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BREEDING SEASON ECOLOGY AND DEMOGRAPHY OF LESSER SCAUP

(*Aythya affinis*) AT RED ROCK LAKES NATIONAL WILDLIFE REFUGE

by

Jeffrey M. Warren

A dissertation proposal submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Breeding Season Ecology and Demography of Lesser Scaup (*Aythya affinis*) at Red Rock

Lakes National Wildlife Refuge

by

Jeffrey M. Warren, Doctor of Philosophy

Utah State University, 2018

Major Professor: Dr. David N. Koons
Department: Wildland Resources

Decisions of if and when to breed, and how much to invest in raising offspring,

have implications for reproductive success and survival of both parent and offspring. Pre-

breeding body condition is an important determinant of breeding propensity and timing of

breeding in birds. For female lesser scaup (*Aythya affinis*), body condition gain on the

breeding grounds prior to breeding was strongly influenced by environmental conditions.

Pre-breeding periods with early phenology and lower water levels resulted in greater rates

of female body condition gain, independent of female age (though older females arrived

on the breeding grounds in better condition than yearlings). Moreover, after accounting

for lay date, the rate of body condition gain during the pre-breeding period was positively

correlated with clutch size ($\hat{\beta} = 0.08 \pm 0.039$), as predicted by the condition-dependent

optimization model. Breeding propensity was also positively influenced by body

condition ($\hat{\beta} = 0.032 \pm 0.005$) and habitat conditions, but not by age. Drought reduced the

proportion of breeding females to 0.85 (SE = 0.05) from 0.94 (SE = 0.03) during normal

water years. After accounting for capture date and body condition, females with evidence of reproductive success on the study site the prior year were more likely to breed ($\hat{\beta} =$ 1.55 ± 0.742), providing evidence of individual heterogeneity in the population that is attributable to factors other than immediate body condition. Demographic consequences of breeding were evident as a carry-over effect from breeding to non-breeding seasons, via a serial survival cost of reproduction. Breeding season water level, a demonstrated proxy for reproductive effort, was negatively correlated with female survival the subsequent non-breeding season, resulting in non-breeding season survival ranging from 0.492 (SE=0.042) following the wettest breeding season of the study (2011), to 0.969 (SE=0.003) following the driest (2007). Habitat conditions favorable to breeding may result in proportionally more females experiencing a constrained period of molt and body condition recovery prior to fall migration. Conversely, survival during the breeding season was positively correlated with breeding season water levels, i.e., a concurrent survival cost of reproduction was not found.

(168 pages)

PUBLIC ABSTRACT

Breeding Season Ecology and Demography of Lesser Scaup (*Aythya affinis*) at Red Rock

Lakes National Wildlife Refuge

Jeffrey M. Warren

It is hypothesized that individuals make reproductive decisions based on current assessments of their physiological condition and environmental conditions. For female lesser scaup (*Aythya affinis*), breeding occurs after an energetically costly spring migration. Increasing fat reserves (i.e., 'body condition') prior to breeding allows a female to produce a larger clutch of eggs, but time spent gaining body condition is costly in terms of time allowed to raise ducklings before freezing conditions in the fall. In Chapter 2 I explored rate of pre-breeding body condition gain in female lesser scaup, and how that rate influenced clutch size. Spring phenology, measured by proxy as water temperature, and water depth strongly influenced the rate at which females increased body condition. Early springs with low water levels led to greater rates of body condition gain in female scaup. The higher the rate of body condition gain, the larger the clutch of eggs females produced. Body condition is also an important determinant of breeding in female ducks; females in poor body condition are more likely to forego breeding. I explored how body condition, wetland conditions, and prior experience influence a female's decision to breed in Chapter 3. Body condition was a strong determinant of when a female bred, with females in good body condition breeding earlier than females in poorer body condition. Habitat conditions were also important, with drought reducing the proportion of breeding lesser scaup females. In Chapter 4 I examined survival costs of

reproduction in female scaup. Nesting exposes females to increased predation risk (a concurrent survival cost), and reduced post-breeding body condition may reduce female survival the subsequent non-breeding season (a serial, or 'downstream', survival cost). Female survival during breeding and non-breeding seasons was most correlated with breeding season water level on the study site, but in opposite directions. Breeding season survival increased with increasing water levels, while non-breeding season survival declined. High water levels on the study site increased the availability of presumably high-security nesting habitat, and also increased female reproductive effort. The former increased breeding season survival, while the latter reduced non-breeding season survival.

ACKNOWLEDGMENTS

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CHAPTER 1

INTRODUCTION

Migratory species utilizing seasonal environments face unique challenges in timing life-cycle events to optimize lifetime reproductive success. Individuals make multiple decisions during the breeding season regarding reproduction, each one with life history consequences. These include the decision to breed, and conditional on breeding, when to breed and the level of effort to invest in the current reproductive event. The decision to breed has potential future survival and fecundity consequences through its influence on an individual's physiological state and exposure to mortality risk (Nur 1984, Golet and Irons 1999, Magnhagen 1991, Low et al. 2010, Arnold et al. 2012). The timing of breeding has implications for fecundity across broad taxa, and is especially well documented in birds. Survival and recruitment of young from early-hatched nests is generally higher than later-hatching conspecifics (Hochachka 1990, Verboven and Visser 1998, Lepage et al. 2000, Blums et al. 2002, Elmberg et al. 2005), and clutch size generally decreases as lay date advances (Klomp 1970, Ankney and MacInnes 1978, Krapu 1981). Timing of breeding can also influence an individual's subsequent survival and fecundity, both of which are often lower in later nesting individuals (Verboven and Visser 1998, Blums et al. 2002, Blums et al. 2005).

Reproductive effort (*sensu* Trivers 1972) represents the total investment an individual makes in producing offspring, inclusive of offspring care for species that care for young. Similar to decisions of if and when to breed, reproductive effort influences an individual's fitness through impacts to future survival and fecundity. For example, female

mallards (*Anas platyrhnchos*) that tended broods to 60 days of age had lower annual survival than females that did not hatch a nest (Arnold and Howerter 2012), while experimentally-reducing reproductive effort during chick-rearing increased fecundity the subsequent year in long-lived seabirds (Catry et al. 2013, Fayet et al. 2016). I consider each of these decisions, in turn, for a long-distance migratory species with an intermediate lifespan, lesser scaup (*Aythya affinis*).

The continental population of scaup (lesser and greater [*A. marila*] scaup combined) reached an all-time low in 2006 of 3.2 million birds, the nadir of an approximately three decade continental decline and nearly two million birds below the North American Waterfowl Management Plan (NAWMP) goal of 5.0 million birds (U.S. Fish and Wildlife Service 2016). Lesser scaup account for 89% of the continental scaup population, and are the most ubiquitous and numerous North American diving duck (Afton and Anderson 2001, Anteau et al. 2014). Two reviews of long-term data sets noted a decrease in the sex and age ratios (number of females relative to males and number of immatures relative to adults, respectively) of lesser scaup in the U.S. harvest (Allen et al. 1999, Afton and Anderson 2001). These results indicated recruitment and female survival of lesser scaup declined concurrent with the population decline. Although the scaup population has rebounded recently, reaching the continental population objective in 2012 and 2016, factors that influence recruitment and female survival are still of interest to elucidate potential drivers of the historic decline and guide future conservation efforts.

The expansive breeding range of lesser scaup (roughly two-thirds of the continental population breeds in the boreal forest of Alaska and Canada; Afton and

Anderson 2001) challenges the utility of inference from a single study site at the southwestern extent of the species' breeding range. The study area in southwestern Montana were the work within this dissertation was conducted is a large (2,332 ha) high-elevation (2,014 m above mean sea level) shallow lake/wetland complex that supports a relatively high breeding density of lesser scaup (>7.7 breeding pairs km^{-2}). Although on the southern extent of scaup breeding range, the study site has one of the harshest and most variable breeding season environments in North America, as measured by growing-season length (Gurney et al. 2011). Moreover, the extensive matrix of seasonally-flooded sedge (*Carex* spp.) interspersed with shallow open-water ponds within the study site is structurally similar to important breeding areas for lesser scaup in Alaska (Yukon Flats and Tanana-Kuskokwim basin), the Yukon (Old Crow Flats), and the Northwest Territories (Mackenzie River Delta) (Baldassarre 2014). Lastly, scaup that breed on the study site winter in areas that support approximately 60% of the continental population of scaup.

Pre-breeding body condition is an important determinant of reproductive success in birds, largely through its influence on the decision to breed, and subsequently, timing of breeding. Females in good body condition are more likely to breed (Devries et al. 2008, Gorman et al. 2008, Martin et al. 2009), initiate nesting earlier (Bêty et al. 2003), and produce larger clutches (Ankney and MacInnes 1978, Krapu 1981). The importance of body condition is compounded by the positive relationship between hatch date and recruitment commonly observed in birds (e.g., Dawson and Clark 2000). A trade-off exists, therefore, between investing time increasing body condition to produce more young (i.e., larger clutches) and initiating breeding activities to produce higher-quality

young (i.e., earlier hatch date). Known as the cost-of-delay hypothesis, the influence of reproductive timing on the trade-off between more young and higher quality young appears nearly ubiquitous among bird species (Rohwer 1992). This hypothesis was formalized into a mathematical model that defines an 'optimal switch curve', i.e., when a female should transition from gaining body condition to clutch formation, conditional on a female's 1) body condition upon arrival at the breeding grounds, 2) rate of body condition gain, and 3) day of the nesting season (Rowe et al. 1994). In Chapter 2, I test predictions of the cost-of-delay hypothesis while simultaneously examining factors that influence female rate of body condition gain during the pre-breeding season.

The decision to breed has obvious consequences for an individual's reproductive success, both immediately and over their lifetime (Blums and Clark 2004), and the proportion of individuals that breed (i.e., breeding propensity) has clear population-level implications. However, little information exists regarding breeding propensity in vertebrates (Reed et al. 2004), and scaup are no exception (but see Devink et al. 2008, Martin et al. 2009). Age and experience are two commonly cited drivers of breeding propensity in iteroparous species, with young, less experienced individuals often breeding at lower rates than older, more experienced conspecifics (Curio 1983, Clutton-Brock 1988, Newton 1989, Cam and Monnat 2000). Variation in breeding propensity is often most pronounced when environmental conditions are not favorable for reproduction, consistent with state-dependent life history theory (McNamara and Houston 1996). This is particularly pronounced in long-lived species that are more likely to have a conservative reproductive strategy, i.e., one that favors adult survival over the current reproductive event (Williams 1966, Charlesworth 1980). For example, poor foraging

conditions have been linked to nonbreeding in adult seabirds (Brandt's cormorant

(*Phalacrocorax penicillatus*), Boekelheide and Ainley 1989; common shag (*P.*

aristotelis), Aebischer and Wanless 1992; snow petrel (*Pagodroma nivea*), Chastel et al.

1995; Arctic terns (*Sterna paradisaea*), Monaghan et al. 1992; and black-legged

kittiwakes (*Rissa tridactyla*), Hamer et al. 1993), and the extent and timing of spring

snowmelt is a strong determinant of breeding propensity in Arctic-nesting geese (Prop

and de Vries 1993, Reed et al. 2004). Individual quality is also an important driver of

breeding propensity, with high-quality individuals surviving and breeding at higher rates

than low-quality conspecifics (Cam et al. 2002, Kennamer et al. 2016). In Chapter 3, I

examine factors influencing breeding propensity in lesser scaup females, including

environmental conditions, age, and body condition. Using stable isotope analysis, I also

test for individual heterogeneity by assessing if females that molted on the site the prior

year, a proxy for prior reproductive success, were more likely to breed the following

year.

Beyond the decision to breed, the level of investment (i.e., reproductive effort) an

individual makes in the current reproductive event may be the reproductive decision with

the greatest influence on future survival and fecundity. In Chapter 4, I examine within-

and among-season survival costs of reproduction using a ten-year data set of uniquely-

marked females and multi-state capture-mark-recapture models. Survival costs of

reproduction may occur concurrently with a given reproductive activity, or in a serial

manner where an individual survives the reproductive event but is in a reduced

physiological condition that influences future survival or fecundity, i.e., a carry-over

effect (COE) from breeding to a subsequent season. Concurrent survival costs of

reproduction are well documented, especially in ground-nesting birds. Increased mortality risks associated with clutch formation and nest attendance can lead to female-biased mortality during the breeding season in ground-nesting birds (Grüebler et al. 2008, Perlut et al. 2008), and habitat conditions favorable to breeding in ducks are negatively related to female breeding season survival, both providing evidence of concurrent survival costs of reproduction (Arnold and Clark 1996, Rotella et al. 2003, Devries et al. 2003, Arnold et al. 2012). Carry-over effects have also repeatedly been found, although most commonly as fecundity effects of winter habitat conditions on reproduction (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Saino et al. 2004, Norris et al. 2004, Gunnarsson et al. 2005, Lehikoinen et al. 2006, Guillemain et al. 2008, Rockwell et al. 2012, Osnas et al. 2016), or fecundity effects of prior reproduction (Hanssen et al. 2005, Catry et al. 2013, Fayet et al. 2016).

Few studies have documented COEs as a survival cost of reproduction from breeding to wintering periods (but see Daan et al. 1996, Blomberg et al. 2013), although decreased post-breeding physiological condition provides a mechanism for this. Waterfowl undertake a complete post-breeding molt, leaving them flightless for a brief period (Hohman et al. 1992). For females, this period can be delayed by breeding activities (Lessells 1986), resulting in a reduced amount of time available to complete molt and regain body condition prior to autumn migration. On my study site, this period is coincident with the lowest observed body condition for females (Stetter 2014). Individuals in poor condition during molt produce lower-quality feathers that lead to higher thermoregulatory costs the subsequent winter (Nilsson and Svensson 1996). Moreover, birds with elevated stress during molt, as measured by feather corticosterone

levels, have reduced survival (Harms et al. 2014, Latta et al. 2016). Therefore, individuals that invest more in the current reproductive event may put themselves at a physiological disadvantage prior to two metabolically-expensive annual events, molt and migration, and pay a survival cost of reproduction the subsequent season. In chapter 4, I explore COEs from breeding to non-breeding seasons as a function of reproductive effort, measured by proxy with breeding habitat conditions and directly with several measures of reproductive success. I also assess the relative role of intra- versus among-seasonal drivers of mortality for females to elucidate the strength of breeding-season COEs by concurrently testing harvest metrics as predictors of non-breeding season survival.

Scaup are intermediate in the spectrum between long- and short-lived species, which should also result in an intermediate response to reproductive risk. Based on residual reproductive value, long-lived species are generally conservative risk takers that hedge their bets against environmental uncertainty, while short-lived species should maximize risks that benefit reproductive success relative to survival costs (Williams 1966, Charlesworth 1980). However, there is a predicted threshold of breeding conditions for long-lived birds where a steep increase in reproductive effort and decrease in adult survival occur (Erikstad et al. 1998). Increased investment in reproduction when recruitment probability is highest should occur in species with low and variable offspring survival because of recruitment's greater influence on fitness than the number of breeding attempts (Gaillard et al. 2000). Recruitment is generally low for *Aythya* females, and reproductive effort varies strongly with environmental conditions (Rogers 1964, Afton 1984, Dawson and Clark 2000, Anderson et al. 2001, Blums and Clark 2004, Warren et al. 2014), corroborating the idea that scaup should be willing to take significant survival

risks when breeding conditions are favorable. This would predict greater breeding propensity and reproductive effort when breeding habitat conditions are good, at the potential expense of concurrent or carry-over survival costs, predictions I explored in Chapters 3 and 4, respectively. Collectively, Chapters 2–4 provide unique insights into life-history strategies of a long-distance migrant with intermediate lifespan, ranging from individual quality (i.e., body condition, prior reproductive success) and environmental (e.g. wetland conditions) influences on decisions of if and when to breed, to survival costs of reproductive effort manifested as a COE to the non-breeding season.

The concept of 'individual quality' as a source of observed heterogeneity among individuals is used throughout subsequent chapters. Individual quality is difficult to define, but generally is viewed as variation among individuals that is positively correlated with fitness (Wilson and Nussey 2010). This should therefore result in 1) high quality individuals surviving and reproducing at greater rates than low quality conspecifics, and 2) the potential for individual quality to mask costs of reproduction. In chapters 2 and 3, I use body condition as a measure of individual quality. This assumes that body condition as a trait is positively related to fitness, i.e., all else being equal, individuals with higher body condition should also have higher fitness. In chapter 4, I posit variation in individual quality as a potential mechanism for the documented relationship between breeding season habitat conditions and non-breeding season survival. I do not, however, attempt to quantify individual quality in this chapter. Further work would be necessary to test the hypothesis that the observed negative relationship between breeding season habitat conditions and female non-breeding season survival results from a higher

proportion of low-quality females breeding when breeding season conditions documented to increase reproductive effort in scaup on our study site occur.

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CHAPTER 2

BODY CONDITION DYNAMICS AND THE COST-OF-DELAY HYPOTHESIS IN A

TEMPERATE-BREEDING DUCK[1]

Abstract

Pre-breeding body condition is an important determinant of reproductive success in birds, largely through its influence on timing of breeding. Declines in clutch size and recruitment probability within breeding seasons indicate a trade-off may exist between the number of young (clutch size) and quality of young (recruitment probability). We explored local drivers of pre-breeding body condition and tested predictions of the cost-of-delay hypothesis in female lesser scaup (*Aythya affinis*). Yearling females arrived on the study site in lower body condition than older females, but both age classes had similar rates of body condition gain on the breeding grounds prior to nesting. Rates of body condition gain were positively influenced by water temperature, a proxy for wetland phenology. The effect of water level was asymptotic and interacted with water temperature, with greater rates of gain in body condition occurring in years with low water levels. Our results supported the predicted response of clutch size to the rate of pre-breeding body condition gain. After accounting for lay date, clutch size was positively related to the rate of body condition gain ($\hat{\beta} = 0.08 \pm 0.039$). We did not find support for a predicted interaction between rate of body condition gain and intra-seasonal decline in clutch size ($\hat{\beta} = 0.01 \pm 0.01$). Our results indicate that local conditions during pre-

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breeding influence body condition dynamics in female lesser scaup, which subsequently affects clutch size.

Introduction

Early birds get not only the worm, but generally have higher reproductive success as well. Survival and recruitment of young hatched from early nests are generally higher than from nests of later breeding conspecifics (Hochachka 1990, Verboven and Visser 1998, Lepage et al. 2000, Blums et al. 2002, Elmberg et al. 2005). Moreover, females that nest earlier generally produce larger clutches (Klomp 1970, Ankney and MacInnes 1978, Krapu 1981). However, few females actually nest early when fitness advantages could be greatest (Lack 1968, Perrins 1970). Strong correlations between body condition, the timing of reproduction, and clutch size in birds indicate that many females may be incapable of nesting early due to inadequate body condition (Dijkstra et al. 1988, Pietiäinen and Kolunen 1993, Devries et al. 2008). Instead, many females face a trade-off between delaying breeding to increase their body condition and potential for a larger clutch, versus breeding earlier in lower body condition and producing fewer, but potentially higher-quality offspring (Drent and Daan 1980). Known as the cost-of-delay hypothesis, the influence of reproductive timing on the trade-off between more young and higher quality young appears nearly ubiquitous among bird species (Rohwer 1992).

Rowe et al. (1994) formalized the cost-of-delay hypothesis in a dynamic mathematical model, facilitating the testing of predictions. In doing so, they defined how a female can maximize individual fitness potential using an "optimal switch curve" (Rowe et al. 1994; Fig. 2-1). The optimal switch curve essentially defines the balance

between the competing values of producing an additional egg versus the likelihood that the egg will successfully produce a recruit. Assuming similar rates of gain in body condition, a female in better initial condition would initiate a nest sooner, producing a larger clutch earlier than a female whose initial condition was lower. Similarly, years in which relatively early nesting occurs in a population are predicted to have larger mean clutches than years in which nesting is delayed. Changes in the rate of body condition gain move the optimal switch curve to the right (increased rate of gain) or left (decreased rate of gain) (Fig. 2-1). Greater rates of gain in body condition result in larger clutches regardless of timing of nesting; lesser rates of gain result in the opposite.

The rate of gain in body condition, and thus the time at which a female will initiate nesting, is likely influenced by the interplay between an individual's age, experience and local environmental factors that determine foraging opportunities. Little direct evidence is available to determine if more experienced individuals have greater rates of gain in body condition than less experienced individuals. More experienced individuals do, however, generally arrive earlier on the breeding grounds, initiate nesting earlier, and produce larger clutches (Birkhead et al. 1983, Sydeman et al. 1991, Devries et al. 2008). Moreover, females commonly increase somatic lipid reserves after arrival on the breeding ground prior to nest initiation (Alisauskas and Ankney 1992), even in species with relatively short periods of time between arrival and nest initiation (e.g., Arctic nesting geese; Budeau et al. 1991, Fox et al. 2006). Environmental conditions on the breeding grounds that influence the ability of females to increase body condition may therefore play an important role in an individual's reproductive success. For example, the influence of snow cover on forage availability has repeatedly been implicated as a driver

of reproductive success in Arctic nesting geese (Barry 1962, Prop and de Vries 1993). Reduced availability of forage resources on the breeding grounds would limit the ability of females to improve or maintain body condition during the period between arrival and nest initiation for these species. Studies have demonstrated both local influences of environmental conditions on reproductive success, and significant increases in body condition on the breeding grounds, but few have explored drivers of gain in body condition during pre-breeding periods (e.g., Mainguy et al. 2002) and how these may simultaneously affect clutch size via cost-of-delay predictions.

Lesser scaup (*Aythya affinis*; hereafter scaup) are one of the latest nesting North American ducks (Bellrose 1980). The prolonged period on the breeding grounds prior to nesting, which can be in excess of a month (Afton 1984, J. M. Warren unpubl. data), provides females considerable opportunities to improve body condition prior to nesting. Scaup utilize somatic reserves for clutch formation (Afton and Ankney 1991, Esler et al. 2001), with a significant proportion of those reserves locally acquired (Warren and Cutting 2011, Cutting et al. 2012). Early nesting scaup also recruit more young than later nesting conspecifics (Dawson and Clark 2000). A prolonged pre-breeding period, reliance on somatic reserves derived from local resources for clutch formation, and a seasonal decline in recruitment make lesser scaup a particularly interesting species to explore body condition dynamics within the context of the cost-of-delay hypothesis.

We undertook the current study to: 1) explore within and among year dynamics of pre-breeding body condition in female lesser scaup, and 2) test predictions of the cost-of-delay hypothesis using mean body condition, nest initiation dates, and clutch sizes during

six years of study on a breeding population of lesser scaup in the southwestern extent of their range.

