

THESIS

TEMPORAL DEMOGRAPHY OF LESSER SCAUP: A SPECIES IN DECLINE

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ABSTRACT

TEMPORAL DEMOGRAPHY OF LESSER SCAUP: A SPECIES IN DECLINE

A central goal of wildlife management and conservation is to determine which demographic parameters have the greatest influence on population growth rate to focus management actions for species of concern. Understanding how environmental conditions influence intra- and interannual variation in demographic parameters, and in turn population growth rates, requires long-term studies. This allows researchers to account for temporal covariation in demographic parameters that may have a greater influence on population dynamics than direct variation in the demographic parameter. One such species that could benefit from a better understanding of temporal variation and covariation in demographic parameters is lesser scaup (*Aythya affinis*, hereafter scaup), which has declined continentally since the early 1980's.

I contributed to and utilized a long-term study of scaup demography at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA to 1) explore how environmental conditions influenced intra- and inter- annual variation in clutch size and nest survival, and 2) incorporate temporal (co)variation in demographic parameters into population models to decouple the influence of parameter variation, *versus* covariation, on population growth rate. To address my first objective, I considered an array of environmental covariates that were hypothesized to influence inter-annual variation in clutch size and nest survival such as water levels, water level phenology, and water temperature. In addition, I considered intra-annual covariates that could influence these vital rates, such as nest initiation date and day of the breeding season, which could serve as proxies for seasonal changes in resources, predators, or

both. Clutch size varied much more within years across nest initiation dates (3.18-10.05), than it did across years (7.51 – 8.38). Given the constrained range of clutch sizes across years, none of the environmental covariates exhibited significant relationships with clutch size. In contrast, nest survival varied little intra-annually (e.g. 2018 nest survival 0.38 ± 0.03), but greatly interannually (0.27 – 0.58). Water level phenology did influence nest survival, such that years when maximum lake levels were reached late in the breeding season relative to mean nest initiation date, had the highest nest survival rates.

To address my second objective, I incorporated results from my first chapter along with annual estimates of female breeding propensity, duckling survival, first-winter survival of females, adult female seasonal survival, process variance of each vital rate, and correlation between each pair of vital rates into a time-variant population model and conducted a prospective and retrospective perturbation analysis of population growth rates. The population model revealed that the study population is declining by approximately 6% each year. Results from the prospective perturbation analysis indicated that breeding season and non-breeding season adult survival had the highest stochastic elasticities (0.84 and 0.82 respectively), and thus had the greatest potential to influence the stochastic population growth rate. Whereas, retrospective analyses indicated that fluctuations in duckling survival made the largest contribution to realized population growth rates in the past (64%). Additionally, covariation in demographic rates explained 37% of variation in realized growth rates compared to 63% being attributable to direct temporal variation in the vital rates.

These findings collectively suggest efforts to manage water phenology at Red Rock Lakes National Wildlife Refuge could positively influence nest survival and efforts should focus on finding ways to increase duckling survival to have the greatest impact on population growth rate.

More broadly, covariation in demographic rates can explain a large proportion of variation in population growth rate and should be incorporated into population models of declining species to more accurately determine points in the life cycle that truly drive population dynamics, and therefore provide sound information to managers aiming to conserve the species.

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CHAPTER ONE
LESSER SCAUP NESTING ECOLOGY: ANNUAL VARIATION IN CLUTCH SIZE AND
NEST SURVIVAL

Introduction

A goal in wildlife management and conservation is to determine which demographic parameters drive population dynamics to identify where to focus management actions. For long- and medium-lived species, adult survival probabilities are often found to have the greatest potential to affect population growth rates (Gaillard et al. 1998, Sæther and Bakke 2000). However, adult survival is often buffered against environmental variation, and because it does not change as much among years compared to other demographic parameters, it often has little influence on realized population growth rates (Pfister 1998, Morris and Doak 2004, Koons et al. 2009). The vital rates which comprise reproductive success, however, often fluctuate greatly among years and in turn may have a greater impact on realized growth rates (Chapter 2, Koons et al. 2017). Although some components of reproductive success may vary little inter-annually, they may vary greatly across individuals and reproductive attempts within a breeding season. Determining the factors governing within- and among-year variation in reproduction could therefore provide insights into how to increase vital rates and positively impact populations in a feasible and efficient manner.

Nesting ecology is the most broadly researched topic in avian ecology and encompasses several important demographic parameters that are components of fertility estimates, such as clutch size and nest survival. Clutch size, which is the number of eggs laid in a single brood, is one of the most studied animal life-history traits (Stearns 1992, Jetz et al. 2008). Nest survival, the probability of at least one egg hatching in a clutch, is also of great attention because it tends

to be one of strongest determinants of population dynamics in ground-nesting birds (Johnson et al. 1992a, Hoekman et al. 2002, Clark et al. 2008, Taylor et al. 2012). Together, clutch size and nest success are major contributors to reproductive success, individual fitness, and variation in population growth rates (Cowardin and Blohm 1992, Johnson et al. 1992a, Martin 1995, Sæther and Bakke 2000, Thackeray et al. 2010).

Variation in clutch size at a given locale and time of year is driven by resource availability and energetic constraints (Lack 1947), as well as individual heterogeneity in the ability to acquire resources and allocate energy to the clutch (Van Noordwijk and De Jong 1986). For example, seasonal declines in food resources can result in seasonal declines in maternal body condition and consequently clutch size, whereby individuals nesting earlier tend to lay larger clutches than those nesting later in the season (Perrins and McCleery 1989, Aparicio 1994, Rowe et al. 1994, Decker et al. 2012). Older, more experienced individuals tend to be best at timing their energy acquisition and nesting phenology to avoid seasonal shortfalls in resources, which in part contributes to the common positive relationship between age/experience and clutch size (Klomp 1970, Hamann and Cooke 1986). Nest predation can also force females to re-nest after they have already expended resources on an initial clutch, leading to lower clutch sizes of re-nests that in part contribute to seasonal declines (Bengston 1972, Milnoff 1991). Inter-annual variation in environmental conditions may also influence food availability, specifically invertebrate resources which provide protein and minerals that are vital for clutch formation (Drobney 1991, Robertson 1995).

Like clutch size, nest survival in waterfowl can vary greatly within and across years, and across habitats (Klett and Johnson 1982, Wilson et al. 2007). Predation is the leading determinant of nest survival that often dictates observed patterns in nest survival across space

and time, but research has focused primarily on spatial variation across habitats (Clark and Shutler 1999, Stephens et al. 2005). A female's ability to choose an adequate nesting site affects the chance of a predator detecting and preying upon her nest. Previous studies have found that nest-site selection and nest concealment influence nest survival in many upland nesting dabbling ducks (Hines and Mitchell 1983, Guyn and Clark 1997, Clark and Shutler 1999). However, studies of diving ducks have found no relationship between nest-site selection and nest survival (Krasowski and Nudds 1986, Maxson and Riggs 1996, Brua 1999, O'Neil et al. 2014).

Apart from spatial variation in nest predation, or lack thereof, predation intensity can also change over time within a breeding season (Fields et al. 2001, Wilson et al. 2007, Colwell et al. 2011). In wetland systems, e.g., high water levels early in the breeding season can prevent mammalian predators from accessing nests (Maxson and Riggs 1996, Albrecht et al. 2006) or ample availability of alternative prey may result in prey-switching among predators and hence lower levels of nest predation (Brook et al. 2005, 2008). In precocial birds such as waterfowl, nest developmental age is also positively related to the daily chances of a nest surviving. This occurs primarily because female hormones lead to increased incubation constancy closer to hatch, which tends to decrease chances of nest predation (Grand et al. 2006).

Finally, nest survival may be driven by inter-annual variation in environmental conditions. For example, weather can influence resource availability and affect average female body condition, resulting in adjustments of incubation constancy that impact nest survival (Skutch 1962, Gloutney and Clark 1991, Bromley and Jarvis 1993, Blums et al. 1997, Newton 2006, Devries et al. 2008). Additionally, warmer Spring temperatures have resulted in higher nest survival, due to higher availability of alternative prey resources to predators (Drever and Clark 2007). Fluctuations in wet and dry periods, wetland density and current-year primary

productivity were also found to influence nest survival in the Prairie Pothole Region (Walker et al. 2013). Thus, when studying nesting ecology, it is important to consider many drivers of clutch size and nest survival to better understand what is driving reproductive success and population dynamics, especially for informing the management of declining populations.

Lesser Scaup (*Aythya affinis*) are a medium-sized diving duck that could benefit from a deeper understanding of the processes driving temporal variation in clutch size and nest survival because their population has declined while other North American waterfowl are thriving. Scaup populations have declined since the late 1970s and the current population estimate (3.6 ± 0.2 million) remains below objectives of the North American Waterfowl Management Plan of 4.9 million (Figure 1.1; note that estimates of scaup abundance represent a combination of Greater Scaup (*Aythya marila*) and Lesser Scaup because these two species cannot be differentiated in aerial surveys, but is comprised of ~90% lesser scaup, Anteau et al. 2014, U.S. Fish and Wildlife Service 2019). The extensive range of Lesser Scaup (hereafter scaup) exposes them to a wide variety of threats that may be contributing to the marked population decline. Previous analyses of long-term wing collections suggested that recruitment and female survival may have both declined since the 1970s (Allen et al. 1999, Afton and Anderson 2001). However, recent analyses of banding data and an integration of monitoring data have found no long-term declines in survival and concluded that recruitment has been the likely driver of decline across the traditional survey area of the Waterfowl Breeding Population and Habitat Survey (Arnold et al. 2016, 2017, Koons et al. 2017).

While nesting ecology has been widely studied in scaup, few studies have been conducted consecutively over long periods of time at one location (Afton 1984, Koons and Rotella 2003a, Walker et al. 2005, Koons et al. 2006, Corcoran et al. 2007). One uninterrupted

long-term study focused on the effects of hatch date and egg size on growth, recruitment, and survival of scaup, but not the effects of environmental variation on demographic performance (Dawson and Clark 1996, 2000). We studied a population of scaup at Red Rock Lakes National Wildlife Refuge, Montana from 2006-2015 and 2017-2018. Our primary objective here is to identify environmental variables related to temporal variation in scaup clutch size and nest survival at our study area. We focus primarily on inter-annual drivers of these two vital rates, while accounting for intra-annual variation, because spatial variation in habitat conditions at the nest site has been previously explored and found to have little influence (O'Neil et al. 2014). We hypothesized that annual water levels, water temperatures and the phenology of peak water levels relative to the mean nest initiation date each year would influence clutch size and nest success at our study site. These environmental conditions were of interest because they are closely related to the hypotheses of scaup decline. In relation to the Climate Change-Habitat Hypothesis (Box 1), we predicted that years with lower water levels would serve as a proxy for decreased aquatic invertebrate abundances, and simultaneously reduced protection of nests from predators, thereby resulting in lower clutch size (because of limited resource availability) and nest survival. As predicted by the Climate Change-Phenological Mismatch Hypothesis (Box 1) we hypothesized that increased water temperatures early in the breeding season and water level phenology relative to nest initiation could influence temporal pulses in primary productivity and invertebrate populations relative to scaups' nutritional needs that would be negatively related to clutch size and nest survival.

Box 1) Several environmental mechanisms for the decline in scaup abundance have been hypothesized, two of which highlight possible changes in the quality of habitat on the breeding grounds. The Global Change-Habitat Hypothesis states that poor wetland conditions on breeding grounds and at stopover locations has reduced food availability and nesting habitat which could result in lower reproductive success (Austin et al. 2014). Changes in wetland conditions are largely due to changes in agricultural practices and climate change. Wetland consolidation in the Prairie Pothole region, which drains multiple smaller wetlands into larger permanent wetlands, can support fish populations throughout the year (smaller wetlands typically freeze over and kill fish populations), resulting in decreased abundances of aquatic invertebrates available to duck populations (McCauley et al. 2015, McLean et al. 2016b). Climate change may also drive changes in precipitation regimes across the scaup breeding range and may have opposing effects in different regions. For example, the Canadian western boreal forest is experiencing warming at faster rates than other terrestrial biomes and is particularly vulnerable to increased drought (Drever et al. 2012, Price et al. 2013). Given the western Boreal Forest encompasses the core scaup breeding range, poor wetland conditions due to drought could decrease nesting habitat and food abundances. The opposite effect on precipitation regimes are predicted in the Prairie Pothole Region, where precipitation is expected to increase. Subsequently leading to deeper permeant wetlands, increased fish abundance, and decreased aquatic invertebrate abundance (McLean et al. 2016b, 2016a, Janke et al. 2019). Once again this could result in decreased food availability to scaup and drive declines in nesting or duckling productivity. Additionally, the Climate Change-Phenology Mismatch Hypothesis suggests earlier spring phenology has led to invertebrate pulses that no longer align with the phenology of scaup dietary needs throughout the breeding season, resulting in lower scaup productivity (Austin et al. 2014). Both hypotheses predict that changes in environmental conditions could be influencing scaup nesting

Methods

Study Site

Our study was conducted on Lower Red Rock Lake (LRRL) at Red Rock Lakes National Wildlife Refuge (RRL) in Southwest Montana (Figure 1.2). Lower Red Rock Lake is a 2,330-hectare, high elevation (2,014 m above mean sea level) montane wetland complex within the Centennial Valley that supports a high density of breeding lesser scaup (>7.7 breeding pairs/km², J. Warren *pers obs*).

This wetland system is characterized by large areas of open water with hardstem bulrush (*Schoenoplectus acutus*) islands and surrounded by vast stands of seasonally flooded Northwest Territory sedge (*Carex utriculata*). Interspersed in the sedge stands are small (< 2 ha) open water ponds, which offer additional nesting habitat (e.g., to nest near open water and escape from predators). Water levels in LRRL do not exceed 1.5 m during the nesting season. Average annual precipitation and temperatures are 49.5 cm and 1.7°C, respectively. This site is one of the most constrained breeding environments for lesser scaup, measured by growing season length, making it similar to the northwest boreal forest core of the scaup breeding range in Canada (Gurney et al. 2011). The wetland complex at RRL has many similarities to wetland systems in the northern boreal forest including shallow waters, fluvial hydrology and large expanses of flooded northwest territory sedge (*Carex utriculata*, U.S. Fish and Wildlife Service 2009, Wells et al. 2010, Gurney et al. 2017). These attributes contrast prairie wetlands that are fed by snow runoff and ground water (Hayashi et al. 2016), and the Prairie Pothole Region where many previous studies of lesser scaup have been conducted (Rogers 1964, Hammell 1973, Afton 1984, Austin and Fredrickson 1986, Koons and Rotella 2003b, 2003a, Rotella et al. 2003, Anteau and Afton 2006). In addition, water levels at our study site can be manipulated by a water control structure

at the out flow of LRRL, which parallels boreal systems which are often regulated by large hydroelectric dams.

Data Collection

To study determinants of inter-annual variation in scaup clutch size and nest success at our study area, we initiated nest searching in June of 2006 and continued nest searching efforts each summer through 2018, except for 2016 due to lack of funding. The study area was divided into 16 survey blocks each containing one to four 750 X 750-meter cells (blocks with predominately open water had one cell whereas blocks that were predominately vegetation had four cells). These survey blocks were systematically searched on foot, with a focus on upland and nearshore habitats for lesser scaup nests. Investigators flushed hens from nests by walking through nesting habitat and disturbing vegetation with willow switches or a trained dog. When a nest was located, we determined clutch size, incubation stage and estimated nest initiation date via candling eggs (Weller 1956). A suite of habitat characteristics was recorded including water depth adjacent to the nest, distance from open water, vegetation type and height, and shore type. Nest locations were recorded in Universal Transverse Mercator coordinates (UTMs) using a GPS, and a willow switch with flagging tape was placed 4 meters to the north of the nest to assist in locating for future visits. We continued to visit nests every 7 – 10 days until fate was determined (i.e., successful, destroyed, abandoned).

We quantified wetland conditions at our study site using a capacitance probe water level and temperature data logger (model WT-HR 1500; TruTrac, Christchurch, New Zealand). In April of each year, we deployed the probe at the outflow of LRRL, which recorded hourly water levels and temperature throughout the breeding season. We also made visual observations of a staff gauge at the same location in case of capacitance probe malfunctions. All field protocols

were approved by Colorado State University Institutional Animal Care and Use Committee (IACUC) 18-7736A.

