88 \pm 0.05$ | $0.89 \pm 0.05$ | $0.89 \pm 0.05$ |
| 2003 | $0.96 \pm 0.04$ | $0.96 \pm 0.04$ | $0.97 \pm 0.03$ | $0.97 \pm 0.03$ |
| 2004 | $0.96 \pm 0.04$ | $0.96 \pm 0.04$ | $0.96 \pm 0.04$ | $0.96 \pm 0.04$ |
| 2005 | 1 | 1 | 1 | 1 |
| 2008 | $0.92 \pm 0.05$ | $0.92 \pm 0.05$ | $0.93 \pm 0.05$ | $0.93 \pm 0.05$ |
| 2009 | $0.92 \pm 0.04$ | $0.92 \pm 0.04$ | $0.92 \pm 0.04$ | $0.92 \pm 0.04$ |

**THESIS SUMMARY:** Members of the sea duck group (tribe: *Mergini*) are thought to exhibit life history traits reflective of long-lived species (i.e., *k* selected, survivor species *sensu* Sæther et al. 1996), such as relatively high and invariant adult female survival contrasted with low and variable breeding probability, and delayed maturity (Stearns 1992, Goudie et al. 1994). My thesis examined life history patterns of Common Goldeneyes (*Bucephala clangula*; hereafter goldeneye) in a nest box population near the northern limit of the breeding range in interior Alaska (Eadie et al. 1995).

My results suggest that goldeneyes exhibit life history traits are most consistent with bet-hedging species, which sharply differ from typical long-lived species by having high annual breeding probability, rather than intermittent annual breeding (Sæther et al. 1996). Though goldeneyes were previously thought to breed annually (Eadie et al. 1995), my thesis research is the first to directly model annual breeding patterns using modern maximum likelihood based approaches. As such, the consistent annual breeding pattern I observed suggests that assumptions of no temporary emigration required by standard CJS capture-mark-recapture studies can be met if sufficiently intensive capture efforts are used; specifically, the capture of females during both egg-laying and near hatch. This finding will inform managers of other capture-mark-recapture nest box studies as to which analytical tools may be appropriate, given their study design.

Furthermore, my thesis findings contrast with several traditional assumptions concerning goldeneyes. For example, average age at first breeding in goldeneyes was thought to be 3 years of age, though highly variable between 2-6 years-old, based on observations of first-time breeding attempts in known-age individuals that did not account for variation in detection probability (Eadie et al. 1995, Milonoff et al. 2002). My

thesis demonstrated that if age-related variation in detection probability is accounted for, individuals had a high probability of entering the breeding population beginning at 2 years of age ($0.96 \pm 0.01$), with no age-related variation.

Additionally, natal and breeding philopatry in goldeneyes has previously been assumed to be near 1 (Savard and Eadie 1999), due to a paucity of suitable nest sites for cavity-nesting species. In contrast, I detected substantial evidence for both immigration and emigration in our study population. I found that nesting densities during the year prior to first breeding (i.e. during nest prospecting, Eadie and Gauthier 1985) are negatively related to per-capita recruitment the following year. I also found that when adjusting for the proportion of marked ducklings in a given year on subsequent population growth, even under maximum marking effort (i.e. 100% of hatched ducklings marked) individuals that hatched outside of the study area continue to enter the study population. Furthermore, population growth rate based only on local recruitment under maximum effort was 0.69, which suggests that in the absence of immigration, our study population would decline.

Among sea ducks, goldeneyes are relatively well-studied, though a lack of demographic parameter estimates throughout their range, particularly from northern latitudes (Eadie et al. 1995, Schmidt et al. 2006), has precluded the construction of a population model (Sea Duck Joint Venture 2008). The demographic estimates presented here are among the first from their Alaska breeding range and will fill a void in our understanding of goldeneye population dynamics. Furthermore, this study is the first in goldeneyes to provide a comprehensive view of life history patterns and their associated tradeoffs using modern maximum-likelihood based approaches. Finally, this study is also

the first to directly evaluate the effects of immigration on population dynamics in goldeneyes, and will provide an avenue for managers of other nest box studies to identify sources of variation in study area population dynamics.

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