Hypotheses and predictions

Body condition dynamics

Primarily carnivorous during the breeding season, scaup forage heavily on amphipods (e.g., *Gammarus* spp. and *Hyalella* spp.) prior to and during clutch development (Rogers and Korschgen 1966; Afton and Hier 1991), which provides females with a great deal of protein and lipids. For example, lipid content of *G. lacustris*, the most common amphipod on our study site, peaks in spring and early summer around 15%, while protein content averages ≈ 40% (Mathias et al. 1982, Arts et al. 1995). The peak of lipid content in amphipods coincides with amphipod reproduction (Arts et al. 1995), which in turn is closely linked to water temperature (Smith 1973). We hypothesized that spring phenology would positively influence the abundance and quality of amphipods on the study site. Thus, our prediction was that mean scaup body condition would increase at a greater rate during springs with relatively early wetland phenology. We therefore predicted a non-linear pseudo-threshold relationship between water temperature and female body condition, given that amphipod reproduction peaks at temperatures similar to maximum water temperatures observed on the study site (Smith 1973). We similarly hypothesized that female body condition would be positively influenced by the availability of preferred foraging areas, i.e., shallow to intermediate depth (50–150 cm) open-water habitat (Torrence and Butler 2006). Higher water levels on the study site correspond to more of the open-water habitat on the study site within

the preferred depth for scaup, so we predicted a positive linear relationship between water

depth and mean body condition gain. Lastly, female experience is an important

determinant of spring body condition in female ducks (Peterson and Ellarson 1979,

Hohman 1986), with more experienced females often arriving on the breeding grounds in

better condition, initiating nests earlier, and producing larger clutches (Krapu and Doty

1979, Baillie and Milne 1982, Devries et al. 2008). Older females were therefore

predicted to be in better body condition and have greater rates of gain in body condition.

Cost-of-delay hypothesis

Based on the cost-of-delay hypothesis, we made two predictions regarding the

relationship between the rate of gain in body condition and clutch size. First, after

controlling for timing of breeding, years with higher rates of gain in body condition were

predicted to have larger clutches. Higher rates of gain in body condition shift the optimal

switch curve to the right (Fig. 2-1), resulting in all females having larger clutches than at

lower rates of gain. Second, the slope of the switch curve should change with varying

rates of body condition gain (e.g. Rowe et al. 1994; Fig. 2-1). After controlling for timing

of breeding among years, we predicted that years with steeper rates of gain in body

condition on the breeding grounds would have steeper declines in clutch size as the

season progresses, assuming a relatively constant decline in offspring quality among

years.

Methods

Data collection

      This study was conducted on Lower Red Rock Lake (Lower Lake) in southwest

Montana (Fig. 2-2). Lower Lake is a large (2,332 ha), high elevation (2014 m above

mean sea level) wetland encompassed by Red Rock Lakes National Wildlife Refuge

(Refuge). Water depths typically do not exceed 1.5 m during the nesting season, with

large open water areas interspersed with hardstem bulrush (*Schoenoplectus acutus*)

islands. Nearly half of the area is extensive stands of seasonally flooded Northwest

Territory sedge (*Carex utriculata*) that contain small (<2 ha), scattered open water areas.

Average annual precipitation is 49.5 cm with 27% occurring during May and June. Annual

average temperature is 1.7ºC. The study site has one of the harshest, and most variable,

breeding season environments utilized by lesser scaup as measured by growing season length

(Gurney et al. 2011).

      Female lesser scaup were captured via spotlighting for 3–6 nights during each

new moon phase during the months of May – June, 2006–2011. Captures occurred on 34

different calendar dates among all years between 9 May – 23 June (overall median nest

initiation date). Females were banded with a US Geological Survey aluminum leg band

and aged (AGE) (second year [SY] or after second year [ASY]) based on eye color

(Trauger 1974). Each female's body mass (nearest 5 g), and tarsus (± 0.1 mm), head (±

0.1 mm), and flattened wing chord (± 1 mm) lengths were recorded.

      Nest searches were conducted within *Carex* spp. dominated habitats on the study

site each year. Scaup nests were located using observational cues of females and trained

dogs during two searches completed between late May and mid-July. Daily searches were conducted between 0600 and 1300 hours; nests found incidentally while conducting other field work were included. When nests were located the number of eggs and incubation stage, as determined by field-candling (Weller 1956), were recorded. Nest initiation date (INIT) was estimated by subtracting the number of eggs and days of incubation from the current date and adding 1 day. Clutch size was recorded for each nest where evidence of incubation was present, but denoted as 'unknown' for nests where intra- or interspecific nest parasitism was evident.

We also quantified spring habitat conditions on the study site each year. A capacitance probe water level and temperature data logger (model WT-HR 1500; TruTrac, Christchurch, New Zealand) was deployed each year in April at the western outflow of Lower Lake. Water levels ($\pm$ 0.1 mm) and temperatures ($\pm$ 0.1°C) were recorded hourly throughout the breeding season. To explore relationships between female body condition and spring phenology and wetland water conditions, we calculated mean water temperatures (TEMP) and levels (LVL) for each day captures occurred. This was done by averaging hourly temperature and level measurements for each capture day and preceding 10 days' data.

Analysis

Our analysis consisted of two primary aspects. First, we explored female body condition dynamics in response to habitat attributes and female age using mixed-effects models. These data were obtained from females captured during the pre-breeding period. Few females were captured more than once, so our analysis explored general patterns in

body condition observed for the breeding population studied. Second, we tested the cost-of-delay hypothesis using the relationship between predicted annual rate of body condition gain and clutch size within and among years.

Female body condition was estimated as a size-adjusted body condition index (BCI) calculated for each female. A principal component analysis was conducted using female head and tarsus measurements, and female body mass was regressed on the first principal component. The resulting regression residual for each female was used as the BCI (e.g., Devries et al. 2008). Negative BCI values indicate females that have a lower than average mass for a given structural size, and positive values indicate the opposite.

Mixed-effects models were used to explore breeding season dynamics of female body condition (package nlme in R 2.15.1; R Development Core Team 2013). We began with a mixed-effect model with a response of female body condition (BCI), fixed-effect interactions among TEMP, LVL, and AGE, and a random intercept for YEAR. TEMP was log-transformed to account for the predicted asymptotic relationship between condition gain and water temperature. Non-significant ($\alpha > 0.10$) fixed-effect parameters were removed in a backwards-stepwise process from the model. Models were fit using restricted maximum likelihood estimation and ranked based on values of Akiake's Information Criterion (AIC; Burnham and Anderson 2002). Residual diagnostic plots from the selected model were used to test for violation of normality and homogeneity (Zuur et al. 2009).

Including YEAR as a random effect provides several benefits. First, we don't assume years are independent and comprise all of the factor levels of interest. Instead, the effect of year is treated as a random variable, with individual year effects realizations of

that distribution. This allows inference to non-sampled factor levels, i.e., years, and acknowledges that different values would be expected if the study were repeated (Kéry 2010). Second, because year effects are not treated as independent, estimated effects of year on the rate of body condition gain are dependent on all factor levels, leading to greater precision when estimating individual year effects (Kéry 2010). This can be contrasted with year as a fixed effect where each year's factor level is estimated independent of information from the other years in the sample, which could lead to bias in our results with variation among years in female arrival and initial capture dates. For example, if the timing of first captures within a year occurred shortly after arrival a higher proportion of early arriving females in better body condition may have been sampled. Conversely, if initial captures occurred relatively later in the spring more late-arriving females of poorer body condition would be available for sampling. This could lead to differences in the rate of body condition change among years due to sampling. Including year as a random factor reduces the risk of that bias by assuming an underlying population-level process of body condition gain that varied randomly among years. Moreover, the timing of captures was such that most females on the site were available for sampling during both capture occasions each year. Uniquely marked scaup females were detected at a consistent and high level (probability of detection, p, approximately 0.77) during surveys conducted mid-May 2006–2008 on the study site (JM Warren unpubl. data), indicating most females had arrived on the site prior to surveys. Additionally, females marked on the study site in 2009 ($n = 6$) with satellite transmitters all returned the following spring on or before 8 May.

We tested for differences among years in clutch size and nest initiation using single factor ANOVA. To test our predictions regarding the response of clutch size to rate of gain in body condition, we used a mixed-effect model with YEAR as a random effect and a fixed-effect structure of standardized nest initiation date (INIT) and the estimated slope of gain in body condition for each year (BCRate). An interaction was included between INIT and BCRate to test our second prediction of steeper seasonal declines for clutch size in years with greater rates of gain in female body condition.

Results

Spring phenology and wetland conditions varied considerably among years during our study. Mean water temperature from 1 May–15 June varied from a low of 7.4°C (SD = 9.8) in 2008 to a high of 14.4°C (SD = 3.0) in 2007 (Table 2-1). Water levels similarly varied from the drought year of 2007 at a level of 2013.6 m above mean sea level (msl) (SD = 0.29) to 2014.2 m above msl in 2006 and 2011 (SD = 0.04 and 0.06, respectively) (Table 2-1). The difference between these years, 0.6 m, represents an approximate halving of mean water depths across the study area between the drought year of 2007 and 2006 and 2011.

We captured 266 females during 2006–2011 that were included in the analysis of body condition dynamics. This sample of individuals from the site included females that were breeding (i.e., egg in the oviduct determined by palpation). Variation in the proportion of breeding females captured among years could bias results, especially during periods of poor wetland conditions when the proportion of breeding females declines and early emigration from breeding areas occurs (Rogers 1964, Afton 1984). We tested for a

difference in the proportion of breeding females in the sample among years using a generalized linear model, log link, and binomially-distributed errors. After accounting for capture date, the proportion of breeders in the sample did not differ among years except 2009, which had fewer breeders captured ($\hat{\beta}_{2009}$ = -1.71, P = 0.06). Mean proportion of breeders captured by year was 0.19, 0.19, 0.0, 0.24, 0.38, and 0.0 for 2006 – 2011, respectively.

The first principal component explained 74% of the variation in female head and tarsus measurements; PCA values ranged from -4.3 to 3.6 (structurally largest to smallest females, respectively). Female body mass was correlated to structural size with structurally larger females being heavier than smaller females, but considerable variation was not explained by the relationship ($\hat{\beta}$ = -17.4, P < 0.001, adjusted R^2 = 0.08). Body condition index values ranged from -206.0 to 193.6, with a mean of 0.06 (SD = 69.0). Assuming a linear relationship between body condition and calendar date, female body condition increased an average of 2.2 index points per day (SE = 0.25) amongst all years of study; this equates to a female of average structural size gaining 2.2 g of mass per day during the pre-breeding period until peak nest initiation. This is corroborated by a small number of individuals (n = 4) that were captured twice within a year – mean mass gain of these females was 2.03 g day^{-1} from mid-May to mid-June.

The best model of female body condition supported our prediction regarding gain in body condition and spring phenology. Mean female body condition increased non-linearly with water temperature, but the relationship was dependent upon water level (i.e., an interaction) such that gains were greatest at lower water levels on the study site, contrary to our prediction regarding the response of body condition gain to water depth

(Table 2-2). The interaction between water temperature and level indicated females had a higher rate of gain in body condition during years with low water. For example, an adult (ASY) female was predicted to have a BCI of -103.6 at 8°C water temperature and a low water level (2013.5 m msl). Increasing water temperature to 18°C increased the predicted BCI to 61.2. However, the same change in water temperature with a high water level (2014.2 m msl) resulted in a narrower range of change in BCI from 6.2 to 81.5 in ASY females. The rate of female body condition gain did not differ based on age class (i.e., interaction terms with AGE had P values > 0.50), however yearling females did have lower mean body condition ($\hat{\beta}_{SY}$ = -27.4, P = 0.001; Fig. 2-3). Graphical tests of normality and variance homogeneity did not indicate violations of these assumptions.

A total of 261 nests were located during the study for which clutch size was determined, ranging from 22 nests found in 2011 to 58 found in 2008. The earliest nest initiation date observed was 22 May 2006, and the latest was 21 July 2011. Mean clutch sizes varied significantly among years ($F_{5, 255}$ = 11.46, P < 0.01) with 2011 having the smallest clutches and 2007 the largest (Table 2-3). Similarly, initiation dates differed among years ($F_{5, 255}$ = 17.15, P < 0.01). Mean nest initiation varied 20 days during the six years studied, with the earliest (2007) and latest (2011) years having the largest and smallest clutch sizes, respectively (Table 2-3). However, peak nest initiation occurred within three days for four of the years studied. Estimates of clutch size and initiation date for 2011, the latest nesting year, may have been biased by second nesting attempts as water levels on the study site rose throughout the normal period of nesting for lesser scaup and some nest flooding was observed.

We found mixed support for our predictions based on the cost-of-delay hypothesis. After accounting for initiation date, annual mean clutch size was positively influenced by the rate of gain in female body condition after arrival (Table 2-4). Conversely, after accounting for initiation date, intra-annual declines in clutch size were not related to the rate of body condition gain (Table 2-4).

Discussion

Body condition dynamics

An individual's body condition during the pre-breeding period strongly influences the timing of breeding in birds (see reviews in Drent 2006, Nager 2006), an important determinant of reproductive success (Rohwer 1992). Few studies, however, have explored local drivers of body condition gain during the pre-breeding period. Our results indicate wetland phenology and water conditions are strong drivers of body condition in female lesser scaup during the pre-breeding period. We found that the rate of body condition gain in lesser scaup was positively influenced by water temperature, a strong proxy for wetland phenology. Earlier wetland phenology may provide greater foraging opportunities for female scaup through higher abundance of invertebrate prey.

The influence of wetland phenology on the rate of body condition gain in female scaup was nevertheless dependent upon the water level of the study site. Deeper levels weakened the relationship between body condition gain and water temperature, resulting in lower rates of body condition gain across the range of temperatures experienced during the study. This is not altogether surprising given that water temperature increases more slowly during high water periods than during low water levels, influencing wetland

phenology and invertebrate abundance. Conversely, low water levels could concentrate important prey items, providing for better foraging efficiency and greater rates of body condition gain. Water level recession has been demonstrated to positively influence reproductive success in wading birds, with a proposed mechanism of increased foraging efficiency through concentration of prey (Kahl 1964, Frederick and Collopy 1989). The lower water levels observed during this study did not reduce the surface area of open water available to pre-breeding females, but instead reduced the overall volume of water. Decreased depth of the water column could concentrate aquatic invertebrates, important prey items for pre-breeding lesser scaup (Rogers and Korschgen 1966, Dirschl 1969, Afton and Hier 1991). Low water levels experienced on the site during this study occurred during periods of regional (i.e., Intermountain West) drought, and females were predicted to have lower body condition upon arrival during these years. The effect of drought on lesser scaup during the breeding season is marked by reduced breeding propensity and early emigration from breeding areas. (Rogers 1964, Afton 1984). Therefore, the observed pattern of greater rates of body condition gain during low water periods could occur if the proportion of breeding females captured on the site was higher during drought years because non-breeding females emigrated from the site prior to peak nest initiation. This would bias estimated rates of body condition gain high relative to non-drought years. We did not find support for this; after accounting for capture date there was not a significantly higher proportion of breeding females in our sample during low water years (i.e., 2007 and 2010).

In migratory birds, older females tend to arrive on the breeding grounds in better body condition (Hohman 1986, Baillie and Milne 1982, Devries et al. 2008). We

similarly found that older females were in better body condition on the breeding grounds at the beginning of the pre-breeding period. However, we did not find evidence that older females had a higher rate of body condition gain during the pre-breeding period than yearling females. This relationship indicates that experience may play a greater role in body condition dynamics prior to arrival, rather than while present, on the breeding grounds. Based on satellite-transmitter marked females ($n = 6$), scaup tend to migrate in a counter-clockwise pattern from the study site to wintering grounds and back (J. M. Warren unpubl. data). Therefore, yearling females may be using spring staging habitats for the first time prior to arrival on the breeding ground, while older individuals would have had previous experience on spring staging habitats. Conversely, yearling females philopatric to their natal area would be utilizing familiar habitat upon return to the breeding grounds. This could result in the observed pattern of lower initial body condition of yearling females relative to older females, but similar rate of body condition gain between the two age classes once on the breeding grounds. Lower initial body condition but similar rates of body condition gain on breeding grounds would similarly lead to consistent differences in body condition during the breeding season between yearling and older females (Krapu and Doty 1979, Krapu 1981).

Cost-of-delay hypothesis

The cost-of-delay hypothesis views the timing of reproduction in birds as a tradeoff between nesting early to produce higher quality young or later to produce a larger clutch (Drent and Daan 1980). Our study provides a unique opportunity to test the cost-of-delay hypothesis, as formalized by Rowe et al. (1994), with respect to the

influence of mean body condition gain on clutch size. After controlling for timing of nest initiation, clutch size was positively related to the rate of body condition gain in lesser scaup. The observed trend followed the prediction regarding the influence of the rate of body condition gain on clutch size; an increase in the rate of body condition gain should result in an increase in the optimal clutch size (Reynolds 1972, Drent and Daan 1980, Rowe et al. 1994). The relationship between the rate of body condition gain and clutch size indicates females are likely responding to local conditions and 'fine-tuning' the timing of breeding. Much of the work regarding pre-breeding body condition influences on breeding in waterfowl have focused on condition of individuals on spring staging areas (e.g., Fox et al. 2006) or shortly after arrival to the breeding grounds (e.g., Devries et al. 2008). This emphasis is well warranted given the considerable reliance on somatic reserves for fueling reproduction and the timing of breeding in most temperate and Arctic nesting waterfowl (Alisauskas and Ankney 1992). Lesser scaup, however, spend a protracted amount of time on the breeding grounds prior to nesting (Afton 1984, this study), and can acquire considerable somatic reserves during this time. Therefore, local conditions on breeding grounds prior to nesting for scaup may be important determinants of the quality (timing) and quantity (clutch size) of a female's reproductive efforts.

Although the intra-seasonal decline in clutch size is quite ubiquitous in birds, considerable variation in the rate of decline among species, populations, and years occurs. For example, greater scaup (*Aythya marila*) clutch size decline was similar among years in a 10 year study conducted in western Alaska (Flint et al. 2006). Mallard (*Anas platyrhynchos*), gadwall (*Anas strepera*), and blue-winged teal (*Anas discors*) clutch size declines were similarly consistent among six years of study in the Prairie Pothole Region

(PPR) (Lokemoen et al. 1990). Conversely, a subsequent study in the PPR found that gadwall and teal, but not mallard, rates of clutch size decline did vary among years (Krapu et al. 2004). Significant differences among years in intra-seasonal clutch size decline were also observed in Arctic-nesting black brant (*Branta bernicla nigricans*) (Lindberg et al. 1997). However, none of the aforementioned studies examined clutch size decline as influenced by rate of body condition gain, making it impossible to directly test Rowe et al.'s (1994) predictions regarding this relationship. Our results, similar to others that found consistent clutch size declines among years, suggest a stronger influence of ultimate (e.g., seasonal decline in quality of young), rather than local, factors on intra-seasonal declines of clutch size for some species. Rowe et al.'s (1994) model of individual optimization implicitly assumes females can recognize, and respond to, local cues such as rate of body condition gain during the pre-breeding period. Among-year variation in clutch size decline provides support for this assumption (e.g., Lindberg et al. 1997). A consistent rate of clutch size decline among years would occur if the timing of clutch formation was triggered by a threshold of body condition dependent upon date, but independent of local cues such as rate of body condition gain. A relatively inflexible strategy such as this is corroborated by observed patterns in scaup. Breeding in scaup is initiated during a narrow window of time across a broad range of latitude and elevation (DeVink et al. 2008, Gurney et al. 2011), a possible product of strong heritability of nest initiation date (Findlay and Cooke 1982). If timing of breeding is the sum of heritable nest initiation date and nonheritable influences of body condition and environmental factors (*sensu* Price et al. 1988), then the latter would appear to have the weakest influence on timing of breeding, and thus clutch size, in scaup. Without information on

heritability of breeding traits, which we lack, it is not possible to test this hypothesis directly. Conversely, local environmental factors were closely linked to the rate of body condition gain in female scaup during this study.

The role of body condition on the timing of, and investment in, clutch formation has long been a topic of interest among ornithologists and ecologists. The influence of body condition on reproductive success underscores the need for a thorough understanding of this dynamic relationship. Our results indicate a strong influence of local drivers on body condition gain in females during the pre-breeding period. Moreover, clutch size was positively related to the rate of body condition gain in females as predicted by Rowe et al. (1994). However, we did not find strong support for the predicted response of clutch size decline to varying rates of body condition gain. Work similar to ours, but at the level of individuals, would provide greater insight into the patterns observed during this study.

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Tables and figures

Table 2-1. Pre-breeding period (1 May – 15 June) mean water temperature and lake level on the Lower Red Rock Lake study area during 2006–2011. Standard deviations are presented parenthetically.

Year	Mean Temperature (°C)	Mean Level (m msl)
2006	12.0 (3.2)	2014.2 (0.04)
2007	14.4 (3.0)	2013.6 (0.29)
2008	7.4 (9.8)	2014.1 (0.48)
2009	11.5 (6.8)	2014.0 (0.45)
2010	8.9 (7.1)	2013.9 (0.58)
2011	13.5 (8.6)	2014.2 (0.06)

Table 2-2. Coefficient estimates, standard errors (SE), and *P* values for covariates in the most parsimonious mixed-model for female lesser scaup body condition on the Lower Red Rock Lake study area. Covariates include age class (Age: SY or ASY), mean water temperature (TEMP) and level (LVL) on the study site for the 10 days preceding capture. A random intercept of year was included in the model, which has an estimated standard deviation of 30.87 (residual deviation = 60.91).

Model Parameter	$\hat{\beta}$	SE ($\hat{\beta}$)	*P*
Intercept	-1407.9	447.3	0.002
Age(SY)	-27.4	7.7	0.001
log(TEMP)	490.0	170.2	0.004
LVL	147.7	56.9	0.010
LVL:log(TEMP)	-48.0	22.0	0.030

Table 2-3. Mean clutch size and nest initiation dates for lesser scaup on the Lower Red Rock Lake study area during 2006–2011. Standard deviations are presented parenthetically.

Year	Clutch Size	Initiation Date
2006	7.0 (1.77)	173 (10.5)
2007	8.5 (1.23)	166 (7.9)
2008	8.4 (1.44)	175 (6.1)
2009	7.2 (1.23)	174 (8.6)
2010	8.2 (1.37)	174 (9.5)
2011	6.7 (2.00)	186 (8.8)

Table 2-4. Coefficient estimates, standard errors (SE), and *P* values for mixed-models exploring relationships between clutch size and rate of body condition gain for female lesser scaup on the Lower Red Rock Lake study area, 2006–2011. Covariates include standardized nest initiation date (INIT) and population-level rate of body condition gain (BCRate). A random intercept of year was included in the model, which had an estimated standard deviation of 0.618 for the additive model and 0.623 for model containing the interaction (residual deviation 1.30 for both models).

