NEST-SITE SELECTION, DUCKLING SURVIVAL, AND BLOOD PARASITE PREVALENCE OF LESSER SCAUP NESTING AT RED ROCK LAKES NATIONAL WILDLIFE REFUGE

by

ANDREW P. STETTER

B.S., University of Wisconsin - Stevens Point, 2011

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2014

Approved by:

Major Professor
Dr. David A. Haukos

Copyright

Acknowledgements

Funding for this research study was provided by the U.S. Fish and Wildlife Service, U.S. Geological Survey, the Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University (KSU), the Avian Health and Disease Program, the Science Support Program, and the Wisconsin Waterfowl Hunters' Conference.

I would like to thank my advisor, Dr. David Haukos, who has been a tremendous source of expertise and guidance throughout the entirety of this project, and has helped me develop the tools and skill set I need to be successful in this line of work. I would like to extend an extra special thank you to Jeff Warren for taking a chance on a Mississippi River rat from Wisconsin and allowing me to partake in this journey, for providing me with this great dataset, for his invaluable insight, and continued encouragement. I am extremely grateful for all of your help and without you none of this would have been possible. I would also like to thank the members of my KSU advisory committee, Dr. Brett Sandercock for assisting me with all aspects of my analyses, especially in MARK and also for teaching me the world of statistics. Also, thank you to Dr. Alice Boyle for her knowledge and guidance of avian biology and for the improvements to my thesis. I would like to thank Dr. Gene Albanese for his suggestions and expert guidance in spatial analysis. Thank you to all the members of the KSU Department of Biology who have helped me along the way.

Thank you to the staff of Red Rock Lakes Refuge Bill West, Kyle Cutting, Jeff Warren, David Farmer, Lance Hicks, and Jackie Vann for providing me with an excellent research facility, the great trailer and shack to live in, all of the equipment and tools to successfully complete my project, and most importantly for accepting me into the family of Lakeview. Thank you to all of the other graduate students and countless technicians who helped who helped out on my project Dave Messmer, Kalen Pokley, Shawn O'Neil, and Cody Deane.

I would like to thank all of the students in my lab: Reid Plumb, Brian Kearns, Joe Lautenbach, Sam Robinson, Dan Sullins, Brandon Weihs, Beth Ross, and John Kraft. I am grateful to have you all in my life and I am truly thankful for the memories that will last a life time. I would also like to thank all the other KSU students who have helped me in one way or another including Bram Verheijen, Kirsten Grond, Eunbi Kwon, Alaina Thomas, Emily Williams, Kyle Anibas, David Spencer, Zak Ratajcak, and Jerad Schroeder.

I would like to thank the staff of my current home at St. Croix Wetland Management District: Tom Kerr, Chris Trosen, Caitlin Smith, Lisa Custer, Dave (Mac) McConnell, Joel Kemm, Tracy Ronnander, Tom Marcouiller, and all of the interns for providing me an excellent opportunity to achieve my life-long goal of becoming a wildlife biologist. Thank you to all of you for everything you have done.

Last, I would like to thank my parents, Sue and Jerry, and my loving girlfriend, Hanna Kruckman, for all of their continued support throughout this entire process. A special thanks to all of my other friends and family, especially my personal editor and best uncle ever, Al Pahl, for his comments, suggestions, and improvements to my thesis.

Table of Contents

List of Tables

List of Figures

Dedication

I would like to dedicate my thesis to my family and friends that can't be with me today Gene Stetter, Nate Stetter, John Stetter, Ruth and Lawrence Stetter, and Zach Zenk.

Abstract – Duckling Survival

Lesser scaup (scaup) populations have been experiencing continent-wide decline since the 1980s. It is important to have complete understanding of the critical factors influencing population change (e.g., duckling survival, nesting success, and health) to advance our understanding of population dynamics and improving species conservation. Duckling survival is a primary driver of scaup demography. I conducted a capture-mark-recapture study using Cormack-Jolly-Seber models in Program MARK to compute apparent daily survival and recapture probabilities for 3256 individually marked ducklings with 620 recaptures during 2010 to 2013. The most parsimonious survival model based on *a priori* hypotheses found that Julian hatch date squared was the most significant predictor of survival and consistent through all four years. Mass at hatch also was significant as a quadratic effect. Duckling survival to 30 days ranged from 29.0 to 80.0. During this study, stabilizing selection played a significant role in duckling survival, which indicates that there was trade-offs for selection of an optimal timing of hatch on survival and a cost associated with hatching too early or too late and being too heavy or to light.

Chapter 1 - Duckling Survival at the Southern Edge of Lesser Scaup Range in Montana

Introduction

Recruitment, the per capita rate at which individuals are added to a population, is the product of several demographic rates. In birds, recruitment includes breeding propensity, clutch size, nesting success, and survival of chicks and juveniles until becoming adults. Survival of pre-fledging young is one of the least-documented demographic rates influencing recruitment in species that produce precocial young, such as waterfowl (Sedinger 1992), even though it is an important determinant of annual recruitment (Koons et al. 2006). Pre-fledgling survival is an important driver of variation in reproductive success (Gurney et al. 2012), yet is characteristic of high variability in waterfowl populations (Sedinger 1992). Estimating reproductive success and recruitment is essential to advancing our understanding of population dynamics and optimizing species conservation; however, estimating recruitment can be difficult.

Lesser scaup (*Aythya affinis*, hereafter scaup), is the most abundant and widespread diving duck species of North American waterfowl (Austin et al. 1998). In 2005, scaup reached an all-time low of 37% below the 1955-2005 long-term average in the traditional survey area and ~ 3 million birds below the North American Waterfowl Management Plan (NAWMP) goal (U.S. Fish and Wildlife Service 2006, hereafter USFWS). The scaup population steadily increased from 2006 to 2012, but decreased in 2013, and currently remains ~ one and a half million birds below the NAWMP goal of 6.3 million (Fig. 1.1; USFWS 2014). Though the scaup population has recently been increasing, factors that caused the decline are still of primary concern, particularly for lesser scaup that account for 89% of the continental population of lesser and greater scaup, combined (*A. marila;* Afton and Anderson 2001).

Within avian species, scaup life history is most representative of a 'bet-hedging' strategy (Saether et al. 1996). A characteristic of a bet-hedging strategy is high variability in reproductive success (Table 1.1), primarily driven by temporal variability in resource availability (Anteau and Afton 2004, Gurney et al. 2011), climatic variability (Rogers 1964, Warren et al. 2014), or predation rate (Saether et al. 1996, Walker and Lindberg 2005, Corcoran et al. 2007). This variation may influence factors such as size at hatch and hatch date, which are known to

affect survival of scaup ducklings (Dawson and Clark 1996, Dawson and Clark 2000, Gurney et al. 2012).

It is widely recognized that selection favors early breeding in a variety of birds (Perrins 1970); however, scaup demonstrate a strong selection for a later optimal breeding time than most other waterfowl (Bellrose 1976, Daan et al. 1990). A variety of hypotheses attempt to explain the factors driving selection for early or late hatch dates including timing of hatch with other species of waterfowl for predator saturation (Flint et al. 2006), parental quality (Devink et al. 2008, Devries et al. 2008, Gurney et al. 2012), resource availability (Dawson and Clark 2000, Anteau and Afton 2004, Gurney et al. 2011), and adequate time for development (Dzus and Clark 1998, Gurney et al. 2012). Mixed results have been found in studies investigating the influence of timing of hatch has on duckling survival. Advantages for earlier hatched and larger ducklings at hatch are widely recognized within many waterfowl species, and results from a study on greater scaup support this hypothesis where earlier hatched ducklings were twice as likely to survive to fledging than later hatched ducklings (Flint et al. 2006). In contrast, structurally larger and later hatched scaup ducklings were more likely to survive to 14 days (Dawson and Clark 1996), and a follow-up study determined larger ducklings had greater recruitment probability and size decreased with increasing hatch date (Dawson and Clark 2000). A study at Cardinal Lake, Canada, showed that duckling survival was negatively correlated with increasing hatch date when raised by lighter females, but did not find the same result with ducklings raised by heavier females (Gurney et al. 2012). Another study found greater annual survival in both structurally smaller, lighter weight female ducklings and adults (Rotella et al. 2003). These studies demonstrate that optimal size and timing of hatch for scaup ducklings clearly varies across the breeding grounds, and appears to be a function of individual optimization based on local environmental factors. Timing of nesting during the breeding season and the resulting influence on hatch date, size, and survival of pre-fledgling scaup ducklings remain unclear throughout much of their range. Thus, these hypotheses should be further investigated to determine the relative influence of factors affecting reproductive choices made by female scaup during the breeding season.

Most duckling mortality occurs within 10 days after hatch due to poor thermoregulatory abilities shortly after hatch (Sedinger 1992, Flint et al. 2006), with survival generally stabilizing by day 30 (Sedinger 1992, Grand and Flint 1996, Guyn and Clark 1999). Inclement weather

(below-average temperatures and above-average precipitation events) has clearly been demonstrated to negatively affect survival of ducklings in mallards (*Anas platyrhynchos*; Stafford and Pearse 2007) and redheads (*Aythya americana*; Korschgen et al. 1996). For example, inclement weather reduced mallard duckling survival immediately after hatch via hypothermia, and had a longer-term influence on survival through increased energetic demands that reduced body condition and lead to increased mortality (Amundson and Arnold 2011). Duckling survival is also positively related to greater water conditions (measured by the amount of water in a wetland) in mallards (Rotella and Ratti 1992, Krapu et al. 2006) and gadwalls (*A. strepera*; Pietz et al. 2003). Greater water levels results in more flooded emergent vegetation, which is often proximal to dry land. Female scaup often use flooded emergent vegetation to conceal ducklings from predators, and help ducklings that have poor thermoregulatory systems conserve body heat, which should result in greater duckling survival (Afton 1984). However, studies on scaup have found little to no support for duckling survival being related to water conditions (Afton 1984, Walker and Lindberg 2005, Corcoran et al. 2007, Gurney et al. 2012). Due to the lack of consistency between these studies and the importance of duckling survival on population growth, further investigation is warranted to assess the influence that inter-annual variation in extrinsic factors such as environmental conditions and wetland phenology cues have in the reproductive decisions female scaup make regarding when to breed and the resulting effects of variation in duckling size and hatch date on duckling survival.

My objective was to determine the relative influence of factors affecting scaup duckling survival in the southern extent of the species' breeding range. I predicted duckling survival would be negatively related to hatch date (i.e., early hatched ducklings will have greater survival than ducklings that hatched later). I also predicted duckling survival was positively related to water levels in Lower Red Rock Lake, Montana, USA, with duckling survival rates greater in years with higher-water levels due to more emergent vegetation available for escape cover. I predicted duckling survival would be influenced by inclement weather patterns - precipitation events and lower mean minimum daily temperatures occurring post hatch will reduce duckling survival rates. Finally, I predicted that duckling size at hatch would influence survival, where ducklings with greater body mass at hatch would have greater survival rates.

Study Area

The majority of scaup population studies have been conducted in the core of the breeding grounds throughout much of the boreal forest in Canada. This study improves upon that body of knowledge by adding the first duckling survival estimate from the southwestern portion of their breeding range. Red Rock Lakes National Wildlife Refuge (hereafter, Refuge) provided an ideal location to further assess hypotheses related to the recent decline; thus, examine long-term changes in scaup demography and susceptibility to time constraints of a high elevation complex during the breeding season.

The Refuge is located in the high-elevation Centennial Valley in southwest Montana (MT; 44° 37'N, 111° 50'W), USA. The Refuge encompasses ~ 10,000 ha of natural and created montane wetlands, providing breeding habitat for a variety of water birds (Cutting et al. 2011). Data collection for this study was on Lower Red Rock Lake, a 2,332 ha montane wetland complex, which was classified as palustrine consisting of a mix of clear, open water, submerged aquatic vegetation (SAV), interspersed islands of hardstem bulrush (*Schoenoplectus acutus*; Cutting 2010). Available habitats surrounding Lower Red Rock Lake are primarily dominated by seasonally flooded Northwest Territory sedge (*Carex utriculata*; Fig. 1.2).