Clutch Size

To estimate within- and among-year variation in clutch size, we used generalized linear mixed-effect models (GLMMs) with Poisson error and a log-link in the R (R Development Core Team 2018) lme4 package that uses maximum likelihood estimation (Bates et al. 2012). The nest initiation date (INIT) of each nest was included as a fixed effect because previous studies have found nests initiated earlier in the breeding season have larger clutch sizes in scaup and other waterfowl species compared to nests initiated later in the season, largely because of the mechanisms presented in the Introduction (Reynolds 1972, Krapu 1981, Batt et al. 1992, Alisauskas and Ankney 1994, Esler et al. 2001), and because this effect had previously been detected for scaup at our study site (Warren et al. 2013). We also considered fixed effects for both the mean pre-breeding season water level (PRELVL, May 1st – June 16th) and water temperature (PRETEMP) because both variables can influence primary productivity and available invertebrate food resources (Vannote and Sweeney 1980, Cayrou and Céréghnio 2005, Devries et al. 2008), which scaup are known to acquire once arriving on the breeding grounds before clutch formation (Cutting et al. 2011). As an alternative, we also considered mean breeding season water level (LVL, May 1st – August 30th) because females must continue to forage throughout the egg laying period to continue to supply nutrients for egg production (Arnold and Rohwer 1991). We also considered an index of nesting phenology (PHENIND) relative to water level by subtracting the annual mean nest initiation date from the ordinal date of maximum water level each year. A large PHENIND indicates water levels peaked late in the nesting season relative to mean nest initiation date, whereas a small PHENIND indicates that

water levels peaked early in the breeding season. We included this index because phenology of peak water levels may influence invertebrate resource pulses that align or misalign (Winder and Schindler 2004, Thackeray et al. 2010) with scaup nutrient needs during egg production. All explanatory water variables were standardized (mean 0 and s.d. of 1). We similarly standardized nest initiation dates within each year relative to the respective annual mean in order to account for intra-annual variation among nests that could be attributable to unmeasured individual heterogeneity in female reproductive investment (Aubry et al. 2009).

Our suite of considered models included univariate fixed effects of each covariate, bivariate additive effects between nest initiation date and each inter-annual water covariate (LVL and INIT, PRELVL and INIT, PRETEMP and INIT, and PHENIND and INIT) and relevant interactions. We also included a random intercept for nest year (YEAR) to estimate inter-annual variation not explained by the fixed effects. Conditional Akaike's Information Criterion (cAIC) was used for model selection because it appropriately accounts for the dimension of the random effect in the penalty term (Saefken et al. 2014). We considered parameters imprecise and uninformative if their 95% confidence intervals overlapped zero and if addition of such parameters to a nested simplification increased the cAIC value of a model, as opposed to decreasing it. Whereas the addition of parameters with explanatory power should decrease the cAIC value of a model (Arnold 2010).

Nest Survival

We estimated daily survival rates (DSR) of nests using the 'nest survival model' in the RMark package for R (Laake 2013, R Development Core Team 2018) that calls program MARK (White and Burnham 1999). This model allowed us to examine environmental covariates for temporal variation in DSR of nests on the logit scale (Dinsmore et al. 2002, Rotella et al. 2004,

Rotella 2007). The influence of nest-site habitat characteristics at our study site was previously considered, and generally induced little selective force on choice of nesting sites (O'Neil et al. 2014). Our focus here was therefore on variables hypothesized to influence temporal variation in nest survival at our study site.

To test if DSR varied over time within breeding seasons, we included models with a linear (TIME) and quadratic (TIME + TIME²) seasonal time trend. Previous work with nesting birds has found that DSR can increase as the nesting season progresses due to decreased rates of nest predation as alternative prey become available to predators (Wilson et al. 2007, Colwell et al. 2011). DSR may also decrease throughout the breeding season due to declines in female body condition (Fields et al. 2001, Brook et al. 2005, Devries et al. 2008). We also considered a univariate model for the effect of nest age (NAGE) because DSR is known to increase with nest age as females increase incubation constancy (Forbes et al. 1994, Flint 2003).

We next considered the same covariates for inter-annual variation in wetland conditions that we used in the clutch size analysis, which allowed us to explore how they might simultaneously influence nest survival. For example, water levels during the pre-breeding period (PRELVL) could influence food availability for females. In turn we may expect nest survival to decrease in years of lower pre-breeding water levels because females tend to be in poorer body condition (Warren et al. 2013), which may require females to take more frequent incubation breaks that can attract attention from predators (Blums et al. 1997). Pre-breeding season water temperatures (PRETEMP) could also affect nest survival because water temperatures could influence invertebrate hatches when females are acquiring nutrients for incubation and affect nest survival via the same mechanisms as pre-breeding water levels. Breeding season water levels (LVL) could also influence nest survival by restricting predator access to nests. Nest predators

such as coyotes and skunks are less likely to wade or swim through large expanses of flooded sedge during high water years, whereas during low water years predators may easily walk to nests (Jobin and Picman 1997). The phenological index (PHENIND: mean nest initiation date – ordinal date of maximum water level) may reveal a match or mismatch between nesting females' nutritional needs and food resources, which may influence female body condition, incubation constancy, and therefore nest survival (Winder and Schindler 2004, Thackeray et al. 2010).

We took a tiered approach to model selection, as we were interested in inter-annual drivers of nest survival while accounting for intra-annual variation in nest DSRs, and wanted to avoid data dredging by considering all possible combinations of covariates (Franklin et al. 2000). First, we built a set of models with explanatory variables describing inter-annual variation in wetland conditions that included univariate effects of PRELVL, LVL, PRETEMP, PHENIND, and a null model with CONSTANT DSR. Bivariate additive effects of PRELVL + PRETEMP, LVL + PRETEMP, PRELVL + PHENIND, LVL + PHENIND were also considered (though bivariate additive effects of PRETEMP and PHENIND were not considered due to multicollinearity). As with the clutch size analysis, if additional parameters did not decrease AICc values, we considered the effects uninformative (Arnold 2010). We then took the top model(s) from the first step and considered additional effects of covariates serving as proxies for biological mechanisms that could affect intra-annual variation in nest mortality, including TIME, TIME + TIME², and NAGE. We used Akaike's information criterion adjusted for sample sizes (AICc) for model selection in both steps (Akaike 1998, Burnham and Anderson 2002). After determining the top model with fixed-effect covariates describing inter- and intra-annual variation in nest survival, we aimed to add a random effect for nest year to estimate inter-annual variation that could not be explained by the covariates. However, we could not implement this in

RMark due to the complexity of our model and limitations of implementing mixed-effect models in RMark. As an alternative, we added year (YEAR) as a fixed effect. To determine the explanatory power of focal covariates in our top models we conducted an analysis of deviance (ANODEV), which indicates the proportion of deviance (R_{DEV}^2) explained by covariates in a model compared to full inter-annual variability in DSR (Equation 1, Skalski 1996).

$$R_{Dev}^2 = \frac{Dev_{TIME+TIME^2} - Dev_{PHENIND+TIME+TIME^2}}{Dev_{TIME+TIME^2} - Dev_{YEAR+TIME+TIME^2}} \quad \text{Equation 1)}$$

Finally, we used the fitted DSR estimates from the top model and the delta method (Powell 2007) to estimate a nest survival probability for each year (using a 34-day period of laying and incubation).

Results

Environmental Conditions

Pre-breeding water levels at LRRL averaged 2013.87 (± 0.17) msl with the highest mean pre-breeding water levels in 2008 (2014.13 ± 0.10 msl) and the lowest in 2007 (2013.61 ± 0.05 msl). During the years of 2015, 2017, and 2018 the capacitance probe malfunctioned, and we were unable to obtain average water temperature readings. For the purposes of modeling we included the average water temperature over the entirety of the project during pre-breeding for these years with missing data (which should lead to conservative estimated effects, if any). Pre-breeding water temps averaged 13.12 (± 2.30) °C and ranged from 0.43 – 28.49 °C. Water temperatures were lowest in April of 2008 and highest in July of 2016. Breeding season water levels averaged 2013.87 (± 0.19) meters above sea level (msl) and ranged between 2013.14 – 2014.33 msl. The highest mean water levels occurred in 2011 (2014.13 ± 0.08 msl) and the

lowest mean water levels occurred in 2013 (2013.67 ± 0.05 msl). The ordinal date of the maximum water level throughout the breeding season averaged day 169 (± 41 days) with the earliest date being 121 (2009 and 2010) and the latest being 243 (2015). Our phenology index demonstrated that maximum water levels rarely ‘matched’ with mean initiation dates ranging from an index of -53 (ordinal date of maximum water level was earlier than mean nest initiation for that year) to 71 (ordinal date of maximum water level was later than mean nest initiation date for that year) with a median of -9 (Appendix Figure A1.1).

Clutch Size Estimates

Over 12 years we monitored a total of 825 nests. For the clutch size analyses, we removed any nest with a clutch size < 4 because these were not considered full clutches (e.g., the likely result of partial egg predation, accidental ejection of eggs by the female or are likely re-nest as waterfowl clutch are smaller in re-nesting attempts (Batt and Prince 1979, Esler and Grand 1994, Anteau et al. 2014)), which left 711 nests for analysis. Across years the mean clutch size was 7.93 (± 1.67) eggs (Figure 1.3), and annual means across nests ranged from 7.07 (year 2006) to 8.96 (year 2012) eggs (Figure 1.4). Mean nest initiation date for the study period was day 172.21 (± 9.42), with the earliest mean nest initiation date occurring in 2007 (day 166) and the latest in 2011 (day 187) (Appendix Figure A1.2).

The univariate model with nest-specific initiation date within a year (INIT) was the top model among our candidate set designed to explain inter- and intra-annual variation in lesser scaup clutch size at our study area (Table 1.1). Several other models were within two cAIC points of our top model; however, these were all additive or interaction models that included the top model as a nested simplification deeming these more complex models as uninformative and they were also imprecise, (i.e., 95% CI highly overlapped 0). In our top-ranking model, nests

initiated later in the season had significantly smaller clutch sizes (log-scale Intercept: $\hat{\beta} = 2.06 \pm 0.02$, 95% CI: 2.02 to 2.10, INIT: $\hat{\beta} = -0.11 \pm 0.01$, 95% CI: -0.14 to -0.09, Figure 1.5). After controlling for relative nest initiation dates within each year, the variance for the YEAR random effect (0.002 ± 0.047 on the log scale) indicated that clutch size varied little between years.

Daily Survival Rate and Nest Survival Estimates

We monitored a total of 783 nests until fate was determined, of which 537 were successful (68.6% apparent nest survival). In our first tier of model selection only three models outperformed a null model, and the top included a univariate effect of PHENIND that carried 51% of the model weight (logit-scale Intercept: $\hat{\beta} = 3.87 \pm 0.07$, 95% CI: 3.74 to 4.00, PHENIND: $\hat{\beta} = 0.18 \pm 0.07$, 95% CI: 0.05 to 0.30, see Table 1.2 for model selection table). The second and third models included the addition of LVL (LVL + PHENIND) and PRELVL (PRELVL + PHENIND), which resulted in the maximum penalty of +2 AIC_c points, deeming the LVL and PRELVL variables as uninformative. Therefore, we retained only PHENIND in the second tier of model selection in which we added explanatory variables for intra-annual variation in DSR.

In this next tier of model comparison, the data indicated greatest support for additive effects of PHENIND and the quadratic model of TIME + TIME², which carried nearly 100% of the model weight (logit-scale Intercept: $\hat{\beta} = -0.45 \pm 0.62$ 95% CI: -1.66 to 0.76, PHENIND: $\hat{\beta} = 0.19 \pm 0.67$, 95% CI: 0.06 to 0.32, TIME: $\hat{\beta} = 0.15 \pm 0.03$, 95% CI: 0.10 to 0.20, TIME²: $-1.20 \times 10^{-3} \pm 2.91 \times 10^{-4}$, 95% CI: -1.75×10^{-3} to 6.12×10^{-4} , see Table 1.3 for model selection table). Within a single year, DSR was lower at the beginning of nesting season, increased and peaked in the middle of the season, and generally plateaued after the peak (Figure 1.6). The positive effect

of PHENIND indicated that DSR was generally higher in years when the ordinal date of maximum water level was much later than the mean nest initiation date (Figure 1.7). For example, 2014 had the highest PHENIND, where the date of maximum water level was on day 243 (August 31st), the mean nest initiation date was on day 171 (June 20th), and reached a maximum DSR within the season of 0.990 ± 0.002 (95% CI: 0.986 – 0.993). The years with the lowest PHENIND were 2009 and 2010, with a date of maximum water level of 121 (May 1st) and a mean nest initiation date of 174 (June 23rd). The maximum DSR throughout the season was 0.983 ± 0.003 (95% CI: 0.978 to 0.987) and 0.982 ± 0.003 (95% CI: 0.784 to 0.984) for 2009 and 2010 respectively. Results from the ANODEV indicated that PHENIND explained 42% of the inter-annual variation in DSR compared to the YEAR + TIME + TIME² model.

Because the PHENIND + TIME + TIME² was our top-ranked model according to AIC_c, we used predicted DSRs from this model to calculate an annual estimate of nest survival using the delta method. Nest survival at LRRL averaged 0.43 (± 0.02 , 95% CI: 0.38 to 0.48) among all years. Annual nest survival was highest in 2011 (0.58 ± 0.03 , 95% CI: 0.52– 0.64, Figure 1.8) and lowest in 2007 (0.28 ± 0.04 , 95% CI: 0.21 to 0.35).

Discussion

Determining the environmental variables that drive variation in reproductive success can provide information to managers to help the enact positive influences on population growth rates (Rushing et al. 2016, 2017). We examined the influence of seasonal water levels and temperature on both clutch size and nest survival because these easily measured abiotic variables can affect aquatic invertebrate abundances and accessibility of nests to predators, thereby serving as potential proxies for these more difficult to measure biotic drivers of scaup reproductive performance. As is common in waterfowl, clutch size declined seasonally (Krapu et al. 1983,

Duncan 1987, Flint et al. 2006), but exhibited little variation across years and did not respond to inter-annual fluctuations in the water variables we considered. Nest survival, however, varied substantially across years and was positively correlated with the index of water level phenology, indicating that nest survival was highest in years when water reached peak levels well after nest initiation at the LRRL study area. Contrary to being consistent with the concept of a resource-consumer phenology mismatch, this result more so suggests that rising wetland levels to a late-season peak provided protection against mammalian predators and nest flooding.

Clutch Size

The small inter-annual variability of clutch size at our study site (process variance = 0.0022) was similar to that at other sites in the northern boreal, prairie-parklands, and prairie pothole region (Corcoran et al. 2007, Gurney et al. 2011). It is hypothesized that observed variation in clutch sizes intra-annually is likely due to individual heterogeneity in specific females such as age and ability to improve body condition just prior to breeding (Lindberg et al. 2013, Warren et al. 2013). Re-nesting attempts could have also influenced the observed variation in clutch size given females are known to lay fewer eggs in re-nesting attempts (Batt and Prince 1979, Eldridge and Krapu 1988), however we were unable to accurately estimate re-nesting probability at our study site. Furthermore, mean clutch sizes at our study site were slightly lower than at other nesting locations for scaup, likely due to the high elevation which, similar to high latitude, generally leads to lower clutch sizes in most species (Krementz and Handord 1984, Johnson et al. 2006, Boyle et al. 2016). For example, Koons et al. (2006), reported clutch size estimates for SY and ASY female lesser scaup as 7.88 and 9.74 respectively in the boreal forest region, and 8.82 and 10.68 respectively in the prairie-parkland region.

The seasonal decline in clutch size at LRRL is well documented at other locations for scaup and other waterfowl species (Perrins and McCleery 1989, Aparicio 1994, Rowe et al. 1994, Decker et al. 2012). Gurney et al. (2011) found a seasonal decline in clutch size across the entire breeding range of scaup. However, scaup did not respond to seasonal environmental constraints by increasing the rate of clutch size declines at locations with shorter growing season lengths, resulting in low levels of inter-annual variation in clutch size. Furthermore, studies have found that scaup rely heavily on endogenous nutrients obtained at stopover locations prior arriving on the breeding grounds (Afton and Ankney 1991, Esler et al. 2001), which could explain why environmental variables at our study site explained little of the inter-annual variation in clutch size. Yet, Cutting et al. (2011) found that scaup at LRRL rely heavily on endogenous nutrients when local conditions are poor and exogenous nutrients when local resources are readily available, suggesting scaup might readily adapt their energetic acquisition and allocation strategy for clutch formation. The small process variance in clutch size, and lack of response to local environmental variables further suggests that these plastic energetic strategies help scaup buffer their clutch size against inter-annual fluctuations in environmental conditions.