Model Parameter	$\hat{\beta}$	SE ($\hat{\beta}$)	*P*
Intercept	5.29	1.12	<0.001
INIT	-0.76	0.08	<0.001
BCRate	0.08	0.04	0.093
Intercept	6.31	1.12	<0.001
INIT	-1.04	0.35	0.002
BCRate	0.08	0.04	0.097
INIT*BCRate	0.01	0.01	0.404
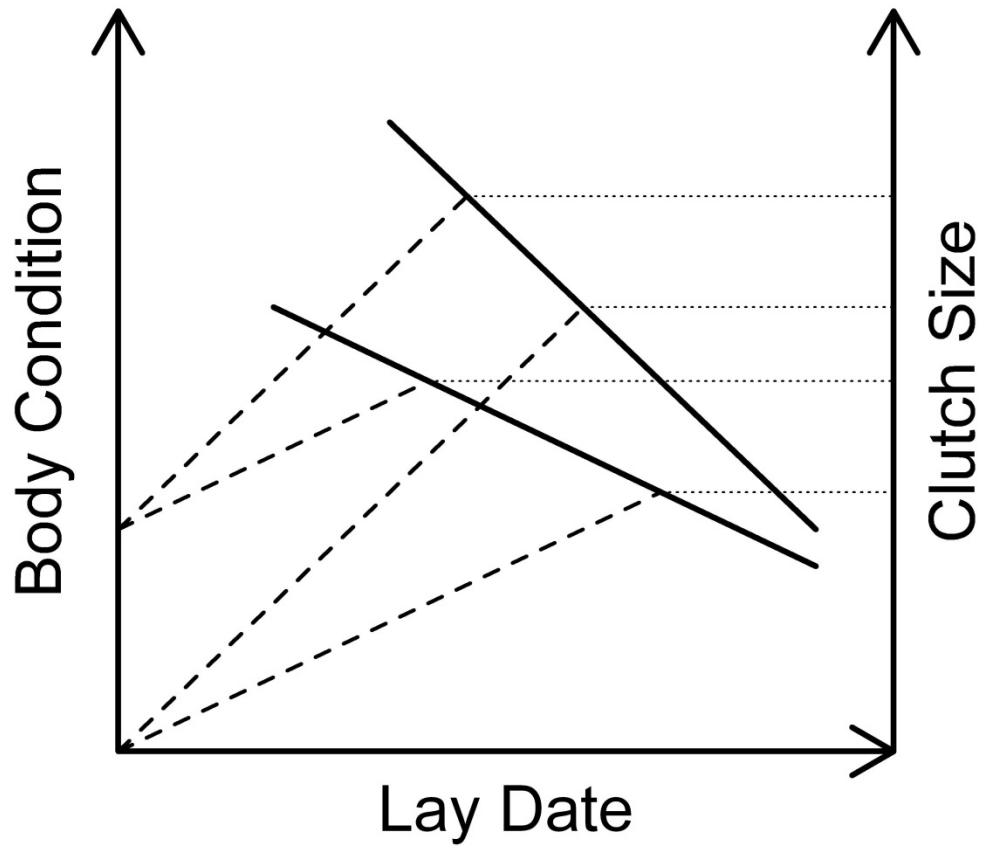
Figure 2-1. Predicted relationships among body condition, lay date, and clutch size from the cost-of-delay hypothesis (modified from Rowe et al. 1994). Bold lines indicate the optimal time, i.e., optimal switch curve, for an individual to initiate nesting based on initial body condition (y-axis intercept) and the rate of body condition gain (slope of dashed lines). Higher rates of body condition gain result in 1) larger clutches, and 2) a steeper intra-seasonal decline in clutch size across individuals in a population.
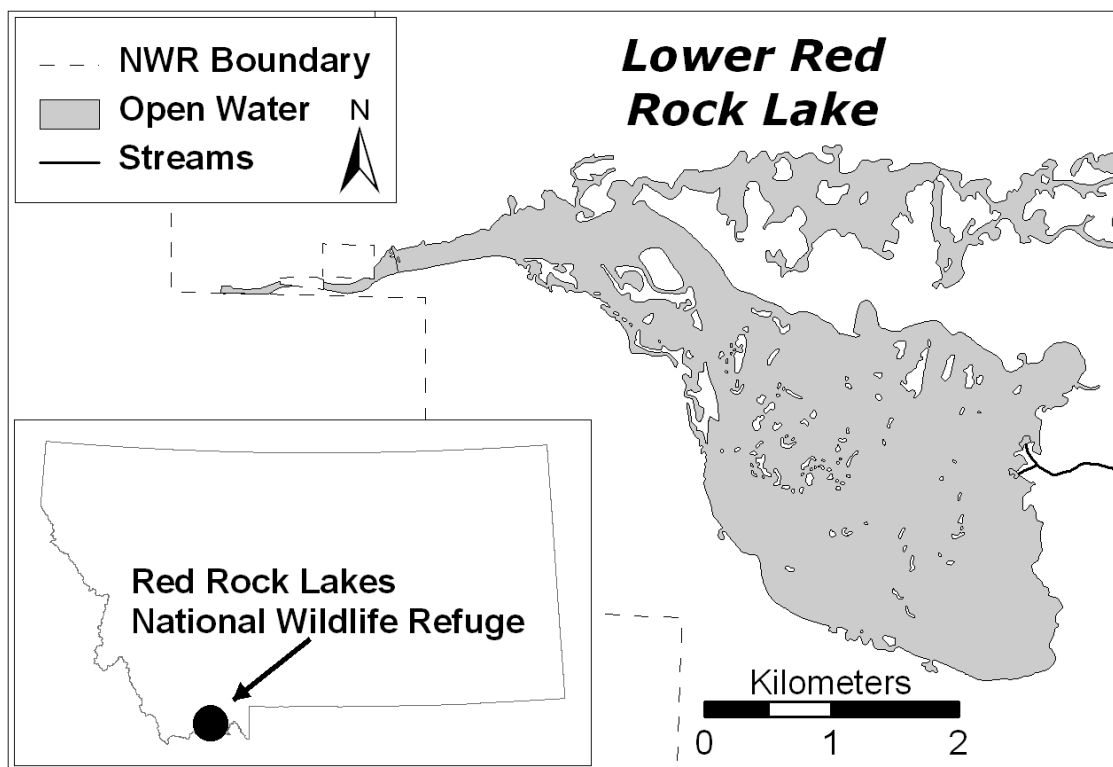
Figure 2-2. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge, southwest Montana, USA.
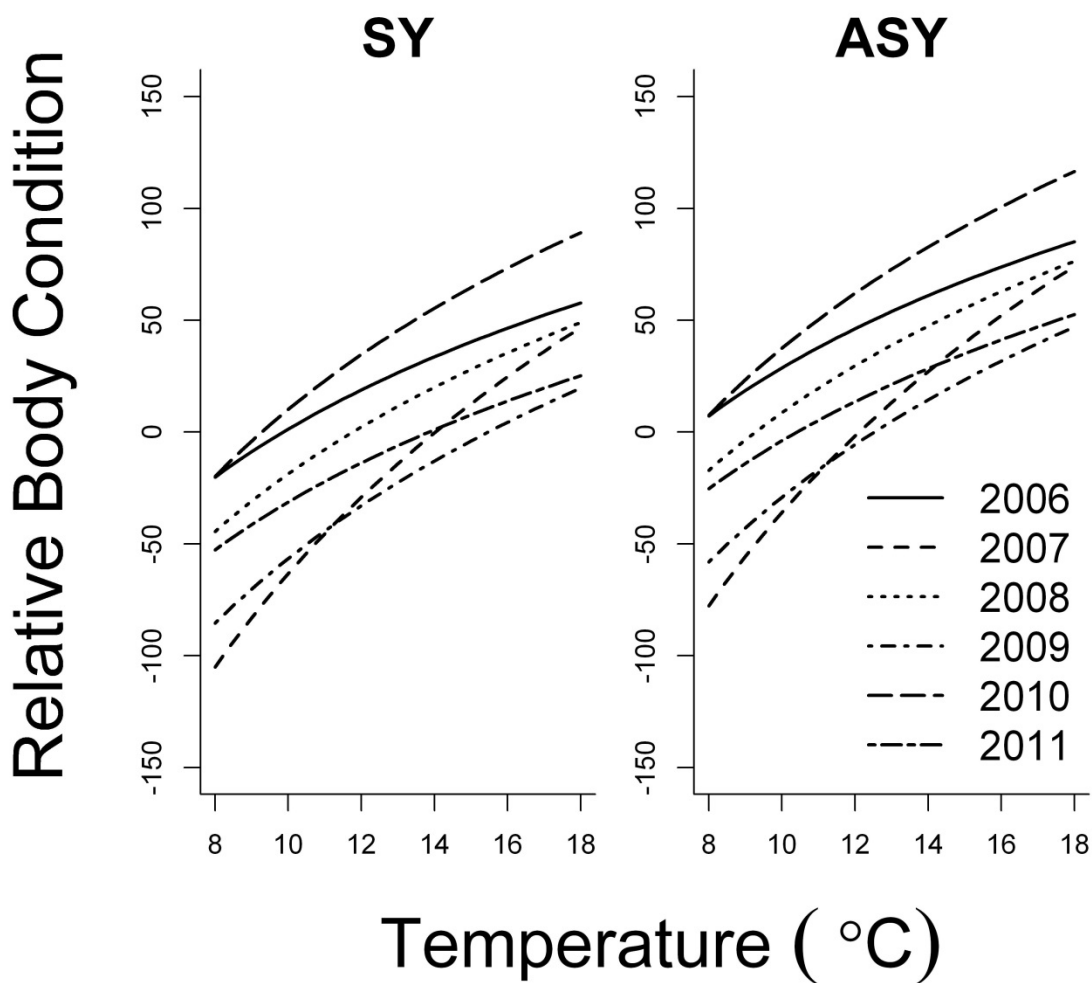
Figure 2-3. Relationship between relative body condition of female lesser scaup and water temperatures by year based on the most parsimonious model $BCIndex = Age + \log(TEMP) * LVL$. Relative body condition is predicted for the mean water level for each year.

CHAPTER 3

PREVIOUS SUCCESS AND CURRENT BODY CONDITION DETERMINE

BREEDING PROPENSITY IN LESSER SCAUP: EVIDENCE FOR THE

INDIVIDUAL HETEROGENEITY HYPOTHESIS[2]

ABSTRACT

The decision to breed influences an individual's current and future reproduction, and the proportion of individuals that breed is an important determinant of population dynamics. Age, experience, individual quality, and environmental conditions have all been demonstrated to influence breeding propensity. To elucidate which of these factors exerts the greatest influence on breeding propensity in a temperate waterfowl, we studied female Lesser Scaup (*Aythya affinis*) breeding in southwestern Montana. Females were captured during the breeding seasons of 2007–2009, and breeding status was determined based on 1) presence of an egg in the oviduct, or 2) blood plasma vitellogenin (VTG) levels. Presence on the study site the previous year, a proxy for adult female success, was determined with stable isotope signatures of a primary feather collected at capture. Overall, 57% of females had evidence of breeding at the time of capture; this increased to 86% for females captured on or after peak nest initiation. Capture date and size-adjusted body condition positively influenced breeding propensity with a declining body condition threshold through the breeding season. We did not detect an influence of female age on breeding propensity. Drought conditions negatively affected breeding propensity,

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[2] Coauthored by J. M. Warren, K. A. Cutting, J. Y. Takekawa, S. E. De La Cruz, T. D. Williams, and D. N. Koons

reducing the proportion of breeding females to 0.85 (SE = 0.05) from 0.94 (SE = 0.03) during normal water years. A female present the previous breeding season was 5% more likely to breed than a female not present the prior year. The positive correlation between age and experience makes it difficult to differentiate the role of age, experience, and individual quality in reproductive success in vertebrates. Our results indicate that individual quality, as expressed by previous success and current body condition, may be among the most important determinants of breeding propensity in female Lesser Scaup, providing further support for the individual heterogeneity hypothesis.

INTRODUCTION

An individual's reproductive success is the product of several life-cycle events, and the decision to breed has clear implications for reproductive success. The decision to breed in a given year influences an individual's lifetime reproductive value assuming a trade-off between current reproduction and future survival or reproduction exists (Williams 1966, Stearns 1992, Aubry et al. 2009). At a population level, the proportion of individuals who breed within a year is an important determinant of population growth (Cam et al. 1998). The broad relevance of the propensity or decision to breed has resulted in considerable theoretical (e.g., Goodman 1974, Charlesworth 1980, Stearns 1992) and empirical (e.g., Boekelheide and Ainley 1989, Aebischer and Wanless 1992, Chastel et al. 1995, Reed et al. 2004, Bohec et al. 2007) work exploring optimal decisions from a life-history perspective and proximate drivers of variation in this demographic rate.

The probability of breeding commonly varies with age in iteroparous species. Delayed maturation in long- and medium-lived species is common (Clutton-Brock 1988,

Newton 1989), with age-at-first-breeding positively related to density (Weimerskirch and Jouventin 1987, Krüger 2005), and negatively related to wetland numbers (a proxy for drought) (Afton 1984) and prey availability (Boekelheide and Ainley 1989, Brommer et al. 1998). After the onset, breeding probability generally increases with age, often reaching an asymptotic value that in some species later declines with the onset of senescence (Afton 1984, Sedinger et al. 2001, Crespin et al. 2006).

Various hypotheses have been posited to explain this commonly observed pattern in breeding probability, or more generally, breeding success. For example, the greater sensitivity of breeding propensity in young, inexperienced individuals to proximate environmental conditions could result from limited resources differentially influencing inexperienced individuals that lack the skills to acquire the resources to breed ('constraint' hypothesis; Curio 1983). Reproductive experience is gained through breeding attempts, which increases monotonically with age but can vary among individuals of the same age (e.g., a four-year old individual who bred each year of life will be twice as reproductively experienced as a comparably aged individual who bred only twice). Increased experience would permit individuals to better overcome constraints to breeding as they age, resulting in greater breeding probability in older age classes. Alternatively, young individuals may forego breeding in an unfavorable year to optimize their residual reproductive value (RRV) based on the tradeoff between the cost of breeding in the current year relative to the probability of reproductive success ('restraint' hypothesis; Goodman 1974, Curio 1983). An individual's RRV decreases with age, increasing the value, and likelihood, of reproductive events as an individual ages. Variation in the quality of individuals could also result in increased breeding

propensity and success with age if individuals that are less likely to breed also have lower survival, resulting in an increased proportion of high-quality individuals in a cohort through time ('heterogeneity' hypothesis; Curio 1983, Barbraud and Weimerskirch 2005, Bohec et al. 2007).

Variation in breeding propensity is most pronounced when environmental conditions are not favorable, i.e. a necessary resource (e.g., prey) for breeding is limited. For example, yearling female diving ducks (*Aythya* spp.) will often breed when wetland conditions are good but will forego breeding during drought (Canvasback [*Aythya valisineria*], Anderson et al. 2001; Lesser Scaup [*A. affinis*], Afton 1984; Ring-Necked Duck [*A. collaris*], Hohman 1986; Redhead [*A. americana*], Sorenson 1991). Environmental conditions averse to breeding have been demonstrated to reduce the probability of breeding in adult seabirds. Examples of non-breeding in response to poor foraging conditions include Brandt's Cormorant (*Phalacrocorax penicillatus*, Boekelheide and Ainley 1989), Common Shag (*Phalacrocorax aristoelis*, Aebischer and Wanless 1992), Snow Petrel (*Pagodroma nivea*, Chastel et al. 1993), Arctic Terns (*Sterna paradisaea*, Monaghan et al. 1992), and Kittiwakes (*Rissa tridactyla*, Hamer et al. 1993). Similar to many seabirds, Arctic nesting geese, e.g., Barnacle Geese (*Branta leucopsis*) and Greater Snow Geese (*Chen caerulescens atlantica*), breed in highly variable and unpredictable environments that can result in high rates of non-breeding when spring conditions are poor. The extent and timing of spring snowmelt has repeatedly been correlated with breeding propensity in Arctic nesting geese, with unusually late snow cover often leading to high levels of non-breeding (Prop and de Vries 1993, Reed et al. 2004).

A threshold body condition level needed for breeding may connect breeding propensity and environmental conditions that influence forage resource availability. Numerous studies have provided evidence that a minimum mass must be reached prior to commencement of breeding. For example, female Wandering Albatross (*Diomedea exulans*) only become first-time breeders after attaining a mass of ca. 8.0 kg (Weimerskirch 1992). Male and female Mute Swans (*Cygnus olor*) need to reach mass thresholds of 10.6 and 8.8 kg, respectively, prior to undertaking breeding (Reynolds 1972). Lower nutrient reserves in non-breeding versus breeding female ducks also supports the hypothesis of a body condition threshold necessary for breeding. Such differences have been noted in Greater Scaup (*Aythya marila*, Gorman et al. 2008), Lesser Scaup (Esler et al. 2001), Ring-Necked Duck (Hohman 1986), and Gadwall (*Anas strepera*, Ankney and Alisauskas 1991). While the threshold appears to be static for some species (e.g., Weimerskirch 1992, Gorman et al. 2008), a seasonally-declining threshold is evinced in other species by 1) declining levels of somatic reserves in females entering rapid follicle growth (RFG) as the season progresses, but 2) a constant proportion of somatic reserves within clutches throughout the nesting season (Esler et al. 2001). This relationship is further corroborated by the widespread intra-seasonal decline in clutch size in birds (Klomp 1970). Whether environmental conditions prevent an individual from reaching their body condition threshold or individuals recognize poor conditions and do not invest effort in increasing body condition (i.e. the restraint hypothesis), has not been determined.

Here, we present data on the breeding status of female Lesser Scaup, a small-bodied diving duck common in North America. Our first objective was to examine

variation in breeding propensity of females relative to body condition, age class, and drought. We predicted: 1) a declining threshold of body condition necessary for initiation of breeding as the season progressed (Esler et al. 2001, Warren et al. 2013), 2) older females would breed at a greater rate than younger females (Afton 1984), and 3) drought conditions would reduce the rate of breeding in female ducks with a more negative influence of drought predicted for young females (Afton 1984, Anderson et al. 2001). The second objective of this work was to explore individual heterogeneity as a driver of breeding propensity using a subset of the data analyzed for the first objective. Using reproductive success during the prior year as a proxy for individual quality (Cam et al. 1998, Sedinger et al. 2008), we predicted that a greater likelihood of breeding would occur in females that had evidence of reproductive success on the study site the previous year.

METHODS

Study Area

This study was conducted on Lower Red Rock Lake (Lower Lake) in southwest Montana, USA (Figure 3-1). Lower Lake is a large (2,332 ha), high elevation (2014 m above mean sea level) wetland encompassed by Red Rock Lakes National Wildlife Refuge. Water depths typically do not exceed 1.5 m during the nesting season, with large open water areas interspersed with hardstem bulrush (*Schoenoplectus acutus*) islands. Nearly half of the area is extensive stands of seasonally flooded Northwest Territory sedge (*Carex utriculata*) that contain small (<2 ha), scattered open water areas. Average annual precipitation is 49.5 cm with 27% occurring during May and June. Annual average

temperature is 1.7ºC. The study site has one of the harshest and most variable breeding

season environments used by Lesser Scaup as measured by growing season length (Gurney et

al. 2011), but it supports a relatively high density of breeding Lesser Scaup (i.e., >7.7

breeding pairs km^{-2}; J. Warren, personal observation).

Field Methods

Female Lesser Scaup ($n = 213$) were captured via spotlighting for 3–6 nights

during each new moon phase in the months of May and June, 2007–2009. Females were

banded with a U.S. Geological Survey aluminum leg band and aged (AGE) (1–2 years

old [YNG] or ≥3 years old [OLD]) based on eye color (Trauger 1974). Each female's

body mass (nearest 5 g), and tarsus (± 0.1 mm) and head (± 0.1 mm) lengths were

recorded.

The oviduct of each female was palpated to determine if an egg was present. If an

egg was not present, a blood sample (~3 ml) was collected by venipuncture of the basilic

vein. Blood samples were immediately placed in heparin-treated Vacutainer tubes and

kept cool until centrifuged (within 12 hours of collection). Plasma samples were pipetted

from the centrifuged samples and stored frozen. Plasma samples were assayed for

vitellogenic zinc (Zn; zinc kit, Wako Chemicals USA, Inc., Richmond, VA) at Simon

Fraser University following the methods in Mitchell and Carlisle (1991). Vitellogenin

(VTG) was estimated as the difference between the concentration of Zn (μg Zn mL^{-1}) in

whole plasma and that found in plasma depleted of very high density lipoprotein

(Mitchell and Carlisle 1991, Gorman et al. 2009). We classified females exceeding the

threshold value of 1.4 μg Zn mL^{-1} as breeders (Gorman et al. 2009). Blood samples were

taken from four females with an oviductal egg to validate breeding classification based on plasma Zn concentration.

Postbreeding waterfowl commonly migrate from breeding grounds to alternate sites for completion of wing molt prior to fall migration (Hohman et al. 1992), and Lesser Scaup are no exception (Austin and Frederickson 1986). Several lines of evidence indicate that successful females (i.e. those that successfully hatched a clutch of eggs) are the primary adult scaup molting on the study site. For example, of 9 females captured in August 2009 as part of an ancillary study, 8 (89%) had a brood patch. During banding operations mid-August through early September 2010–2012, 1933 scaup were banded. Most (92%) were ducklings; of the remaining 8% (138 individuals), only 21 were males. Therefore, stable isotope primary feather signatures that match those of feathers produced on the study site represents a proxy for adult female success the prior breeding season. In 2008 and 2009, the distal 2 cm of the 1st primary feather was collected from each female for stable isotope analysis to determine if the female had molted on the study site the previous year. Feather signatures of females that were captured in 2008 or 2009 and known to have molted on the study site the previous year (2 adult females 2008, one adult and 5 yearlings 2009) were used to classify previous breeding season reproductive status (successful or unsuccessful) of the remaining females. Feather samples were rinsed with a 2:1 chloroform-methanol rinse to remove surface oils. Samples were then weighed (~1 mg) into tin capsules for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis. Isotope analyses for $\delta^{13}C$ and $\delta^{15}N$ were conducted at the University of California-Davis Stable Isotope Facility with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer. Based on

international measurement standards (Vienna Pee Dee Belemnite for carbon and

atmospheric N_2 for nitrogen) the estimated analytical error for $\delta^{13}C$ and $\delta^{15}N$ was ±0.2 ‰

and ±0.3 ‰. A minimum convex polygon (MCP) was created in bivariate space based on

feather $\delta^{13}C$ and $\delta^{15}N$ values from females known to have molted on the site buffered by

the estimated analytical error for each isotope. Females with feather signatures within the

MCP were classified as having been present on the study site during the previous

breeding season (PBSP). We believe this is a reasonable estimate of 1) natal origin for

yearling females, or 2) female success during the previous breeding season for adults (≥2

years old).

Data Analysis

Female body condition was estimated as a size-adjusted body condition index

(BCI) calculated for each female. A principal component analysis was conducted using

female head and tarsus measurements, then female body mass was regressed on the first

principal component (Devries et al. 2008, Warren et al. 2013). The resulting regression

residual for each female was used as the BCI. Negative BCI values indicated females had

lower than average mass for a given structural size, and positive values indicated they

had a higher than average mass.

Based on a review of relevant literature and resultant hypotheses and predictions,

we created a suite of competing *a priori* models for each objective. Our first objective

was to examine the relative role of drivers of variation in breeding propensity, and our

second objective was to explore the influence of individual heterogeneity on breeding

propensity. We evaluated the strength of support for each model within a suite by ranking

models with Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) and by calculating the normalized relative model likelihoods (w_i) for each model (Burnham and Anderson 2002). Variation in breeding propensity was modeled with generalized linear models, binomially distributed errors, and a logit link in R 2.15.1 (R Development Core Team 2013). Relative annual capture date (CDate = *capture date - median annual scaup nest initiation date*) was included in each model to account for variation in breeding propensity due to when a female was captured within a breeding season. Model goodness-of-fit was tested for the most general model (i.e. most highly parameterized) within a model suite, assuming a χ^2 distribution for the estimated deviance with *n-k* degrees of freedom, where *n* is the sample size and *k* is the number of estimated parameters (Neter et al. 1996).