The Refuge is home to one of the highest density stable breeding populations of scaup in North America with >7.7 pairs/km^2 (Cutting 2010). The climate and high elevation (2,333 m) of the Centennial Valley provided a narrow window of breeding opportunity for the local population of scaup, comparable to that of areas in the western boreal forest (WBF) such as Minto Flats (MF) State Game Refuge located in Alaska (latitude 65°), USA. The WBF is the core breeding area for scaup hosting upwards of 50% of scaup breeding pairs each year, and of chief concern due to consistent declines in the BPOP estimates (Austin et al. 2000). The low latitude and high altitude of the Refuge contribute to some of the harshest conditions scaup experience during the breeding season (Gurney et al. 2011), which made it a relevant area to assess factors that influence duckling survival for comparsion with other study sites.

Weather Measurements

Weather data included mean minimum ambient air temperature and precipitation events to assess annual variations in duckling survival. Data were obtained from the Lakeview Ridge snow telemetry ~ 2 km from Lower Red Rock Lake at an elevation of 2428 m

(www.wcc.nrcs.usda.gov/nwcc/site?sitenum=568&state=mt). The average annual precipitation is 49.5 cm, 27% of which occurs during May and June. The mean annual temperature is 1.8° C; mean January temperature is -11.6° C and mean July temperature is 14.8° C. Average water level and average water temperature were recorded by a data logger at the western outflow of Lower Red Rock Lake (Fig. 1.3) and used as covariates in analyses. All environmental data for analyses were collected during 8 July and 11 September for each year.

Methods

Data Collection

Nest Searching

Nest searching was conducted for six weeks, from late May to late July during eight year period of 2006-2013 in wetland habitat surrounding Lower Red Rock Lake (Table 1.2). Lower Red Rock Lake was divided into 16 survey blocks, each 750 m^2, each block was searched twice, with the exception of blocks that had no suitable nesting habitat (e.g., blocks in the middle of the lake comprised of open-water habitat with interspersed islands of hardstem bulrush). Investigators flushed female scaup by walking and disturbing vegetation with willow sticks, and through using trained dogs to locate nests. Nest initiation date (±2 days) was estimated by candling eggs, which allowed for timing the last visit (see 'Duckling Capture – Nest Site') before hatch (Weller 1956). This study was conducted under the Federal Bird Banding permit: 06266, and was approved through Northern Prairie Wildlife Research Center's Animal Care and Use Permit project number: 3210APN.

Duckling Capture – Nest Site

Nests were revisited every 6 to 10 days, or as needed depending on incubation stage of each nest, to minimize disturbance at the nest site, until fate was determined (i.e., abandoned, destroyed, or hatched). The second to last revisit to each nest occurred one day prior to the expected hatch date (i.e., day 27 of incubation for scaup; Austin et al. 1998). When at least one egg pipped (i.e., duckling beginning to crack out of the egg), all eggs were placed in a loose black mesh bag, ~ 60 x 40 cm, with a drawstring opening, to contain ducklings in the nest bowl for marking (Guerena et al. 2012). Nests were revisited later that day or the following day or as

necessary to allow all eggs to hatch. Ducklings at the nest were primarily captured using the containment method; however, additional ducklings were also captured opportunistically at nest bowls that were not originally discovered during nest searching. Nest hatch primarily occurred during from 8 July to 11 September. A nest was considered successful if at least one duckling or one intact egg membrane was found at the nest.

At capture, the following duckling morphological measurements were recorded: head length (±0.1 mm; using calipers), tarsus length (±0.1 mm; using calipers), and mass (±1g; using a Pesola spring scale). Each duckling received a web-tag on the distal portion of the web, which allowed estimation of web-tag retention, using a uniquely numbered Monel tag (size 1005-1; National Band and Tag Co., Newport, Kentucky, USA; Alliston 1975). Due to issues with web-tag loss in 2010, we double marked ducklings in 2012 and 2013 with passive integrated transponder (PIT) tags (9.0 x 1.5 mm; Biomark, Boise, Idaho, USA). PIT tags were injected directly under the skin between the shoulders of the ducklings, using a sterile 14-ga needle and syringe (Carver et al. 1999). PIT tags and needles were sterilized before each use in a 250 ml glass jar containing a 1:10 household bleach (5.25% sodium hypochlorite) bath for 30 seconds, and then rinsed in a saline solution prior to implanting. Following implantation of PIT tags and web-tagging, ducklings were placed in a second mesh bag in a shaded area, until all captured ducklings from the nest were tagged. Ducklings were then placed back into the nest bowl and covered with down or other nest material and left to await return of the hen.

Duckling Capture – Post Nest-Departure

Marked ducklings were recaptured during two, five-day drive-trapping sessions in August and September (Table 1.2). The first drive-trapping session was conducted two weeks after the peak of hatching and the second, two weeks after the end of the first drive-trapping session. The same morphological measurements (head and tarsus length, mass) were recorded during each drive-trapping session. Ducklings smaller than age class 1B (tarsus <30 mm in length) received a web-tag, and ducklings larger than age class 1B (tarsus >30 mm in length) were banded with a federal numbered aluminum leg band from the U.S. Geological Survey Bird Banding Lab (Gollop and Marshall 1954). During drive-trapping, ducklings were captured by extending nets out from a cage in a V shape and funneling ducklings into a trap using canoes and kayaks.

Data Analysis

Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999) were used to compute apparent daily survival (φ_i) and recapture probability (p_i) of individually marked ducklings. Estimated φ in CJS models assumes an instantaneous marking period (Cooch and White 2006); to meet this assumption, survival was estimated for two intervals: interval one was 24 days and interval two was 22 days. The first interval was equal to the difference between the medians of the nest marking period and the first drive-trap session and the second interval was equal to the difference between the medians of first and second drive-trapping sessions. Due to unequal intervals, the two intervals were scaled to bi-weekly periods by dividing by 14 days (1.71 and 1.57, respectively). I developed and tested a set of *a priori* models based on the set of hypotheses for factors influencing duckling survival. A goodness-of-fit (GOF) test median (ĉ) was used to determine whether the global model met the assumptions of mark-recapture analyses (Cooch and White 2006). I ran a logistic regression model in MARK with a Lower Bound of 1.00 and Upper Bound of 1.30 with 100 replications for each of 100 steps for a total of 12,000 simulations, which resulted in a median ĉ of 0.995 (SE = 0.018). The variance inflation factor (ĉ) was set to 1.00 and the ranking of the most parsimonious models was based on Akaike Information Criterion (AIC_c), which provides an unbiased criterion for model selection (Lebreton et al. 1992). AIC_c has two components: negative log-likelihood, which measures lack of model fit to the observed data, and a bias correction factor, which increases as a function of the number of model parameters (Johnson and Omland 2004). ΔAIC_c is the difference between any particular model of interest and the model with the lowest AIC_c value. Any value for ΔAIC_c that is '$X \leq 2$' is thought to be equally parsimonious and considered a good fit of the observed data (Burnham and Anderson 2002). AIC_{wi} is the weight each model has at explaining the unknown truth (i.e., the 'relative plausibility' likelihood of the model given the data set) and normalized across the set of candidate models to sum to one. As a model's weight approaches 1, it is unambiguously supported by the data, and models with ~ equal weights have a similar level of support in the data (Johnson and Omland 2004)

Duckling growth curves were generated annually for 2010, 2012, and 2013 using mass from ducklings that were marked at the nest (known hatch date) and recaptured during drive-trap session one and/or drive-trap session two for 2010, 2012, and 2013 (Fig. 1.4; Dawson and Clark

1996). Age 0 (day of hatch) was excluded from analyses to avoid artificial inflation of R^2 values. All of the birds used for those three years were then combined for an average growth curve estimation for 2011 because of the small sample size of ducklings recaptured from the nest in 2011 (n = 1; Table 1.3, Fig. 1.4). The results of the linear regression models were used to predict age in days from mass for ducklings that lost their web-tag or unmarked at time of initial capture during the drive-trapping sessions (hatch date unknown). Estimated age of ducklings was used to back-date (±2-3 days) an individual's estimated date of hatch (Dawson and Clark 1996). This individual covariate estimated Julian date of hatch (hereafter, hatch date) for all ducklings in the survival analysis that were unmarked at initial capture. Hatch date^2 was also included in analyses to test for a quadratic effect of hatch date throughout the season. Mass at hatch (hereafter, mass) was used as a covariate for each duckling marked at the nest, and the average annual mass for ducklings marked at the nest was inputted for ducklings captured during the drive-trapping sessions that were not marked at a nest, which was specific to each year, to correct for missing data and for convergence of parameters. Mass^2 was also included in analyses to test for quadratic effects of mass at hatch on survival throughout the season. I tested the effect of cohort-specific weather and habitat variables on survival of scaup during each survival interval. These included mean minimum daily temperature (TEMP), mean accumulated precipitation (PRECIP), mean water temperature (WATER TEMP), mean water level (WATER). For all analyses, nonsignificant main effects and covariates were iteratively removed from analyses and data reanalyzed (Lebreton et al. 1992).

Results

In 2010, mean minimum daily temperature was 7.1º C and 4.8º C, accumulated precipitation was 17.8 mm and 7.6 mm, and mean water temperature was 17.6º C and 13.0º C during survival intervals one and two, respectively. In 2011, mean minimum daily temperature was 6.4º C and 6.9º C, accumulated precipitation was 17.8 mm and 12.7 mm, and mean water temperature was 22.0º C and 21.7º C during survival intervals one and two, respectively. In 2012, mean minimum daily temperature was 8.6º C and 6.8º C, accumulated precipitation was 0.0 mm and 22.9 mm, and mean water temperature was 23.5º C and 21.0º C during survival intervals one and two, respectively. In 2013, mean minimum daily temperature was 7.9º C and

9.5º C, accumulated precipitation was 0.0 mm and 0.0 mm, and mean water temperature was 17.4º C and 14.4º C during survival intervals one and two, respectively.

Given an unknown hatch date at first capture, I used equations generated from the linear regression models of known-age ducklings to predict ages of 2617 ducklings (i.e., 2010 n = 682; 2011 n = 135; 2012 n = 1153; and 2013 n = 647, respectively) in days using their mass at time of capture. Age was then used to backdate each ducklings estimated hatch date (±2-3 days), and could be done so with confidence as the generated growth curve model fit the data (i.e., all R^2 values >0.88).

Model selection based on *a priori* hypotheses for hatch date performed best when hatch date^2 was added to the null model (Lebreton et al. 1992). The most parsimonious was φ (g+ hatch date+hatch date^2) p (g+t) (Table 1.4), which indicated that survival was influenced by additive effects of both hatch date and hatch date^2 and group (hereafter, year), while recapture rate was influenced by additive effects of year and time. The $\hat{\beta}$ estimate for the effect of hatch date^2 indicated a significant quadratic effect on survival with all years combined ($\hat{\beta}$ = -0.33, 95% CI = -0.47 – -0.19; Fig. 1.5). There were no other credible models (AIC_c < 2.00). Because I corrected for unequal intervals by setting the time intervals to 1.71 and 1.57, the real function parameters of mean survival were bi-weekly for all years.

The effects of cohort-specific environmental covariates were tested by *a priori* hypotheses using the highest ranked model including each variable to assess effects on duckling survival. The $\hat{\beta}$ estimate for the effect of PRECIP had a significant negative effect on survival ($\hat{\beta}$ = -2.41, 95% CI = -3.30 – -1.54). The $\hat{\beta}$ estimate for the effect of TEMP had a negative effect during survival intervals but had a wide confidence interval overlapping zero ($\hat{\beta}$ = -1.83, 95% CI = -12.25 – 8.59). The $\hat{\beta}$ estimate for the effect of WATER TEMP had a significant positive effect during survival intervals was ($\hat{\beta}$ = 4.65, 95% CI = 2.11 – 7.21). The *a priori* test for effect of high vs low-water levels (i.e., WATER) resulted in the $\hat{\beta}$ estimate having a negative effect during survival intervals but had a wide confidence interval overlapping zero ($\hat{\beta}$ = -0.34, 95% CI = -1.26 – 0.53).

Models for mass at hatch performed best when mass^2 was added (Lebreton et al. 1992). The most parsimonious duckling survival model for the effect of mass at hatch on duckling survival was φ (g+mass+mass2+hatch date+hatch date2) p(g+t) (AIC_{wi} = 1.00, ΔAIC_c = 0.00). There were no other competing models (ΔAIC_c < 2.00). The best fitting approximating model stated that survival was influenced by additive effects of mass, mass^2, hatch date, hatch date^2, while recapture rate was influenced by additive effects of year and time. The $\hat{\beta}$ estimate for effect of mass^2 on survival was a significant quadratic effect on survival for all years ($\hat{\beta}$ = -0.15, 95% CI = -0.22 – -0.09; Fig. 1.6).