Nest Survival

We additionally found that water level phenology had a greater influence on nest survival than mean water levels. Specifically, nest survival was highest when water reached peak levels late in the breeding season, which maintains protective flooded sedge habitats during the relatively late nesting phenology of scaup compared to other species. Maintaining flooded sedge habitats likely protected nesting females from mammalian predators such as coyotes, foxes, and skunks, which are not inclined to wade through flooded sedge habitats to search for overwater

nests (Jobin and Picman 1997). However, nests were still susceptible to mink and to predation from avian predators such as ravens and gulls. Also beneficial during periods of high water levels, females can discretely swim off their nests to take incubation breaks. Whereas low water periods force females to fly off the nest, revealing the nest location to predators and resulting in increased rates of nest failure. More conspicuous incubation behavior resulted in higher rates of predation in shorebirds which is also likely the case in waterfowl since they are exposed to similar nest predators (Smith et al. 2012). Finally, maximizing water levels extremely late in the breeding season compared to mean nest initiation date may have also led to decreased rates of nest flooding, since many nests would have already hatched. Nest flooding is a known cause of nest failure at LRRL (Navarre, *pers obs*), was the second leading cause of nest failure in the boreal (Walker et al. 2005), and is often a cause of nest failure in other diving duck species (Bouffard et al. 1987, McAuley and Longcore 1989).

Historically (1950s – 1990s), nest survival of scaup varied among years and locations with average rates in the prairie grasslands, prairie parklands, and northern boreal of 37.3%, 29.5%, and 57.2% respectively (Anteau et al. 2014). More recent studies in these locations found nest survival rates of 32% in the northern boreal and 33% in the prairie-parklands (Koons et al. 2006), with rates ranging from 11-27% in the Alaskan boreal forest (Walker et al. 2005, Corcoran et al. 2007, Martin et al. 2009). With a mean rate of 43% at LRRL, nest survival is slightly higher than many of the recent estimates in other locations, but lower than historic estimates in the northern boreal. These elevated nest survival rates at LRRL, compared to other sites is likely due to relatively high and maintained water levels (due to historic water control structures), which can act as a buffer against drought cycles.

Management Implications

Given the lack of response to inter-annual environmental variation, management actions have little potential to influence clutch size in lesser scaup. Manipulations of water levels are likely to have no effect on clutch size. However, our results demonstrate that water levels could be managed to remain high, or slowly increase throughout the breeding season to positively influence nest survival. In years with ample snowpack and runoff, water levels could be manipulated via a water control structure on LRRL. Managers historically increased water levels early in the breeding season to provide ample nesting habitat for the trumpeter swan (*Cygnus buccinator*), then let them decrease throughout the breeding season, and finally increased water levels again to maximize recreational opportunities such as waterfowl hunting in the autumn. Altering wetland management practices to maintain or slightly increase water levels throughout the breeding season at RRL may benefit scaup populations, however, one would need to consider the management of scaup, trumpeter swans, arctic grayling (a species of conservation concern, *Thymallus arcticus*), as well as downstream water users. Co-optimizing all the needs and concerns among species and stakeholders would best be considered through a Structured Decision Making framework (Gregory et al. 2012). Structured Decision Making could also help develop collaborative projects with industry, First Nations, and governments in the boreal, where many systems have large hydro-electric dams that could manage water levels to benefit scaup nest survival and other species while generating ample power.

Table 1.1) Comparison of models with variables hypothesized to affect lesser scaup (*Aythya affinis*) clutch size between 2006 to 2018 (excluding 2016) at the Lower Red Rock Lake study area in southwestern Montana, USA. Shown are the modeled variables (Model), conditional log likelihood (CLL), degrees of freedom (df), and conditional Akaike Information Criterion (cAIC). INIT = nest-specific initiation date within a year, PRELVL = pre-breeding season water level, LVL = breeding season water level, PHENIND = phenological index, PRETEMP = pre-breeding season water temperature. All models included a random effect for nest year (YEAR_{RAN}).

Model	CLL	df	cAIC
INIT + YEAR _{RAN}	-1474.30	8.57	2965.75
PRELVL + INIT + YEAR _{RAN}	-1474.34	8.54	2965.75
LVL + INIT + YEAR _{RAN}	-1475.40	7.59	2965.97
PHENIND + INIT + YEAR _{RAN}	-1474.30	9.03	2966.67
PRETEMP + INIT + YEAR _{RAN}	-1474.30	9.09	2966.79
PRELVL * INIT + YEAR _{RAN}	-1473.95	9.52	2966.94
PHENIND * INIT + YEAR _{RAN}	-1473.82	10.04	2967.72
LVL * INIT + YEAR _{RAN}	-1475.37	8.55	2967.84
PRETEMP * INIT + YEAR _{RAN}	-1473.88	10.09	2967.94
INTERCEPT + YEAR _{RAN}	-1508.70	7.58	3032.56
PRELVL + YEAR _{RAN}	-1508.74	7.54	3032.56
LVL + YEAR _{RAN}	-1509.80	6.58	3032.75
PHENIND + YEAR _{RAN}	-1508.71	8.03	3033.47
PRETEMP + YEAR _{RAN}	-1508.70	8.10	3033.60

Table 1.2) Comparison of models for first step in model selection for nest daily survival rates with inter-annual covariates for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site in Montana, USA between 2006 to 2018 (excluding 2016). Shown are the modeled variables (Model), deviance, number of parameters (K), Akaike Information Criterion adjusted for sample size (AIC_c), difference in AIC_c relative to the top model (ΔAIC_c), and model weight (w_i). PRELVL = pre-breeding season water level, LVL = breeding season water level, PHENIND = phenological index, PRETEMP = pre-breeding season water temperature, CONSTANT = a null model with constant DSR.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
PHENIND	1423.62	2	1427.62	0.00	0.51
PRELVL + PHENIND	1423.59	3	1429.59	1.97	0.19
LVL + PHENIND	1423.62	3	1429.62	2.00	0.19
CONSTANT	1430.90	1	1432.90	5.28	0.04
PRELVL	1429.78	2	1433.78	6.16	0.02
PRETEMP	1430.42	2	1434.42	6.80	0.02
LVL	1430.47	2	1434.48	6.85	0.02
PRELVL + PRETEMP	1429.71	3	1435.71	8.09	0.01
LVL + PRETEMP	1429.97	3	1435.928	8.36	0.01

Table 1.3) Comparison of models for second step of model selection for lesser scaup (*Aythya affinis*) nest daily survival rates (DSR) at the Lower Red Rock Lake study site, Montana, USA between 2006 to 2018 (excluding 2016), where intra-annual covariates were added to the inter-annual covariate(s) supported in the first step of model selection. Shown are the modeled variables (Model), deviance, number of parameters (K), Akaike Information Criterion adjusted for sample size (AIC_c), the difference in AIC_c relative to the top model (ΔAIC_c), and model weight (w_i). PHENIND = phenological index, TIME = linear time trend in DSRs across the breeding season, TIME² = additional term for a quadratic time trend, and NAGE = nest developmental age.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
PHENIND + TIME + TIME ²	1360.21	4	1368.21	0.00	1
PHENIND + TIME	1374.31	3	1380.31	12.10	0
PHENIND + NAGE	1377.46	3	1383.46	15.25	0
PHENIND	1423.62	2	1427.62	59.41	0

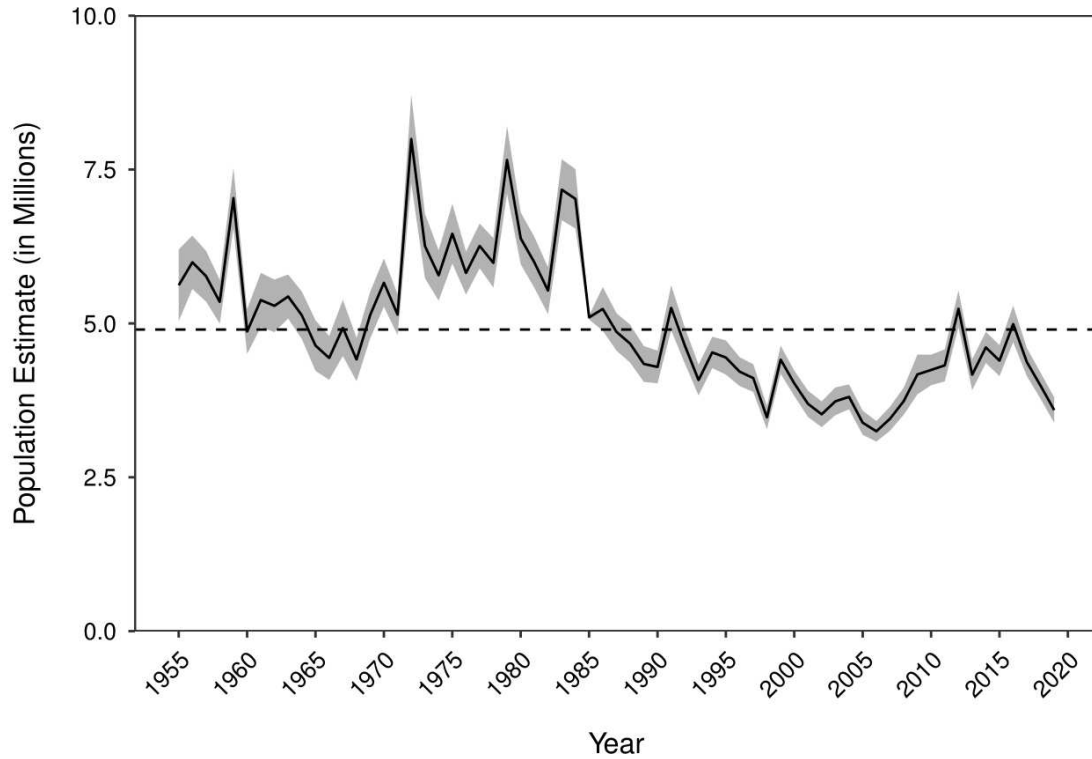


Figure 1.1) Breeding population estimates (solid line) of combined lesser scaup (*Aythya affinis*) and greater scaup (*Aythya marila*) abundance (the two species cannot be differentiated during aerial surveys) and standard errors (grey area). The dashed line indicates the North American Waterfowl Management Plan population goal. Estimates are from the Waterfowl Breeding Population and Habitat Survey traditional survey area which comprises coastal, boreal, prairie-parklands, and prairie pothole habitats in parts of North-Central United States, Canada, and Alaska (U.S. Fish and Wildlife Service 2019).

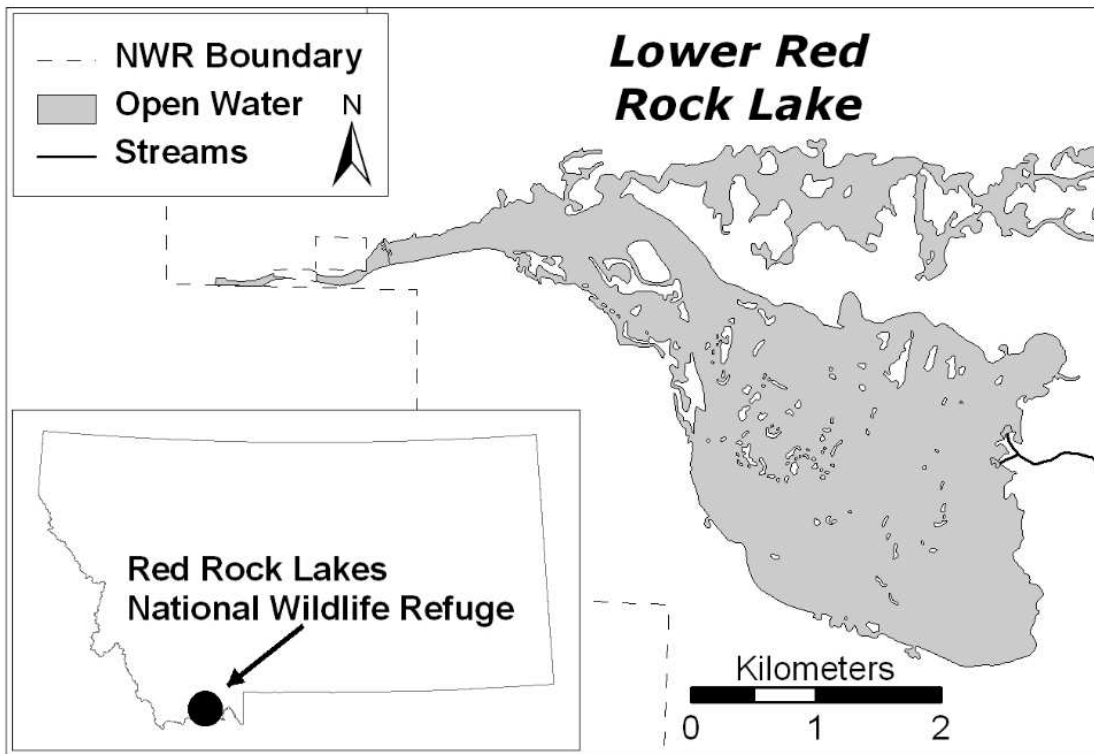


Figure 1.2) Map of Lower Red Rock Lake study site and location of Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA.

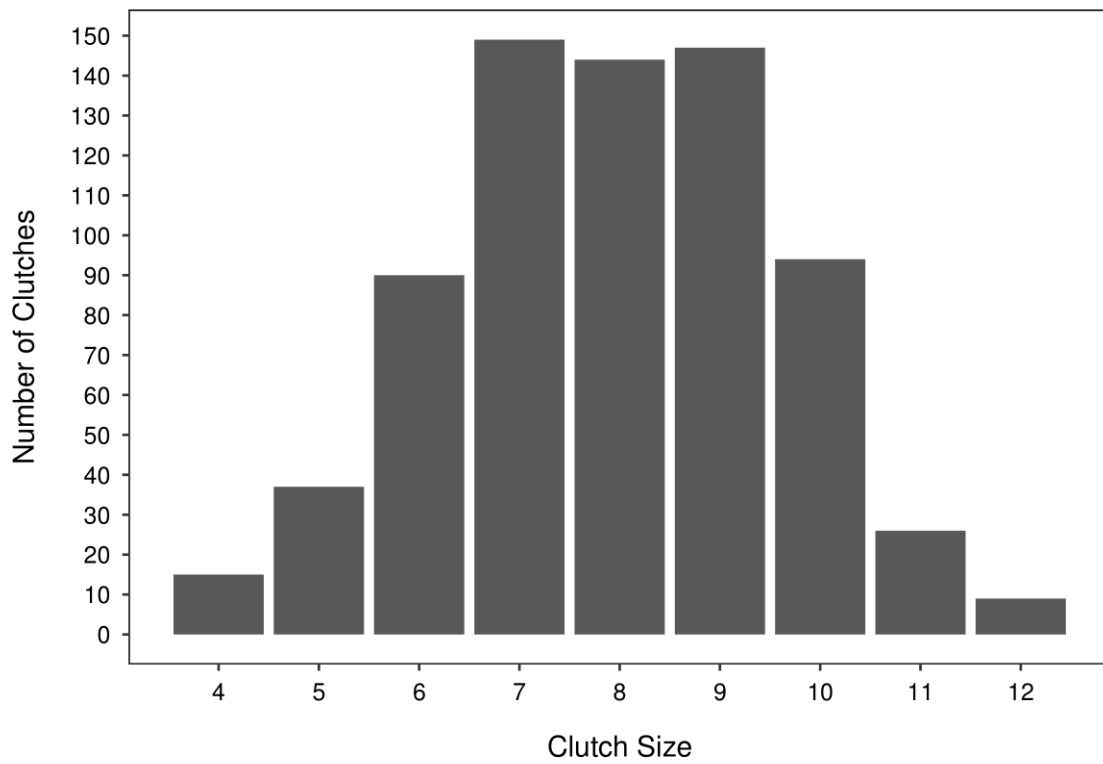


Figure 1.3) Distribution of lesser scaup (*Aythya affinis*) clutch sizes from 2006-2018 (excluding 2016) at the Lower Red Rock Lake study area in Montana, USA.