For the first objective, we examined a suite of models for variation in female scaup breeding propensity in relation to relative capture date (CDate), body condition index (BCI), age class (AGE), and drought (DROUGHT) for females captured 2007–2009. An interaction between AGE and BCI was explored in several models to determine if a different body condition threshold existed for older versus younger females. An interaction between CDate and AGE was tested to account for potential differences in the timing and likelihood of breeding between younger and older females. Similarly, an interaction between CDate and DROUGHT was examined to account for potential differences in the timing and likelihood of breeding during drought (2007) versus years with normal water conditions (2008 and 2009). Lastly, an AGE and DROUGHT interaction was included to test for potential variation in breeding propensity between age classes of females in response to poor wetland conditions (Dufour and Clark 2002).

The suite of models for the second objective to explore the role of individual quality in breeding propensity differed from the first by including the variable PBSP and excluding DROUGHT. We were only able to determine PBSP for females in 2008 and 2009, so exploring the effect of drought in this suite of models was not possible.

RESULTS

Conditions on the site varied considerably among the three study years. For example, mean water temperature from May 1st – June 15th was >4°C cooler in 2008 (7.4°C, SD = 9.8) than in 2007 or 2009 (14.4°C, SD = 3.0; and 11.5°C, SD = 6.8). Similarly, 2008 had greater mean water levels during May 1st – June 15th than either 2007 (0.5 m lower) and 2009 (0.1 m lower). The differences of conditions resulted in the median scaup nest initiation date in 2007 being 9 and 8 days earlier than 2008 and 2009, respectively (Warren et al. 2013).

We determined the breeding status of 213 females captured during the breeding seasons of 2007–2009 including 4 recaptured females ($n = 217$). Overall, 57% of females had evidence of breeding, with 80 having an oviductal egg present and 44 having elevated blood plasma VTG levels (i.e., >1.4 μg Zn mL^{-1}). Mean blood plasma VTG level for 4 females with oviductal eggs was 4.35 μg Zn mL^{-1} (SD = 1.69), significantly greater than the threshold value we used to classify females as breeders ($t_3 = 3.499$, $P = 0.02$) . There was a relationship between age class and capture date, with older females (OLD) captured 6.0 days (SE = 2.7) earlier than 1–2 year-old females ($F_{1,215} = 4.8$, $P = 0.03$). Thus, we included the interaction of age with capture date in the model.

The first principal component explained 74% of the variation in female head and tarsus measurements; PCA values ranged from -4.3 to 3.6 for the structurally largest to smallest females. Female body mass was correlated with structural size, with structurally larger females being heavier than smaller females, but considerable variation was not explained by the relationship ($\hat{\beta}$ = -18.9, $P < 0.001$, adjusted R^2 = 0.09). BCI values ranged from -214.7 to 148.1 with SD = 69.9.

Stable isotope signatures from females who produced feathers on the study site had δ^{13}C and δ^{15}N values of -17.9 (SD = 0.34, range = -18.5 – -17.3) and 6.7 (SD = 0.40, range = 6.4 – 7.6), respectively. We examined 145 females with feather isotopic signatures, and 32 (22%) were determined to be present on the study site the year prior to capture. Of these females, 20 (63%) were identified as breeders in the current year.

The most general breeding status probability model in each model suite fit the data well (χ^2 = 117.9, df = 211, P = 1.00; χ^2 = 68.6, df = 139, P = 1.00, respectively; Tables 3-1 and 3-3). Top models from both suites indicated strong support for a positive relationship between body condition and breeding propensity, as well as a greater probability of a female being in breeding status when captured later in the season (Tables 3-1 through 3-4). An effect of age on the breeding propensity was only weakly supported in each model suite. Models that included AGE were 0.61 and 1.59 AIC_c units lower than the most supported model (Tables 3-1 and 3-3). Moreover, the effect of age on breeding propensity overlapped zero in each model ($\hat{\beta}_{ASY}$ = -0.609, SE = 0.505 and $\hat{\beta}_{ASY}$ = -0.471, SE = 0.633, objective one and two, respectively).

Objective 1: Variation in Breeding Propensity

The most general breeding status probability model for the first objective model suite fit the data well ($\chi^2 = 117.9$, df = 211, $P = 1.00$; $\chi^2 = 68.6$; Table 3-1). Top models from this model suite indicated strong support for a positive relationship between body condition and breeding propensity, as well as a greater probability of a female being in breeding status when captured later in the season (Tables 3-1 and 3-2). Drought conditions were related to lower probability of breeding (Tables 3-1 and 3-2). For example, the probability that a female in average body condition was in breeding status at the peak of nest initiation (i.e. median nest initiation date) during a drought year was 0.85 (SE = 0.05) compared with 0.94 (SE = 0.03) for a normal water year (Figure 3-2). An effect of age on breeding propensity was only weakly supported. Models that included AGE were ≥0.61 units lower than the most supported model (Table 3-1). Moreover, the effect of age on breeding propensity overlapped zero ($\hat{\beta}_{ASY} = -0.609$, SE = 0.505).

Objective 2: Individual Heterogeneity

The second objective's most general breeding status probability model fit the data well ($\chi^2 = 68.6$, df = 139, $P = 1.00$; Table 3-3). Models in this model suite provided further support for strong effects of body condition and capture date on breeding propensity in female scaup (Tables 3-3 and 3-4). Previous success, a proxy for individual quality, positively influenced the probability of breeding (Tables 3-3 and 3-4). The probability of breeding at the peak of nest initiation for an average body condition female successful the previous year was 0.98 (SE = 0.01), whereas females without evidence of success on the site the previous year had a probability of 0.93 (SE = 0.04) (Figure 3-3).

Similar to model results from the first objective, the hypothesized effect of age on breeding propensity was weakly supported. The best model that included AGE was ≥1.59 AIC_c units lower than the most supported model (Table 3-3) and the estimated effect overlapped zero ($\hat{\beta}_{ASY}$ = -0.471, SE = 0.633).

DISCUSSION

Differentiating the role of age, experience, and individual quality in reproductive success in vertebrates is difficult, because these factors are often confounded. Our study used feather isotopic signatures to determine if a female was present on the study site the previous year during wing molt, a strong proxy of success for adult females and natal origin for yearlings, allowing us to explore relationships among female breeding status, individual quality, experience, and age. Lack of experience has long been evoked to explain poor reproductive success, including relatively low breeding probability, in young birds (Curio 1983, Forslund and Pärt 1995). Age should convey greater ability to obtain limited resources, thereby permitting older individuals to invest more time in activities beyond those necessary for somatic maintenance that will ultimately lead to successful reproduction. This would predict a strong positive relationship between age and breeding propensity. Experience and age are confounded, arguably synonymous for some behaviors (e.g., foraging behavior). Reproductive experience will increase with age, but can vary among individuals of the same age due to differing numbers of reproductive attempts, resulting in varying levels of correlation between age and reproductive experience. Lesser Scaup are a medium-lived species that can breed as yearlings and have

relatively high breeding propensity (Afton 1984, Devink et al. 2008, this study) that will lead to high correlation between age and experience (including reproductive experience).

If the primary driver of age-correlated increases in breeding propensity and success is individual heterogeneity, i.e. high quality individuals are more likely to breed and survive, previous success would be a better predictor of breeding propensity and success than age or experience. Birkhead et al. (1983) found that a female's genotype was an important determinant of lay date in Mute Swans, which ultimately influenced the number of cygnets fledged. Their findings provide a mechanism for selection of phenotypic traits as hypothesized in the individual heterogeneity hypothesis (Curio 1983, Cam et al. 1998). The effect of age on reproductive success was ambiguous in Mute Swans, but there was strong evidence of a breeding pair effect on lay date and clutch size (Birkhead et al. 1983). We similarly found an ambiguous influence of age on breeding propensity in female Lesser Scaup, contrary to our prediction that older females would breed at a higher rate. Our results did, however, support our prediction that females present on the site the previous year were more likely to breed the following year. This could be the result of increased reproductive experience or evidence of individual heterogeneity. We believe it is more likely the latter than the former; if the relationship was primarily due to experience a stronger influence of age would be expected given the observed high level of breeding propensity on the study area and therefore high correlation between reproductive experience and age. Individual heterogeneity in reproductive success is common in wildlife populations, with considerable evidence that superior individuals have greater survival probabilities and lifetime reproductive output (see review in Conner and White 1999). It has been repeatedly observed that a few

individuals may contribute the majority of offspring to a waterfowl population (Owen and Black 1989, Williams 1999, Blums and Clark 2004). In Tufted Duck (*Aythya fuligula*) and Common Pochard (*A. ferina*), species closely related to Lesser Scaup, only 26% and 29% of females, respectively, recruited at least one offspring (Blums and Clark 2004). These studies, and our results, provide indirect evidence for variation in phenotypic quality resulting in some individuals achieving disproportionately high reproductive performance relative to 'lower quality' individuals.

Greater than half (57%) of female Lesser Scaup captured had evidence of breeding, with the proportion increasing to 86% for females caught on or after the peak of nest initiation in a given year. This is comparable to female scaup in the western boreal forest of Canada, where 90% of females collected after June 3rd had initiated rapid follicle growth (RFG) (Devink et al. 2008). Conversely, Martin et al. (2009) found relatively low breeding propensity in radio-marked Lesser Scaup females in central Alaska. In that study, breeding propensity was estimated as 0.12, although the proportion of females determined to have initiated RFG based on levels of blood plasma yolk precursors was nearly four times that (46%) (Martin et al. 2009). The disparity of breeding propensity estimates may be driven by methodological differences. Radio-transmitters increase energy expenditure and decrease nesting in birds (see review in Barron et al. 2010). Conversely, we cannot rule out a positive bias that could result from an increasing rate of temporary emigration by non-breeding females. Both of these scenarios highlight the difficulties of estimating breeding propensity in highly mobile species.

Life history theory predicts that an individual's residual reproductive value declines with age, which should result in a concomitant increase in reproductive effort (Williams 1966, Gadgil and Bossert 1970, but see Charlesworth and León 1976). With respect to breeding propensity, the predicted pattern of increasing likelihood of breeding by sexually mature individuals as they age is well documented (Afton 1984, Brommer et al. 1998, Sedinger et al. 2001, Krüger 2005, Aubry et al. 2009). However, we did not find evidence for an increase in breeding propensity with age class. Including age class in models actually led to higher AIC_c values. This was in contrast to Afton's (1984) study that detected monotonically increasing breeding propensity with age in Lesser Scaup from yearling (breeding propensity 0.71) to ≥ three-years old (breeding propensity = 1) females. Unlike Afton (1984), we did not have known age females in our sample which limited us to two age classes. In addition, classification error associated with relying on eye color to determine a female's age cannot be ruled out as influencing our ability to detect an effect of age on breeding status.

Female body condition exhibited a strong, positive influence on breeding propensity. This is consistent with a broad body of work that has demonstrated the importance of body condition on the decision to breed (e.g., Reynolds 1972, Weimerskirch 1992, Chastel et al. 1995). The strong correlation between body condition and breeding propensity provides support for a threshold body condition that must be attained for breeding to commence (Ankney and Alisauskas 1991, Weimerskirch 1992). Waterfowl invest proportionately greater amounts of energy into a clutch than birds that produce altricial young (King 1973), often relying on somatic reserves for clutch

formation (see review in Alisauskas and Ankney 1992). This strategy likely predisposes waterfowl to a body condition threshold for breeding.

Our results supported our prediction for a declining threshold of body condition necessary for breeding. Females in better body condition bred earlier, with a declining threshold of body condition as the season progressed. The timing of breeding has significant consequences for reproductive success, with early-nesting females generally laying larger clutches (Klomp 1970, Ankney and MacInnes 1978, Warren et al. 2013) of higher quality young (Verboven and Visser 1998, Lepage et al. 2000, Blums et al. 2002). Esler et al. (2001) similarly found evidence for a declining threshold of body condition in Lesser Scaup females. A declining level of body condition at which females initiate breeding is predicted by the condition-dependent individual optimization model (Rowe et al. 1994). The model predicts the optimal time for a female to initiate a nest, and the resultant clutch size, based on body condition (including the rate of condition gain or loss) and the intra-seasonal decline in the quality of young (Rowe et al. 1994). The declining level of body condition predicted, therefore, is not a threshold *per se*, but an optimal decision of when to breed based on the factors outlined above. The model also predicted the nearly ubiquitous nature of intra-seasonal clutch size decline in birds, which has also been documented on our site (Warren et al. 2013). We did not know where in the sequence of clutch formation a female was when captured which may have been the cause of a declining threshold. The proportion of females late in the laying sequence, in lower body condition, would likely increase with capture date.

We found mixed support for our predictions of the response of breeding propensity to drought conditions experienced during the study. Drought demonstrated a

strong negative effect on breeding propensity, but we did not find support for younger females being more negatively influenced by drought than older females (i.e., models that allowed breeding propensity to differ for each age class in response to drought were poorly supported). The predicted difference in breeding propensity between normal water conditions and drought (a difference of 0.09) was less in this study than reported for Lesser Scaup in the Prairie Pothole Region (PPR) of Canada (a difference of 0.54 in Rogers 1964, and 0.17 in Afton 1984). Our study site is part of a shallow lake–emergent wetland complex with significant snowmelt runoff inputs from perennial streams. Even under extreme drought, the area of open water habitat during pre-breeding was comparable to the other years with the primary difference being lower water levels (0.4-0.5 m lower) (Warren et al. 2013). This resulted in over half of the open water area being <0.50 m in depth during the drought year. This can be contrasted with the PPR, where closed-basin wetlands predominate and drought conditions can result in >90% of basins being dry (Warren et al. 2008) and available water area being reduced by nearly two-thirds (Rogers 1964). While the negative effect of drought is consistent across studies in Lesser Scaup, and more broadly in waterfowl, the mechanism leading to reduced breeding propensity has yet to be determined. Whether females are constrained from environmental conditions experienced during drought or demonstrate restraint in response to low likelihood of reproductive success is unknown.

Three general explanations exist for the commonly observed pattern of increasing reproductive success with age and experience in birds – individuals are constrained by a lack of resources necessary to breed, individuals demonstrate restraint in the face of a lack of resources necessary to breed, and individuals vary in quality with high quality

individuals having higher rates of survival and reproduction than low quality individuals. The constraint and restraint hypotheses view poor reproduction of young birds as primarily a function of age class. Our results provided ambiguous support for age class as an important determinant of breeding propensity. By contrast, the individual heterogeneity hypothesis considers the disparity in reproductive success as primarily driven by differences in the quality of individuals. We found evidence of variation in individual quality during this study, with previously successful females more likely to breed in the subsequent year, providing support for the individual heterogeneity hypothesis.

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TABLES AND FIGURES

TABLE 3-1. Model rankings for analyses of breeding propensity in 213 female Lesser Scaup captured during the breeding season, 2007–2009. Covariates include a size-adjusted body condition index (BCI), age class (AGE: 1–2 years old or ≥3 years old), and drought. Relative capture date (CDate = *capture date - median annual nest initiation date*) was included in each model to account for variation attributable to when a female was captured during the breeding season. Only models within 4 AIC_c units of the top model are presented.

Model	K^a	AIC_c	ΔAIC_c	w_i^b
CDate + BCI + DROUGHT	4	127.78	0.00	0.260
CDate + BCI + AGE + DROUGHT	5	128.39	0.61	0.192
CDate * DROUGHT + BCI	5	129.08	1.30	0.136
CDate + BCI	3	129.23	1.45	0.126
CDate + BCI + AGE	4	129.32	1.54	0.120
CDate * AGE + BCI + DROUGHT	6	130.29	2.51	0.074
CDate * AGE + BCI	5	131.12	3.34	0.049

[a]Number of estimated parameters

[b]Normalized relative model likelihoods.

TABLE 3-2. Coefficient estimates, standard errors (SE), and *P* values for the most supported model of breeding probability for female Lesser Scaup captured during the breeding seasons of 2007–2009.

Model Parameter	$\hat{\beta}$	SE ($\hat{\beta}$)	P
Intercept	2.082	0.391	<0.001
CDate[a]	0.082	0.014	<0.001
BCI[b]	0.032	0.005	<0.001
Drought	-0.984	0.537	0.07

[a]Relative annual capture date (*capture date - median annual nest initiation date*)

[b]Body condition index

TABLE 3-3. Model rankings for analyses of breeding propensity of 145 female Lesser Scaup captured during the breeding season, 2008–2009. Covariates include a size-adjusted body condition index (BCI), age class (AGE: 1–2 years old or ≥3 years old), and prior breeding season presence (PBSP). Relative capture date (*capture date - median annual nest initiation date*) was included in each model to account for variation attributable to when a female was captured during the breeding season. Only models within 4 AIC_c units of the top model are presented.

Model	K^a	AIC_c	ΔAIC_c	w_i^b
CDate + BCI + PBSP	4	77.57	0.00	0.479
CDate + AGE + BCI + PBSP	5	79.15	1.59	0.217
CDate + BCI	3	80.31	2.74	0.122
CDate * AGE + BCI + PBSP	6	81.24	3.67	0.076
CDate + AGE + BCI	4	81.46	3.90	0.068

[a]Number of estimated parameters

[b]Normalized relative model likelihoods.

TABLE 3-4. Coefficient estimates, standard errors (SE), and *P* values for the most supported breeding propensity model for female Lesser Scaup captured during the breeding seasons of 2008–2009.

Model Parameter	$\hat{\beta}$	SE ($\hat{\beta}$)	P
Intercept	1.695	0.475	<0.001
CDate[a]	0.085	0.020	<0.001
BCI[b]	0.040	0.008	<0.001
PBSP[c]	1.553	0.742	0.04

[a]Relative capture date (*capture date - median annual nest initiation date*)

[b]Body condition index

[c]Prior breeding season presence
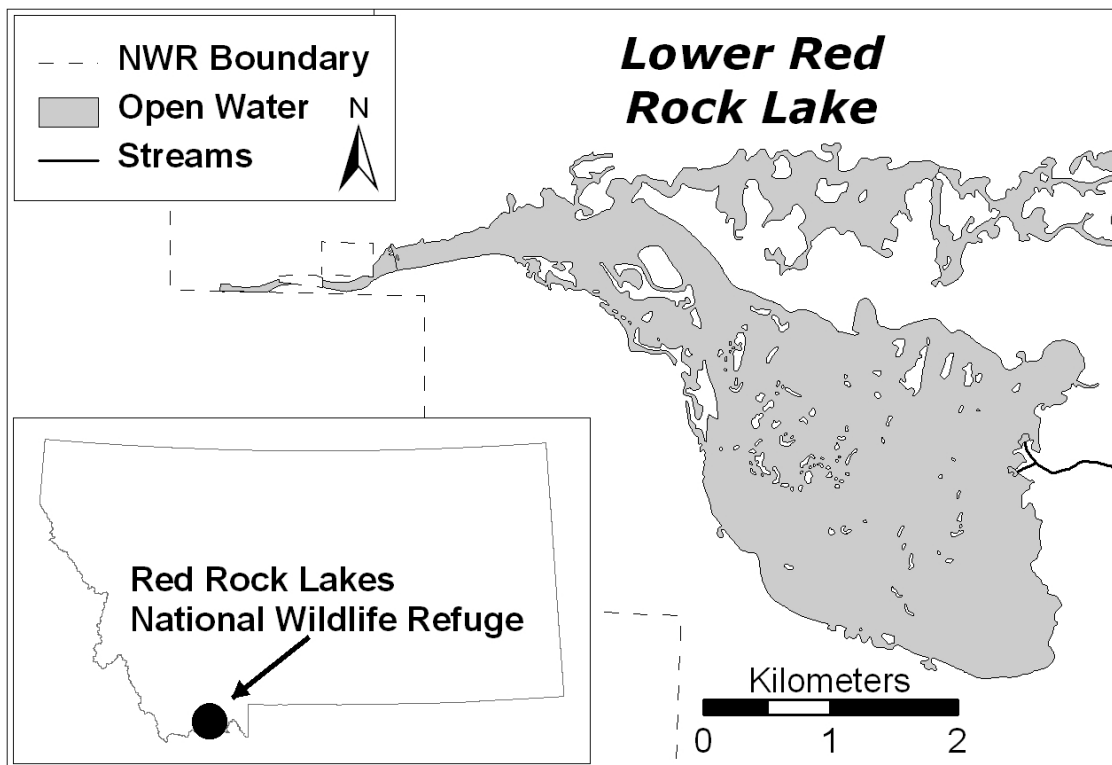
FIGURE 3-1. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge, southwest Montana, USA.
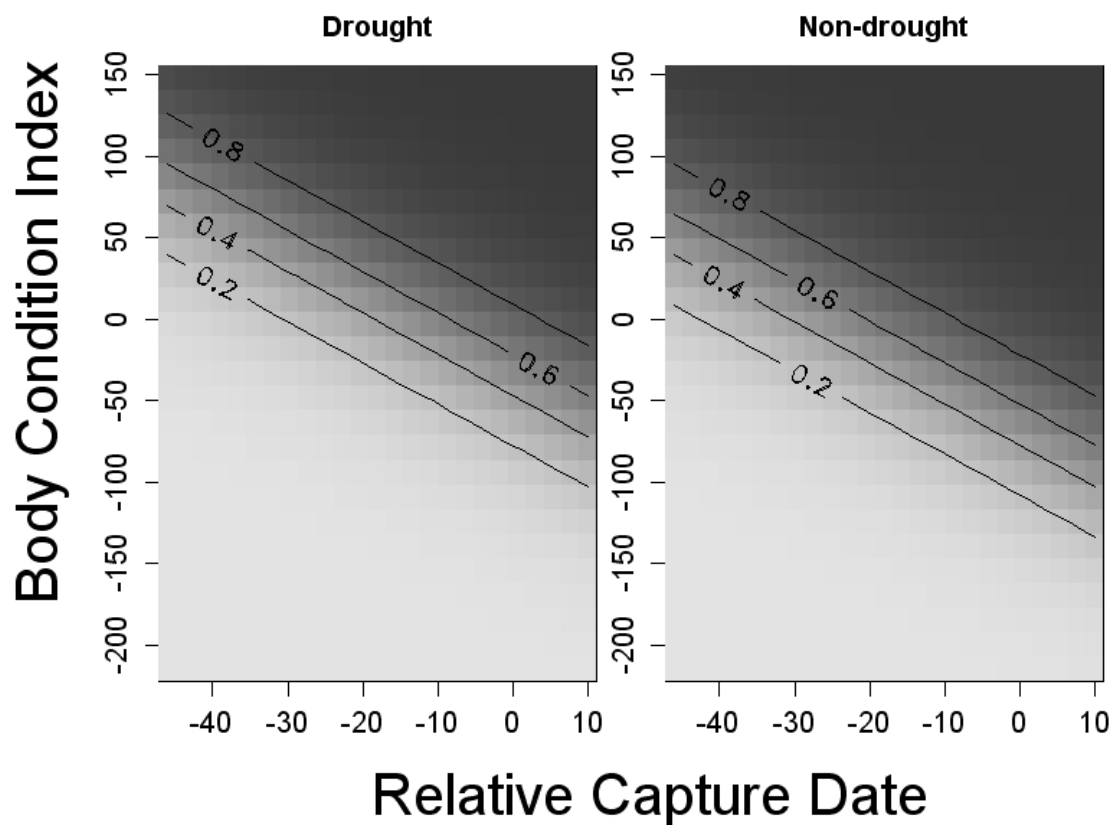
FIGURE 3-2. Female Lesser Scaup breeding propensity, 2007–2009, based on body condition index, relative capture date (*capture date - median annual nest initiation date*), and drought. Gray scale represents female breeding probability from low (light) to high (dark); female breeding probability isoclines are also provided.
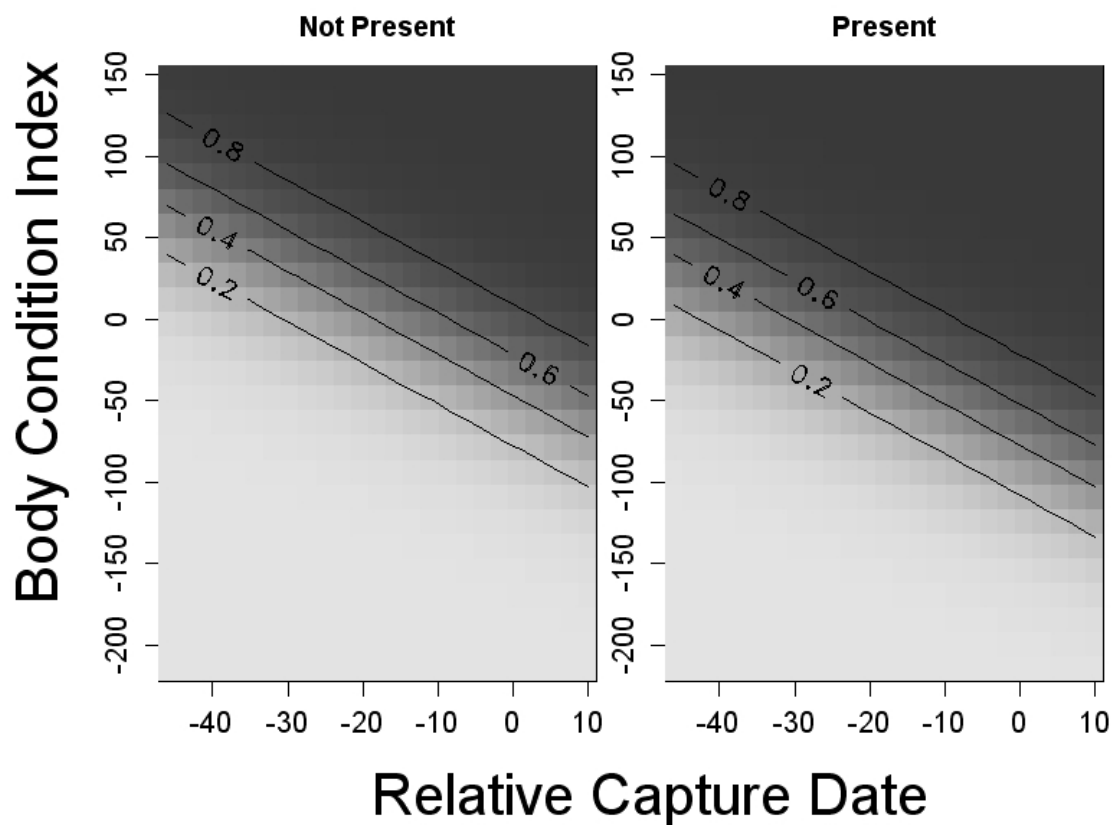
FIGURE 3-3. Female Lesser Scaup breeding propensity, 2008–2009, based on body condition index, relative capture date (*capture date - median annual nest initiation date*), and presence on the study site during molting in the previous breeding season. Gray scale represents female breeding probability from low (light) to high (dark); female breeding probability isoclines are also provided.