Survival was also scaled to 30 days for ease of comparison to other scaup duckling survival studies (Table 1.1, Fig. 1.7; e.g., Walker and Lindberg 2005, Corcoran et al. 2007, Gurney et al. 2012). Recapture rates were estimable for the top model (Fig. 1.8). Estimates of survival for 2010 were initially biased low due to problems with web-tag loss. Therefore, I calculated a maximum likelihood estimate of marker loss, which I used to correct for marker loss in 2010 (Nichols et al. 1992). A total of 150 ducklings were marked at the nest and over the course of both drive-trap sessions 48 ducklings were recaptured (Table 1.3). Of those, 36 ducklings had torn right webs, resulting in a marker loss rate of 75%.

Discussion

A consistent annual, quadratic curve was evident in all four years of this study, which was inconsistent with my hypothesis of survival being negatively related to hatch date. The quadratic pattern found in this study indicates a stabilizing selection trend for an optimal timing of hatch on survival and a cost associated with hatching to early or too late. Results of other scaup studies found directional selection toward early (Gurney et al. 2012) or late hatched ducklings (Dawson and Clark 2000), which is a common evolutionary strategy found in birds (Price et al. 2000). Our results when paired with results of other studies indicate scaup experience multiple trade-offs associated with larger clutch sizes and higher quality young but low survival early in the year (Dawson and Clark 2000, Flint et al. 2006), whereas delaying breeding is linked with increased nest success, smaller clutch sizes, and lower recruitment rates due to ducklings not reaching an asymptotic body size by the time freeze up occurs (Dawson and Clark 1996, Warren et al. 2013).

Contrary to the prediction of heavier ducklings having greater survival than lighter ducklings, I found strong support for an annual trend of stabilizing selection on mass at hatch, consistent with the quadratic trend found for hatch date on duckling survival. These findings contrast with a study that found directional selection towards lighter female ducklings having greater survival than heavier ones (Rotella et al. 2003). Other studies on great tits (*Parus major*) found survival can actually decrease when individuals become too heavy, which decreases maneuverability resulting in a greater risk of predation (Gosler et al. 1995, Krams 2000). Decreased mobility could be the underlying cause of the observed decline in survival with ducklings that were too heavy at hatch during this study. However, many advantages of larger ducklings at hatch are widely recognized across many waterfowl species. Larger ducklings have increased nutrient reserves resulting in a reduction of thermogenic costs due to greater surface area to volume ratios (Rhymer 1988, Dawson and Clark 1996), and are more insulated (Alisauskas 1986, Rhymer 1988) resulting in prolonged resilience against the elements after hatch until first feeding (Kear 1965, Marcström 1966). Ducklings hatching from larger eggs were structurally larger, had a greater recruitment probability, and size decreased with increasing hatch date (Dawson and Clark 1996, 2000). The large sample size of scaup ducklings captured and used in these analyses resulted in a significant quadratic curve suggesting stabilizing selection for an optimal duckling mass at hatch with limiting survival costs of being too heavy or too light at this Refuge.

A review of eight different studies that took place across the scaup breeding range, spanning latitudes 44° to 66°, found that mean clutch initiation date across all years varied from 9 June to 23 June for a window of 15 days (Gurney et al. 2011). Scaup have a relatively late nesting date (Dawson and Clark 2000) that does not seem to vary despite changes in spring phenology across the extent of the breeding range (Gurney et al 2011). During the four years of this study, average clutch initiation date spanned a greater range of dates than the aforementioned studies (i.e., 21 days) from 15 June to 5 July. Birds that rely on environmental cues for breeding are more prone to mismatches between timing of breeding and peak food abundance, which may limit reproductive success (Helm 2009). Failure to alter life-history strategies in response to seasonal variation in wetland phenology, spring snow cover duration, or food supply may result in a "mismatch" between optimal time for breeding and peak resource availability for ducklings (Thomas et al. 2001, Schlaepfer et al. 2002, Drever et al. 2012a). This

concept known as the "mismatch hypothesis" is a central problem in evolutionary and applied ecology today, and contributes to many theories regarding scaup decline (Drever et al. 2012b). The delayed and expanded window of clutch initiation exhibited by scaup at Lower Red Rock Lake during this study supports previous results that found females nested later on average at lower latitudes and higher altitudes (i.e., Lower Red Rock Lake), than areas in more northern parts of the breeding range at lower altitudes (e.g., WBF and MF State Game Refuge). From 1988-2007, Lower Red Rock Lake had one of the shortest growing season lengths on average at 100 days (SD = 24) compared to the growing season lengths at other breeding areas such as: MF State Game Refuge = 116 days (SD = 8), and the Missouri Coteau (latitude 46°) = 257 days (SD = 20; Gurney et al. 2011). Lower Red Rock Lake experienced water levels in 2011 that were significantly greater than in other years as a result of above average snow pack and late run off, but duckling survival estimates did not differ between high and low-water years. Although water levels were not a significant predictor of duckling survival, scaup females responded to the seasonal variation in wetland phenology in 2011 by delaying nest initiation. Mean clutch initiation was 5 July in 2011 and the next latest annual mean clutch initiation in other years of this study was 22 June 2010. Results of the current study provide important insights into how scaup cue in on environmental factors and changes in spring phenology and adjust timing of breeding to maximize breeding success. Understanding how and why scaup respond to spring phenology and adjust timing of breeding is becoming increasingly important due to changes in climate.

By separating out the effects of the cohort-specific environmental and weather explanatory variables and testing each one based on *a priori* hypotheses, I was able to determine the effect each of these variables had on survival of scaup ducklings. Water temperature (a proxy for wetland phenology; Warren et al. 2013), had a significant positive effect on survival (i.e., as water temperature increased, survival increased). For example, duckling survival was lower in 2010 and 2013 when Lower Red Rock Lake's water temperature was below average, and duckling survival was greater in the 2011 and 2012 when water temperatures were above average. A similar study conducted on the Refuge found that rates of body condition gain in adult females were greater with warmer water temperatures (Warren et al. 2013). In prairie nesting ducks, wetland phenology is positively correlated with duckling survival (Gendron 1999, Krapu et al. 2000). If this is true with scaup ducklings at the Refuge, then greater levels of body

condition could be the cause for greater survival rates, because it is common in waterfowl for larger individuals to have survival advantages over smaller individuals (Krementz et al. 1997). The model with precipitation affecting survival suggested that as precipitation increased survival decreased, which is consistent with other studies conducted in waterfowl for example, mallard duckling mortality was found to be 1.6 times greater with each additional cm of precipitation (Stafford and Pearse 2007). Mean minimum daily temperature had no effect on survival of scaup ducklings during this study. Results of the current study provide evidence that water temperature and precipitation events were the only environmental factors that influenced duckling survival during the first 30 days of life.

Some of the previous studies on scaup duckling survival were constrained by short time frames or small sample sizes, as most were only one or two years and only a couple hundred ducklings, which may be the cause for inconsistent findings among studies. The current study had ~10 times the sample size of one of the larger duckling survival studies conducted on scaup (n = 334 ducklings; Afton 1983) with 3256 ducklings marked and 620 recaptures over a four-year period without a radio-effect. The large sample size in my study allowed for testing of varying effects of hatch date across years while increasing precision of survival and recapture estimates and reducing model-selection uncertainty. Estimates of 30 day duckling survival from this study across all four years were similar to or greater than other studies conducted on scaup (Table 1.1).

In conclusion, the results of a consistent stabilizing selection trend in hatch date^2 and mass^2 across all four years of this study provide support for an individual optimization hypothesis, in that female scaup can recognize and respond to trade-offs with extrinsic factors such as environmental conditions and wetland phenology cues in the local environmental and adjust their timing of breeding accordingly (Rowe et al. 1994, Warren et al. 2013). Females recognize that there is an optimal time for utilization of available resources for ducklings (Dawson and Clark 2000, Anteau and Afton 2004, Gurney et al. 2011) and ducklings need adequate time for development (Dzus and Clark 1998, Gurney et al. 2012). The trade-offs female scaup experience in variations of clutch size, timing of clutch initiation, and resources invested in reproduction are all underlying factors that result in the observed stabilizing selection trend for an optimal time and size at hatch of ducklings, and are especially important factors to consider when moving forward with the management of the species.

Literature Cited

Afton, A. 1983. Male and female strategies for reproduction in Lesser Scaup. Dissertation. University of North Dakota, Grand Forks, ND, USA.

Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. Auk 101:255-265.

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management: 65:781-796.

Alisauskas, R. T. 1986. Variation in the composition of the eggs and chicks of American coots. Condor 88:84-90.

Alliston, W. G. 1975. Web-tagging ducklings in pipped eggs. Journal of Wildlife Management 39:625-628.

Amundson, C. L., and T. W. Arnold. 2011. The role of predator removal, density-dependence, and environmental factors on mallard duckling survival in North Dakota. Journal of Wildlife Management 75:1330-1339.

Anteau, M. J., and A. D. Afton. 2004. Nutrient reserves of lesser scaup (*Aythya affinis*) during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. Auk 121:917-929.

Austin, J. E., C. M. Custer, and A. D. Afton. 1998. Lesser scaup (*Aythya affinis*). In The Birds of North America, no. 47 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C, USA.

Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and J. K. Ringelman. 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin 28:254-263.

Bellrose, F. C. 1976. Ducks, geese & swans of North America, 3rd ed., Stackpole Books, Harrisburg, PA, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, USA.

Carver, A. V., L. W. Burger, Jr., and L. A. Brennan. 1999. Passive integrated transponders and patagial tag markers for northern bobwhite chicks. Journal of Wildlife Management 63:162-166.

Cooch, E., and G. White. 2006. Program MARK: a gentle introduction. available online with the MARK programme 7. http://www.phidot.org/software/mark/docs/book/

Corcoran, R. M., J. R. Lovvorn, M. R. Bertram, and M. T. Vivion. 2007, Lesser scaup nest success and duckling survival on the Yukon Flats, Alaska. Journal of Wildlife Management 71:127-134.

Cutting, K. A. 2010. Nutrient allocation to egg formation of lesser scaup. Dissertation. Montana State University. Bozeman, Montana, USA.

Cutting, K. A., K. A. Hobson, J. J. Rotella, J. M. Warren, S. E. Wainwright-de la Cruz, and J. Y. Takekawa. 2011. Endogenous contributions to egg protein formation in lesser scaup (*Aythya affinis*). Journal of Avian Biology 45:505-513.

Dawson, R. D., and R. G. Clark. 1996. Effects of variation in egg size and hatching date on survival of lesser scaup (*Aythya affinis*) ducklings. Ibis 138:693-699.

Dawson, R. D., and R. G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. Condor 102:930-935.

Devink, J. M., R. G. Clark, S. M. Slattery, and D. L. Trauger. 2008. Are late-spring boreal lesser scaup (*Aythya affinis*) in poor body condition. Auk 125:291-298.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618-628.

Drever, M. C., R. G. Clark, C. Derksen, S. M. Slattery, P. Toose, and T. D. Nudds. 2012a. Population vulnerability to climate change linked to timing of breeding in boreal ducks. Global Change Biology 18:480-492.

Dzus, E. H., and R. G. Clark. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. Auk 115:311-318.

Flint, P. L., J. B. Grand, T. F. Fondell, and J. A. Morse. 2006. Population dynamics of greater scaup breeding on the Yukon-Kuskokwim Delta, Alaska. Wildlife Monographs 162:1-22.

Fournier, M. A., and J. E. Hines. 2001. Breeding ecology of sympatric greater and lesser scaup (*Aythya marila* and *Aythya affinis*) in the subarctic Northwest Territories. Arctic 54:444-456.

Gendron, M. and R. G. Clark. 2002. Survival of gadwall and mallard ducklings in southcentral Saskatchewan. Journal of Wildlife Management 66:170-180.

Gollop, J. B., and W. H. Marshall. 1954. Guide for aging duck broods in the field. Mississippi Flyway Council Technical Section Report.

Gosler, A. G., J. J. D. Greenwood, and C. Perrins. 1995. Predation risk and the cost of being fat. Nature 377:621-623.

Grand, J. B., and P. L. Flint. 1996. Survival of northern pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. Condor 98:49-55.

Guerena, K. B., P. M. Castelli, T. C. Nichols, and C. K. Williams. 2012. Evaluation of a clutch-containment method during hatch in geese: Using resident Canada geese as an example. Wildlife Society Bulletin 36:376-379.

Gurney, K., R. Clark, S. Slattery, N. Smith-Downey, J. Walker, L. Armstrong, S. Stephens, M. Petrula, R. Corcoran, and K. Martin. 2011. Time constraints in temperate-breeding species: influence of growing season length on reproductive strategies. Ecography 34:628-636.