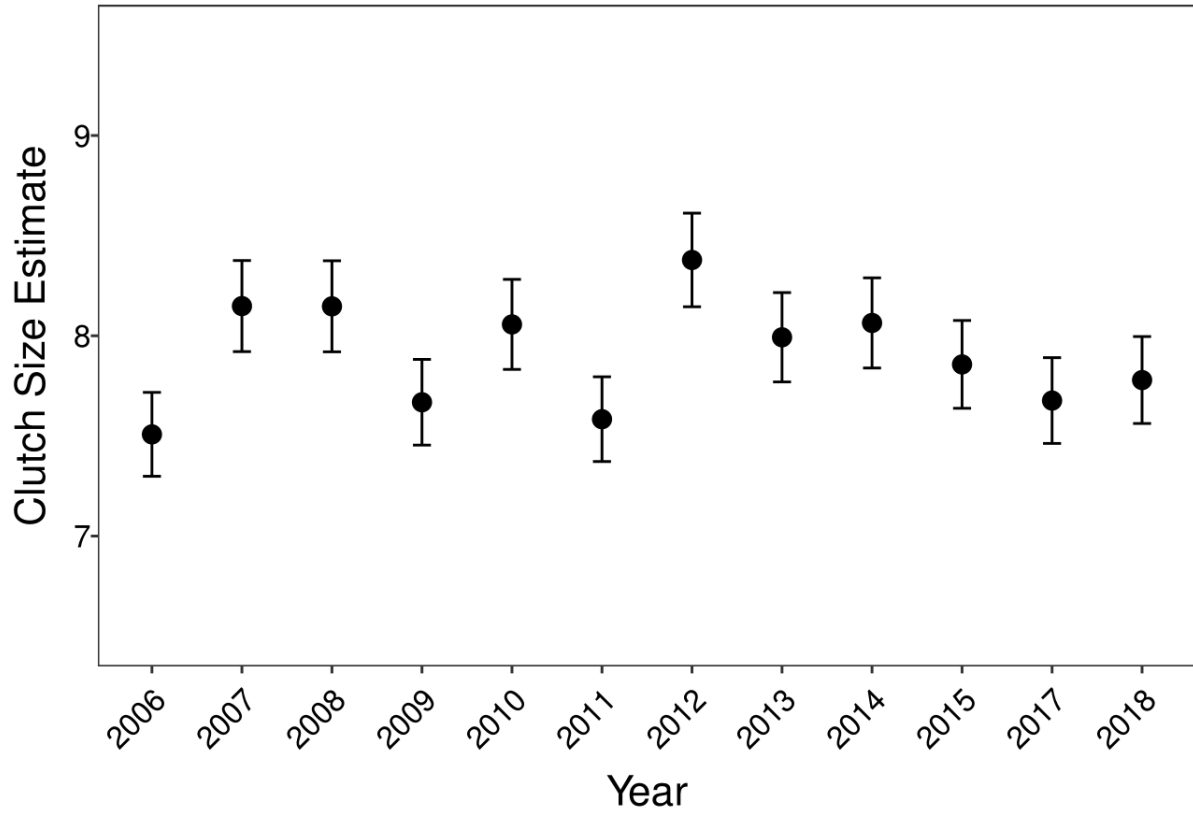


Figure 1.4) Predicted annual mean clutch sizes for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site in southwestern Montana, USA during 2006-2018 (excluding 2016) based on the top model (INIT + YEAR_{RAN}), and associated 95% confidence intervals (error bars).

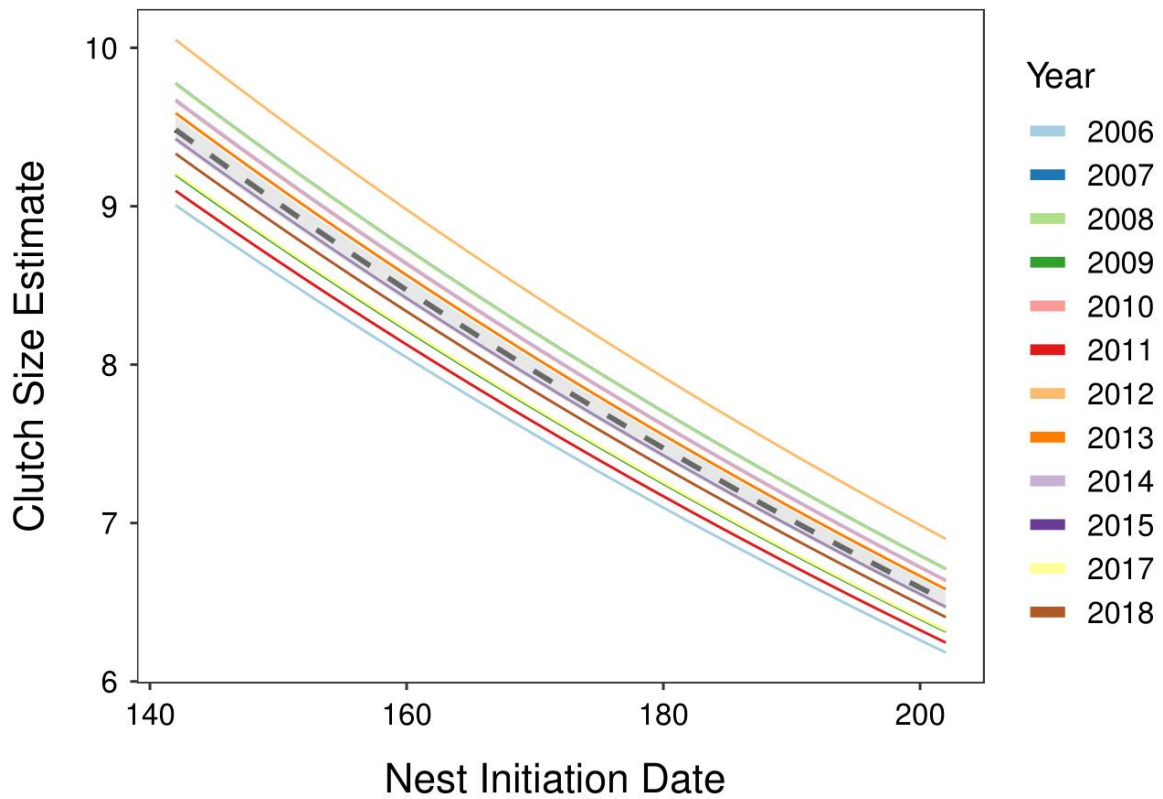


Figure 1.5) Predicted clutch sizes for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site in southwestern Montana, USA from the earliest (ordinal day 143) to the latest (ordinal day 202) nest initiation dates (x-axis) within each year (colored lines). The black dashed line represents the mean among all years with gray 95% confidence interval.

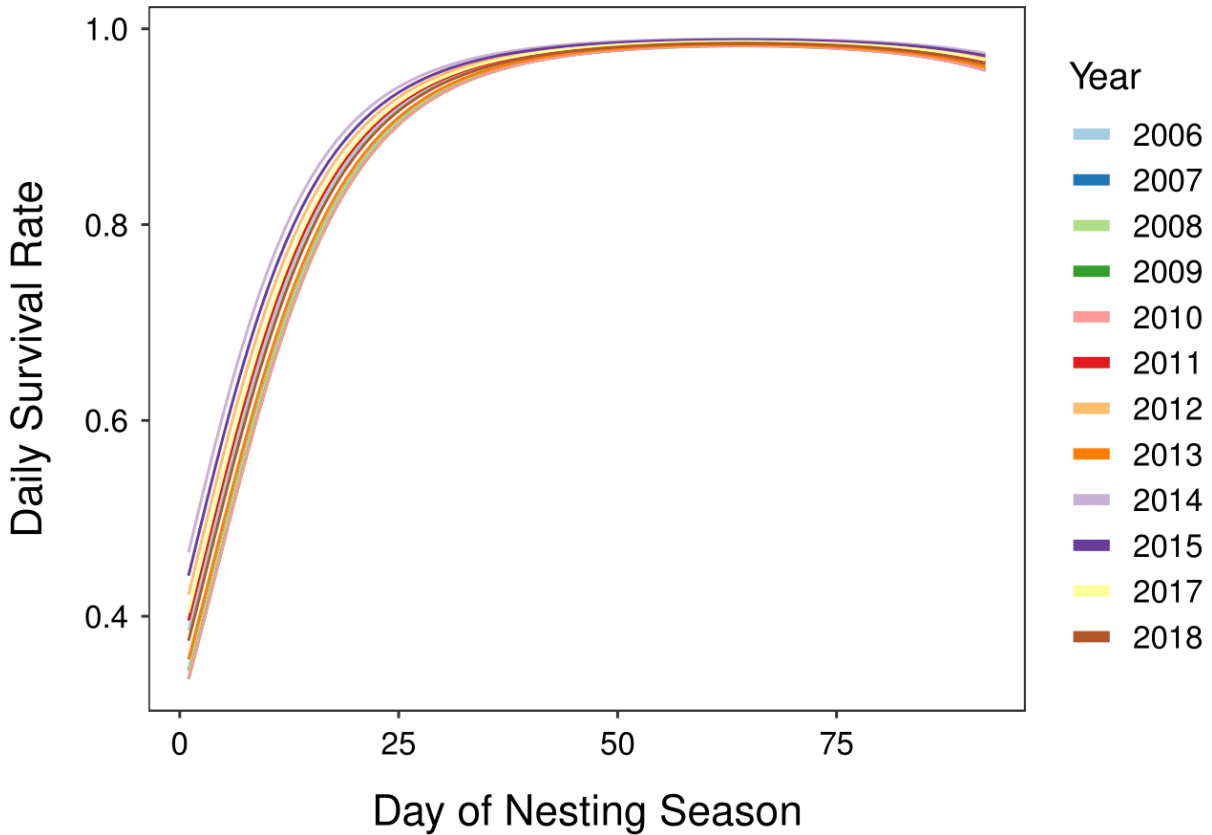


Figure 1.6) Daily survival rate (DSR) for lesser scaup (*Aythya affinis*) nests at the Lower Red Rock Lake study site, Montana, USA across the entire nesting period, demonstrating the variation in DSRs intra-annually (x-axis, and across years (colored lines). Day 0 is the earliest known nest initiation date for the entire study period (ordinal day 143) from the PHENIND + TIME + TIME² model. PHENIND = annual phenological index, TIME = linear time trend in DSRs across days within a breeding season, TIME² = additional term for a quadratic time trend.

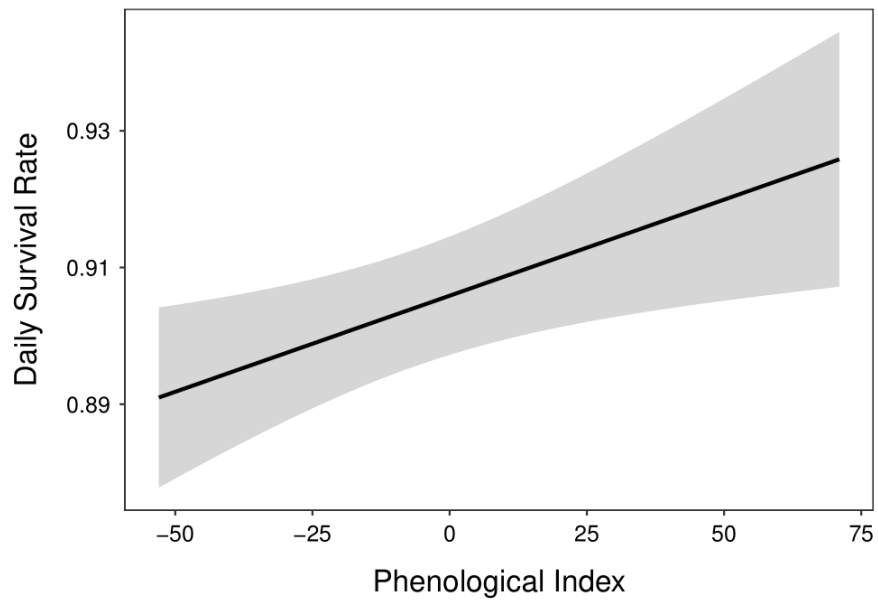


Figure 1.7) Relationship between daily survival rate (DSR) of lesser scaup (*Aythya affinis*) nests at the Lower Red Rock Lake study site, Montana, USA and the annual phenological index (PHENIND) and the associated 95% confidence interval (grey region).

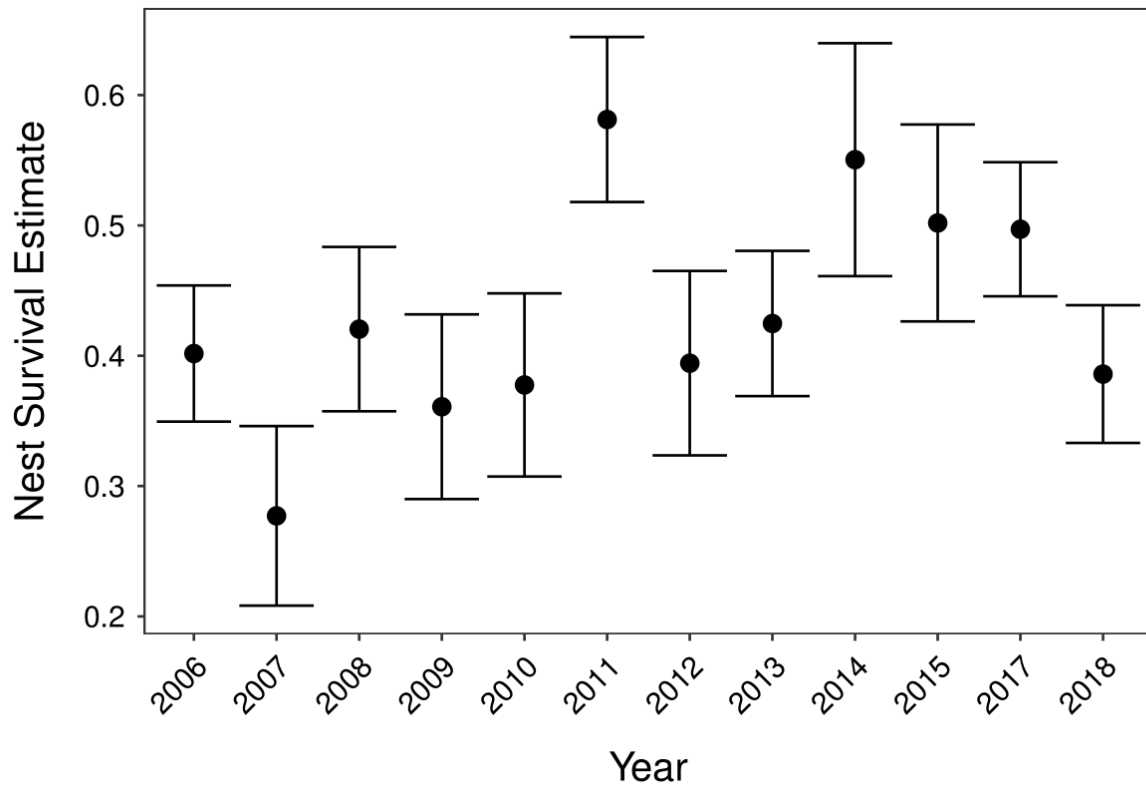


Figure 1.8) Predicted annual nest survival rates for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site, Montana, USA with associated 95% confidence intervals (error bars), which were calculated by taking the product of daily survival rates from the PHENIND + TIME + TIME² model from the mean nest initiation date until day 34 of incubation for each year. PHENIND = phenological index, TIME = linear time trend in DSRs across the breeding season, TIME² = additional term for a quadratic time trend.

CHAPTER TWO

IMPLICATIONS OF VITAL RATE COVARIANCE ON LESSER SCAUP POPULATION DYNAMICS

Introduction

Population abundance, a component of biodiversity, is foundational to ecology and understanding how populations respond to environmental conditions enables informed conservation actions. For decades, researchers have used population models to determine how variation in vital rates influences population growth rates (Caswell 2001). However, many studies combine vital-rate estimates from various locations (Koons et al. 2006, Schamber et al. 2009), which confounds spatial and temporal variation and does not allow for explicit treatment of temporal covariation in vital rates.