CHAPTER 4

A TALE OF TWO SEASONS: WITHIN-SEASON AND CARRY-OVER EFFECTS OF

REPRODUCTIVE EFFORT ON SURVIVAL IN A LONG-DISTANCE MIGRANT

ABSTRACT

Reproduction may be costly if an individual invests limited resources toward current reproduction at the expense of self-maintenance, or if reproduction increases mortality risks. Both costs can occur concurrently with reproduction, but physiological costs on demography can occur serially where an individual survives reproduction in a reduced condition that influences future survival or fecundity, i.e., a carry-over effect (COE) from breeding to a subsequent season. We examined concurrent and serial survival costs of reproduction in female lesser scaup (*Aythya affinis*) using multistrata capture-mark-recapture models. Breeding habitat conditions, a proxy for reproductive effort, strongly influenced survival during breeding and non-breeding seasons, but in opposing directions. Breeding season survival was positively related to breeding season water levels, whereas non-breeding season survival was negatively related. The latter result suggested a COE of reproductive effort from breeding to non-breeding seasons when breeding habitat conditions were favorable. Increased proportion of young and/or low quality females breeding when conditions are favorable could produce the observed relationship if those individuals are less capable of completing molt and recovering condition after breeding than higher quality individuals. Complex seasonal interactions documented during this study underscore the importance of understanding when in an annual cycle costs of reproduction occur.

INTRODUCTION

"It was the best of times, it was the worst of times…it was the spring of hope, it was the winter of despair" (Dickens 1859). Charles Dickens's portrayal of pre-revolutionary times in Paris and London in *A Tale of Two Cities* also aptly describes the disparity between breeding and non-breeding seasons for populations in seasonal environments (Fretwell 1972). The breeding season represents a period of population growth as adults undertake reproduction with the 'hope' of recruiting young as carriers of their genetic legacy. Those individuals, adults and newly born, that survive to the subsequent non-breeding season will be reduced in number by mortality during winter, a period of population decline (i.e., no birth, only death occurs). The winter season has been referred to as 'a waiting interval' between breeding seasons for migratory birds; a period when individuals migrate to exploit seasonally-abundant resources and avoid the dangers of remaining at high-latitude breeding areas that are frozen (Lack 1968, Weller and Batt 1988).

More than 'waiting in despair' occurs during winter, however. The importance of habitat and an individual's energetic condition during winter for successful reproduction in the subsequent breeding season has been repeatedly demonstrated in migratory birds, mammals, and fish (birds: Ebbinge and Spaans 1995, Marra et al. 1998, Béty et al. 2003, Saino et al. 2004, Gunnarsson et al. 2005, Guillemain et al. 2008. mammals: Testa and Adams 1998, Pachkowski et al. 2013, Monteith et al. 2014. fish: Henderson and Wong 1998, Blanchard et al. 2003, Bunnell et al. 2007). Relatively large-bodied birds capable of acquiring endogenous reserves during one season and exporting them to a subsequent season to fuel metabolically-costly activities such as reproduction (i.e., a capital

reproduction strategy, *sensu* Drent and Daan 1980) provided early evidence that conditions during one season could influence fitness in a subsequent season. Commonly referred to as carry-over effects (COEs) or seasonal interactions, these among-season relationships underscore the difficulty of understanding within- and among-season drivers of an individual's demographic performance. Conditions during the preceding winter have been positively correlated with the proportion of juveniles in the population the following winter (Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Lehikoinen et al. 2006, Osnas et al. 2016), fledging success (Saino et al. 2004, Rockwell et al. 2012), and other parameters of reproductive success (Norris et al. 2004, Gunnarsson et al. 2005, Guillemain et al. 2008) in migratory birds. Individuals in better body condition than conspecifics at the onset of spring migration initiate nests earlier and lay larger clutches (Béty et al. 2003), are more likely to reproduce successfully (Prop et al. 2003), and produce more offspring (Ebbinge and Spaans 1995). These studies, and more (see reviews in Harrison et al. 2011, Sedinger and Alisauskas 2014), demonstrate the potential for habitat use and energetic condition during winter to influence reproductive success in the ensuing breeding season.

Investigations of COEs from breeding to non-breeding seasonal components of survival are less common (Daan et al. 1996), but costs of reproduction could result in such a seasonal interaction. Life history theory considers reproduction costly, because an individual may be obliged to invest limited resources toward the current reproductive effort or self-maintenance; investing in the former over the latter could reduce survival and future fecundity (Williams 1966, Stearns 1992). But costs of reproduction can occur concurrently with a given reproductive activity, or in a serial manner where an individual

survives the reproductive event but is in a reduced condition that results in 1) higher mortality during the following non-breeding season, or 2) reduced reproductive success the subsequent breeding season.

Concurrent costs of reproduction, e.g., reduced survival during reproduction, are well documented in ground-nesting birds. Female-biased mortality during the breeding season in ground-nesting birds provides evidence for concurrent costs associated with producing a clutch and nest attendance, costs not incurred by males (Grüebler et al. 2008, Perlut et al. 2008). Similar patterns are found when habitat conditions favor high breeding propensity (Arnold and Clark 1996, Rotella et al. 2003, Arnold et al. 2012). This is likely the result of females being exposed to greater mortality risk from terrestrial mammalian predation during laying and incubation, and as the result of repetitive re-nesting attempts upon previous nest failure (Sargeant et al. 1984; Low et al. 2010, Arnold et al. 2012). These examples demonstrate the array of survival costs to reproduction, within the season of reproduction (Magnhagen 1991).

Serial survival costs of reproduction are less well studied than either concurrent survival costs or serial fecundity costs (Daan et al. 1996, Sedinger and Alisauskas 2014, Latta et al. 2016). Overall survival costs, i.e., reduced annual survival for breeding individuals (Clutton-Brock et al. 1983, Pugesek and Diem 1990, Barbraud and Weimerskirch 2005, Tavecchia et al. 2005, Hadley et al. 2007), and experimentally-induced fecundity costs in breeding season $t+1$ (Hanssen et al. 2005, Catry et al. 2013, Fayet et al. 2016) have been repeatedly demonstrated. The former provide evidence for a survival cost to reproduction, but do not differentiate if costs occur concurrent with, or serial to, the reproductive event. Unlike concurrent survival costs that terminate an

individual's life and likely the chance of recruiting already produced offspring, serial survival costs may have little influence on the probability of recruitment, and thus induce a lesser net cost to lifetime fitness. This scenario would be the case for iteroparous species whose offspring care ends with the breeding season – serial survival costs to reproduction are independent of recruitment from the prior reproductive event. Moreover, if an individual is unable to predict upcoming non-breeding season conditions, current reproductive effort should maximize recruitment as a function of breeding season conditions conditional on residual reproductive value (Williams 1966), while 'accepting' greater risk associated with potential serial survival costs. In such cases, serial survival costs of reproduction represent the extreme end of a spectrum of potential COEs from the breeding season, with reduced fecundity the subsequent breeding season at the opposite end of the COE spectrum.

We undertook the current study to test for concurrent and serial costs of reproduction in a long-distance migratory bird. We hypothesized that breeding habitat conditions conducive to high breeding effort result in high concurrent survival costs among female lesser scaup (Sargeant and Raveling 1992, Rotella et al. 2003). Conversely, we hypothesized that concurrent survival costs would be low when nest predation risks were also low (i.e., when nest survival is high; Lokemoen et al. 1990, Cam et al. 1998, Kennamer et al. 2016).

We also tested for serial survival costs (COEs) of breeding effort on female non-breeding season survival. Reproductive investment during the preceding breeding season may compress the time available for molt and migration, both metabolically-costly annual activities (Hohman et al. 1992, McWilliams et al. 2004). Waterfowl undergo an

annual molt during the latter part of the breeding season that leads to a short period of

flightlessness, a relatively costly undertaking due to energetic costs associated with

replacing feathers, decreased thermoregulatory capacity, and limited mobility (King

1981, Guillemette et al. 2007). Reproductively successful lesser scaup females must molt

later than non-breeding or unsuccessful females (Austin and Fredrickson 1986),

providing less time for successful females to regain body condition for migration. Lighter

birds during fall and early winter do indeed experience lower survival (Haramis et al.

1986, Conroy et al. 1989, Pfister et al. 1998), and are more susceptible to hunter harvest

(Dufour et al. 1993, Pace and Afton 1999) than heavier conspecifics, thus providing a

mechanism for serial survival costs to reproduction for females that successfully breed.

METHODS

Study Description

We conducted this study on lesser scaup, a long-distant migratory waterfowl with

a relatively large clutch ($\bar{x}$ = 7.7, SD = 0.8, Warren et al. 2013) and intermediate life

expectancy. Conditional on surviving the first year, <10% of females would participate in

≥5 breeding seasons (Arnold et al. 2016, this study). This study was conducted in the

southwestern extent of lesser scaup breeding range on Lower Red Rock Lake (Lower

Lake) in the Centennial Valley of southwest Montana, USA (Figure 4-1) (described in

Warren et al. 2014). Lower Lake is a large (2,332 ha), high elevation (2,014 m above

mean sea level [msl]) wetland within a larger shallow lake/wetland complex. Water

depths typically do not exceed 1.5 m during the nesting season, with large open water

areas interspersed with hardstem bulrush (*Schoenoplectus acutus*) islands. Nearly half of

the area consists of extensive stands of seasonally flooded Northwest Territory sedge (*Carex utriculata*) that contain small (<2 ha), scattered open water areas. The study site supports a relatively high density of breeding scaup (i.e., >7.7 breeding pairs / km^{-2}; J. Warren, unpubl. data) even though it is one of the harshest and most variable breeding season environments used by scaup as measured by growing season length (Gurney et al. 2011). The study area is in the eastern extent of the Pacific Flyway administrative zone of the U.S. Fish and Wildlife Service (USFWS), and ~80% of hunter recoveries of marked scaup from the site occur within this flyway (J. Warren, unpubl. data).

Field Methods

A capacitance probe water level data logger (model WT-HR 1500; TruTrac, Christchurch, New Zealand) was deployed at the western outflow of Lower Lake shortly after ice melt each spring. Water levels (± 0.1 mm) and temperatures (± 0.1 °C) were recorded hourly throughout the breeding season as proxies for wetland condition and phenology on the study site, respectively.

Female lesser scaup were captured each summer via spotlighting (adult [≥1 yr old] only) (Lindmeier and Jessen 1961) and during late summer using drive-trapping (adult and juvenile [hatch-year individuals]) (Cowan and Hatter 1952). Spotlighting occurred during new moon phases in May – August 2005, May and June 2006–2012, and June 2013–2015. Drive-trapping was conducted in September 2008 and 2009, and August and September in 2010–2014. Females were banded with a U.S. Geological Survey (USGS) aluminum leg band and fitted with a nasal marker (juveniles with a head length ≥70 mm and adults). Nasal markers comprised a combination of uniquely

identifiable nylon pieces attached through the nares using 1.6 mm 316L stainless steel welding wire and stainless steel washers (Lokemoen and Sharp 1985). During 2005–2008 it was observed that movement of the steel washers wore the crimped ends of the steel wire on the nasal markers, leading to marker loss beginning after ca. 20 months of a female being marked (J. Warren, unpubl. data). Starting in 2009 a small (ca. 3 mm diameter) piece of epoxy (WaterWeld, J-B Weld Co., Sulphur Springs, TX) was put on the distal crimped ends of the steel wire to minimize marker loss. The oviduct of each female captured during May and June spotlighting was palpated to determine laying status (i.e., absence or presence of an egg).

Pre- and post-breeding season (May and late August/early September, respectively) resight surveys were conducted each year for marked female lesser scaup beginning in September 2005. The study area was divided into 16 survey blocks of approximately equivalent open water area. Each block comprised 1–4 750m x 750m plots that were visited twice during a resight survey. Each visit to a survey block was conducted for 4 hours, beginning at sunrise for morning visits and 4 hours prior to sunset for evening visits. If a block was visited in the morning during the first visit, it was visited in the evening on the second visit, and vice versa. Visit order was randomly established during the initial resight survey, and that order was maintained for subsequent surveys.

Data Analysis

Temporal variation in seasonal survival of female scaup was investigated using multi-state capture-mark-recapture (CMR) models implemented in program MARK

(White and Burnham 1999) using the RMark package (Laake 2013) in R version 3.2.2 (R
Development Core Team 2017) to construct models. Multi-state models permitted the
use of resight, recapture, and hunter recovery data (Gauthier and Lebreton 2008), while
simultaneously accounting for marker loss (e.g., Meixell et al. 2013). Pre-breeding (May
/ June) and post-breeding (August / September) CMR survey periods occurred annually.
Resight surveys were combined with spotlighting and drive-trapping sessions for pre- and
post-breeding surveys, respectively. Seasonal survival was modeled over two open
intervals each year with breeding season defined as June through August and the non-
breeding season September through May. Hunter recoveries of marked birds during the
non-breeding season were obtained from the USGS Bird Banding Laboratory.

Three states were included to allow for modeling of marker loss and incorporation
of harvest data. Two live states were defined based on auxiliary marker status – live, leg
band and nasal marker present (AN), and live, leg band only (AB). Females released in
the AN state could be reencountered in either live state while on the study area. A single
dead state (D) was included to model mortality transitions from either live state, which
were directly informed by observations of females that were harvested within North
America and reported to the USGS Bird Banding Laboratory (and indirectly informed by
live re-encounters). Harvest occurred during non-breeding seasons (i.e., between a post-
breeding survey and pre-breeding survey); females harvested and reported between time t
and $t + 1$ were coded as observations in state D at time $t + 1$ (Gauthier and Lebreton
2008). Survival probability, S, was fixed to 1, 1, and 0 for AN, AB, and D states,
respectively. These constraints result in transition probabilities $\psi^{AN \cdot D}$ (i.e., alive and
nasal-marked to dead) and $\psi^{AB \cdot D}$ that represent female mortality probabilities from each

respective state (hereafter, we refer to the complement of mortality transition probabilities as survival). We assumed no effect of nasal-marking on adult female survival, so constrained $\psi^{AN \cdot D}$ and $\psi^{AB \cdot D}$ to be equal (Brook 2002). Juvenile females were included in the analysis because they augment the sample size for adult survival upon recruitment at age one. We allowed mortality transitions for juvenile females to differ between live states due to inherent bias in head-size selection criteria for nasal-marking. Moreover, we tested for an effect of nasal-marking on juvenile (i.e., immature) mortality, and constrained juvenile mortality to be independent of breeding season metrics in models testing for carry-over effects of breeding effort and success on adult female mortality. Due to relatively low numbers of nasal-marked juvenile females in 2011 ($n =$ 12), the subsequent first-winter mortality probability in 2011 was constrained to be the same as 2009 in time-varying models; juvenile females nasal-marked in 2011 and 2009 had the most similar head lengths ($\bar{x} = 78.6$ mm [SD = 4.76], and 78.8 [3.26], respectively), a reasonable proxy for juvenile female age at marking ($\hat{\beta}_{Age} = 0.91$, SE = 0.020, $R^2 = 0.93$, $n = 170$), and subsequently first-winter survival in juvenile *Aythya* (Anderson et al. 2001, Stetter 2014). Juvenile nasal-marked females from 2005 and 2008 ($n = 2$ and 3, respectively) were also constrained, due to low sample sizes, to have the same transition probabilities as 2009 and 2011.

Transition probabilities from D to either live state, $\psi^{D \cdot AN}$ and $\psi^{D \cdot AB}$, were fixed to zero (i.e., D was modeled as an 'absorbing state'). Females were only allowed to transition from AN to AB, and not vice versa, so $\psi^{AB \cdot AN}$ was fixed to zero. Females recaptured alive during the study that had 1) lost their nasal marker and were fitted with a new marker ($n = 14$), 2) retained their nasal marker but were fitted with a new steel pin

due to wear of the original ($n = 16$), or 3) been released with only a leg band (state AB) and nasal marked during a subsequent recapture, were right-censored at that occasion and a new encounter history was started (Meixell et al. 2013). Four females released with a nasal marker were later recovered during the non-breeding ($n = 2$) and breeding ($n = 2$) seasons without a marker, resulting in a total of 18 individuals available to estimate $\psi^{AN \cdot AB}$ during two periods (2005–2008 [no epoxy] and 2009–2015 [epoxy]). Estimating marker loss ($\psi^{AN \cdot AB}$) was done externally to the multi-state CMR model because 1) encounters of marker loss were too few to achieve convergence on a marker-loss transition probability in the multi-state CMR model amidst low detection probabilities, and 2) combining resights and physical recaptures of AN females during survey occasions (i.e., May–June and August–September) precluded use of physical recaptures of marked females in estimation of marker loss within the multi-state CMR model.

To more fully utilize these data in estimating the transition probability from AN to AB, we modeled marker loss as a function of months since marking and marking period (see above) using a generalized linear model (GLM) with binomially-distributed errors and a logit-link in R version 3.2.2. We then used predicted marker loss for each marking period to fix the probability of a female losing her marker (i.e., $\psi^{AN \cdot AB}$ in the multi-state CMR model) as a function of months since marking to the end of the interval of interest. Of 10 females marked 2005–2008 and recaptured or recovered ≥ 36 months since marking, none retained their marker. To account for this, we fixed transition probability $\psi^{AN \cdot AB}$ such that marker loss was 1 for ≥ 36 months post-marking for females marked during the first marking period when epoxy was not used (2005–2008).

The probability of female *i* being observed in state *k* at time *t* was conditional on state-dependent detection probabilities $p_{i,t}^k$. Nasal-marked females could be resighted or recaptured, with detection probability defined as $p_{i,t}^{AN}$. Conversely, a female that had lost her marker was only available for recapture with detection probability $p_{i,t}^{AB}$. Detection probability for AB females, $p_{i,t}^{AB}$, was fixed to 0 for time periods when captures were not attempted (2006–2007 post-breeding periods and 2013–2014 pre-breeding periods), or no recaptures occurred (2006 and 2012 pre-breeding periods and post-breeding periods excluding 2011). Yearling *Aythya* females commonly have lower fidelity to breeding areas than older females (Johnson and Grier 1988, Serie et al. 1992, Arnold et al. 2002, Blums et al. 2002), which in our study would result in lower detection probability for females marked the previous year as juveniles. We assessed this possibility by including models that allowed detection probability of yearling females to differ from adult females when determining an event probability structure for use in modeling (see below).

Given our model formulation, the probability of a newly dead female being harvested, recovered and reported ($p_{i,t}^D$) was modeled according to the Seber formulation (Seber 1971). As recoveries were only possible during the non-breeding season, $p_{i,t}^D$ was estimated for pre-breeding encounter periods (which occur at the trailing end of the non-breeding season that encompasses the hunting season) but fixed to 0 for post-breeding periods (i.e., August-September).

Detection of nasal-marked females ($p_{i,t}^{AN}$) accounted for the majority of post-release encounters of individuals used to inform model fitting (see Results below), allowing greater flexibility in exploring variation in $p_{i,t}^{AN}$. We considered 12 model

formulations based on combinations of pre- and post-breeding survey detection

probability as 1) constant, 2) time varying, 3) a function of mean water level during May

and August, and 4) hen reproductive success (post-breeding survey $p_{i,t}^{AN}$ only).

Modeling Strategy

We employed a step-down approach similar to Lebreton et al. (2009) to create a

model set focused on biological hypotheses of temporal variation in adult female seasonal

mortality. We started by determining suitable event probability structures for p^{AB} and p^{D},

which were our most data-limited event probabilities (see Results below). Three

formulations for each probability were considered – time-varying, periods defined by

naïve direct recapture or recovery rates, and time-invariant. Naïve direct recapture and

recovery rates were calculated as the proportion of individuals banded the prior fall and

recaptured during the subsequent breeding season (0–0.3%, 2005–2008 and 2013; 2.3–

3.3%, 2010–2011, and 2014; and 5.9–8.2%, 2009, 2012, and 2015), and the proportion of

individuals recovered during the interval after banding (0–10.0%, 2005–2008, 2010,

2012, and 2013; and 15.6–23.0%, 2009, 2011, and 2014), respectively. The nine possible

combinations were fitted with a model that allowed full time-varying estimates of 1)

mortality transition probabilities by age class (juvenile and adult) with an additive nasal-

marker effect for juvenile females, and 2) detection probability of nasal-marked females

(p^{AN}) with, and without, an additive yearling effect. Relatively few resights of AN

females during the first pre-breeding survey conducted May 2006 ($n = 21$) led to

estimation issues, so May 2006 p^{AN} was constrained to be the same as May 2007.