Gurney, K. E. B., R. G. Clark, and S. M. Slattery. 2012. Seasonal variation in pre-fledging survival of lesser scaup (*Aythya affinis*): hatch date effects depend on maternal body mass. Journal of Avian Biology 43:68-78.

Guyn, K. L., and R. G. Clark. 1999. Factors affecting survival of northern pintail ducklings in Alberta. Condor 101:369-377.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of mid-continent mallards. Journal of Wildlife Management 66:883-900.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101-108.

Kear, J. 1965. The internal food reserves of hatching mallard ducklings. Journal of Wildlife Management 29:523-528.

Koons, D. N., J. J. Rotella, D. W. Willey, M. Taper, R. G. Clark, S. Slattery, R. W. Brook, R. M. Corcoran, and J. R. Lovvorn. 2006. Lesser scaup population dynamics: what can be learned from available data? Avian Conservation and Ecology 1(3):6. URL: http://www.ace-eco.org/vol1/iss3/art6/

Korschgen, C. E., K. P. Kenow, W. L. Green, D. H. Johnson, M. D. Samuel, and L. Sileo. 1996. Survival of radiomarked canvasback ducklings in northwestern Minnesota. Journal of Wildlife Management 60:120-132.

Krams, I. 2002. Mass-dependent take-off ability in wintering great tits (*Parus major*): comparison of top-ranked adult males and subordinate juvenile females. Behavioral Ecology and Sociobiology 51:345-349.

Krapu, G. L., P. J. Pietz, D. A. Brandt and R. R. Cox, Jr. 2000. Factors limiting mallard brood survival in prairie pothole landscapes. Journal of Wildlife Management 64:553-561.

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox Jr. 2006. Mallard brood movements, wetland use, and duckling survival during and following a prairie drought. Journal of Wildlife Management 70:1436-1444.

Krementz, D. G., R. J. Barker, and J. D. Nichols. 1997. Sources of variation in waterfowl survival rates. Auk 114:93-102.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

Marcström, V. 1966. Mallard ducklings (*Anas platyrhynchos*) during the first days after hatching. Viltrevy 4:343-370.

Natural Resources Conservation Service. 2014. National Water and Climate Center 2010-2013. Available: http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=568&state=mt. February 2014.

Nichols, J. D., J. Bart, R. J. Limpert, W. J. Sladen, and J. E. Hines. 1992. Annual survival rates of adult and immature eastern population tundra swans. Journal of Wildlife Management 53:485-494.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Pietz, P. J., G. L. Krapu, D. A. Brandt, and R. R. Cox Jr. 2003. Factors affecting gadwall brood and duckling survival in prairie pothole landscapes. Journal of Wildlife Management 67:564-575.

Pledger, S., K. H. Pollock, and J. L. Norris. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. Biometrics 59:786-794.

Price, T., M. Kirkpatrick, and S. J. Arnold.. 1988. Directional selection and the evolution of breeding date in birds. Science 240:798-799.

Rhymer, J. M. 1988. The effect of egg size variability on thermoregulation of mallard (*Anas platyrhynchos*) offspring and its implications for survival. Oecologia 75:20-24.

Rogers, J. P. 1964. Effect of drought on reproduction of the lesser scaup. Journal of Wildlife Management 28:213-222.

Rotella, J. J., and J. T. Ratti. 1992. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. Journal of Wildlife Management 56:499-507.

Rotella, J. J., R. G. Clark, and A. D. Afton. 2003. Survival of female lesser scaup: effects of body size, age, and reproductive effort. Condor 105:336-347.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist 143:698-722.

Saether, B. E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose (*Alces alces*). Ecology 77:1493-1500.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474-480.

Sedinger, J. S. 1992. Ecology of prefledgling waterfowl. Pages 109-127 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney,D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598-2600.

Traylor, J. J., and R. T. Alisauskas. 2006. Effects of intrinsic and extrinsic factors on survival of white-winged scoter (*Melanitta fusca deglandi*) ducklings. Auk 123:67-81.

U.S. Fish and Wildlife Service. 2006. Waterfowl population status, 2006. U.S. Department of the Interior, Washington, D.C., USA.

U.S. Fish and Wildlife Service. 2014. Waterfowl population status, 2014. U.S. Department of the Interior, Washington, D.C., USA.

Walker, J., and M. S. Lindberg. 2005. Survival of scaup ducklings in the boreal forest of Alaska. Journal of Wildlife Management 69:592-600.

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

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

Weller, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20:111-113.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-139.

Tables

Table 1.1. Summary of survival estimates for lesser scaup ducklings. Estimates and latitude and longitude readings were taken from original studies. Survival estimates are followed by 95% confidence intervals unless otherwise stated. Some of the studies estimated duckling survival at the brood level (B.S.).

Author (Year)	Years of Study	Study Area	Survival Estimate	Time Length
Afton (1984)	1977-1980	SE of Erickson, MB, Canada (50°30′N, 99°55′W)	Single B.S. = 0.74 (n=132). Amalgamated B.S. = 0.86 (n=36)	Age Class II
Dawson and Clark (1996)	1990-1992	St. Dennis NWA, SK, Canada (52°13′N,106°04′W)	0-14 days = 0.40 (0.32-0.53), 15-48 days = 0.96 (0.87-1.05)	0-14 days
Brook (2002)	1999-2000	Yellow Knife, NT, Canada (62°N,114°W)	0.61	0-47 days
Koons and Rotella (2001)	2002-2003	Erickson, MB, Canada (50°30′N, 99°55′W)	0.20 (0.00-0.58, n=54), B.S. = 0.48 (0.19-0.79, n= 9)	0-28 days
Walker and Lindberg (2005)	2002-2003	Minto Flats SGR, AK, USA (64°50′N, 148°50′W)	2002 = 0.24 (0.16-0.36), 2003 = 0.03 (0.00-0.19)	0-30 days
Flint et al. (2006)	1991-2000	Y-K Delta, AK, USA (61°10′N, 165°30′W)	1999 = 0.22 (0.12-0.31, n=253), 2000 = 0.53 (0.39-0.67, n=245)	0-30 days
Corcoran et al. (2007)	2001-2003	Yukon Flats, AK, USA (66°N, 148'W)	1-10 = 0.32 (0.12-0.77),11-20 = 0.99 (0.89-1.04), 21-30 = 0.92 (0.80-1.04)	0-10, 11-20, 21-30 days
Gurney et al. (2012)	2005-2007	Cardinal Lake, NT, Canada (67°36′N, 133°39′W)	2005 = 0.02 (85%CI: 0.00-0.04), 2007 = 0.27 (85%CI: 0.12-0.42)	0-30 days
This Study	2010-2013	Red Rock Lakes NWR, MT, USA (44°37′N, 111°50′W)	2010 = 0.29 (0.27-0.31), 2011 = 0.59 (0.42-0.76), 2012 = 0.80 (0.55-1.00), 2013 = 0.51 (0.46-0.56) & 2010 = 0.12 (0.11-0.14), 2011 = 0.44 (0.24-0.64), 2012 = 0.71 (0.35-1.00), 2013 = 0.35 (0.30-0.40)	0-30 days, & 0-47 days

Table 1.2. Dates for all periods used in lesser scaup duckling survival analyses from 2010-2013 at Red Rock Lake National Wildlife Refuge, Montana. Ducklings were marked at the nest and recaptured during two, five-day drive-trapping sessions, one in August and one in September.

Year	Nest Searching	Nest Marking	August Drive-Trapping	September Drive-Trapping
2010	June 1-July 16	July 8-August 10	August 16-20	September 7-11
2011	June 6-July 22	July 31-August 12	August 16-19	September 6-10
2012	May 20-July 18	July 9-August 14	August 13-17	September 4-8
2013	May 30-July 15	July 8-August 13	August 12-16	September 3-7

Table 1.3. Lesser scaup mark-recapture efforts resulted in a total of 3,256 ducklings marked and 620 recaptures during the 2010-2013 field seasons at Red Rock Lakes National Wildlife Refuge, Montana. Recaptures were not conducted during the nest marking (Nest) period. Recaptures occurred during two, five-day drive-trapping sessions, one in August and one in September. Each row represents the number of ducklings marked and recaptured throughout each specific year in subsequent marking sessions. Each row in Total Recaptures is the total number of individuals recaptured from each marking cohort.

	Session	Marked	Recaptures August Drives	Recaptures September Drives	Total Recaptures
2010	Nest	150	12	0	12
	August Drive	571	-	170	170
	September Drive	294	-	-	-
	Total	1015			182
2011	Nest	34	0	1	1
	August Drive	20	-	10	10
	September Drive	126	-	-	-
	Total	180			11
2012	Nest	181	18	9	27
	August Drive	764	-	82	82
	September Drive	542	-	-	-
	Total	1487			109
2013	Nest	273	63	22	85
	August Drive	491	-	233	233
	September Drive	473	-	-	-
	Total	1237			318
	Total	3256			620

Table 1.4. Summary of model selection results for estimation of apparent survival (Φ) and recapture probability (p) for lesser scaup at Red Rock Lakes National Wildlife Refuge from 2010-2013. Models are ranked by ascending AICc with the best fit model listed first. Model covariates include: 1) actual and estimated Julian hatch date for each duckling (hatch date; 8 July = day 1), 2) Julian hatch date squared (hatch date2), 3) mean minimum daily temperature during each survival interval (TEMP), 4) mean accumulated precipitation during each survival interval (PRECIP), 5) mean water temperature during each survival interval (WATER TEMP), 6) mean water level during each survival interval (WATER). Variance inflation factor ($\hat{c}$ = 1.00).

Model[a]	K[b]	Deviance	AIC_c[c]	ΔAIC_c[d]	AIC_{wi}[e]
φ (g+hatch date+hatch date 2) p(g+t)	11	2622.7	2644.8	0.0	0.940
φ (t+hatch date+hatch date2) p(g+t)	9	2632.3	2650.3	5.54	0.006
φ (g+t+PRECIP) p(g+t)	11	2642.5	2664.6	19.86	0.000
φ (g+t+hatch date) p(g+t)	10	2645.5	2665.5	20.76	0.000
φ (t+TEMP) p(g+t)	14	2640.0	2668.2	23.43	0.000
φ (g+t+WATERTEMP) p(g+t)	14	2643.0	2671.1	26.35	0.000
φ (WATER) p(g+t)	7	2714.3	2728.3	83.56	0.000

a Model notation: Φ apparent survival, p = recapture probability, g = group (year), t = survival intervals 1 & 2, + = additive term.
b Number of estimable parameters
c Akaike's Information Criterion
d Akaike's Information Criterion Difference
e Akaike's Information Criterion Weight

Table 1.5. Summary of model selection results for estimation of apparent survival (Φ) and recapture probability (p) for lesser scaup at Red Rock Lakes National Wildlife Refuge from 2010-2013. Models are ranked by ascending AICc with the best fit model listed first. Model covariates include: 1) actual and estimated Julian hatch date for each duckling (hatch date; 8 July = day 1), 2) Julian hatch date squared (hatch date2), 3) mass at hatch (mass), 4) mass at hatch squared (mass2). Variance inflation factor ($\hat{c}$ = 1.00).