Many studies also assume that vital rates vary independently over time (Figure 2.1, panel one), which is a costly assumption because covariation among vital rates can sometimes have a greater influence on population dynamics than the direct impact of temporal variances (Coulson et al. 2005, Doak et al. 2005). Omitting temporal covariation from population models could therefore lead to spurious conclusions about population dynamics and inappropriate management actions, since these co-varying relationships are often caused by vital-rate responses to common environmental drivers that can be targeted by managers (Coulson et al. 2005). For example, positive temporal covariation is caused by vital rates responding similarly to underlying environmental conditions (Figure 2.1, panel two). Whereas negative covariation arises when vital rates respond differently to environmental conditions, or when greater investment in one part of the life-cycle results in a trade-off at another part, e.g., a cost of reproduction (Figure 2.1, panel three; Hoekman et al. 2002, Aubry et al. 2009, Amundson et al. 2013). Understanding and

including these relationships among vital rates into population models could identify environmental variables that may cause changes in multiple vital rates that managers can then manipulate to efficiently benefit population growth rates (Fieberg and Ellner 2001). Considering such correlations among demographic rates could be particularly important for population viability analyses, as these are used to determine extinction risk and management actions for imperiled species (Boyce 1992, Brook et al. 2000). However, to estimate covariation among vital rates, demography must be studied over long periods of time at the same geographic location (or via longitudinal studies at multiple locations).

Long-term studies can incorporate temporal covariation in vital rates as well as inform perturbation analyses (Miller et al. 2011, Morris et al. 2011). Both prospective and retrospective perturbation analyses provide insights as to which vital rates to target for management actions (Mills and Lindberg 2002, Morris and Doak 2002). Prospective perturbation analysis examines how equivalent changes in vital rates could affect population growth rate in the future. Whereas, retrospective analyses quantify how non-equivalent changes in vital rates affected population growth rates in the past (Caswell, 2000, 2001), from which historical information can be used (with care) to inform future actions (Koons et al. 2016).

Lesser scaup (*Aythya affinis*) are a medium-sized diving duck that could benefit from a deeper understanding of these processes because their population has declined while other North American waterfowl are thriving. The continental population of scaup (*Aythya* spp., 3.6 ± 0.2 million birds, U.S. Fish and Wildlife Service, 2019) remains well below the North American Waterfowl Management Plan objectives of 4.9 million birds, continuing a nearly three-decade long deficit relative to objectives (Figure 1.1; note that estimates of scaup abundance represent a combination of greater scaup (*A. marila*) and lesser scaup because these two species cannot be

differentiated in aerial surveys, but is comprised of ~90% lesser scaup, Anteau et al. 2014, U.S. Fish and Wildlife Service 2019). The extensive range of lesser scaup (hereafter scaup) exposes them to a wide variety of threats that may be contributing to the marked population decline. Previous analyses of long-term wing collections by hunters suggested that recruitment and female survival may have both declined since the 1970s (Allen et al. 1999, Afton and Anderson 2001). However, recent analyses of banding data and an integration of monitoring data have found no long-term declines in survival and concluded that recruitment was the likely driver of population declines (Arnold et al. 2016, 2018, Koons et al. 2017). These results highlight the need to better understand the factors limiting recruitment in scaup.

Recruitment is defined as the number of young that survive to breed the following season (Cowardin and Blohm 1992) and thus entails multiple vital rates throughout the annual life cycle. For lesser scaup and other waterfowl these vital rates include breeding propensity, clutch size, nesting success, re-nesting probability, duckling survival, and first year survival of fledged offspring. Understanding drivers of recruitment is crucial to waterfowl management because each component of recruitment is affected by different habitats and potentially even various times of the year when considering cross-seasonal effects, and because it is helpful to accurately forecast recruitment (to at least the next fall flight) to set sustainable harvest regulations (Cowardin and Blohm 1992).

Koons et al. (2006) first applied prospective tools to examine how changes in vital rates could affect lesser scaup population growth rate. However, this study amalgamated rates from different locations and could not incorporate temporal covariation of vital rates into population models. Recent work utilized prospective and retrospective transient perturbation analyses to identify recruitment as the likely driver of long-term declines in scaup abundance across the

large-scale traditional survey area (Koons, Arnold, & Schaub, 2017), however the use of a large-scale integrated population model prevented inference at local scales where the mechanisms driving temporal covariation among vital rates is most meaningful to management. Finer-scale studies that can address temporal covariation in vital rates are thus needed to better understand the local environmental drivers that affect recruitment and population dynamics, and to better identify habitat drivers that can be managed.

Wetland basin densities and water levels are potential habitat variables that managers can manipulate. On the breeding grounds, variation in wetland abundance is known to have strong impacts on recruitment, but water level manipulation is rarely considered as a tool for affecting recruitment; though it is a common tool used for maximizing food availability to wintering waterfowl (Smith et al. 1989, Dzus and Clark 1998). Variation in water levels and water level phenology can plausibly affect scaup recruitment because they rely on wetlands for nearly every component of their life cycle; however, managers need a better understanding of correlations between wetland conditions and vital rates to successfully influence recruitment through management (Anteau et al. 2014, Baldassarre 2014).

Correlations between wetland condition and various vital rates have been observed in scaup. For example, wetland condition was positively correlated with breeding propensity (Rogers 1964, Warren et al. 2014) and negatively correlated with female seasonal survival at sites in Canada (Rotella et al. 2003). However, at our study site wetland levels were positively correlated with adult female breeding season survival and negatively correlated with adult non-breeding season survival (Warren 2018). Thus, correlations between wetland conditions and vital rates could potentially affect scaup population growth rate by driving co-variation among important vital rates.

We collated information from a long-term study of lesser scaup demography at Red Rock Lakes National Wildlife Refuge and created time-variant population models. We were uniquely able to estimate and incorporate covariation among vital rates into our models to explore its impact on local lesser scaup population dynamics. We created stochastic population models and conducted a transient life-table response experiment (LTRE) to 1) determine stochastic population growth rate (λ_S) and prospective sensitivities of λ_S to proportional changes in the vital rates, 2) examine the contribution of temporal variance and covariance of vital rates to past variation in realized growth rates, and 3) decompose variation in realized growth rates into direct effects from variance in vital rates and indirect effects from covariance among vital rates.

Methods

Study Site

Our study was conducted on Lower Red Rock Lake (LRRL) at Red Rock Lakes National Wildlife Refuge (RRL) in Southwest Montana (Figure 2.3). Lower Red Rock Lake is a 2,330-hectare, high elevation (2,014 m above mean sea level) montane wetland complex within the Centennial Valley that supports a high-density of breeding lesser scaup (>7.7 breeding pairs/km², J. Warren *pers obs*). This wetland system is characterized by large areas of open water with hardstem bulrush (*Schoenoplectus acutus*) islands and surrounded by vast stands of seasonally flooded northwest territory sedge (*Carex utriculata*). Interspersed in the sedge stands are small (< 2 ha) open water ponds, which offer additional nesting habitat (e.g., to nest near open water and escape from predators).

Research on the scaup population on LRRL began in 2005 to estimate seasonal and age-specific survival using capture-mark-recapture techniques (Warren 2018). Then in 2006 field

methods were added to enable the estimation of certain reproductive parameters (Warren et al. 2013, 2014). Finally, procedures were added to estimate duckling survival in 2010 (Stetter 2014, Warren 2018). A detailed description of study site can be found in chapter one of Navarre (2020).

While LRRL is on the southern extent of the scaup breeding range, it hosts many similarities to wetland complexes in scaup's core breeding area in the northwest boreal forest of Canada. Similarities include growing season length, shallow waters, fluvial hydrology and large expanses of flooded northwest territory sedge (U.S. Fish and Wildlife Service 2009, Wells et al. 2010, Gurney et al. 2017). Underlying environmental similarities between LRRL and the boreal forest may provide better insights as to what could be potentially driving declines than many of the previous studies on scaup that were conducted in prairie-parkland habitats (Afton 1984, Koons and Rotella 2003b, 2003a, Rotella et al. 2003, Anteau and Afton 2006), but see (Slattery and Clark 2019). Prairie habitats differ from LRRL and the boreal ecosystem as prairie systems are fed by snow-melt and ground water, have longer growing season lengths, and landscapes are dominated by agriculture (wheat, barley, canola, and flax, Koons and Rotella 2003a, Gurney et al. 2011).

Vital Rate Estimates and Life-Cycle Model

Using the rich array of scaup research at the RRL study site, we collated a set of published and unpublished estimates of vital rate means and sampling variances for each year possible. Vital rates of interest included breeding propensity (BP), clutch size (CS), nest survival (NS), duckling survival (DS), juvenile survival from fledging until the following breeding season (JS), adult female breeding season survival (BS), and non-breeding season survival of adult females (NBS).

Previously published estimates of breeding propensity controlled for capture date, age class and drought conditions (Warren et al. 2014) and were estimated directly in 2007-2009. Using the estimated relationship between drought and BP from Warren et al. (2014), we modeled predicted BP for all other years based on annual mean water levels. Within- and among-year variation in clutch size was estimated during 2006-2015 and 2017-2018 (Chapter One). A previous study (Koons et al. 2006) found both breeding propensity and clutch size to be age-specific (rates differed between second-year (SY) and after-second-year (ASY) birds). At our study site we were unable to determine the age of most nesting hens, and thus we calculated age-specific estimates in a *post hoc* fashion. To do so we took each annual estimate of clutch size at our study site (which conflates any effect of age) and partitioned it into two age classes using the relative difference between age classes reported in Koons et al. (2006) and the stable age distribution from Koons et al. (2006). Next, we used estimates of nest survival from Chapter One, which were estimated each year during 2005-2015 and 2017-2018. Duckling survival was estimated during 2010-2015 and 2017-2018 (Stetter 2014). Juvenile survival, adult breeding season survival, and adult non-breeding season survival were estimated each year during 2005-2015 and 2017-2018, while accounting for marker loss (Warren 2018). Finally, we calculated the among-year mean and temporal process variance for each vital rate using the method described by (White 2000), which were later used in building time-variant population models.

We approximated the annual life cycle of Lesser Scaup (Figure 2.4) with two age classes: SY (birds entering their second year of life) and ASY (after second year). Based on this life cycle, our matrix projection model (Equation 2.1) was parameterized with a fertility value for each age class assuming a pre-breeding census and female limited birth-pulse reproduction (Caswell 2001).

$$\mathbf{A} = \begin{bmatrix} f_{SY,t} & f_{ASY,t} \\ S_{SY,t} & S_{ASY,t} \end{bmatrix} \quad \text{Equation 2.1)}$$

Age-specific fertility (Equation 2.2) is the product of the sex ratio (0.5 for lesser scaup (Arnold et al. 2016), age-specific breeding propensity (BP_x), age-specific clutch size (CS_x), and the probabilities of nest survival (NS), duckling survival (DS), and juvenile survival between fledging in year t and the start of nesting in year $t+1$ (JS).

$$f_{x,t} = 0.5 * BP_{x,t} * CS_{x,t} * NS_t * DS_t * JS_t \quad \text{Equation 2.2)}$$

For the purposes of this analysis we assumed scaup do not re-nest due to limitations of our study, though evidence indicates that at least some should (Afton 1984, Flint et al. 2006). Survival probabilities were assumed to be equivalent for both age classes and annual adult survival was parameterized as a product of breeding season survival (BS) and non-breeding season survival (NBS, Equation 2.3).

$$S_{x,t} = BS_t * NBS_t \quad \text{Equation 2.3)}$$

Population Modeling

To relax assumptions of the commonly used deterministic matrix projection model (MPM), we sought to account for the realities of variation and covariation among vital rates over time. To do so, we first generated probability distributions for each vital rate using its estimated mean and temporal process variance for years in which we had direct estimates of vital rates (BP: 2007-2009, CS: 2006-2015 and 2017-2018, NS: 2006-2015 and 2017-2018, DS: 2010-2015 and 2017-2018, JS: 2005-2017 BS: 2005-2017, NBS: 2005-2017). Beta distributions were used to summarize the temporal variability of any vital rate constrained between 0 and 1 (BP, NS, DS,

JS, BS, NBS) and gamma distributions were used for CS. We then incorporated covariation among vital rates by calculating Pearson correlation coefficients between each pair of vital-rate point estimates for years when all vital rates were estimated (2010-2015 & 2017; wherein BP was predicted based on water levels). We then utilized copulas to generate correlated temporal distributions of vital rates using the copula package in R (Hofert et al. 2018). Next, we generated a Monte Carlo sequence of 10,000 randomly selected values for each vital rate. This sequence was used to estimate λ_S (Tuljapurkar 1984, Caswell 2001):

$$\widehat{\log \lambda_S} = \frac{1}{T} \sum_{t=0}^{T-1} r_t \quad \text{Equation 2.4)}$$

where $r_t = \log(N(t+1)/N(t))$. Finally, we calculated lower-level elasticities of λ_S to proportional changes in the mean ($E_{ij}^{S\mu}$), temporal process variance ($E_{ij}^{S\sigma}$), and the coefficient of variance (E_{ij}^S) of each vital rate, as previously outlined by others (Equation 2.5 - 2.7, Doak et al. 2005a, Haridas and Tuljapurkar 2005, Tuljapurkar and Haridas 2006).

$$E_{ij}^{S\mu} = \frac{\partial \log \lambda_S}{\partial \log \mu_{ij}} \quad \text{Equation 2.5)}$$

$$E_{ij}^{S\sigma} = \frac{\partial \log \lambda_S}{\partial \log \sigma_{ij}} \quad \text{Equation 2.6)}$$

$$E_{ij}^C = \lim_{T \rightarrow \infty} \left(\frac{1}{T} \right) \sum_{t=1}^T \frac{v_i(t) C_{ij}(t) u_j(t-1)}{\lambda(t)(\mathbf{v}(t), \mathbf{u}(t))} \quad \text{Equation 2.7)}$$

Equation 2.7 is the general formula for calculating elasticities and which can yield $E_{ij}^{S\mu}$ when, $C_{ij}(t) = \mu_{ij}$, $E_{ij}^{S\sigma}$ when $C_{ij}(t) = X_{ij}(t) - \mu_{ij}$, and E_{ij}^S when $C_{ij}(t) = X_{ij}(t)$. Where $\mathbf{u}(t)$ is the sequences of population structure vectors, $\mathbf{v}(t)$ is the sequences of reproductive value vectors at each time step t , and $X_{ij}(t)$ is the matrix element perturbed by a proportional amount $C_{ij}(t)$.

To additionally account for possible non-stationary changes in the local scaup demography over time and to exploit the insights provided by retrospective perturbation analyses, we analyzed population dynamics over the observed timeframe of 2010-2017 (omitting 2016). Lacking knowledge of the age distribution in 2010, we first conducted an asymptotic analysis of a deterministic MPM for 2010 to determine its stable age distribution, which we then used to project future abundances and age structures using the realized time-variant sequence of vital rates thereafter. After accounting for process variance and covariance among vital rates and age structure, we first calculated the sensitivity (Equation 2.8) of λ_t to change in each demographic parameter using symbolic calculus, where λ_t is the realized population growth rate at time step t and $\theta_{i,t}$ is demographic parameter θ_i at time step t (inclusive of both vital rates and population structure):

$$\frac{\partial \lambda_t}{\partial \theta_{i,t}} \quad \text{Equation 2.8)}$$

The calculated sensitivities and the covariation among demographic rates were used to obtain the variation in realized growth rates (Equation 2.9)

$$\text{var}(\lambda_{\text{realized},t}) \approx \sum_i \sum_j \text{cov}(\theta_{i,t}, \theta_{j,t}) \left. \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{i,t}} \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{j,t}} \right|_{\bar{\theta}_{ij}} \quad \text{Equation 2.9)}$$

Finally, contributions of each individual demographic parameter (χ_{θ_i}) to temporal variance in realized population growth rates was calculated by summing over the vital-rates covariances (Equation 2.10, Horvitz et al. 1997).

$$\chi_{\theta_i} \approx \sum_j \text{cov}(\theta_{i,t}, \theta_{j,t}) \left. \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{i,t}} \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{j,t}} \right|_{\bar{\theta}_{ij}} \quad \text{Equation 2.10)}$$

A vital rate may contribute little to variation in λ_t due to a low sensitivity (it is insensitive to change), low variance in demographic parameter θ_i , and/or the effect of negative covariation between θ_i and θ_j nullifying the direct effect of variation in θ_i (Koons et al. 2016). The contribution of θ_i to variation in λ_t reveals how strongly fluctuations in λ_t are driven by θ_i . We also decomposed variation in realized growth rates into contributions of direct effects of variation in vital rates and indirect effects of covariation among vital rates, by summing over the variances and covariances separately.