Models were ranked using Akaike's Information Criterion adjusted for sample size

(AIC$_c$; Burnham and Anderson 2002). In our second step we focused on comparing model structures for variation in first-winter (juvenile) female mortality. Formulations considered were 1) time-varying, 2) time-invariant, 3) mortality as a function of nesting season water level (a proxy for wetland conditions during early life), 4) daily bag limit, and 5) estimated Pacific Flyway harvest. These five formulations were fitted, with and without an additive effect of nasal-marking, using the most supported model structure for p^{AB} and p^{D} determined during step one, and the same adult mortality and p^{AN} structures used in step one.

Two critical assumptions are made in fitting capture-recapture models; independence among 1) marked individuals, and 2) each release and subsequent reencounter (if any) of individuals (Choquet et al. 2009). Program U-CARE V2.3.2 (Choquet et al. 2005, Choquet et al. 2009) provides the ability to test these assumptions for multi-state capture-recapture models. We assessed transience (test 3G) and trap dependence (test M) for two groups, juvenile and adult females, and three states (AB, AN, and D). Our global model allowed full time-varying p^{AN}, except, due to estimation issues, pre-breeding surveys during 2006 and 2011 were constrained to be the same as they had similar mean May water levels. Detection of band-only females, p^{AB}, was allowed to vary among capture sessions in years 2009–2014, but fixed to 0 in 2005–2006 (see above) and constrained to be the same for sessions 2007–2008 due to low numbers of recaptures. Recoveries by hunters, p^{D}, were allowed to vary annually 2008–2014 but constrained 2005–2007 due to low numbers of recoveries. Transition probabilities were allowed to vary by year and age class in the global model, with an additive effect of being nasal-marked for juveniles.

Explanatory Variables

Three sets of variables were considered as predictors of variation in seasonal survival of adult female scaup, the focal parameters of this study. First, breeding effort, measured by proxy with water level on the study area and directly with breeding propensity, was considered as a predictor of breeding season survival and survival during the subsequent non-breeding period. Water level (WL) data collected hourly on the study area was used to calculate annual mean water level from the first to third quartile of nest initiation dates. Increased water levels on the study site could influence female breeding season survival by providing more secure nesting habitat; high water during summer results in hundreds of hectares of shallowly-flooded sedge habitat available for nesting hens. Predation of females nesting in large, contiguous areas of flooded sedge may be lower than in adjacent terrestrial nesting sites, as nest success has been documented higher in over-water nests than ground nests (Arnold et al. 1993, Koons and Rotella 2003a). Breeding propensity (BP), a direct measure of breeding effort that we hypothesized to affect seasonal rates of survival in a similar fashion, was estimated for the population each year based on the observed relationship in 2007-2009 between breeding propensity, female body condition, and habitat conditions on our study site (Warren et al. 2014**,** Appendix).

Second, we considered relationships between reproductive success and concurrent breeding season survival because mammalian predators (e.g., mink [*Mustela vison*]) may prey upon nests as well as attendant females (Koons and Rotella 2003a, Arnold et al. 2012). We quantified reproductive success in two ways – nest daily survival rate (DSR) and hen reproductive success (HRS, the product of annual estimates of breeding

propensity and nesting success, assuming no renesting; Appendix). We estimated nest

DSR for each year between 2006 and 2014, but given a lack of data, we used the

temporal average of DSR as the covariate value in 2005 (Appendix). We also assessed

the ability of HRS to predict non-breeding season survival, testing for a serial carry-over

effect of reproductive success. Higher HRS leads to a greater proportion of females in the

population that raise offspring, molt, and regain body condition on the study site prior to

fall migration. The sequential nature of these events leads to successful females having

less time for molt and regaining body condition than unsuccessful females, which can

negatively influence survival the subsequent winter (Nilsson and Svensson 1996, Harms

et al. 2014).

Last, the influence of change in harvest regulations (i.e., daily bag limit changed

in response to continental scaup populations) and estimated harvest were considered as

variables that could influence non-breeding season survival as scaup are a game species,

and harvest occurs on our study site as well as off the study site upon migration. We

explored the relationship between non-breeding season survival of females and variation

in Pacific Flyway 1) daily bag limit (DBL) and 2) estimated lesser scaup harvest

(HARV). Daily bag limit varied between 2 (2008), 3 (2005–2007, 2009–2011, 2013 and

2014) and 7 (2012) scaup day^{-1} during this study. Annual estimates of lesser scaup

harvest in the Pacific Flyway were obtained from http://www.flyways.us/regulations-and-

harvest/harvest-trends. Variables were z-standardized to have mean = 0 and standard

deviation = 1, excluding DBL, which was scaled to start at zero.

All models were fitted using simulated annealing due to evidence of models

converging on local minima (Lebreton and Pradel 2002). Models that did not converge

after six attempts at fitting were discarded from the analysis, resulting in a final model set

of 375 from a possible set of 420. We assessed the relative amount of biological variation

explained by each model using the ratio of deviance reduction (R) of a model between a

null and global model. First, we calculated Zheng's (2000) deviance reduction measure

for each model i, $D_i = 1 - \left(\frac{dev_i}{dev_{Null}}\right)$, where dev_i is model i's deviance, and the

denominator is the deviance of a null model. Our null model for this calculation had

constant 1) detection probabilities for each state, p^{AB}, p^{AN}, and p^D, 2) survival (i.e.,

transition) probabilities for each season, 3) first-winter juvenile female survival, and 4) an

additive effect of nasal-marking for juvenile females. Each model's D was then divided

by the deviance of a global model, providing a relative reduction in deviance, R.

RESULTS

We released 1,180 nasal-marked and banded and 1,025 band-only females

between May 2005 and September 2014, and received 177 hunter-shot recoveries, 72

(40.7%) of which occurred on the study site. Most (~80%) of recoveries were juvenile

females marked prior to the season of harvest; only 15 adult females were recovered by

hunters on the study site. We obtained 1,349 resightings and 384 recaptures from 2005–

2014, with 62 of the recaptures being band-only females that had been banded in a prior

year and were nasal-marked upon recapture. Of 16 females that were known to have lost

a nasal-marker, 13 were recaptured individuals and 3 were recovered individuals. Marker

retention for females marked 2005–2008, prior to application of epoxy, declined

significantly with months since marking (β on logit scale = -0.22, SE = 0.06). Marker

retention improved with addition of epoxy to the distal ends of markers during 2009–

2014 (β = -0.11, SE = 0.03) (Figure 4-2).

Overall goodness-of-fit tests were not significant for adult females, but were

significant for juveniles (Table 4-1). Estimated variance inflation factors were, with a

single exception, < 2, indicating modest heterogeneity in the dataset (Burnham and

Anderson 2002). The exception was Test M for juvenile females ($\chi^2_{16} = 47.0$, $P < 0.001$,

$\hat{c} = 2.9$; Table 4-1), a test of trap-dependence. The significant Test M result for juvenile

females indicated there was a difference in the probabilities of reencountering juvenile

females in different states after initial release, conditional on being present during both

periods. We believe the significant Test M result was a function of right-censoring

individuals who changed from AB to AN states upon recapture, making these transitions

for yearlings 'invisible' to GOF efforts. Right-censoring upon recapture resulted in all

juvenile females reencountered as a yearling either 1) in their original release state (i.e.,

no transitions among alive states), or 2) in the dead state, and thus led to a significant

Test M for our data set. Lastly, the focus of this study was adult female seasonal survival;

we included juveniles and modeled variation in first winter survival so we could

incorporate juvenile females in analysis upon recruitment at age one. For adult females,

the primary focus of this study, there was no evidence for overdispersion ($\hat{c} = 1.05$),

with only a slightly higher global $\hat{c} = 1.27$. We therefore did not inflate model variances.

Our study encompassed considerable environmental and biological variation;

breeding season water levels varied by 0.7m (2011 level - 2013 level) in a system

generally <1m deep (Table 4-2). Median nest initiation ranged from 14 June – 5 July, and

nest daily survival rate ranged from 0.966 – 0.986, resulting in mean annual nesting

success (i.e., DSR[34]) from 30.8% – 61.9% (Table 2). Pacific Flyway scaup daily bag limit varied from 2 (2008) to 7 (2012), with all remaining years 3 (Table 4-2).

Event Probabilities

The top model structure for detection probabilities, which was used in subsequent modeling of female seasonal survival (Lebreton et al. 2009), included 1) full temporal variation in adult p^{AN}, 2) three direct recapture periods for p^{AB}, and 3) constant recovery and reporting rate conditional on death p^D (Table 4-3). We found weak support for lower detection probability of yearling scaup females and direct recovery periods (Table 4-3), so employed the simpler top model without these effects throughout remaining modeling efforts to examine variation in seasonal survival of scaup females.

First-winter Survival

The main thrust of this work was exploring adult female seasonal survival, but considerable numbers of juvenile females were nasal-marked and 'graduated' into adulthood after their first winter. We therefore modeled female first-winter survival similar to event probabilities. Our best model of female first-winter survival indicated constant survival during the 7 non-breeding seasons during which enough juvenile females were marked and released (AB and AN states) during preceding banding periods to estimate survival. Only 6 juveniles were released in state AN between 2005–2008; juvenile AN releases between 2009 and 2014 ranged from 18 (2011) and 195 (2012). All top models also included a nasal-marker effect on first-winter survival, indicating nasal-marked juveniles had lower survival than band-only juvenile females. All subsequent

modeling of adult survival included constant first-winter survival with a respective

additive marker effect on transition probability structures.

Adult Seasonal Survival

The most supported model for seasonal survival of adult females indicated that

both breeding and non-breeding season survival were most influenced by breeding season

water level (Table 4-5, Figure 4-3). There was considerable support for the top model;

model weight for the top model was 0.767 and the residual reduction in deviance, R, was

0.723 (Table 4-5). Moreover, the second best model was > 4 AIC_c away from the top

model and had a model weight of only 0.088, 11.5% of the top model. More direct

measures of reproductive effort and success, i.e., breeding propensity (BP), hen

reproductive success (HRS), and nest daily survival rate (DSR) were thus not supported

as predictors for either breeding or non-breeding season survival (Table 4-5). Nor did we

find support for an influence of harvest metrics (DBL, HARV) on non-breeding season

survival; all models within 7 AIC_c units of the top model included breeding season water

level as the best predictor of non-breeding season survival (Table 4-5). Based on the top

model, resighting rates for adult nasal-marked females ranged from 0.107 (95%CI =

0.058–0.192) in August 2013, to 0.794 (95%CI = 0.498–0.937) in May 2007, both

drought years. Recovery rate, i.e., the probability of being found and reported conditional

on death, for females was 0.136 (95%CI = 0.115–0.159).

The top model indicated a positive relationship between adult breeding season

female survival and breeding season water levels, resulting in breeding season female

survival ranging from 0.686 (SE=0.059) in 2007, the driest breeding season of the study,

to 0.911 (SE=0.038) in 2011, the wettest breeding season during the study (Figure 4-3). Conversely, a possible carryover effect was indicated by the negative relationship between reproductive effort (as measured by proxy with water level on the study site) and adult female non-breeding season survival (Figure 4-3). Adult non-breeding season female survival ranged from 0.492 (SE=0.042) in 2011, to 0.969 (SE=0.003) in 2007 (Figure 4-3). Adult annual survival ranged from 0.448 (SE=0.012) in 2011 to 0.712 (SE=0.008) in 2010 (Figure 4-3). First-winter survival of band-only females was 0.521 (SE=0.052), and we did find evidence of a marker effect on juveniles – estimated first-winter survival of nasal-marked females was only 0.256 (SE=0.025).

Given the effect of nasal markers on juvenile survival, we explored marker effects on adult females in a *post hoc* analysis. Building off our top model, we included an additive effect of being nasal marked for adult female survival during the non-breeding season (too few AB adult females were captured during post-breeding banding to provide stable estimation of a possible effect during the breeding season). Estimated non-breeding season survival of adult AN females for the ten-year period was 0.687 (95%CI = 0.654–0.719), and adult AB female survival was 0.657 (95% CI = 0.535–0.761); thus indicating no effect of nasal markers on adult female survival during the non-breeding season. Juvenile AN and AB survival estimates from this *post hoc* analysis were consistent with those from the top model presented above.

DISCUSSION

We found that complex seasonal interactions resulted in serial survival costs to reproduction in lesser scaup as a function of habitat conditions during breeding. Although

we had predicted that habitat conditions favorable to breeding would induce concurrent survival costs of reproduction because of a documented increase in reproductive investment (Warren et al. 2013) and associated exposure to predation, female breeding season survival was positively correlated with breeding season habitat conditions. This is contrary to the many studies that have found a negative relationship between breeding habitat conditions and female survival during the breeding season (e.g., Sargeant and Raveling 1992, Arnold and Clark 1996, Rotella et al. 2003, Arnold et al. 2012). Increased water levels on our study site result in greater contiguous area of flooded emergent vegetation (predominantly *Carex* spp.) available to nesting females. When emergent vegetation is flooded during the breeding season females commonly swim off the nest when approached, flushing tens of meters from the nest and approaching disturbance. When emergent vegetation is not flooded, females remain on the nest longer when approached, often flushing directly from the nest, potentially making them more susceptible to predation (JMW, pers. obs.). Corroborating this, over-water nests have higher survival than ground nests (Arnold et al. 1993, Koons and Rotella 2003a), and female mortality risk during the breeding season tends to be greatest during incubation of terrestrial nests and lowest during brood rearing when females occupy aquatic habitats (Koons and Rotella 2003b, Arnold and Howerter 2012). In addition, we found that more direct measures of breeding effort and/or success, i.e., breeding propensity, nest survival, and hen reproductive success, were poor predictors of breeding season survival.

Breeding season survival of female lesser scaup on our study area was instead lowest during years with poor habitat conditions for reproductive investment. Reduced annual survival during years with poor breeding conditions has been documented in

female common eider (*Somateria mollissima*, Coulson 1984) and canvasback (Hochbaum 1944), although the season of mortality was not determined in either study. Breeding season drought conditions result in fewer females breeding (Rogers 1964, Afton 1984), although breeding propensity is still relatively high on our study site during drought (0.85, SE=0.05; Warren et al. 2014). Therefore, reduced breeding season survival during years with poor habitat conditions could result from either an exogenous habitat effect, or from females that do breed paying a higher concurrent survival cost than when habitat conditions are good. Increased susceptibility to predation during drought-year nesting could increase mortality risk for breeding females (see above), or mortality could increase for all females as a function of deteriorating environmental conditions. Either, or both, mechanisms could influence drought-year female survival on our study site, and further work would be necessary to determine their relative role in breeding season mortality of scaup and similar species.

Despite the lack of evidence for hypothesized concurrent survival costs of reproduction, scaup females experienced a serial survival cost to reproduction through a COE from breeding to non-breeding seasons. Non-breeding season survival was relatively high following breeding seasons with poor to average habitat conditions, but declined sharply as habitat conditions improved and breeding propensity approached unity (Figure 4-3, Warren et al. 2014). Breeding season COEs have largely been identified as a fecundity cost to reproduction the subsequent breeding season through manipulative studies of reproductive effort (Lessells 1986, Catry et al. 2013, Fayet et al. 2016), with few documenting serial survival costs to reproduction (but see Daan et al. 1996, Nilsson and Svensson 1996). A population-level decline in non-breeding season

survival following a breeding season with high reproductive effort could result from all breeding females experiencing an equal cost of reproduction. Conversely, the decline could be driven by young and/or low quality females experiencing a disproportionately higher survival cost of reproduction. Younger and/or lower-quality females commonly breed at higher rates when environmental conditions are favorable (Boekelheide and Ainley 1989, Barbraud and Weimerskirch 2005, Tavecchia et al. 2005), and reduced post-breeding survival for first-time breeders is well documented (Viallefont et al. 1995, Cam and Monnat 2000, Barbraud and Weimerskirch 2005, Sanz-Aguilar et al. 2008). Moreover, individual quality has been documented across a broad spectrum of species, and on the study site, providing evidence that 'high-quality' individuals survive and reproduce at higher rates than 'low-quality' conspecifics (Cam et al. 1998, Arnold and Howerter 2012, Warren et al. 2014, Kennamer et al. 2016). This further corroborates the hypothesis that the COE documented during this study could result from increased young and/or poor quality individuals breeding when habitat conditions are favorable.

Mechanism(s) leading to a serial survival cost of reproduction may also be related to individual condition at the termination of breeding, which coincides with molt and the need to regain body condition prior to migration. Increased reproductive effort can lead to reduced body condition and delayed molt prior to migration (Lessells 1986), a physiologically challenging time for waterfowl that undergo a flightless period between reproduction and migration (Hohman et al. 1992, McWilliams et al. 2004). Lesser scaup are one of the latest-nesting waterfowl species in North America (Baldassarre 2014), and our study site represents one of the harshest scaup breeding areas in North America due to a short growing season (Gurney et al. 2011), reducing the amount of time for

completing these activities. Female breeding season body condition and health on the study site, the latter measured as the ratio of heterophiles to lymphocytes, are lowest during this period (Stetter 2014). Molt constrained by time and/or energy can be costly in terms of subsequent survival. For example, experimentally delayed breeding in blue tits (*Parus caeruleus*) resulted in birds expending about 15% more energy in thermoregulation than did control birds during the subsequent winter due to poorer quality feathers produced during a time and/or energy constrained molt (Nilsson and Svensson 1996). Elevated stress during molt has also been linked to reduced survival in birds (Harms et al. 2014, Latta et al. 2016), further corroborating that the timing of, and body condition during, molt provides a mechanism for a COE from breeding to non-breeding seasons in scaup females. Post-breeding females in poor body condition may also incur higher harvest rates (Dufour et al. 1993, Pace and Afton 1999), although we did not find support for our hypothesized relationships between female non-breeding season survival and harvest metrics.

The opposing responses of seasonal survival rates to breeding season water levels resulted in annual survival peaking near mean habitat conditions experienced during the breeding season, and declining as conditions deteriorated or improved. Annual survival was lowest in years when breeding habitat conditions were most favorable to reproduction, indicating an overall cost of reproduction to scaup females. Rotella et al. (2003) similarly found a negative correlation between wetland conditions and female lesser scaup annual survival in the Prairie Pothole Region, a pattern also documented in dabbling ducks (Arnold and Clark 1996). Annual survival varied considerably during our study (range 0.448–0.712, SD=0.098, CV=15.4%), with a similar range of values, but

with an overall mean survival (0.636, SE=0.031) slightly higher than prior studies

(Rotella et al. 2003, Arnold et al. 2016).

Survival costs of reproduction are well documented, but often do not differentiate

the seasons when the costs are incurred (Clutton-Brock et al. 1983, Pugesek and Diem

1990, Barbraud and Weimerskirch 2005, Tavecchia et al. 2005, Hadley et al. 2007),

which precludes determining if the cost incurred was a COE or concurrent with the

reproductive event. Understanding when in the annual cycle a survival cost of

reproduction occurs provides important information for understanding life history

evolution and informing conservation decisions. Conservation efforts for long-distance

migratory species, such as lesser scaup, necessarily consider the annual life cycle at a

continental scale (Austin et al. 2010). Vital rates (e.g., seasonal female survival) that

demonstrate the greatest influence on population growth rate are identified, and

management actions (e.g., harvest management, habitat acquisition) are targeted to

increase them. The finite population growth rate of lesser scaup is most sensitive to

proportional changes in female breeding season survival, followed by non-breeding

season survival (Koons et al. 2006). Our results indicate breeding season survival could

be increased via water management on the study site, although this may be unique to our

study system. However, increased female breeding season survival may come at a high

cost to non-breeding season survival, and subsequently annual survival, outweighing

potential gains in population growth rate. Improving non-breeding season habitat

availability and quality for females does not have this hidden potential cost to survival,

but may have other effects that are not well understood. This underscores the importance

of understanding seasonal interactions for migratory species, i.e., where reproductive costs are experienced by species living in seasonal environments.

Female scaup breeding on our study site employ diverse migratory and wintering strategies, wintering as close as riverine systems <350 km distant and as far as estuarine systems of the Pacific Ocean and Gulf of Mexico 1,000–2,800 km distant (JMW, unpublished data). Females from the study site use wintering areas common to three of the four North American Flyways (i.e., Pacific, Central, and Mississippi), resulting in 'overlap' during winter with ≈ 60% of the continental population of lesser scaup (Baldassare 2014). While the broad winter distribution of females from the study site precludes estimating mean conditions experienced during that period, it indicates non-breeding season survival rates estimated during this study may be representative of a much broader portion of the continental population. This is significant in that our estimates of non-breeding season survival are the first published that included the entire non-breeding season. Moreover, our study design allowed understanding non-breeding season survival in the context of breeding season conditions, giving us the ability to examine seasonal interactions (COEs) and costs of reproduction manifested as a serial survival cost. Further work will be necessary to clarify potential mechanisms for the high serial survival cost to reproduction documented during our study, and other drivers of seasonal survival in migratory species.

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TABLES AND FIGURES

TABLE 4-1. Goodness-of-fit test results for female lesser scaup banded and resighted or recovered from 2005 to 2014 at Red Rock Lakes National Wildlife Refuge, Montana. Potential extra-binomial heterogeneity in the data due to transience (Test 3G) and trap-dependence (Test M) was assessed for adults and juveniles.

$\hat{c}$ = variance inflation factor.

	Adults			Juveniles		
	χ^2	df	P	χ^2	df	P
Test 3G	35.6	41	0.71	3.3	18	1.00
Test M	21.0	13	0.07	47.0	16	<0.001
Overall test	56.7	54	0.38	50.4	34	0.04
$\hat{c}$		1.05			1.48	
Global $\hat{c}$			1.27			

TABLE 4-2. Table of covariate values used to test concurrent and serial survival costs of reproduction for female lesser scaup 2005–2014, southwestern Montana. All continuous covariates were *z*-standardized for analysis; daily bag limit was scaled to start at zero (i.e., 2 was subtracted from all values).

Year	Breeding Season Lake Stage (msl)[a]	Median Nest Initiation	Breeding Propensity	Nest Daily Survival Rate	Hen Reproductive Success[c]	Daily Bag Limit	Pacific Flyway Harvest
2005	2014.06	22 June[b]	0.943	0.975[b]	0.409*	3	28070
2006	2014.16	22 June	0.941	0.986	0.588	3	34170
2007	2013.55	15 June	0.910	0.974	0.367	3	51410
2008	2013.91	24 June	0.942	0.977	0.421	2	27110
2009	2013.90	21 June	0.945	0.975	0.403	3	30210
2010	2013.76	24 June	0.852	0.971	0.311	3	23180
2011	2014.37	5 July	0.878	0.969	0.296	3	22050
2012	2013.91	14 June	0.914	0.966	0.281	7	62590
2013	2013.67	24 June	0.845	0.980	0.429	3	40530
2014	2014.11	19 June	0.883	0.985	0.522	3	37610

[a]Mean lake stage, meters above sea level (msl), from 1st to 3rd quantiles of nest initiation for each year.