Model[a]	K[b]	Deviance	AICc[c]	Δ AICc[d]	AICc wi[e]
φ (g+mass+mass2+hatch date+hatch date2) p(g+t)	13	2575.3	2601.5	0.0	1.000
φ (g+mass+mass2+hatch date) p(g+t)	12	2605.8	2630.0	28.5	0.000
φ (g+mass+mass2) p(g+t)	11	2666.6	2688.7	87.2	0.000
φ (g+mass) p(g+t)	8	2685.1	2701.2	99.7	0.000
φ (.) p(g)	6	2714.7	2726.8	125.3	0.000
φ (.) p(t)	7	2714.1	2728.2	126.7	0.000

Figures

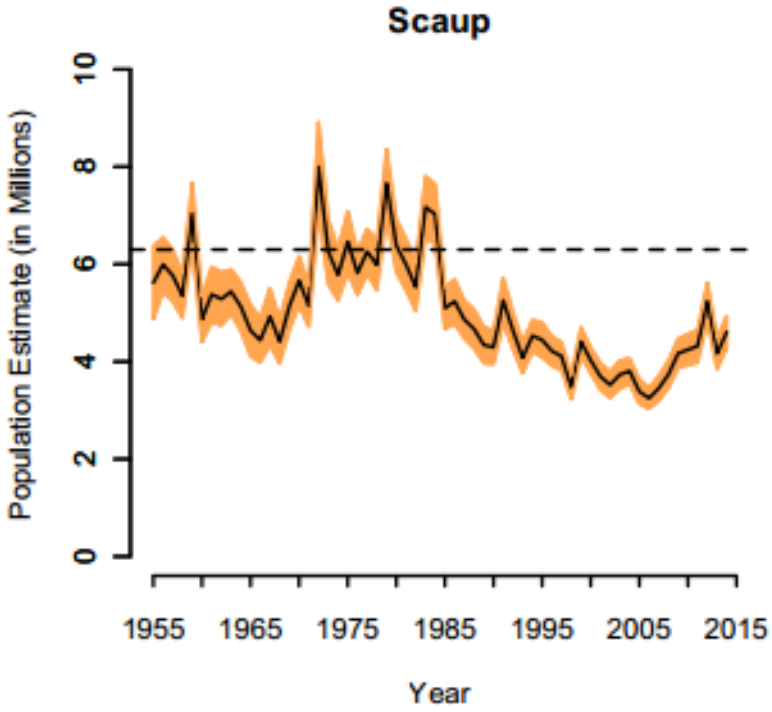

Figure 1.1. Breeding population estimates, 95% confidence intervals, and North American Waterfowl Management Plan population goal (dashed line) for selected species in the traditional survey area (strata 1-18, 20-50, 75-77) for scaup (U.S. Fish and Wildlife Service 2014).

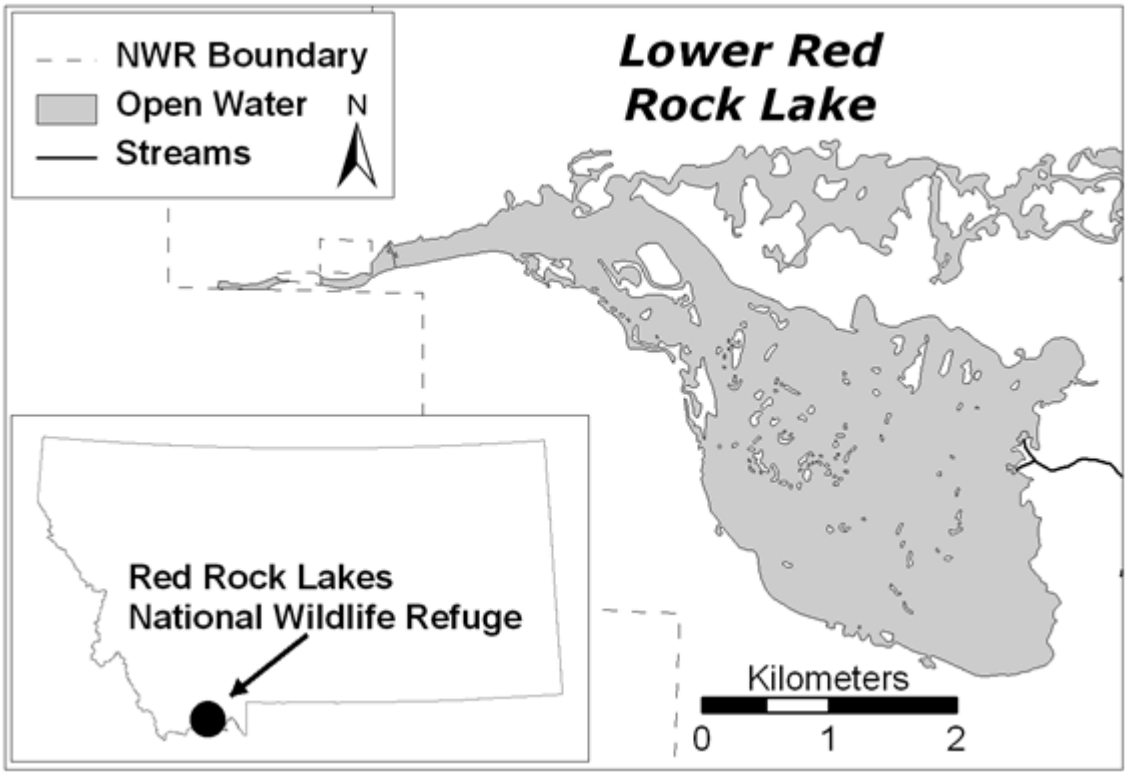

Figure 1.2. Lower Red Rock Lake and River Marsh study site on Red Rock Lakes National Wildlife Refuge (NWR), Montana, USA. Inset shows location of Red Rock Lakes NWR within Montana.

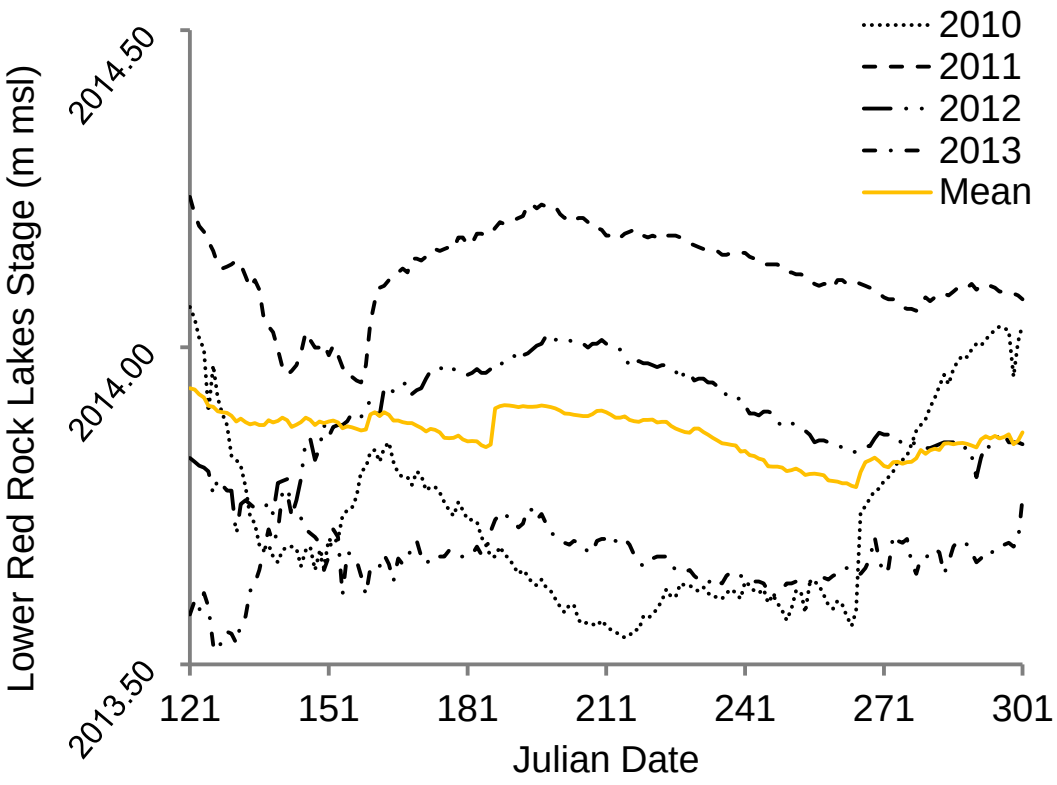

Figure 1.3. Daily lake stage (meters above mean sea level) of Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA, from 1 May to 27 October 2010-2013. The mean water level (orange line) is over the same period of dates (1 May to 27 October) from 2004 to 2013.

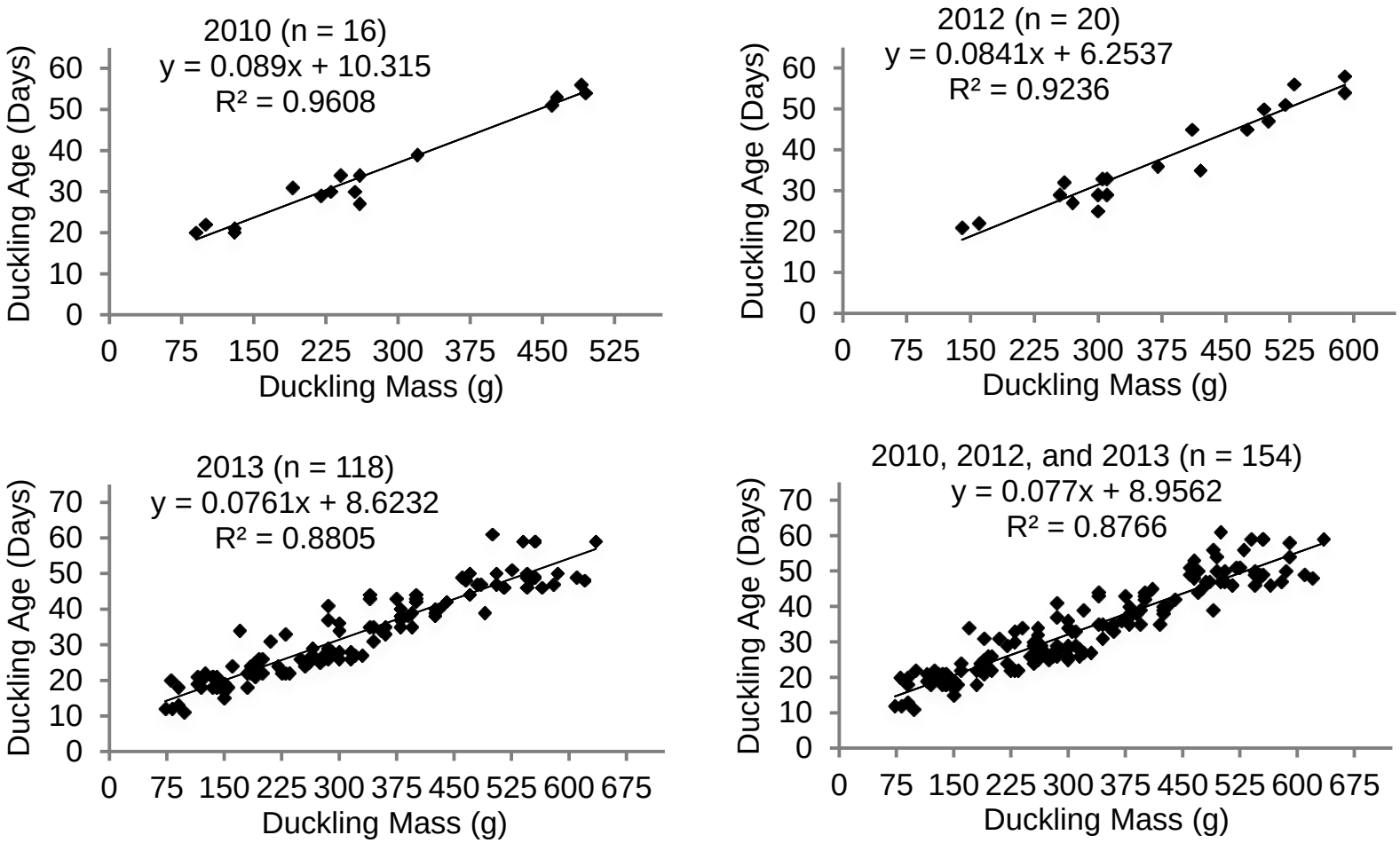

Figure 1.4. Estimated growth curves showing relationship between age and mass for all ducklings marked at the nest and then recaptured in 2010, 2012, and 2013 (n = 154) at Red Rock Lake National Wildlife Refuge, Montana, USA. The equation of this line was used in estimating age for ducklings captured during drive trapping in 2011.