Results

We found that NS and DS experienced the highest levels of temporal process variance during our study, whereas BP_{SY} and BP_{ASY} experienced the lowest levels. The process variance of CS_{SY} and CS_{ASY} were also low. Mean vital rate estimates, process variances, and the years which were used to calculate these statistics can be found in Table 2.1 for the prospective analysis and Table 2.2 for the retrospective analysis. We found strong positive correlations between BS and JS and strong negative correlations between NS and CS, JS and NBS and BS and NBS. All other correlations were moderate to weak (between -0.70 and 0.70). Pearson's correlations used in the prospective perturbation analysis can be found in Table 2.3 and correlations used in the retrospective perturbation analysis can be found in Table 2.4. We also note that correlations between BP_{SY} and BP_{ASY}, and CS_{SY} and CS_{ASY}, were intrinsically close to 1.00 because rates for SY and ASY birds were differentiated from one another *post hoc* using a composite estimate of BP and CS which included both estimates.

The stochastic population growth rate over the study period was 0.94, which suggests the studied scaup population was declining at an average rate of 6% each year (but was fluctuating

and did not decline at this rate every year). The stochastic elasticities of λ_S to changes in the mean of lower level vital rates $E_{ij}^{S\mu}$ were highest for BS (0.84) and NBS (0.82), indicating proportional changes in mean BS and NBS have the greatest potential to influence population growth rate into the future (Figure 2.5 Panel 1). In contrast $E_{ij}^{S\mu}$ for BP_{SY} (0.02) and CS_{SY} (0.02) were lowest, indicating that equivalent proportional changes in these vital rates would have little influence on λ_S . Changes to mean BP_{ASY} , CS_{ASY} , NS, DS, JS also had relatively low $E_{ij}^{S\mu}$. Elasticities of λ_S to changes in the process variance of vital rates ($E_{ij}^{S\sigma}$) was highest for NS (0.05), followed by NBS (0.02), suggesting that increased variation in NS and NBS would positively influence λ_S (Figure 2.5, Panel 2). Conversely, $E_{ij}^{S\sigma}$ was negative for DS (-0.12), indicating increased rates of variation in DS would result a decline in λ_S . Finally, elasticities of λ_S to changes in the coefficient of variation (CV) of vital rates (E_{ij}^S) demonstrated similar patterns as changes in mean vital rates with BS and NBS (both 0.84) having the highest E_{ij}^S and BP_{SY} and CS (both 0.02) having the lowest (Figure 2.5, Panel 3).

Results from the transient LTRE demonstrated that temporal variation in DS (0.64) made the greatest contribution to temporal variation in λ_t , followed by NS (0.27) and NBS (0.20, Figure 2.6). A subset of demographic parameters (CS_{SY} , CS_{ASY} , JS, BS) had small negative contributions ($-3.65 * 10^{-3}$, -0.02, -0.08, -0.04 respectively) to variation in λ_t . SY (-0.03) and ASY (-0.01), the demographic rates which accounted for the proportion of the population in each age class, also had small negative contributions to variation in λ_t . BP_{SY} , BP_{ASY} , had little to negligible positive contributions to variation in realized growth rates. Finally, comparing direct and indirect contributions of vital rates to variation in realized growth rates indicated that

covariation among demographic parameters explained 37% of the variation in λ_t , while direct variation in demographic parameters explained 63% (Figure 2.7, Table 2.6).

Discussion

Understanding population dynamics requires knowledge of how demographic parameters temporally covary with one another because such processes can explain a large proportion of variation in population growth rates (Coulson et al. 2005, Doak et al. 2005). Here we accounted for temporal covariation in vital rates across the annual cycle of lesser scaup and conducted prospective and retrospective perturbation analysis to determine which demographic parameters had the greatest influence on population growth rate. We found that covariation among parameters explained 37% of the variation in realized growth rates, which is a non-negligible amount that stresses the importance of including temporal covariation into population analyses. Utilizing prospective and retrospective tools, while accounting for temporal covariation will allow managers to make well-informed decisions regarding species in decline.

Prospective Analysis

Like the continental population, the population of scaup at LRRL may be declining (U.S. Fish and Wildlife Service 2019). The stochastic growth rate of 0.94 at LRRL is slightly higher than that of 0.91, estimated across several populations in the boreal and prairie-parklands (Koons et al. 2006). Regardless, we suspect our estimate of λ_S is biased low because the study population has remained locally abundant throughout the study period. It is possible there are high rates of immigration supplementing this population, or birds may return to the Centennial Valley, but not LRRL and remain undetected by our re-sight surveys. Recent work at our study site also indicates that nasal markers negatively influence survival (Deane 2017), that once finalized and accounted for, could increase the estimate of λ_S .

We found the highest elasticities were to changes in mean BS and NBS survival, which is similar to many prospective perturbation analyses conducted on waterfowl such as mallards (*Anas platyrhynchos*, Hoekman et al. 2002) and many species of sea duck (Schamber et al. 2009, Flint 2015). Like our study, Koons et al. (2006) found that modeled population growth rates were most elastic to changes in mean BS and NBS, however they were unable to account for temporal covariation among vital rates, which may explain dissimilar results between our studies and theirs to perturbations of variance in vital rates. Koons et al. (2006) found elasticities to changes in variance to be negative for all vital rates with the largest magnitudes for NS and DS, indicating fluctuation in variance would negatively impact population growth rate. In contrast, we found a positive elasticity to changes in the variance of NS, which may lead to increased population growth rates by allowing for more “boom” years and in turn higher recruitment rates (Boyce et al. 2006, Lawson et al. 2015, Iles et al. 2019)

Retrospective Analysis

Our goal was to pin-point which vital rates were driving scaup population dynamics using retrospective tools, which explore how a vital rate’s sensitivity value and temporal variation contributed to realized growth rates. There is evidence across taxa that vital rates with high elasticities, such as adult survival, have little influence on realized growth rates due to low interannual variation, especially in species with longer generation times (Gaillard et al. 1998, Sæther and Bakke 2000). Adult survival is hypothesized to be buffered against temporal variation, whereas vital rates which contribute to fertility tend to be more variable and potentially more labile to temporal changes in environmental conditions, which can result in larger contributions to realized growth rates (Pfister 1998, Morris and Doak 2004, Koons et al. 2009).

Vital rates with high elasticities are also found to have small contributions to realized

growth rates in waterfowl (Koons et al. 2014). For example, in both snow geese (*Chen caerulescens*) and barnacle geese (*Branta leucopsis*) components of recruitment were found to contribute most to realized growth rates, while adult survival had the highest prospective elasticities (Rockwell et al. 1997, Cooch et al. 2001, Layton-Matthews et al. 2019). There is a similar trend in species with intermediate life histories, such as sea ducks, as well as with scaup (Flint 2015). Koons et al. (2017) conducted a transient LTRE on lesser scaup utilizing an Integrated Population Model (IPM) and found that JS had the largest contribution to realized growth rates at 52%, while adult survival had the highest prospective elasticity. In contrast we found that DS contributed most to realized growth rates, which is likely due to incorporating covariation among vital rates that is being driven by local environmental variables (e.g., Chapter 1). DS had relatively high process variance as well as moderately high realized sensitivity (Table 2.5), which resulted in its large contribution to realized growth rates (See equation 2.9). Unlike Koons et al. (2017), we found a slightly negative contribution of JS to realized growth rates due to negative covariation with several other vital rates, nullifying the direct effect of variation (Table 2.3, Table 2.6). While our results were somewhat different than those of Koons et al. (2017), our conclusions support the broader hypothesis that recruitment is driving scaup population dynamics because DS is an important component of recruitment (Arnold et al. 2016, Koons et al. 2017). Recruitment has had a large influence on the population dynamics of many waterfowl species including mallard, canvasback (*Aythya valisineria*), and lesser scaup (Johnson et al. 1992b, Anderson et al. 1997, Walker and Lindberg 2005), and duckling survival may have a greater influence on population growth rates in populations with high nest survival such as at LRRL (Amundson and Arnold 2011)

Contribution of Temporal Covariation

Our study as well as many others found significant correlations among demographic parameters. For example, Sæther and Bakke (2000) examined the contribution of variation in vital rates on population growth rate for several avian species and found positive correlations between fecundity and juvenile survival, and between adult survival and juvenile survival. Sim et al. (2011) also found positive correlations between reproductive success and adult survival for ring ouzels (*Turdus torquatus*). We also found positive correlations between juvenile and adult survival rates, which indicates that these vital rates respond similarly to underlying environment conditions. For example, if environmental conditions are favorable on the breeding grounds both age classes would have high rates of survival. However, we also found significant negative correlations between BS and NBS of adults, implying a cost-of-reproduction that was examined in depth by Warren et al. (2018) at our study site.

When comparing the contribution of covariation among demographic parameters to the direct contributions of variation, we found that covariation accounted for 37% of the temporal variation in realized growth rates. Closer examination of the proportional contributions of individual pairs of demographic rates found the largest positive contributions came from covariation between JS and BS, additionally supporting the conclusion these rates respond similarly to environmental conditions (Table 2.6). Whether environmental conditions on the breeding grounds (due to carry-over effects) or wintering grounds is driving rates of JS warrants further study. In contrast, the largest negative contributions were a result of covariation between JS and NBS followed by BS and NBS, further supporting the conclusion that scaup experience decreased levels of fitness after breeding (Table 2.6). Understanding these relationships allows managers to weigh the cost and benefits of specific management actions.

Our results are similar to those of Coulson et al. (2005) who found that covariation explained between $\frac{1}{3}$ and $\frac{1}{2}$ of the variation in population growth rates for several ungulate populations. This conclusion supports our hypothesis that covariation in demographic parameters can greatly contribute to population growth rate, and though commonly done, researchers should not assume independence among demographic parameters. To truly understand demographic and evolutionary processes, studies must account for temporal covariation among vital rates (Doak et al. 2005).

Management Implications and Future Research Needs

Accounting for temporal covariation is especially important for applied management, since we often prioritize influential vital rates for management actions (Wisdom et al. 2000, Davison et al. 2013). Assuming that vital rates are temporally independent could lead to spurious conclusion about the demographic processes that are most influential on population dynamics, such inference could misinform management and possibly have negative impacts on declining populations. Efforts should be made to account for temporal covariation among demographic parameters in population viability analysis to correctly estimate extinction thresholds, compare management actions, and determine which demographic parameters have the greatest influence on population dynamics (Boyce 1992, Mills and Lindberg 2002, Boyce et al. 2006). Our results further support the need for long-term studies that enable the estimation of process variance and covariance in order to understand demographically what is driving populations and make the best management decisions (Menges 2000, Sæther and Bakke 2000).

In addition, our findings provide insights into needed management actions as well as future research need for scaup at LRRL and other regions such as the boreal forest. The results of the prospective analysis indicated that BS and NBS survival have the greatest potential to

influence population growth rate, however, these rates are currently high, and vary little interannually. Thus, we might have little potential to positively influence these survival probabilities, and if hunting has compensatory impacts on NBS (Arnold et al. 2016, Warren 2018), then harvest might have little potential to negatively impact survival as well. However, work to incorporate a correction factor for the effect of nasal markers on survival will be necessary for an accurate estimate of JS, BS, and NBS. Given that the vital rates with the highest prospective elasticities contributed little to realized growth rates, management might consider directing focus at increasing DS and possibly other components of recruitment in other populations. Efforts to increase, stabilize the large amount of variation around DS, or positively influence vital rates which are positively correlated with DS, could lead to notable increases in population growth rate. One possible action could be to manipulate water levels to positively influence breeding propensity (which is highly correlated with duckling survival), because water levels are known to influence BP at our study site (Warren et al. 2013). Our findings from chapter one found that manipulating water levels could also positively influence NS, which could increase population growth rate since NS was found to have the second highest contribution to realized growth rates. However, Stetter (2013) explored drivers of duckling survival and found no effect of water levels, but a positive effect of water temperature (a proxy for wetland phenology), which often drives primary productivity and available invertebrate food resources (Vannote and Sweeney 1980, Cayrou and Céréghnio 2005, Devries et al. 2008). Management of scaup populations would benefit from a better understanding of drivers of invertebrate resources on which scaup ducklings rely (Dawson and Clark 1996).

While our study site does not perfectly emulate boreal forest habitats where scaup predominantly breed, our results could offer some insights into research needs for boreal

populations due to similarities between locations which include similar growing season lengths, large expanses of flooded sedge habitats, fluvial hydrology, and dammed systems (U.S. Fish and Wildlife Service 2009, Wells et al. 2010, Gurney et al. 2011, 2017). Determining rates and drivers of duckling survival in these locations should be a priority. However, it should be noted that the boreal forests are realizing the effects of climate change at a faster rate than sites at lower latitudes such as RRL and efforts should be made to determine how vital rates vary and covary at boreal sites in response to climate change and commensurate impacts on wetlands and hydrology.

Table 2.1) Summary of vital rate means and temporal process variances for lesser scaup (*Aythya affinis*) used for the prospective perturbation analysis, as well as years in which vital rates were directly measured at the Lower Red Rock Lake study area. BP_{SY}: SY breeding propensity, BP_{ASY}: ASY breeding propensity, CS_{SY}: SY clutch size, CS_{ASY}: ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival.

Vital Rate	Mean	Process Variance	Years
BP _{SY}	0.723	1.435*10 ⁻³	2007-2009
BP _{ASY}	0.984	1.435*10 ⁻³	2007-2009
CS _{SY}	7.455	1.512*10 ⁻¹	2006-2015, 2017-2018
CS _{ASY}	8.132	1.512*10 ⁻¹	2006-2015, 2017-2018
NS	0.431	1.351*10 ⁻²	2006-2015, 2017-2018
DS	0.285	1.325*10 ⁻²	2010-2015, 2017-2018
JS	0.442	8.623*10 ⁻³	2005-2017
BS	0.843	3.409*10 ⁻³	2005-2017
NBS	0.904	9.637*10 ⁻³	2005-2017

Table 2.2) Summary table of mean and temporal process variance for each demographic parameter from 2010-2015 and 2017 for lesser scaup (*Aythya affinis*), which were used for the transient LTRE at the Lower Red Rock Lake study area. BP_{SY} : SY breeding propensity, BP_{ASY} : ASY breeding propensity, CS_{SY} : SY clutch size, CS_{ASY} : ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival, SY: the proportion of SY females in the local population, ASY: the proportion of ASY females in the local population.

Vital Rate	Mean	Process Variance
BP_{SY}	0.711	$2.05 \cdot 10^{-3}$
BP_{ASY}	0.956	$2.05 \cdot 10^{-3}$
CS_{SY}	7.447	$1.51 \cdot 10^{-1}$
CS_{ASY}	8.108	$1.51 \cdot 10^{-1}$
NS	0.448	$1.90 \cdot 10^{-2}$
DS	0.293	$1.49 \cdot 10^{-2}$
JS	0.428	$1.41 \cdot 10^{-2}$
BS	0.838	$1.55 \cdot 10^{-3}$
NBS	0.910	$1.14 \cdot 10^{-2}$
SY	0.308	$9.73 \cdot 10^{-3}$
ASY	0.692	$9.73 \cdot 10^{-3}$

Table 2.3) Pearson's correlation coefficients between vital rates used in the prospective perturbation analysis for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site (years in which data were collected for each vital rate are listed in table 2.1). BP_{SY}: SY breeding propensity, BP_{ASY}: ASY breeding propensity, CS_{SY}: SY clutch size, CS_{ASY}: ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival.

	BP _{SY}	BP _{ASY}	CS _{SY}	CS _{ASY}	NS	DS	JS	BS	NBS
BP _{SY}	-	1.000	-0.675	-0.673	0.556	0.319	0.623	0.525	-0.610
BP _{ASY}	-	-	-0.675	-0.673	0.556	0.319	0.623	0.525	-0.610
CS _{SY}	-	-	-	1.000	-0.717	0.078	-0.552	-0.386	0.687
CS _{ASY}	-	-	-	-	-0.717	0.083	-0.553	-0.388	0.689
NS	-	-	-	-	-	-0.137	0.007	-0.086	-0.100
DS	-	-	-	-	-	-	-0.093	-0.240	0.002
JS	-	-	-	-	-	-	-	0.966	-0.946
BS	-	-	-	-	-	-	-	-	-0.843

Table 2.4) Pearson's correlation coefficients between vital rates used in the retrospective perturbation analysis for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site (years for each vital rate listed in table 2.1). BP_{SY}: SY breeding propensity, BP_{ASY}: ASY breeding propensity, CS_{SY}: SY clutch size, CS_{ASY}: ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival, SY: proportion of the population comprised of SY females, ASY: proportion of the population comprised of ASY females.