[b]Overall mean values during the study; nest searching and monitoring did not occur in 2005.

[c]Product of breeding propensity and nesting success (probability of hatching at least one egg), assuming renesting does not occur.

TABLE 4-3. Top models for detection probabilities among nasal-marked and banded (AN) and band-only female lesser scaup (AB), as well as recovery and reporting rates conditional on death (r). Event probabilities were fitted with a transition probability (Ψ) structure that allowed full temporal variation in seasonal adult female survival (breeding and non-breeding seasons, 2005–2014) and juvenile first-winter survival, and an additive effect of being nasal-marked for juveniles. Only models within 7 AIC$_c$ units of the top model are presented.

Event Probability Structure	k^a	ΔAIC$_c$	Weight[b]	Deviance
$AN_{(t)} + AB_{(period)} + r_{(.)}$	51	0.00	0.375	5886
$AN_{(t+yearling)} + AB_{(period)} + r_{(period)}$	53	1.22	0.204	5883
$AN_{(t+yearling)} + AB_{(period)} + r_{(.)}$	52	1.98	0.140	5886
$AN_{(t)} + AB_{(year)} + r_{(period)}$	57	2.37	0.115	5876
$AN_{(t)} + AB_{(year)} + r_{(.)}$	56	3.23	0.075	5879
$AN_{(t+yearling)} + AB_{(year)} + r_{(period)}$	58	4.35	0.043	5876
$AN_{(t+yearling)} + AB_{(year)} + r_{(.)}$	57	5.25	0.027	5879
$AN_{(t)} + AB_{(period)} + r_{(year)}$	58	6.63	0.014	5878

[a]Number of estimated parameters.

[b]Normalized relative model likelihoods.

TABLE 4-4. Model results for first-winter survival of juvenile lesser scaup females banded (state AB), or nasal-marked and banded (state AN) between 2005–2014 at Red Rock Lakes National Wildlife Refuge, Montana, USA. Event probabilities for each state were 1) temporally-varying for AN females, 2) direct recapture periods for AB females, and 3) constant recovery conditional on death (state D). Adult female seasonal survival (i.e., breeding and non-breeding seasons) was fully time varying. Only models within 7 AIC$_c$ units of the top model are presented.

First-winter Survival	k^a	ΔAIC$_c$	Weight[b]	Deviance
constant	45	0.00	0.367	5890
water level	46	0.87	0.238	5889
Pacific Flyway harvest	46	0.95	0.228	5889
daily bag limit	46	1.64	0.161	5889

[a]Number of estimated parameters.

[b]Normalized relative model likelihoods.

TABLE 4-5. Comparisons of alternative multi-state models for explaining temporal variation in seasonal survival of female lesser scaup marked in southwestern Montana, 2005–2014. Only models within 7 AIC$_c$ units of the most supported model are presented. All models include parameters for hatch-year female survival with an additive effect of being nasal-marked, and allow encounter probabilities to 1) vary temporally across all survey periods for nasal-marked females, 2) vary among periods for physical recaptures, and 3) have constant recovery and reporting probability conditional on death (described in methods). Null and global model deviances, used in calculating R, were 6142 and 5871, respectively.

Survival						
Breeding Season	Non-breeding Season	k[a]	ΔAIC_c	Weight[b]	Deviance	R[c]
water level	*water level*	30	0.00	0.767	5946	0.723
constant	*water level*	29	4.34	0.088	5953	0.699
breeding propensity	*water level*	30	5.71	0.044	5952	0.702
nest daily survival rate	*water level*	30	6.10	0.036	5952	0.701
hen reproductive success	*water level*	30	6.37	0.032	5953	0.700

[a]Number of estimated parameters.

[b]Normalized relative model likelihoods.

[c]Relative reduction in model deviance when compared to the global model (see methods).
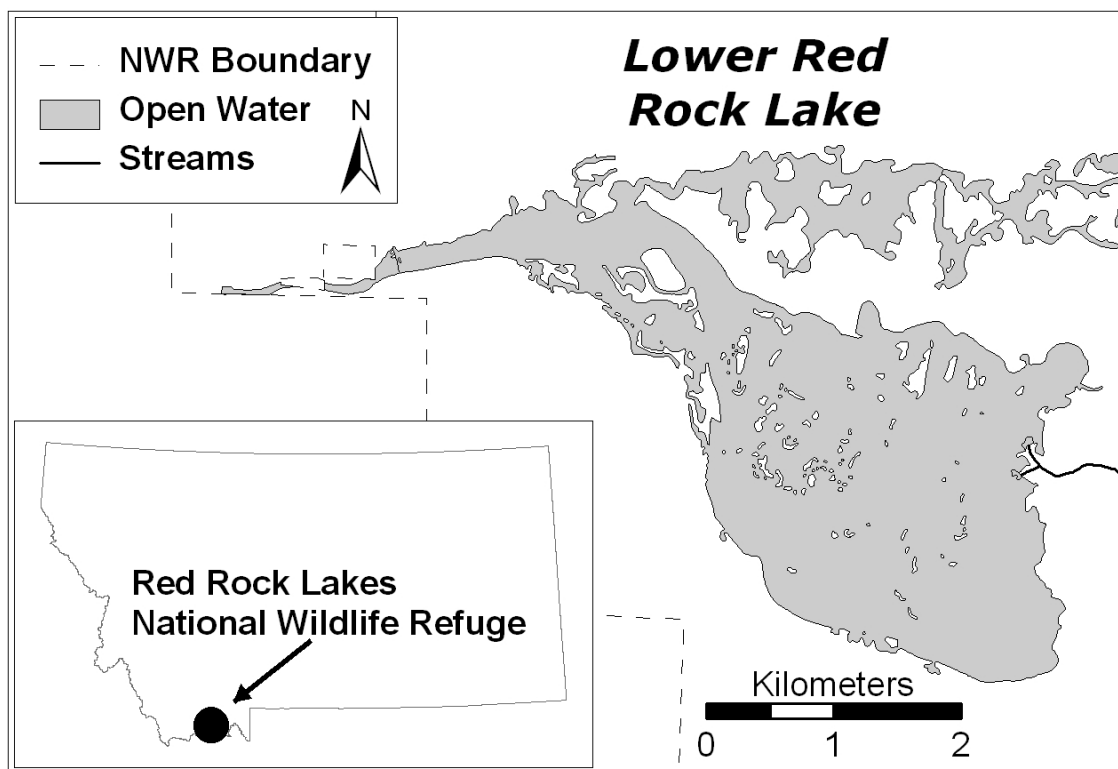
FIGURE 4-1. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge, Montana, USA.
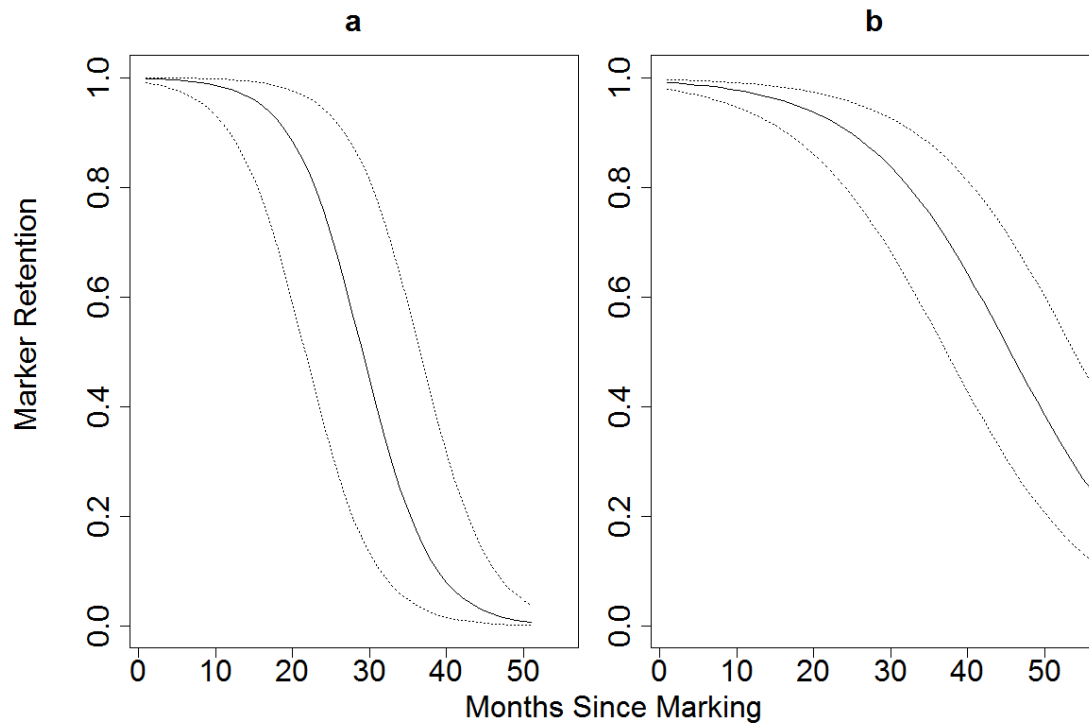
FIGURE 4-2. Nasal-marker retention as a function of months since marking a) 2005–2008, prior to addition of epoxy on distal ends of markers, and b) 2009–2015, when epoxy was used to aid marker retention.
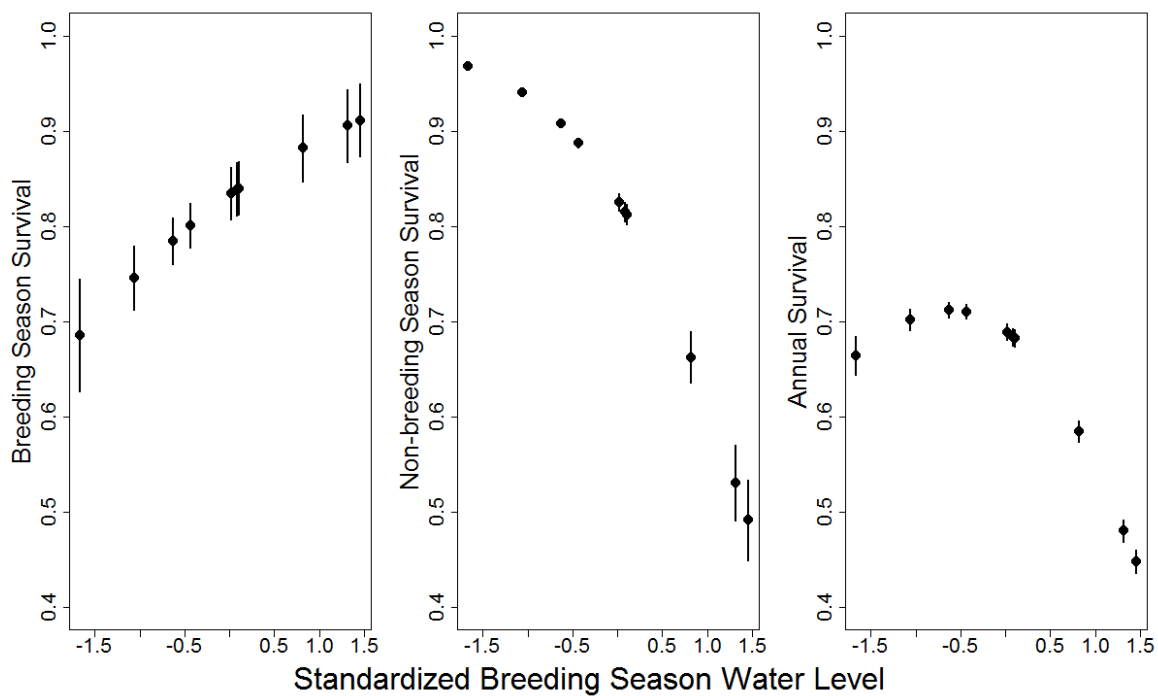
FIGURE 4-3. Seasonal and annual survival (±1 SE) of female lesser scaup (*Aythya affinis*) in relation to breeding season water levels at the Lower Red Rock Lake study area. Breeding season was defined as mid-May–early September and non-breeding season was defined as early September–mid-May.

CHAPTER 5

CONCLUSION

An individual's life may be a linear sequence of events from birth to death, but species in seasonal environments are shaped by the circular nature of seasonality. The influence of annual life-cycle events on individuals may strongly interact among seasons, creating the opportunity for carry-over effects and seasonal interactions. For example, conditions experienced by an individual during winter can have reproductive consequences the subsequent breeding season (Marra et al. 1998, Saino et al. 2004, Gunnarsson et al. 2005, Guillemain et al. 2008). Similarly, reproductive decisions may influence an individual's survival and fecundity the subsequent non-breeding and breeding seasons, respectively (Daan et al. 1996, Hanssen et al. 2005, Blomberg et al. 2012, Fayet et al. 2016). The decision to breed is likely the most significant fitness-related decision an individual makes within a year, but is only the first of several decisions with life history consequences if reproduction is undertaken. Timing of reproduction, and parental effort invested, are also important reproductive decisions that influence current and future fecundity and survival (Hochachka 1990, Verboven and Visser 1998, Lepage et al. 2000, Golet et al. 2004). In Chapters 2 and 3, I examined intrinsic (e.g., body condition, age) and extrinsic (e.g., water conditions) drivers of a female's decision of if, and when, to breed in lesser scaup (*Aythya affinis*), a long-distant migrant with intermediate life span. In Chapter 4, I assessed survival consequences of female reproductive effort within and among seasons, the ultimate cost of reproduction in iteroparous species.

The decision of if, and when, to breed is strongly influenced by a female's pre-breeding body condition. Lesser scaup spend a protracted pre-breeding period on breeding areas, providing opportunity to increase body condition prior to clutch formation. Quality of young declines with advancing lay date, however, resulting in a trade-off between how much time a female should spend increasing body condition to produce a larger clutch and initiating a nest in lower body condition and producing fewer, but higher quality, young (Béty et al. 2003, Descamps et al. 2011). In Chapter 2, I found that a female's ability to increase pre-breeding body condition on the breeding area was strongly influenced by environmental conditions, i.e., spring phenology and water depth. Springs with early phenology and low water levels had the highest rates of pre-breeding body condition gain. Female age influenced arrival body condition, with yearlings arriving in poorer condition than older conspecifics, but rate of pre-breeding body condition gain was similar between age classes. Corroborating the cost-of-delay hypothesis as formalized in the condition-dependent individual optimization model of Rowe et al. (1994), the rate of body condition gain during the pre-breeding period was positively related to clutch size. However, I did not find support for the predicted relationship between the intra-annual decline in clutch size and rate of body condition gain, another prediction of the cost-of-delay hypothesis and Rowe et al.'s model.

The decision to breed is similarly influenced by a female's age, body condition, and environmental conditions. In Chapter 3, I found that female lesser scaup breeding propensity is strongly positively related to body condition, providing support for a threshold body condition that must be achieved prior to undertaking breeding. This threshold declined during the breeding season, i.e., females in better condition bred

earlier in the season and breeding female condition was negatively correlated with date. This is also consistent with the condition-dependent individual optimization model (Rowe et al. 1994), which predicts that a female's optimal decision regarding when to breed is a function of her body condition and the intra-seasonal decline in quality of young, the latter of which has been documented on the study site (Stetter 2014). Breeding propensity also declined during drought years, a common phenomenon in *Aythya* females (Afton 1984, Anderson et al. 2001), although it is not known if females are constrained or demonstrate restraint when conditions are not favorable for breeding (Curio 1983). I found weak support for an age effect on breeding propensity, and evidence of individual heterogeneity among females. Females with evidence of prior reproductive success on the study site bred at higher rates than females lacking this evidence. Individual heterogeneity is relatively common in birds (Cam et al. 2002, Kennamer et al. 2016), leading to positive correlation between survival and fecundity in 'high-quality' individuals.

Survival costs of reproduction can occur concurrent with, or serial to, a reproductive event. An individual that survives the reproductive event but is in a reduced physiological state, or has less time to complete metabolically-costly annual events such as post-breeding molt, may have reduced survival during the subsequent non-breeding season. In Chapter 4, I used a ten-year data set of uniquely-marked females to investigate drivers of within- and among-season survival as a function of reproductive effort. Female breeding and non-breeding seasonal survival was most correlated with breeding season water levels on the study site, but in opposing directions. Female breeding season survival was positively related to water levels, likely the result of increased area of

highly-secure nesting habitat (i.e., shallowly-flooded sedge [*Carex* spp.]). Conversely, breeding habitat conditions documented to increase reproductive effort in scaup on the study site (Warren et al. 2014) led to reduced non-breeding season survival, i.e., a carry-over effect (COE) of reproduction. Reproduction reduces physiological state of females (Stetter 2014), and constrains a female's time to molt (Austin and Fredrickson 1986, Lessells 1986), which can have survival consequences the subsequent non-breeding season (Nilsson and Svensson 1996, Harms et al. 2014). If this hypothesized mechanism for the documented COE is correct, breeding early would convey fitness benefits to a female beyond increased quality of young and thereby increase the importance of pre-breeding body condition. Optimization of the trade-off between the current reproductive event and lifetime reproductive success for an individual would necessarily have to include survival costs of delay for both parent and offspring. Most explanations of breeding cost of delay focus on the latter, likely due to the greater demonstration of declining survival of young with increasing hatch date.

I provide the first estimates of seasonal survival for lesser scaup that I am aware of, but perhaps more importantly, I was able to provide estimates of non-breeding season survival in the context of breeding season conditions, demonstrating a breeding season COE of reproduction on female survival. Future work could build upon results presented herein and explore age-specific seasonal survival as a function of reproductive effort and environmental conditions, testing the hypothesis that the increase in young and/or low quality females breeding in years with habitat conditions favorable to reproduction resulted in the strong survival cost of reproduction documented as a breeding season COE. This study is also uniquely situated to explore optimal reproductive decisions based

on increasing nest survival (Pokely 2014) and decreasing duckling survival (Stetter 2014) with advancing lay date, and adult female seasonal survival. Lastly, examining the response of population growth to temporal covariation in vital rates to inform conservation actions should be pursued. This study has concurrently estimated vital rates since 2006 (female seasonal survival, breeding propensity, and nest survival), with studies of duckling and juvenile survival starting in 2010.

This study is also the first I am aware of that estimated and accounted for marker loss for a marking technique common in ducks (Lokemoen and Sharp 1985, Arnold and Clark 1996, Rotella et al. 2003). Given the high rate of marker loss we documented early in the study, it is likely that prior studies using similar marking techniques underestimated survival. I also found a significant marker effect on juvenile, but not adult, survival. As this and similar studies progress it will be important to address ethical considerations associated with marker effects, and consideration of marker loss effects on estimation of demographic parameters. Lastly, long-term demographic studies like the Red Rock Lakes lesser scaup study provide a unique opportunity to advance our understanding of harvest and habitat impacts on species as they make life history decisions when confronted with changing environmental conditions, and the consequences of those decisions, i.e., trade-offs, that have population-level ramifications.

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APPENDIX

Breeding Propensity

We estimated annual female breeding propensity of lesser scaup following Warren et al. (2014). First, we estimated a size-adjusted body condition for females captured during pre-breeding and nesting periods. Body condition of females captured during the nesting season (i.e., 9 June – 5 July) was then regressed with date of capture using a linear mixed-effects model with a random intercept of year. An annual estimate of mean body condition was then predicted using each year's median nest initiation date and random intercept. Because no nest searching was conducted in 2005 the overall median nest initiation date for 2006–2013 was used (22 June). We then predicted annual breeding propensity using the best breeding propensity (BP) model (a generalized linear model with binomially-distributed errors and a logit link) from Warren et al. (2014)

$$BP = 2.082 + 0.082 * CDate + 0.032 * BCI - 0.984 * Drought,$$

where *CDate* is relative capture date (median nest initiation date = 0), *BCI* is female body condition index, and *Drought* is a categorical variable based on breeding season water levels on the study site (2007, 2010, and 2012–2014 were drought years and the remaining years non-drought).

Nest Monitoring

Nest searches were conducted within *Carex* spp. dominated habitats on the study site each year beginning in 2006. Observational cues of females and trained dogs were used to locate scaup nests during two searches completed between late May and mid-July. Searches were conducted between 0600 and 1300 hours daily; nests found incidentally while conducting other field work were included. When nests were located

the number of eggs and incubation stage, as determined by field-candling (Weller 1956), were recorded. Nest initiation date was estimated by subtracting the number of eggs and days of incubation from the current date and adding 1 day. Nests were revisited every 6–10 days until fate was determined (i.e., successful [at least 1 egg hatched], destroyed, or abandoned).

Reproductive Success

Annual estimates of nest daily survival rate (DSR) were calculated for 2006–2014 using the package RMark in R version 3.0.3 to implement nest survival models in program MARK. Nests abandoned, damaged or destroyed due to investigator activity were not included in analysis. Nest monitoring did not occur during the first year of the study, so mean nest DSR was used for 2005's DSR covariate value in female seasonal survival analyses. All variables were z-standardized to have a mean of zero and standard deviation of one. An index of annual hen reproductive success (HRS) was calculated as BP*DSR[34].