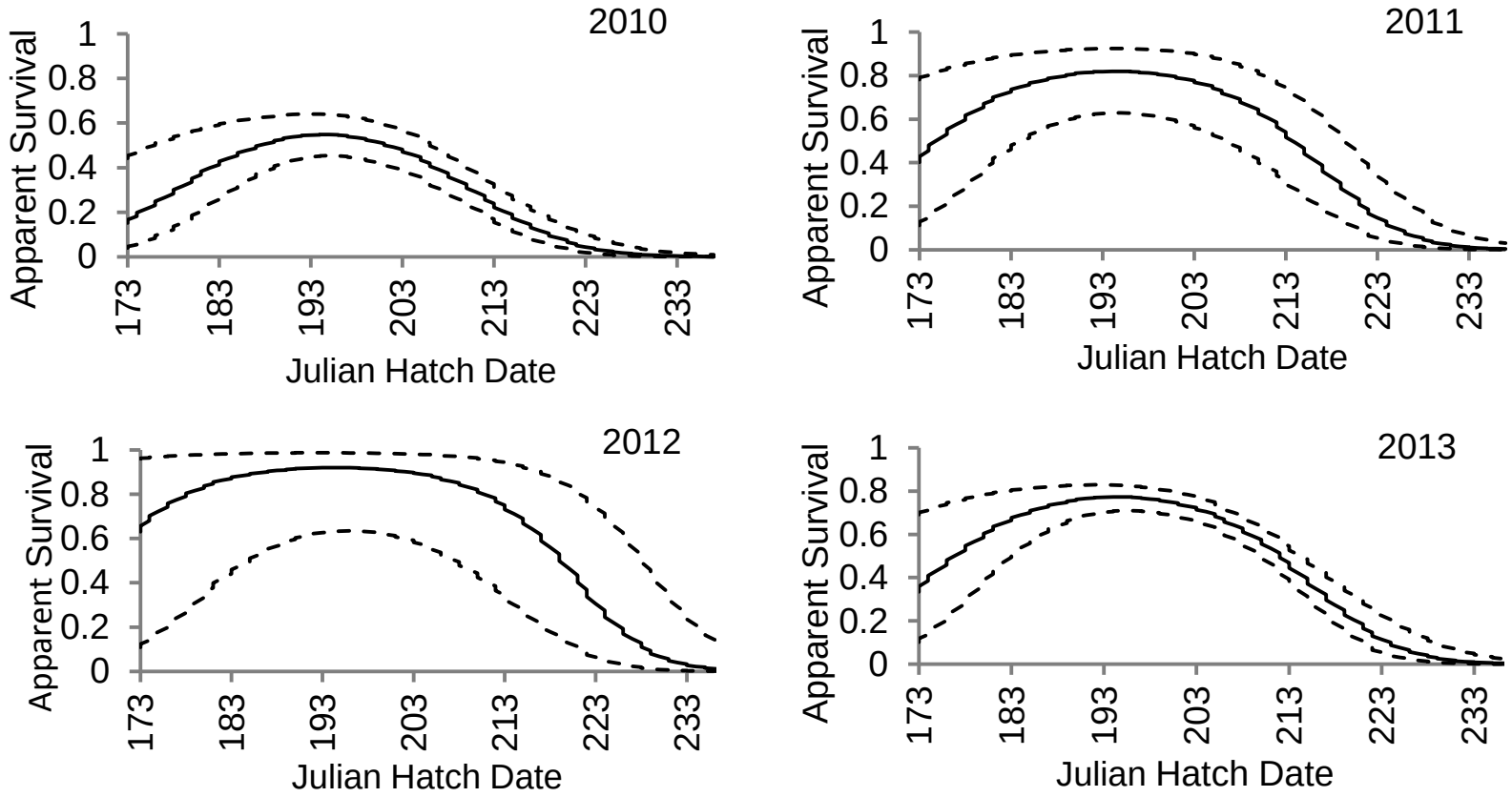

Figure 1.5. Relationship between duckling hatch date (Julian) and model-based bi-weekly apparent survival estimates with 95% confidence intervals (dashed lines) of lesser scaup ducklings in 2010, 2011, 2012, and 2013 at Red Rock Lakes National Wildlife Refuge, Montana, USA. Estimated survival was based on an additive model that included duckling hatch date (Julian) for each year of the study. Hatch date was back dated using the growth curve equation generated specific to each year (day 173 = 22 June, day 237 = 25 August), with the exception of 2011, that used all of the ducklings combined from the other growth curves.

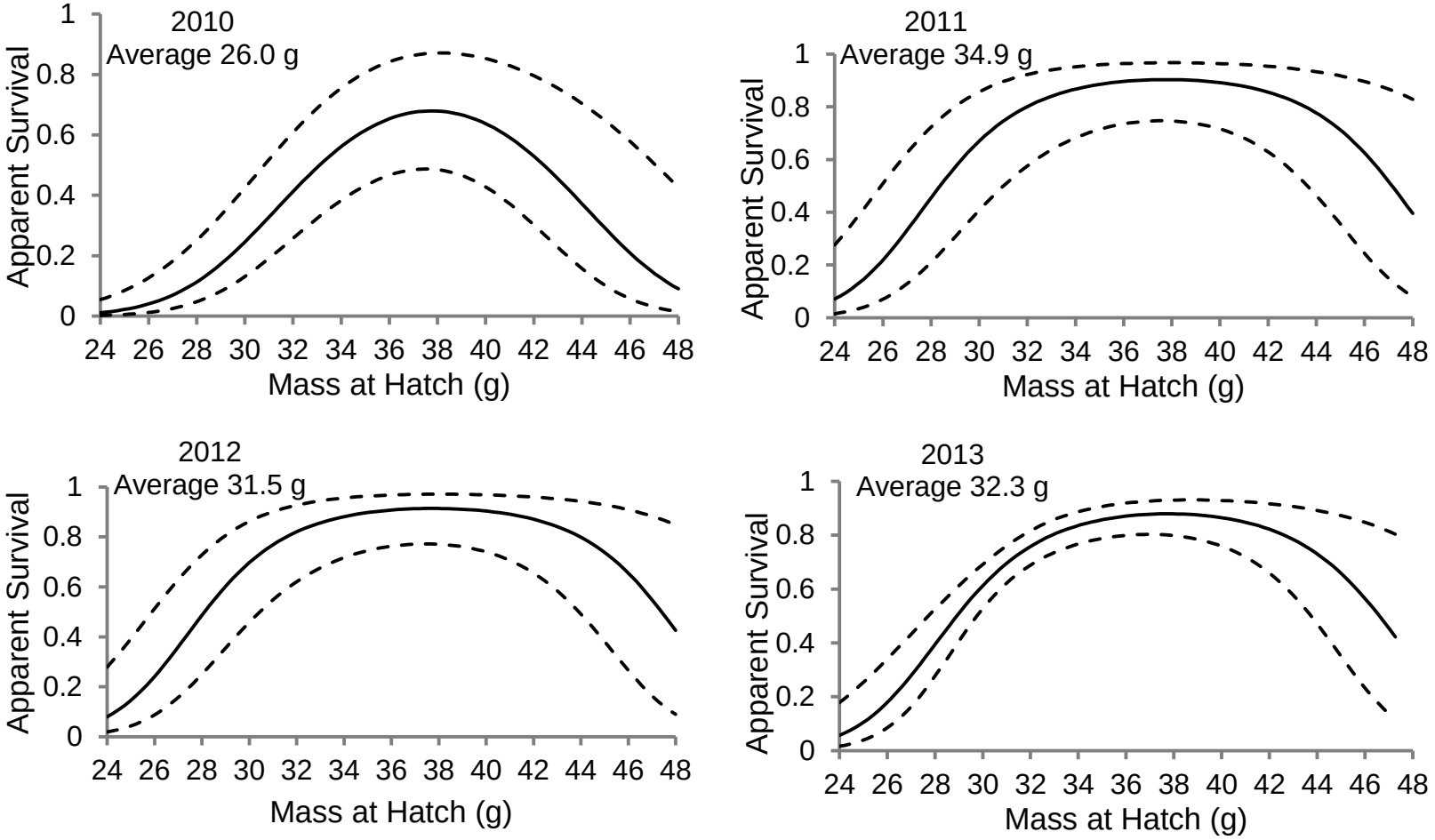

Figure 1.6. Relationship between duckling mass at hatch (g) and model-based bi-weekly apparent survival estimates with 95% confidence intervals (dashed lines) of lesser scaup ducklings from 2010-2013 at Red Rock Lakes National Wildlife Refuge, Montana, USA. Estimated survival was based on a model that included duckling hatch date (Julian) for each year of the study, duckling mass at hatch, duckling mass at hatch squared. Average duckling mass for all ducklings captured at the nest was inserted for missing values of ducklings not captured at the nest in 2010 for convergence of parameters.

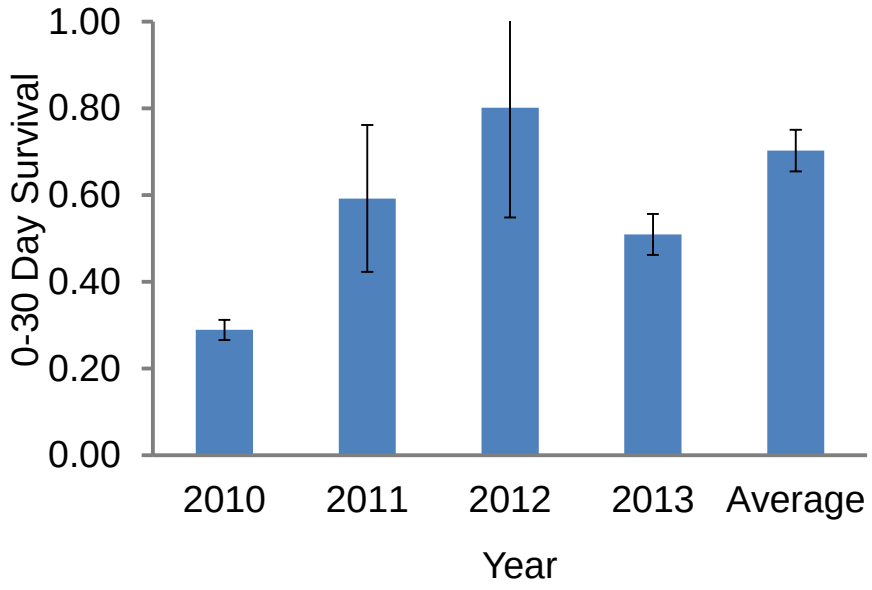

Figure 1.7. Duckling survival (0-30 days) estimates for ducklings at Red Rock Lakes National Wildlife Refuge, Montana, USA, during the summers of 2010 to 2013 (n = 3256). Error bars represent 95% confidence intervals.

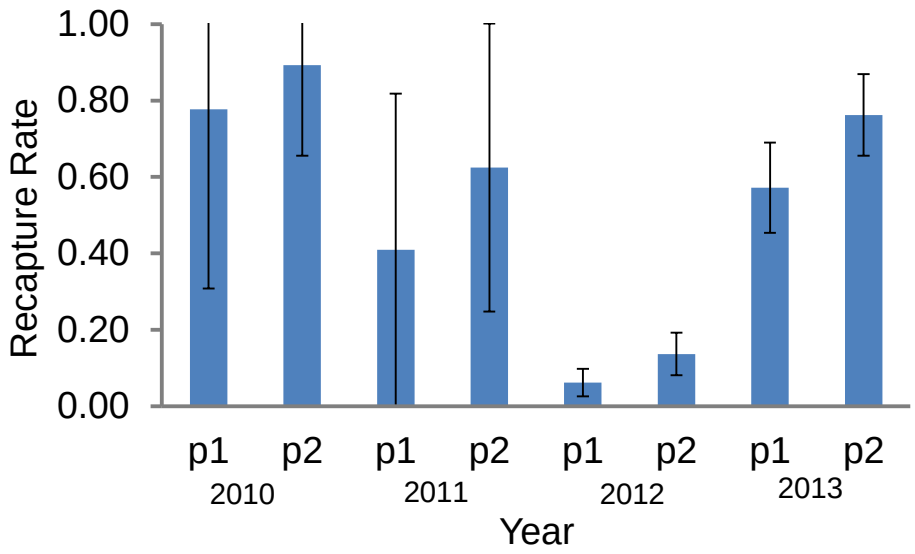

Figure 1.8. Recapture rates of ducklings based on top model "Φ(g+JHATCH +JHATCH2) p(g + t)" for ducklings at Red Rock Lakes National Wildlife Refuge, Montana, USA, during the summers of 2010 to 2013 (n = 3256). Error bars represent 95% confidence intervals. The first recapture period with in each year is represented by a 1 and the second is represented by a 2.