	BP _{SY}	BP _{ASY}	CS _{SY}	CS _{ASY}	NS	DS	JS	BS	NBS	SY	ASY
BP _{SY}	-	1.000	-0.683	-0.683	0.556	0.319	0.560	0.550	-0.502	0.854	-0.854
BP _{ASY}	-	-	-0.683	-0.683	0.556	0.319	0.560	0.550	-0.502	0.854	-0.854
CS _{SY}	-	-	-	1.000	-0.718	0.049	-0.476	-0.400	0.560	-0.811	0.811
CS _{ASY}	-	-	-	-	-0.718	0.049	-0.476	-0.400	0.560	-0.811	0.811
NS	-	-	-	-	-	-0.137	-0.042	-0.068	-0.020	0.514	-0.514
DS	-	-	-	-	-	-	-0.166	-0.212	0.121	0.453	-0.453
JS	-	-	-	-	-	-	-	0.973	-0.943	0.514	-0.514
BS	-	-	-	-	-	-	-	-	-0.843	0.418	-0.418
NBS	-	-	-	-	-	-	-	-	-	-0.602	0.602
SY	-	-	-	-	-	-	-	-	-	-	-1.000

Table 2.5) Estimates of process variance (2010-2015,2017), realized sensitivity, and prospective elasticity to changes in mean vital rates ($E_{ij}^{S\mu}$) for each vital rate for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site. Note DS has relatively high process variance, moderate prospective elasticity, high retrospective sensitivity, and contributed most to realized growth rates (λ_t). BP_{SY}: SY breeding propensity, BP_{ASY}: ASY breeding propensity, CS_{SY}: SY clutch size, CS_{ASY}: ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival.

Vital Rate	Process Variance	Realized Sensitivity	Prospective Elasticity
BP _{SY}	2.05*10 ⁻³	0.04	0.02
BP _{ASY}	2.05*10 ⁻³	0.18	0.14
CS _{SY}	1.51*10 ⁻¹	3.90 * 10 ⁻³	0.02
CS _{ASY}	1.51*10 ⁻¹	0.02	0.15
NS	1.90*10 ⁻²	0.47	0.10
DS	1.49*10 ⁻²	0.71	0.27
JS	1.41*10 ⁻²	0.460	0.16
BS	1.55*10 ⁻³	0.90	0.84
NBS	1.14*10 ⁻²	0.84	0.82

Table 2.6) Proportional contributions of demographic parameter variation (diagonal) and covariation (off-diagonal) to variation in realized growth rates of lesser scaup (*Aythya affinis*) at the Lower Red Rock Lakes study site. Positive values indicate a positive contribution to realized growth rates while negative values represent a negative contribution.

	BP _{SY}	BP _{ASY}	CS _{SY}	CS _{ASY}	NS	DS	JS	BS	NBS	SY	ASY
BP _{SY}	3.39*10 ⁻⁴	1.49*10 ⁻³	-1.90*10 ⁻⁴	-1.06*10 ⁻³	6.71*10 ⁻³	5.16*10 ⁻³	5.69*10 ⁻³	3.64*10 ⁻³	-8.38*10 ⁻³	-8.90*10 ⁻⁴	-2.20*10 ⁻⁴
BP _{ASY}	-	6.54*10 ⁻³	-8.50*10 ⁻⁴	-4.64*10 ⁻³	2.95*10 ⁻²	2.27*10 ⁻²	2.50*10 ⁻²	1.60*10 ⁻²	-3.68*10 ⁻²	-3.90*10 ⁻³	-9.70*10 ⁻⁴
CS _{SY}	-	-	2.35*10 ⁻⁴	1.29*10 ⁻³	-7.22*10 ⁻³	6.63*10 ⁻⁴	-4.03*10 ⁻³	-2.21*10 ⁻³	7.79*10 ⁻³	7.03*10 ⁻⁴	1.75*10 ⁻⁴
CS _{ASY}	-	-	-	7.06*10 ⁻³	3.96*10 ⁻²	3.63*10 ⁻³	-2.21*10 ⁻²	-1.21*10 ⁻²	4.27*10 ⁻²	3.86*10 ⁻³	9.57*10 ⁻⁴
NS	-	-	-	-	4.30*10 ⁻¹	-7.88*10 ⁻²	-1.51*10 ⁻²	-1.59*10 ⁻²	-1.21*10 ⁻²	-1.91*10 ⁻²	-4.73*10 ⁻³
DS	-	-	-	-	-	7.71*10 ⁻¹	-8.05*10 ⁻²	-6.69*10 ⁻²	9.60*10 ⁻²	-2.25*10 ⁻²	-5.58*10 ⁻³
JS	-	-	-	-	-	-	3.05*10 ⁻¹	1.93*10 ⁻¹	-4.71*10 ⁻¹	-1.61*10 ⁻²	-3.99*10 ⁻³
BS	-	-	-	-	-	-	-	1.29*10 ⁻¹	-2.74*10 ⁻²	-8.48*10 ⁻³	-2.11*10 ⁻³
NBS	-	-	-	-	-	-	-	-	8.21*10 ⁻¹	3.08*10 ⁻²	7.66*10 ⁻³
SY	-	-	-	-	-	-	-	-	-	3.20*10 ⁻³	7.93*10 ⁻⁴
ASY	-	-	-	-	-	-	-	-	-	-	1.97*10 ⁻⁴

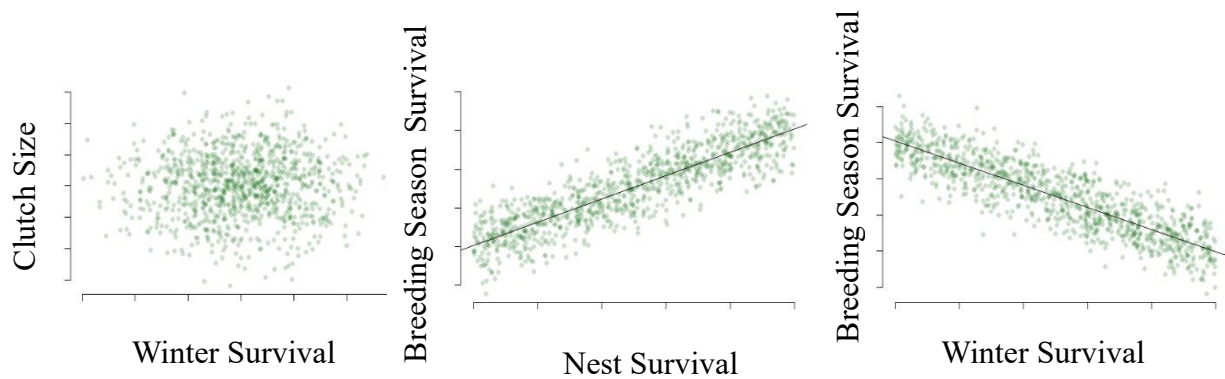


Figure 2.1) Examples of no covariation (Panel 1), positive covariation (Panel 2) and negative covariation (Panel 3) based on hypothesized relationships between a subset of vital rates for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site. Positive covariation between nest survival and breeding season survival indicates these vital rates are responding similarly to an underlying environmental variable (e.g., predation). Negative covariation between winter survival and breeding season survival indicates there is a trade-off between these two vital rates.

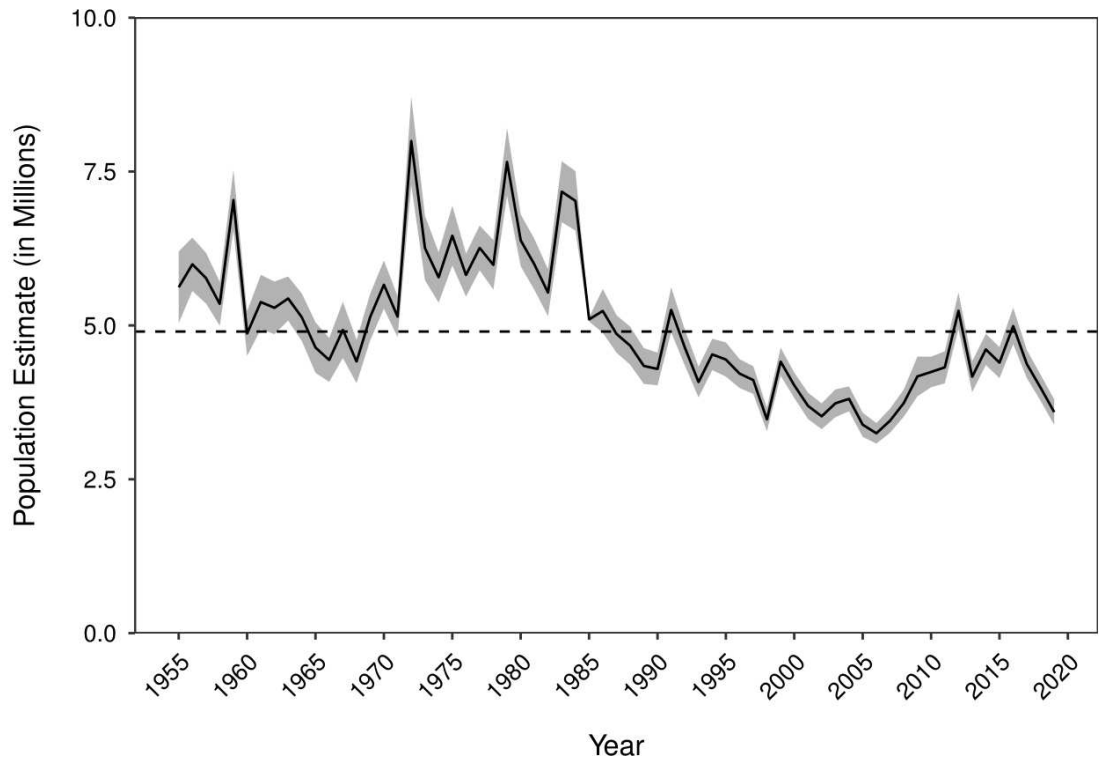


Figure 2.2) Breeding population estimates (solid line) of combined lesser scaup (*Aythya affinis*) and greater scaup (*Aythya marila*) abundance (the two species cannot be differentiated during aerial surveys) and standard errors (grey area). The dashed line indicates the North American Waterfowl Management Plan population goal. Estimates are from the Waterfowl Breeding Population and Habitat Survey traditional survey area which comprises coastal, boreal, prairie-parklands, prairie pothole habitats in parts of North-Central United States, Canada, and Alaska (U.S. Fish and Wildlife Service 2019)

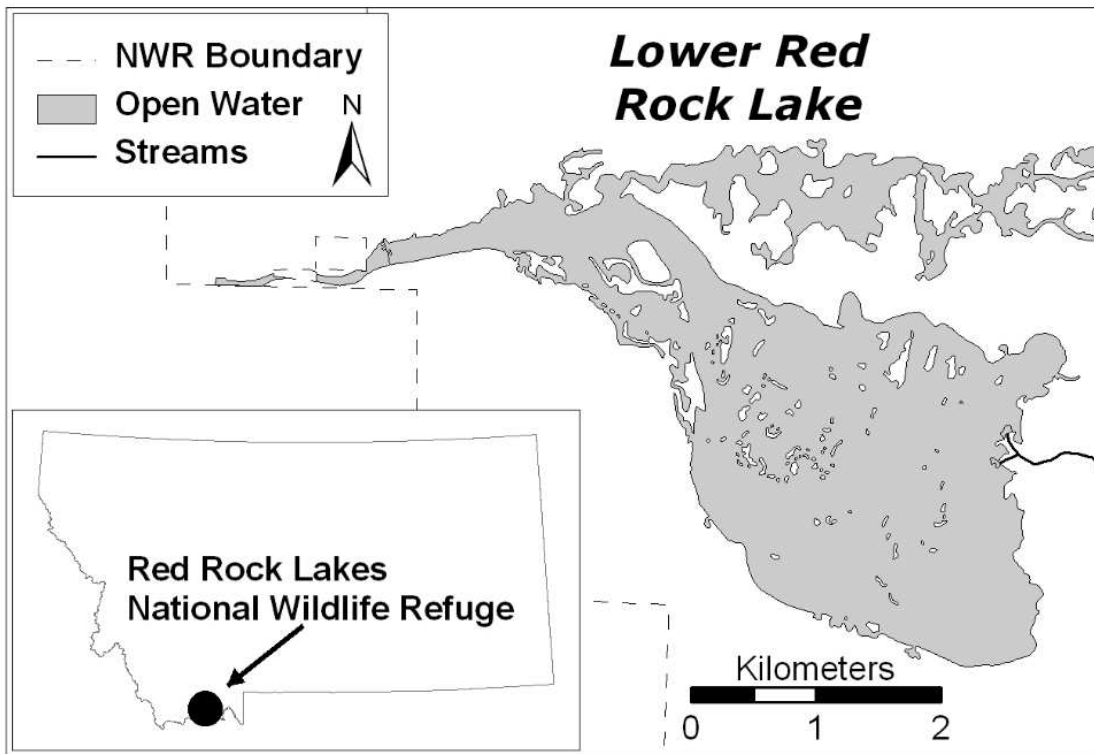


Figure 2.3) Map of Lower Red Rock Lake study site and location of Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA.

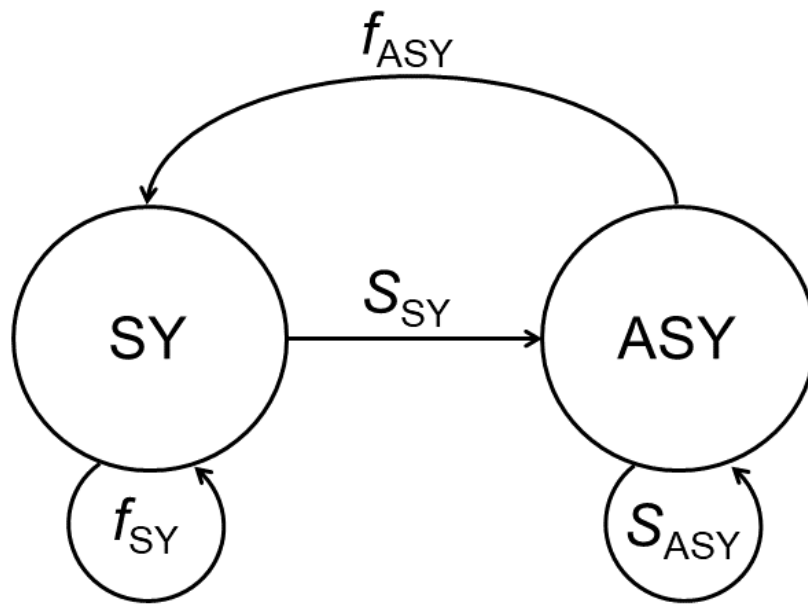


Figure 2.4) Age-structured life cycle model for a pre-breeding census of lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site. Second-year (SY) and after-second year (ASY) age classes can have different fertility (f_x) and survival estimates (S_x), but as explained in the text we constrained adult survival probabilities to be equivalent between SY and ASY females.