CURRICULUM VITAE

Jeffrey Michael Warren
Red Rock Lakes National Wildlife Refuge
27650 B South Valley Road
Lima, Montana 59739
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jeffrey_warren@fws.gov

Education   *Utah State University – Logan, UT*
Doctor of Philosophy, Wildlife Biology
Enrolled January 2010, current GPA 3.83, expected graduation date 2017

Montana State University - Bozeman, MT
Master of Science, Fish and Wildlife Management.
Graduated August 2004, GPA 3.72

Michigan Technological University - Houghton, MI
Bachelor of Science, Biological Sciences with Ecology minor
Graduated June 1996, cumulative GPA 3.41, departmental GPA 3.48

Experience   *Wildlife Biologist, Inventory and Monitoring*
November 2010 – current, GS-13
US Fish and Wildlife Service, Mountain Prairie Region
Red Rock Lakes National Wildlife Refuge
27650 B South Valley Rd
Lima, MT 59739
Supervisor: Steven Kettler, M.Sc. (303)236-4369
- Responsible for providing science support for National Wildlife Refuges within the states of Montana, Utah, and Wyoming, including
  o Develop and lead data management and analysis workshops across the USFWS Mountain-Prairie Region
  o Advise students of the Master of Science in Science Education program (Montana State University) while conducting ecological research projects on National Wildlife Refuges
- Assist Refuge System staff with managing and analyzing data and reporting inventory and monitoring results
- Participate in protocol development and assignment for inventory and monitoring efforts on National Wildlife Refuges, Wetland Management Districts, and surrounding lands
- Lead development of Adaptive Management projects for resource management

- o Arctic grayling conservation in the Centennial Valley
- o Winter feeding of elk and bison on the National Elk Refuge
- Coordinate collaborative science and monitoring
  - o Lead developer of Intermountain West Wetland Working Group
  - o Developing wetland state-and-transition modeling approaches for wetland management

Wildlife Biologist
March 2004 – November 2010
Red Rock Lakes National Wildlife Refuge
27650 B South Valley Rd
Lima, MT 59739
Supervisor: Bill West, M.Sc. (406)276-3536

- Responsible for developing, prioritizing, and implementing the Refuge's biological program
- Initiate and develop partnerships with state and federal agencies, and non-government organizations, to address complex resource management issues faced by the Refuge, including
  - o Moose willow browse study with Montana Fish, Wildlife & Parks
  - o Integrated pest management with The Nature Conservancy
  - o White-faced ibis annual survival study with Idaho Department of Fish and Game
  - o Master of Science in Science Education internship program with Montana State University
- Design and implement monitoring to assess response of target organisms to management activities
- Build diverse teams of stakeholders to address complex natural resource issues at local, regional, and national scales
- Obtain funding and oversee all aspects (design, analysis, report and manuscript preparation) of research projects, including
  - o "The role of habitat quality and climate in waterbird fitness in montane wetland ecosystems"; 4 year study of waterbird survival and recruitment
  - o "Alternate hypotheses for the continental decline of Lesser Scaup"; 1 year study of contaminant levels in Lesser Scaup eggs
  - o "The role of winter and spring resources on breeding propensity of Lesser Scaup: could the spring condition hypothesis explain the continental decline of scaup?"; 3 year study of breeding propensity and breeding season survival of Lesser Scaup

- o "Temporal covariation of Lesser Scaup demographic rates and implications for management"; 8 year study of covariation in breeding season demographic rates of Lesser Scaup
- Authored, or supervised writing of, Comprehensive Conservation Plan sections dealing with habitat and wildlife
  - o Integrated Refuge's target species with state, regional, and national priorities and objectives
  - o Synthesized available data to provide management strategies for target species
- Hire and supervise seasonal technicians
- Coordinate fall and winter Tri-state trumpeter swan surveys for Montana, Idaho, and Wyoming
- Represent the Refuge at various meetings, e.g. Pacific Flyway Council, Greater Yellowstone Trumpeter Swan Working Group
- Design and manage databases (Microsoft® Access, Visual Basic for Applications [VBA], and SQL), manage and analyze spatial data (ArcGIS 9.2) and conduct analyses (R 2.9.0, Program MARK, PRESENCE 2.0) for Refuge research and monitoring programs
- Produce peer-reviewed manuscripts from Refuge monitoring and research projects
- Subject editor for the *Journal of Fish and Wildlife Management*, a USFWS on-line peer-reviewed publication

Range Technician/Firefighter
July 1997 – March 2004, GS-5, intermittent
June 1996 – February 1997, GS-4, temporary
Red Rock Lakes National Wildlife Refuge
27650 B South Valley Rd
Lima, MT 59739
Supervisor: Greg Dehmer (406)276-3536

- Responsible for experimental design, fieldwork, and analysis for study investigating the relationships among abiotic factors, submerged aquatic vegetation, and waterbirds in Lower Red Rock Lake
- Developed Adaptive Management Resource plan for Lower Red Rock Lake, which is used to direct water-level management as well as reduce the uncertainty associated with the response of the wetland complex to water-level manipulations
- Assisted with proposal development to monitor fall migration routes and winter habitat usage of trumpeter swans via satellite telemetry
- Performed winter neck collar surveys, brood observations and banding of trumpeter swans
- Acted as aerial survey observer for fall and winter trumpeter swan surveys of southwest Montana

- Coordinated winter waterfowl and bald eagle surveys and prepared biological reports
- Mapped locations and organized control of noxious weeds
- Assisted with Refuge tours and provide visitors with information and directions
- Performed fire suppression and prescribed burning (FFT1, Engine Boss Trainee)
- Responsible for various maintenance duties around Refuge that included fencing, vehicle maintenance, grounds maintenance

Graduate Research Assistant
May 2001 – May 2003
Montana State University
Department of Ecology
Bozeman, MT 59717
Supervisor: Jay Rotella, Ph.D. (406)994-5676
- Investigated relationships among intensity of cattle grazing and nest density and nesting success of upland-nesting ducks in the western Aspen Parkland
- Organized methodology, coordinated logistics, selected study sites (n = 97), and obtained permission from landowners to access property for field-data collection
- Selected, trained, and supervised crew of 2 crew leaders and 4 technicians during 2001 and 2002 field seasons
- Responsible for daily data collection activities, including: systematic nest searches of upland and wetland cover for duck and shorebird nests using vehicle-pulled cable drags, nest-site habitat characterization, vegetation sampling, pair and brood surveys, predator observations, and range health assessment
- Organized and supervised entry and editing of data by technicians
- Performed data analysis (SAS 9.0) and completed Master's thesis
- Led project tours for Ducks Unlimited Canada field managers and Alberta Department of Agriculture Extension Specialists
- Project has been written up in Alberta Outdoorsman and Birdscapes

Research Assistant
October 2002 – December 2002
Montana State University
Department of Ecology
Bozeman, MT 59717
Supervisor: Jay Rotella, Ph.D. (406) 994-5676
- Assisted with study of Weddell seal population dynamics, McMurdo Sound, Antarctica

- Lived in remote camp and traveling to breeding colonies via snowmobile to mark newborn seal pups with uniquely coded flipper tags
- Tagged unmarked adults and replaced worn or broken tags of marked adults
- Performed surveys of breeding colonies

Graduate Teaching Assistant
September 2000 – May 2001
Montana State University
Department of Cell Biology and Neurosciences
Bozeman, MT 59717
Supervisor: Susan Gibson, M.Sc. (406)994-3151

- Prepared and presented weekly lectures for Human Anatomy & Physiology I & II laboratory sections
- Responsible for ~ 50 students each semester, including testing and grading
- Maintained laboratory and cadavers

Biological Technician/Project Leader
February 2000 – July 2000
Montana State University
Department of Ecology
Bozeman, MT 59717
Supervisor: Jay Rotella, Ph.D. (406)994-5676

- Organized pilot-year study investigating duck productivity in large intact grasslands of northcentral Montana
- Selected study site, acquired access from private landowners, organized/constructed necessary equipment to decoy trap, mark, and radio-track 25 mallard females
- Performed prong and suture transmitter attachment surgeries. Oversaw and performed data collection, including: banding records, daily telemetry locations, nest monitoring, daily predator observations, carnivore track count, stick nest survey, and land use
- Created reports for dissemination to cooperators and funding agencies

Research Assistant
September 1999 – February 2000
Wildlife Conservation Research Center
Department of Natural Resources Management and Engineering
Storrs, CT 06269-4087
Supervisor: John S. Barclay, Ph.D. (860)486-0143

- Reviewed literature relevant to greater scaup productivity, winter habitat, and contaminant levels

- Synthesized a proposal to investigate the relationship of winter habitat and contaminant levels to the productivity of greater scaup nesting on the west coast of Alaska
- Organized permits at the state and federal levels
- Presented proposed project to the Director's Committee of the WCRC

Biologist/Site Leader
October 1998 – September 1999
Institute for Wetland and Waterfowl Research
P.O. Box 1160
Stonewall, MB R0C 2Z0
Supervisor: Dave Howerter, Ph.D. (204)467-3000
- Obtained access from private landowners on 25 mi^2 study site in central Alberta
- Responsible for project logistics such as crew housing, vehicles, budget, personnel, and equipment
- Interviewed and selected 13 personnel to perform tasks associated with trapping, marking, and radio-tracking 136 mallard females and nest searching
- Oversaw training of personnel for decoy trapping, data management, telemetry, nest searching, and wetland classification
- Coordinated trapping and marking of 136 mallard females
- Performed transmitter implant surgeries and prong and suture transmitter attachments
- Responsible for data collection, including: daily telemetry locations, nest monitoring, brood observations, daily predator observations, carnivore track count, stick nest survey, land use, and wetland classification on study site
- Responsible for monthly updates

Telemetry Crew Leader
March 1998 – August 1998
Institute for Wetland and Waterfowl Research
P.O. Box 1160
Stonewall, MB R0C 2Z0
Supervisor: Glenn Mack, M.S. (780)489-8110
- Responsible for training and supervising five telemetry technicians in all aspects of the daily tracking of 135 radio-implanted mallard females
- Trained telemetry and nest search crews for decoy trapping and morphological measurements of ducks
- Tracked mallard females daily via null-array and hand-held telemetry systems
- Performed weekly aerial telemetry surveys to locate missing females

- Mist-netted and purse trapped mallard females on nests
- Attached prong and suture transmitters to nest-trapped females
- Performed brood observations
- Assisted with obtaining GPS locations for all waterfowl nests found
- Assisted with wetland classification on 25 mi^2 study site

Biological Technician
January 1998 – March 1998
Ducks Unlimited, Inc**.**
4974 Central Avenue, Suite A
Monroe, LA 71203-6102
Supervisor: Seth White, M.S. (318)340-1020

- Oversaw Wetland Restoration Program (WRP) sites in the Mississippi Delta of Louisiana
- Monitored seedling planting on bottomland hardwood wetland restorations. Collected compliance data to ensure plantings met Natural Resources Conservation Service (NRCS) specifications
- Coordinated with NRCS on site preparation and planting schedule logistics
- Worked as liaison between landowners, forestry contractors, Ducks Unlimited, and NRCS

Telemetry Technician
April 1997 – July 1997
Institute for Wetland and Waterfowl Research
P.O. Box 1160
Stonewall, MB R0C 2Z0
Supervisor: Glenn Mack, M.S. (780)489-8110

- Decoy trapped mallard females for radio-marking
- Performed banding, weighing and measuring (tarsus, head, keel and wing chord) of mallards
- Assisted with implantable transmitter surgeries and prong and suture transmitter attachment
- Tracked mallard females daily with vehicle mounted null-array and hand-held telemetry systems
- Assisted with aerial telemetry surveys to locate missing mallard females
- Completed nest habitat data for nests found via telemetry or incidentally
- Performed raptor stick nest surveys, daily predator observations and brood observations
- Responsible for telemetry vehicle maintenance

Undergraduate Research Volunteer

September 1995 – May 1996
Clearcut Avian Diversity Project
Michigan Technological University
School of Forest Resources and Environmental Science
Houghton, MI 49931-1295
<u>Supervisor</u>: Tom Waite, Ph.D. (614)292-5549
- Responsible for researching and reviewing relevant literature
- Performed point counts of over-wintering bird species in Michigan's northwestern
  Upper Peninsula
- Snowshoed to sites to identify bird species by sight and sound
- Performed data analysis and initial draft production

<u>Volunteer Positions</u> *Subject Editor*, Journal of Fish and Wildlife Management

<u>Publications</u> **Warren, J. M.**, J. Rotella, and J. E. Thompson. 2008. Contrasting effects of cattle grazing intensity on upland-nesting duck production at nest and field scales in the Aspen Parkland, Canada. Avian Conservation and Ecology 3:6 [online] <u>URL:http://www.ace-eco.org/vol3/iss2/art6/</u>

Olson, D, **J. Warren**, and T. Reed. 2009. Satellite-tracking the seasonal locations of Trumpeter Swans *Cygnus buccinator* from Red Rock Lakes National Wildlife Refuge, Montana, USA. Wildfowl 59:3–16.

Pollard-Wright, H. M., M. T. Wright, and **J. M. Warren**. 2010. Use of a portable tower and remote controlled launcher to improve physical conditioning in a rehabilitating wild mallard (*Anas platyrhynchos*). Journal of Avian Medicine and Surgery 24:308–315.

Gurney, K. E. B., R. G. Clark, S. M. Slattery, N. V. Smith-Downey, J. Walker, S. E. Stephens, M. Petrula, R. M. Corcoran, K. H. Martin, K. A. DeGroot, R. W. Brook, A. D. Afton, K. Cutting, **J. M. Warren**, M. Fournier, and D. N. Koons. 2010. Geographic variation in reproduction in a temperate–breeding bird species: strategies for coping with time constraints. Ecography 34:628–636.

Warren, J. M. and K. A. Cutting. 2011. Breeding strategy and organochlorine contamination in eggs of lesser scaup (*Aythya affinis*). Ecotoxicology 20:110–118.

Cutting, K. A., J. J. Rotella, K. A. Hobson, **J. M. Warren**, J. Y. Takekawa, and S. E. Wainwright. 2012. Endogenous contributions to egg

protein formation in lesser scaup *Aythya affinis*. Journal of Avian Biology 42:505–513.

Warren, J. M., K. A. Cutting, and D. N. Koons. 2013. Body condition dynamics and the cost-of-delay hypothesis in a temperate-breeding duck. Journal of Avian Biology 44:575-582.

Cutting, K. A., K. A. Hobson, J. J. Rotella, **J. M. Warren**, J. Y. Takekawa, S. E. W. De La Cruz, and M. Parker. 2013. Relative contribution of lipid sources to eggs of lesser scaup. Journal of Avian Biology 44:1-5.

Hopkins, J. B., III, K. A. Cutting, and **J. M. Warren**. 2013. Use of stable isotopes to investigate keratin deposition in the claw tips of ducks. PLoS ONE 8:e81026.

Sharp, J. L., R. S. Sojda, M. Greenwood, D. O. Rosenberry, and **J. M. Warren**. 2013. Statistical classification of vegetation and water depths in montane wetlands. Ecohydrology 6:173-181.

O'Neil, S. T., **J. M. Warren**, J. Y. Takekawa, S. E. De La Cruz, K. A. Cutting, M. W. Parker, and J. L. Yee. 2014. Behavioural cues surpass habitat factors in explaining prebreeding resource selection by a migratory diving duck. Animal Behaviour 90:21-29

Whelham, N. J., **J. M. Warren**, and M. R. Frisina. 2013. Effects of cattle grazing on small mammal communities at Red Rock Lakes National Wildlife Refuge, Montana. Intermountain Journal of Sciences 19:9-21.

Warren, J. M., K. A. Cutting, J. Y Takekawa, S. E. De La Cruz, T. D. Williams, and D. N. Koons. 2014. Previous success and current body condition determine breeding propensity in Lesser Scaup: evidence for the individual heterogeneity hypothesis. The Auk 131:287-297.

Cole, E. K., A. M. Foley, **J. M. Warren**, B. L. Smith, S. R. Dewey, D. G. Brimeyer, W. S. Fairbanks, H. Sawyer, and P. C. Cross. 2015. Changing migratory patterns in the Jackson elk herd. Journal of Wildlife Management 79:877-886.

Stadum, J., **J. M. Warren**, and J. J. Rottela. 2016. Breeding season occupancy of long-billed curlews and sandhill cranes in grazed habitats at Red Rock Lakes National Wildlife Refuge, Montana. Intermountain Journal of Sciences 21:15-28.

Austin, J. E., S. T. O'Neil, and **J. M. Warren**. 2017. Habitat selection by postbreeding female diving ducks: influence of habitat attributes and conspecifics. Journal of Avian Biology 48:295-308.

Presentations **Warren, J. M.,** and D. N. Koons. 2016. Within-season and carry-over effects of reproductive effort ion survival in female lesser scaup. Presentation. 7th North American Duck Symposium, Annapolis, Maryland.

Warren, J. M., K. A. Cutting, J. Y. Takekawa, S. E. De La Cruz, T. D. Williams, and D. N. Koons. 2016. Previous success and current body condition determine breeding propensity in lesser scaup: evidence for the individual heterogeneity hypothesis. Poster. 7th North American Duck Symposium, Annapolis, Maryland.

Deane, C. E., J. J. Rotella, **J. M. Warren,** D. N. Koons, and R. A. Garrott. 2016. Harvest and non-harvest mortality relationships for lesser scaup breeding in southwestern Montana. Presentation. 7th North American Duck Symposium, Annapolis, Maryland.

Austin, J. E., S. O'Neil, and **J. M. Warren.** 2016. Habitat use of postbreeding female lesser scaup. Presentation. 7th North American Duck Symposium, Annapolis, Maryland.

Vest, J. L., M. J. Petrie, B. D. Dugger, **J. M. Warren,** and D. W. Smith. 2016. Water issues for the Great Salt Lake: implications to wetlands and waterfowl. Presentation. 7th North American Duck Symposium, Annapolis, Maryland.

Stetter, A. P., **J. M. Warren,** and D. A. Haukos. 2016. Duckling survival at the edge of scaup range in Montana. Poster. 7th North American Duck Symposium, Annapolis, Maryland.

Warren, J. M., K. A. Cutting, and D. N. Koons. 2013. Body condition dynamics and the cost-of-delay hypothesis in a temperate-breeding duck. Plenary Presentation. Ecology and Conservation of North American Waterfowl Symposium, Memphis, Tennessee.

O'Neil, S. T., **J. M. Warren**, J. Y. Takekawa, S. E. De La Cruz, K. A. Cutting, and J. L. Yee. Presentation. Pre-breeding home range attributes and habitat selection of lesser scaup females. Presentation. Ecology and Conservation of North American Waterfowl Symposium, Memphis, Tennessee.

S. R. Couture, and **J. M. Warren**. 2013. Nest-site selection and the habitat heterogeneity hypothesis in trumpeter swans. Presentation. Ecology and Conservation of North American Waterfowl Symposium, Memphis, Tennessee.

Stetter, A. P., **J. M. Warren,** and D. A. Haukos. 2013. Parasitemia, health, and reproduction in lesser scaup at Red Rock Lakes National Wildlife Refuge. Poster. Ecology and Conservation of North American Waterfowl Symposium, Memphis, Tennessee.

Warren, J. M. 2010. The relative contribution of climate and habitat to temporal variation in breeding season demographics of lesser scaup females. Presentation. 4th Annual Wildland Resources Department Pre-project Symposium, Logan, Utah.

Warren, J. M., K. A. Cutting, and R. S. Sojda. 2009. Seasonal survival and breeding-site fidelity of lesser scaup females at Red Rock Lakes National Wildlife Refuge. Presentation. 5th North American Duck Symposium, Toronto, Ontario.

Warren, J. M., K. A. Cutting. 2009. Implications of breeding strategy for cross-seasonal contaminant effects on eggs: a case study with lesser scaup. Poster. 5th North American Duck Symposium, Toronto, Ontario.

Cutting, K. A., J. J. Rotella, **J. M. Warren**, S. E. Wainwright, and J. Y. Takekawa. 2009. Nutrient allocation strategies of female lesser scaup at Red Rock Lakes National Wildlife Refuge, Montana. Presentation. 5th North American Duck Symposium, Toronto, Ontario.

Cutting, K. A., J. J. Rotella, **J. M. Warren**, M. Parker, S. E. Wainwright, and J. Y. Takekawa. 2009. Nutrient allocation in egg formation of female lesser scaup (*Aythya affinis*). Presentation. The Wildlife Society Montana Chapter Annual Conference.

Reed, G., **J. M. Warren**, N. Whelham, and M. R. Frisina. 2009. Effects of cattle grazing on small mammal communities at Red Rock Lakes National Wildlife Refuge. Presentation. The Wildlife Society Montana Chapter Annual Conference.

O'Reilly, M., **J. M. Warren**, and B. Brannon. 2009. Dynamics of a harvested moose population in southwest Montana. Poster. The Wildlife Society Montana Chapter Annual Conference.

Levine, R., **J. M. Warren**, and G. Boltz. 2009. Arctic grayling emergence and development in Odell Creek, Red Rock Lakes National Wildlife

Refuge, Montana. Poster. American Fisheries Society Montana Chapter Annual Conference.

Karagicheva, J., **J. M. Warren**, R. S. Sojda, and K. A. Cutting. 2008. Factors affecting body condition of nestling white-faced ibis. Presentation. International Wader Study Group Annual Conference, Jastrzębia Góra, Poland.

Warren, J.M., G. L. Hadley, and D. Olson. 2008. Annual survival of winter-translocated trumpeter swans. Presentation. Greater Yellowstone Trumpeter Swan Working Group Annual Meeting, West Yellowstone, Montana.

Warren, J. M., R. S. Sojda, and K. A. Cutting. 2008. Seasonal survival and breeding-site fidelity of lesser scaup females at Red Rock lakes National Wildlife Refuge.
Presentation. The Wildlife Society Northwest Section Annual Conference, Spokane, Washington.

Whelham, N., **J. M. Warren**, and M. R. Frisina. 2008. Effects of cattle grazing on small mammal communities at Red Rock Lakes National Wildlife Refuge. Poster. The Wildlife Society Northwest Section Annual Conference, Spokane, Washington.

Warren, J. M., R. S. Sojda, and K. A. Cutting. 2008. Seasonal survival and breeding-site fidelity of lesser scaup females at Red Rock lakes National Wildlife Refuge. Presentation. Spring Wetlands Meeting and Habitat Tour, Dillon, Montana.

Cutting, K. A., J. J. Rotella, **J. M. Warren**, S. E. Wainwright, and J. Y. Takekawa. 2008. Influence of nutrient acquisition and habitat selection on breeding propensity of female Sesser scaup on Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge. Presentation. The Wildlife Society Montana Chapter Annual Conference.

O'Reilly, M., **J. M. Warren**, and K. R. Newlon. 2008. Relationships among ungulate browse, willow community structure and migratory landbirds at Red Rock Lakes National Wildlife Refuge. Presentation. The Wildlife Society Montana Chapter Annual Conference.

Cutting, K. A., **J. M. Warren**, and J. J. Rotella. 2007. Contaminants in eggs of Lesser Scaup nesting on Lower Red Rock Lake, Red Rock Lakes NWR. Poster. The Wildlife Society Montana Chapter Annual Conference.

O'Reilly, M., **J. M. Warren**, and K. Newlon. 2007. Relationships among moose abundance, willow community structure and migratory landbirds at Red Rock Lakes National Wildlife Refuge. Poster. The Wildlife Society Montana Chapter Annual Conference.

Warren, J. M., M. Parker, and R. Sojda. 2004. Adaptively managing Lower Red Rock Lake: current results and related studies. Presentation. Greater Yellowstone Trumpeter Swan Working Group Annual Meeting, West Yellowstone, Montana.

Warren, J. M., J. J. Rotella, and J. E. Thompson. 2004. The effects of cattle grazing on duck production in the Aspen Parkland. Presentation. The Wildlife Society 11th Annual Conference, Calgary, Alberta.

Warren, J. M., J. J. Rotella, and J. E. Thompson. 2003. The effects of cattle grazing on duck production in the Aspen Parkland Ecoregion. Presentation. 3rd North American Duck Symposium, Sacramento, California.

Warren, J. M., J. J. Rotella, and J. E. Thompson. 2001. The effects of cattle grazing on duck production in the Aspen Parkland Ecoregion. Poster. Student and Staff Symposium, Ducks Unlimited, Canada, Stonewall, Manitoba.

Warren, J. M. and J. J. Rotella. 2002. The effects of cattle grazing on duck production in the Aspen Parkland Ecoregion. Presentation. The Wildlife Society Montana Chapter Annual Conference.

Awards STAR Award ($1364), U.S. Fish and Wildlife Service, July 2010.
Non-Monetary Recognition (40 hrs AL), U.S. Fish and Wildlife Service, November 2009.
Non-Monetary Recognition (40 hrs AL), U.S. Fish and Wildlife Service, August 2009.
STAR Award ($1400), U.S. Fish and Wildlife Service, April 2009.
STAR Award ($1500), U.S. Fish and Wildlife Service, July 2006.
STAR Award ($2500), U.S. Fish and Wildlife Service, January 2004.
STAR Award ($800), U.S. Fish and Wildlife Service, August 2003.
STAR Award ($600), U.S. Fish and Wildlife Service, October 2000.
Wynn G. Freeman Award ($650), Montana Chapter of The Wildlife Society, March 2001.
Certificate of Merit, Mathematical Sciences Department, Michigan Technological University, Winter Term 1993–94.