Abstract – Nest-Site Selection

There is a hierarchical process of behavioral and environmental processes that influence habitat selection, which inherently influences the survival and fitness of that individual and contributes to population growth. I investigated nest fate, spatial attributes, and all relationships between high and low-water levels with habitat attributes (distance to upland, distance to open water, nearest neighbor distance) of located nests using general linear models in SAS, *t*-tests in R, and Hot Spot Analysis in ArcGIS of 481 nests over eight years. In low-water years, successful nests ($\bar{x}$ = 1153 m) were located 22.0% farther from upland than unsuccessful nests ($\bar{x}$ = 944 m), but support for a similar relationship was lacking in high-water years. Successful nests were located 21.0% and 23.0% (i.e., 49 and 50 m) closer to conspecific nests than unsuccessful nests in low and high-water levels, respectively. In both high and low-water level years, clusters of nests initiated later in the season coincided with Hot Spots for nest fate (i.e., high-quality habitat patches, clusters of successful nests), whereas areas that tended to be selected first, evidenced by clusters of nests initiated earlier, tended to overlap with clusters of Cold Spots for nest fate. The core Hot Spot for nest fate was in the same spot in both water level conditions and located in flooded emergent vegetation in the heart of Lower Red Rock Lake furthest from any upland habitat. Three out of six Cold Spots for nest fate both in high and low-water years were located in emergent vegetation on the perimeter of Lower Red Rock Lake adjacent to uplands. Density-dependence seems to be a factor affecting late-nesting scaup females that are apparently cuing in on the reproductive performance of conspecifics when determining where to nest. Therefore, management actions focused on survival and reproductive success of scaup should consider managing water levels and habitat for later nesting scaup to increase adult survival and ultimately recruitment of ducklings.

Chapter 2 - Nest-Site Selection and Nest Success at Red Rock Lakes National Wildlife Refuge

Introduction

Habitat patch selection for nest sites is critical to breeding success in waterfowl (Clark and Shutler 1999). Habitat patch selection is thought to be a nonrandom process (Pulliam and Danielson 1991) and theoretically influenced by Ideal Free Distribution (IFD). IFD states that diverse behavioral and environment cues guide habitat selection among patches (Fretwell and Lucas 1969). Later the IFD theory was expanded to Public Information (PI) stating that birds were attracted to large congregations of conspecifics (i.e., individuals of the same species), and patch reproductive success by conspecifics influenced selection of nesting areas (Doligez et al. 2003). Presence of conspecifics has been identified as an indicator of habitat patch quality, which consists of many factors such as: potential mates, foraging opportunities, and safety from predators in a variety of bird species (Muller et al. 1997, Danchin et al. 2004, Stamps and Krishnan 2005, Campomizzi et al. 2008). Limitations on reproductive output of breeding populations of birds are affected by density-dependent competition for nest sites, food resources, predation (Newton 1994, Newton 1998, Larivière and Messier 1998), and density-independent factors such as drought, wetland phenology, and severity of winter (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006). However, the influence of density is not fully understood in the distribution patterns of waterfowl (Johnson and Grier 1988).

Generally, migratory waterfowl, including lesser scaup (*Aythya affinis*; hereafter, scaup), demonstrate high site fidelity and breeding pairs often nest close to locations which they were successful in previous years (Trauger 1971, Afton 1984). Such philopatry is common in closely related species such as redheads (*A. americana*; Arnold et al. 2002) and canvasbacks (*A. valisineria*; Anderson et al. 1997). Previous research on Red Rock Lakes National Wildlife Refuge (hereafter, Refuge) in Montana found that areas of successful nesting during the previous season were a significant predictor of pre-breeding habitat selection for females (i.e., females were more likely to concentrate and spend time in close proximity to areas of successful nesting in prior year locations; O'Neil et al. 2014). O'Neil

et al. (2014) also reported that returning scaup females who nested successfully the previous year on the Refuge used open water habitat and emergent vegetation within 300 m of their previous year's nest site. In general, scaup tend to nest closer to water than most other terrestrial nesting waterfowl species because they are not able to walk effectively on land and therefore, have greater foraging efficiency near water. At Yukon Flats, Alaska, between 2001 to 2003, nests (n = 177) were located on average 4 m from the water edge with 71.4% of nests located within 0.5 m from water; only seven nests were located greater than 25 m from water (Corcoran et al. 2007). Despite increased foraging efficiency, selection for nesting closer to water may negatively impact nest success because nests have a greater chance of becoming inundated should water levels rise. This relationship represents trade-offs between the risk of nest failure by flooding, proximity to land which could increase predation risk, and increased foraging efficiency of nesting close to the water. Further investigation into factors determining nest-site patch selection and nest success of scaup will aid in understanding this complex hierarchical process that influences survival and fitness of individuals (Jones 2001).

Two retrospective analyses of long-term scaup population and harvest databases concluded that female survival and age ratios in the U.S. harvest have decreased (Allen et al. 1999, Afton and Anderson 2001). A mallard life-cycle population model determined that nest success and female survival during the breeding season had the greatest impact on population growth (Hoekman et al. 2002). Koons et al. (2006) also found supporting evidence, through a review of studies from 1934 to 2005, that scaup female survival during the breeding and non-breeding season had the greatest influence on population growth, with nest success and duckling survival accounting for additional variation in past scaup population fluctuations. Declines in female survival could be tied to greater hen mortality during the nesting season, because females are more vulnerable to predation at this time. Thus, management efforts aimed at increasing population growth in waterfowl are often focused on increasing female survival and nest success, as they are inherently connected, which would lead to increased waterfowl recruitment (Cowardin et al. 1985, Emery et al. 2005).

Due to the recent population fluctuations and concerns regarding the status of the scaup population, further insight into the spatio-temporal drivers responsible for variation in demographic rates during the breeding season is necessary across the breeding range (Sauer et al. 2004, Corcoran et al. 2007). Gaining a better understanding of what factors affect female survival and nest success on the breeding grounds is critical to advancing our understanding of population dynamics and improving species conservation. Habitat patch selection and distribution of nest sites on the landscape play an important role in the breeding success of waterfowl (Clark and Shutler 1999). No specific links between population vital rates and continental population decline have been identified (Koons et al. 2006). Thus, further research is needed to investigate potential relationships among patch selection, density dependence, and behavioral cues from conspecifics to assess potential drivers of waterfowl population demography.

My objective was to investigate the spatio-temporal factors affecting nest-site patch selection and nest success of scaup in the southwestern extent of their breeding range. I hypothesized that nest-site selection and nest success of scaup would be affected by local precipitation and consequent changes in water levels in Lower Red Rock Lake within Red Rock Lakes National Wildlife Refuge. Nesting success has been found to be positively associated with the number of inundated ponds (Afton 1984). I predicted that nest success would be greater in years with higher water levels than lower water levels at the Refuge. There is an inherent risk of nest failure when selecting where to place a nest on the landscape due to trade-offs between flooding, predation, PI, and foraging efficiency. I predicted that nests located closer to water would have greater survival due to seclusion from predators. Scaup are gregarious and philopatric in nature (Afton 1984, Johnson and Grier 1988), with many of their life history strategies based on the timing of resource availability and environmental cues (Schlaepfer et al. 2002, Gurney et al. 2011). One example of these cues is the likely influence of conspecific and density-dependent indicators on habitat patch selection during the breeding season (Jamieson and Brooks 2004, Viljugrein et al. 2005, O'Neil et al. 2014). I hypothesized that nest-site selection and clustering of successful (Hot Spots) and unsuccessful (Cold Spots) nests would be related to nest initiation date. Nests initiated later during the breeding season would be influenced by density-dependence of conspecific nests located throughout Lower Red Rock Lake (i.e.,

high-quality patches of habitat demonstrating previous nest success would be selected for earlier in the breeding season and lower-quality areas would be selected for by females who are initiating nests later in the breeding season). Evidence of density-dependence was found at a local scale in nests located in close proximity generally sharing the same fate (Ringelman et al. 2012). I hypothesized that densities of nest locations would affect nest fate. I predicted that more aggregated nests would be more successful than more isolated nests. I also predicted that densities of nest locations would differ between high and low-water years.

Study Area

The 10,000 ha Refuge is located near the southern-most latitudes of the breeding range for scaup in the high-elevation (2,014 m above mean sea level) Centennial Valley in southwest Montana, USA. Although the refuge is at the edge of the breeding range for scaup, the study site has strong climatic similarities to key breeding areas in the boreal forest. Therefore, research conducted on scaup at the Refuge was relevant to other sites. Lower Red Rock Lake is a wetland complex that encompasses 2332 ha of wetland habitat comprised of nearly equal areas of shallow (<2 m) open water, submerged aquatic vegetation, and palustrine emergent vegetation habitats (Fig. 2.1). The climate and high elevation of the Centennial Valley provide a narrow window of breeding opportunity that is one of the harshest experienced by scaup throughout its breeding range (Gurney et al. 2011). Accumulated precipitation data during the first to third quartile range of nest initiation for a given year were obtained from the Lakeview Ridge snow telemetry ~ 2 km from Lower Red Rock Lake at an elevation of 2428 m (www.wcc.nrcs.usda.gov/nwcc/site?sitenum=568&state=mt; Fig. 2.2). Average water levels were recorded by a data logger at the western outflow of Lower Red Rock Lake and measured throughout the nesting season for a given year.

Methods

Data Collection

Nest searching was conducted for six weeks from late May through July during eight year period of 2006-2013 in all habitat types (primarily wetland dominated)

surrounding Lower Red Rock Lake (Table 3.1). Lower Red Rock Lake was divided into 16 survey blocks, each 750 m^2, each block was searched twice, with the exception of blocks with no suitable nesting habitat (e.g., blocks in the middle of the lake comprised of open-water habitat with interspersed islands of hardstem bulrush (*Schoenoplectus acutus*; Cutting 2010). Investigators flushed female scaup by walking and disturbing vegetation with willow sticks, and through using trained dogs to locate nests. All nests were marked with a flagged stick placed 4 m to the north of the nest bowl and the Universal Transverse Mercator (UTM) position recorded. Each Julian date of clutch initiation (hereafter, JDATE) was estimated by candling eggs (±2 days) to determine incubation stage (Weller 1956). Nests were revisited every 6 to 10 days or as needed until fate was determined (i.e., abandoned, destroyed, successful). Nests were considered successful if at least one duckling or one intact egg membrane was found at the nest. Other characteristics recorded at each nest site that were used as dependent variables in these analyses include distance to open water, if the nest was located near edge (within 5 m of open water), tall or short vegetation height (±0.5 m), host eggs hatched, and water depth (±1 mm) if over water, which was measured when the nest was first located and on the final visit. The study methods conducted during this study were approved through Northern Prairie Wildlife Research Center's Animal Care and Use committee under project number: 3210APN.

Data Analysis

I obtained vegetation data from the National Land Cover Database (NLCD), and classes were merged into 10 different categories (i.e., barren land, developed, dry lake bed, emergent vegetation, forest, large open water, pasture, small inundated pond, upland, and woody wetlands) representing the dominant classes of vegetation surround Lower Red Rock Lake (http://www.mrlc.gov/nlcd20 06.php). An existing bathymetric model of the study site was used to estimate the area of flooded emergent vegetation during the first and third quartile of nest initiation for a given year (Fig. 2.3; O'Neil et al. 2014). National Agricultural Imaging Program aerial orthoimagery was classified into an open water and emergent vegetation layer. Each year's bathymetric map was then clipped to the emergent vegetation layer and adjusted for inaccuracies of interpolation methods used in generating the map (±10 cm) resulting in eight layers, each consisting of year specific inundated

emergent vegetation. Each layer was merged back with the open water layer, which resulted in eight individual layers encompassing all the open water and flood emergent vegetation on Lower Red Rock Lake. Estimated NND was determined for each nest to the closest neighboring nest using Environmental Systems Research Institute's ArcGIS 10.2 Geographic Information System (GIS) software (ESRI 2013). Spatial nest characteristics (i.e., distance to upland, NND, and distance to open water) were calculated using the "near tool" in ArcGIS and included as independent variables in these analyses. Water levels were considered high or low if they were greater than two standard deviations above or below the 2004-2013 long-term average (Fig. 2.4). Correspondingly, nests were categorized into high- and low-water level years. Annual scaup daily nest survival rates for nests from 2006 to 2013 were previously estimated in RMark (Warren et al. 2014), and then converted to overall nest success by raising to the power of 35, which is comparable to Mayfield's corrected nesting success method (Johnson 1979). Differences between nest success in high and low-water years were tested by using a Welch Two Sample *t*-test in R 2.15.2 to account for nonhomogeneity of variance (Zar 1984, R Development Core Team 2013). All statistical relationships between habitat attributes and nest characteristics were analyzed using general linear models in SAS (PROC GLM; SAS Institute 1988). Statistical significance was determined at $\alpha = 0.10$.