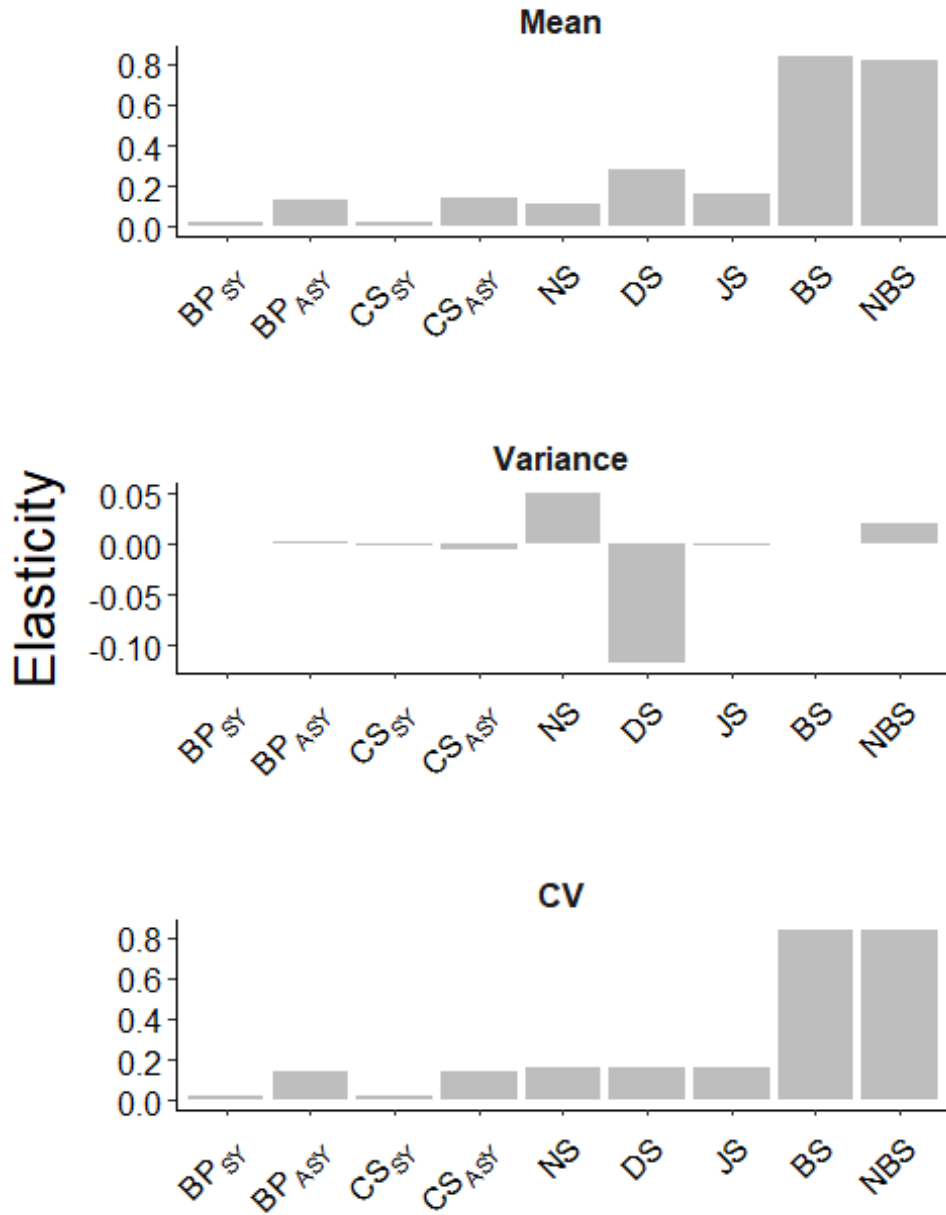


Figure 2.5) Prospective elasticities for changes in vital rate means (panel 1), variances (panel 2) and coefficients of variation (CV, panel 3) for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site. Large positive elasticities indicate that changes in mean/ variance/ CV have a greater positive influence on population growth rate. Conversely, a large negative elasticity such as with DS (panel 2) indicates increasing variance of DS would negatively influence population growth rate. BP_{SY}: SY breeding propensity, BP_{ASY}: ASY breeding propensity, CS_{SY}: SY clutch size, CS_{ASY}: ASY clutch size, NS: nest survival, DS: duckling survival, JS: juvenile survival, BS: breeding season survival, NBS: non-breeding season survival.

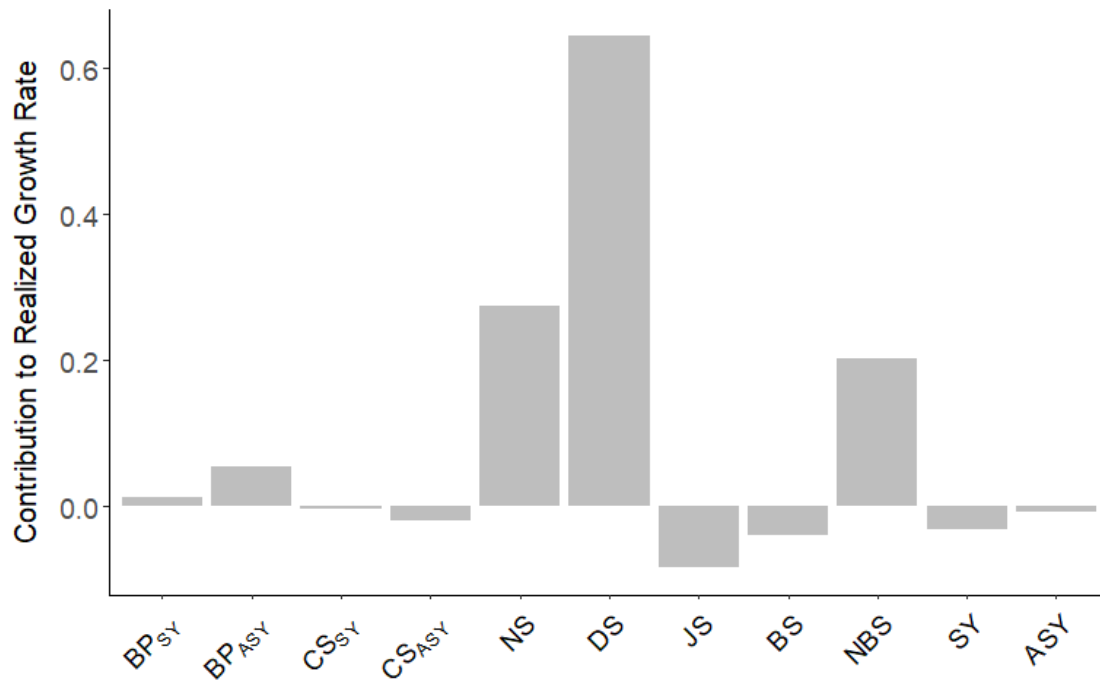


Figure 2.6) Proportional contributions of vital rates and components of age structure to variation in realized growth rates from transient LTRE of lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site.

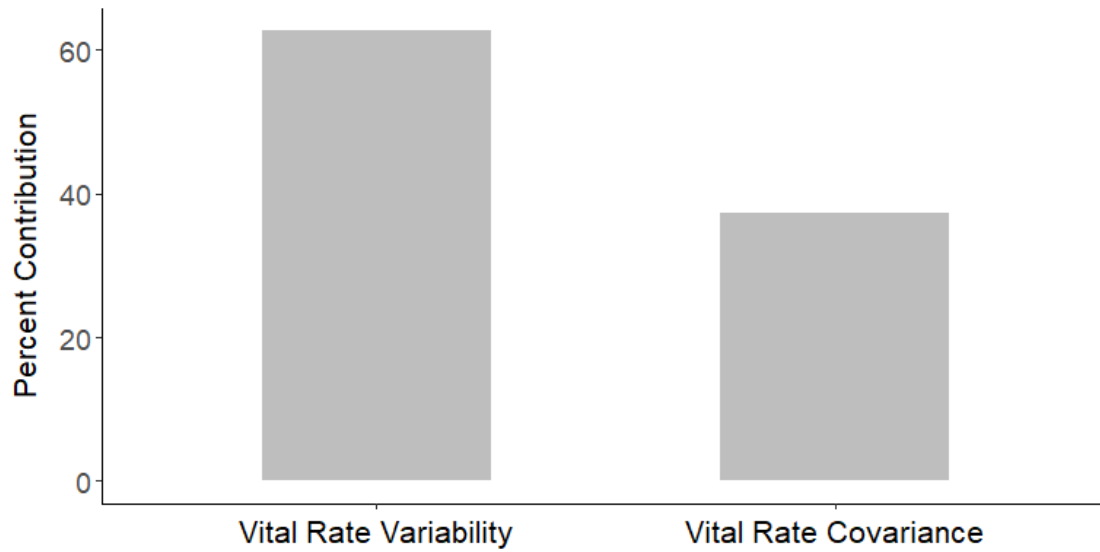


Figure 2.7) The contribution of the direct effect from variability of demographic parameters and the indirect effect of covariation among demographic parameters on variation in realized growth rate from the LTRE for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study site.

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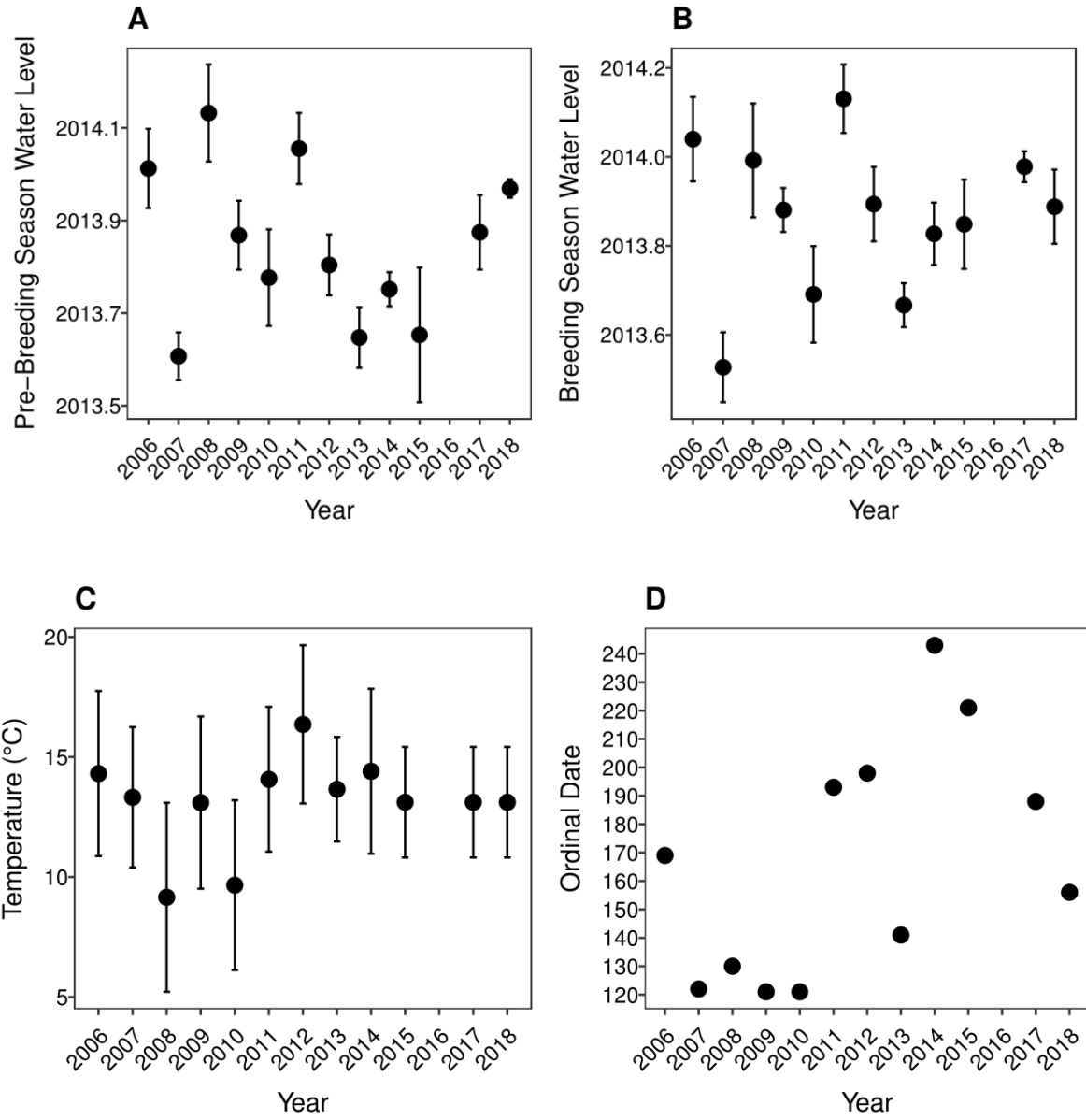
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APPENDIX



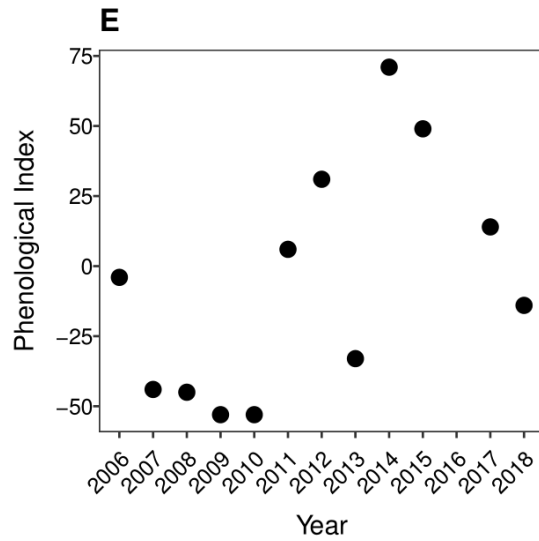


Figure A1.1) Time series of environmental variables measured at the Lower Red Rock Lake study site, Montana, USA. A) Annual mean pre-breeding season water levels (in meters), B) mean breeding season water levels, C) mean pre-breeding season water temperatures, D) ordinal date of maximum water level, and E) phenological index (mean nest initiation date – ordinal date of maximum water level).

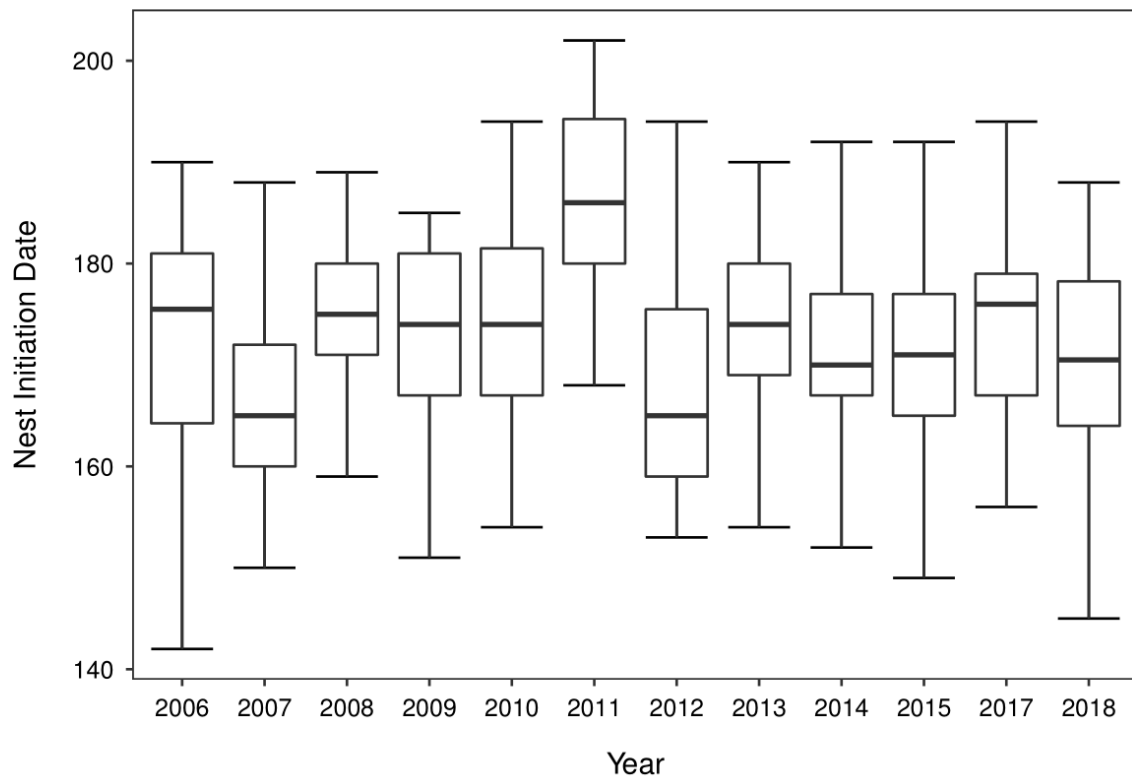


Figure A1.2) Boxplots of nest initiation dates each year for lesser scaup (*Aythya affinis*) at the Lower Red Rock Lake study area, Montana, USA. Shown are the estimated median (bold line), 1st and 3rd quartiles (box) and largest and smallest value within 1.5x interquartile range above 3rd quartile and below 1st quartile (whiskers).