Hot Spot Analysis Rendering is a cluster mapping tool used to identify statistically significant spatial clusters of high values (Hot Spot) and spatial clusters of low values (Cold Spot) using the Getis-Ord Gi* statistic. The tool generates a Getis-Ord Gi* statistic for each weighted feature in the dataset based on similarity of that point with neighboring features (ESRI 2013). The null randomization model tests the distribution of spatial features (i.e., nests), and assumes a randomized distribution of the attribute of interest (e.g., nest fate) across the entire sample. The local sum for a feature and its neighbors is compared proportionally to the sum of all features. Thus, when the local sum is different from the expected local sum, with that difference too large to be the result of random chance, a statistically significant z-score results. For example, a high z-score coupled with an $\alpha = 0.10$ for a feature indicates a spatial clustering of high values. Points with a z-score greater or less than the ±2 standard deviation bin were considered statistically significant Hot Spots or Cold Spots at a 95% confidence level (Fig. 2.5).

The Input Field for the analysis specifies the numeric count field to be evaluated; for example, Piorkowski and O'Connell (2010) used Hot Spot analysis to locate patterns of high site-specific mortality by including information on the number of wind turbines, number of collisions, ground cover, and topographic position within a given area. I applied this same method of locating nesting Hot Spots of scaup around Lower Red Rock Lake. To identify Hot/Cold spots based on nest fate, I set the input field to a binary variable indicating the nest fate (0 for failed nests and 1 for successful nests). I also used JDATE for the input field to test for spatial clustering by timing of clutch initiation. For all analyses, the conceptualization of spatial relationships was set to inverse distance, so that the nearby neighboring features have a larger influence on the computations for a target feature than features that are far away and euclidean distance was used as the distance method. Cowardin et al. (1995) found scaup nesting density to be two breeding pairs/km^2. Therefore, I set the threshold distance as 500 m, so that the features outside 500 m for a target feature were ignored in analyses for that feature.

Results

A total of 481 nests were monitored during the breeding seasons of 2006-2013. Nests that failed due to human activity, livestock, or Refuge operations were removed, with 440 nests remaining in the analyses. Estimates of nest success were estimated for 440 nests and varied from 30 to 62% from 2006-2013 at the Refuge. Of those nests, 280 successfully hatched at least one chick while 160 nests failed due to abandonment, predation and/or hatching failure (Fig. 2.6). Nest failure attributed to predation (70%), weather (2%), nest parasitism (1%), and unknown (27%). Clutch size ranged from four to 12 eggs. Of the nests included in this study, 27% (n = 122) successfully hatched the entire clutch. Average nest success in high-water years was 0.42 (SD = 0.13) and in low-water years was 0.41 (SD = 0.08). Nest success did not differ between high and low-water years (t_6 = 0.11, P = 0.92).

I found a significant relationship was found between distance to upland and fate in low-water years ($F_{1,181}$ = 6.79, P = 0.009). Successful nests ($\bar{x}$ = 1153 m, 95% CI = 1055-1251) were located 22% farther from upland than unsuccessful nests ($\bar{x}$ = 944 m, 95% CI = 820-1068; Fig. 2.7). Support for a similar relationship was lacking in high-water years ($F_{1,257}$ = 0.11, P = 0.74; Fig. 2.7).

Fate of a nest was not associated with the distance to open water in either low-water or high-water years ($F_{1,181} = 2.32$, $P = 0.13$). Successful nests were located 14 m (95% CI = 10-17) and unsuccessful nests were 19 m (95% CI = 14-23) from open water. Similarly, no evidence was found for a relationship between nest fate and distance to open water in high-water years ($F_{1,257} = 0.38$, $P = 0.54$). Successful nests were 15 m (95% CI = 12-18) and unsuccessful nests were 17 m (95% CI = 12-21) from open water.

Distance to nearest neighbor summary resulted in an observed mean distance of 71 m, which differed from the expected mean distance of 116 m (Nearest Neighbor ratio was 0.61, $z = -16$, $P < 0.0001$). This test indicated that there was a less than 1% chance that the clustering pattern of nests observed on Lower Red Rock Lake was due to random chance. Relationships between NND and fate were consistent between high and low-water years. In low-water years, successful nests ($\bar{x} = 185$ m, 95% CI = 149.71-220.32) were located 49 m (21%) closer to conspecific nests than unsuccessful nests ($\bar{x} = 234$ m, 95% CI = 188.89-278.21; $F_{1,181} = 2.83$, $P = 0.09$; Fig. 2.8). In high-water years, successful nests ($\bar{x} = 171$ m, 95% CI 146-196) were located 50 m (23%) closer to conspecific nests than unsuccessful nests ($\bar{x} = 221$ m, 95% CI = 187-256; $F_{1,257} = 5.32$, $P = 0.02$; Fig. 2.8).

Hot Spot analyses of 182 nests in low-water years identified a small significant Hot Spot for nest fate (i.e., clustering of successful nests) in emergent vegetation of the northern part of Lower Red Rock Lake (Fig. 2.9). Three significant Cold Spots for nest fate (i.e., clustering of nest failure) were located along the northwestern, eastern, and southeastern shores of Lower Red Rock Lake in low-water years (Fig. 2.9). A significant Hot Spot for clutch initiation in low-water years (i.e., clustering of nests that were initiated earlier in the year) was found on the eastern shore of Lower Red Rock Lake (Fig. 2.10). Two significant Cold Spots for clutch initiation (i.e., clustering of nests that were initiated later in the year) were located in the emergent vegetation just above the northern part of Lower Red Rock Lake and off two tributaries that flow into the eastern edge of Lower Red Rock Lake in low-water years (Fig. 2.10). Hot Spot analyses of 258 nests in high-water level years identified a Hot Spot for nest fate again in the area of emergent vegetation on the northern shore of Lower Red Rock Lake and along the northwestern shore (Fig. 2.11). Three Cold Spots of nest fate were located along the northeastern shore, along the northern part of the western shore, and just off the western shore on a few scattered islands in high-water years

(Fig. 2.11). Two significant Hot Spots for clutch initiation in high-water years were found along the southern edge and off a tributary east of Lower Red Rock Lake (Fig. 2.12). Three significant Cold Spots for clutch initiation were found along the northwestern, southwestern, and northeastern shores of Lower Red Rock Lake (Fig. 2.12).

Discussion

The effect density has on the distribution patterns of waterfowl during the nesting season remains unclear (Johnson and Grier 1988). The density of nest locations on the landscape and its effects on nest success are frequently argued whether higher densities result in increased or decreased nest success rates (Cowardin et al. 1985, Clark and Nudds 1991, Horn et al. 2005). Clark and Shutler (1999) found in a review of waterfowl nesting studies (n = 270), that higher density nesting patches tended to have relatively higher nest success than lower density nesting areas of conspecifics. During this study, nest-site selection was influenced by a positive relationship between nest fate and the distance to the nearest nest (NND). During both high and low-water years, successful nests were located ~50 m closer to conspecific nests than unsuccessful nests. The relationship between NND and nest success is consistent with another study conducted on the Refuge that also found a positive relationship between habitat utilization and conspecific density, with habitat utilization increasing in young females by 48% ± 0.02 for every increase in density, and habitat utilization increasing in older females by 27% ± 0.30 for every increase in density (O'Neil et al. 2014). The congregations of successful nests with reduced distances in the core Hot Spot at Lower Red Rock Lake indicates that late-nesting females are able to cue in, recognize, and select higher quality habitat patches.

Selection tends to favor early breeding across most avian species (Perrins 1970). To determine the differences between high and low-water level years on nest initiation, I investigated the resulting variation in timing of nest initiation. Successful nests were initiated on average 3 days earlier than unsuccessful nests, which indicate a benefit of nesting earlier in low-water years. However, previous research on the Refuge found, not accounting for differences in water levels, that nesting success was positively related with increasing initiation date (i.e., increases later in the nesting season). For example, nest success for scaup was as low as 0.01 (95% CI = <0.01-0.07) on 1 June but increased to 0.87

(95% CI = 0.75-0.93) on 20 August (Warren et al. 2014). Nesting earlier often induces a larger clutch and higher quality young but a lower chance of successfully hatching (Dawson and Clark 1996, Dawson and Clark 2000), and breeding later results in significantly increased nest success but is coupled with smaller clutch sizes and lower recruitment rates (Flint et al. 2006). Estimates of mean clutch initiation were latest in 2011 when lake levels rose due to melting of an above-average snowpack during scaup nest initiation. This spike in water levels flooded many of the nests and is thought to be the cause for the small sample of nests found that year (Warren et al. 2014). My results indicate that the trade-offs in timing of breeding that female scaup are influenced by density-independent factors (i.e., water levels). Contrary to my prediction, areas that had clusters of nests initiated later in the season coincided with Hot Spots for nest fate (i.e., high-quality habitat patches, clusters of successful nests), whereas areas that tended to be selected for first, evidenced by clusters of nests initiated earlier, overlapped with clusters of Cold Spots for nest fate. This relationship of spatial clustering based on the timing of nest initiation and nest success/failure was evident in both high and low-water level years. These spatial patterns directly conflict with other results of this study that successful nests were on average initiated three days earlier than unsuccessful nests in low-water years. However, these patterns are comparable to the positive relationship between initiation date and nest survival that was found during five of seven years in a study conducted on scaup in the boreal forest (Walker et al. 2005), and the positive relationship found between increasing JDATE and nest success previously found in research conducted on scaup at the Refuge (Warren et al. 2014). These results indicate that there are certain areas around Lower Red Rock Lake that tend to either be more or less successful year after year, which is consistent with other research on the Refuge that found successful breeders used habitat within ~ 300 m of prior years' nest locations from 2007-2009 at the Refuge (O'Neil et al. 2014). Late-nesting scaup females are cuing on the reproductive performance of early-nesting conspecifics for public information when determining patch level nest-site selection. Conversely, early nesters could be cuing on prior years' successful nesting areas, or possibly cuing on public information of earlier nesting females of other species. It is very peculiar that early-breeding females are actually not selecting for the higher-quality habitat patches, rather results of my Hot Spot analyses show just the opposite.

Waterfowl colonize areas as a positive response to precipitation and vacate areas that are dry (Johnson and Grier 1988). Based on the bathymetric map calculations of flooded emergent vegetation, nest distance to open water was not different between high and low-water years. Greater than 90% of the nests were located within 20 m from open water each year during the 2006-2013 nesting seasons at the Refuge. Therefore, the spatial shifts of nest location Hot Spots dependent on water levels were inevitable and hypothesized for this study. Contrary to my prediction, nest success did not differ between years with high and low-water levels. Between 1989-1993 and 2002-2003 at Minto Flats State Game Refuge in Alaska, annual nest success for 554 scaup nests varied between 1 to 61%, only exceeding 20% in two of the seven years (Walker et al. 2005). Walker et al.'s (2005) found that most successful nests were initiated later and further away from water; whereas, least successful nests were initiated earlier and closer to water. Although nest success did not differ between high and low-water levels at the Refuge, Hot and Cold Spots of nest fate locations differed between high and low-water level years. These Hot and Cold Spots were identified as clusters of nests grouped higher in magnitudes of successful or unsuccessful that were greater than expected by random chance. The most pronounced Hot Spot for nest fate in high-water levels, which was in the same location for the Hot Spot in low-water levels, consisted of 52 nests; whereas, it consisted of 10 nests in low-water levels. The core Hot Spot for nest fate was in the same spot in both water levels located in emergent vegetation, flooded dependent on the year, was in the heart of Lower Red Rock Lake furthest from any upland habitat. The second Hot Spot for nest fate in all high-water years encompassed 16 nests, but this same location was identified as a Cold Spot in low-water. There were three Cold Spots for nest fate both in high and low-water years, and they were similar in only one location, which was located off two tributaries on the east shore of Lower Red Rock Lake. The other four Cold Spots for nest fate both in high and low-water years were all located in emergent vegetation on the perimeter of Lower Red Rock Lake adjacent to uplands. The spatial patterns observed in shifting of Hot and Cold Spots with high and low-water levels indicates that scaup respond to changes in wetland phenology and these environmental processes are influencing patch selection and ultimately a driver of breeding success. However, nest success was not found to be different between high and low-water levels.

Distance to upland (non-emergent, seasonally inundated vegetation) was a significant indicator of nest fate in low-water years. Successful nests were located 209 m farther from upland than unsuccessful nests, which supports the trends observed of Cold Spots located on the peripheries of Lower Red Rock Lake adjoining neighboring uplands. However, a conflicting study found support for the pattern that successful nests were located closer to dry land (Fournier and Hines 2001) I speculate this relationship was due to accessibility from predators, emphasizing that nest-site selection is critical to nest survival. The primary cause of nest failure at the Refuge is the predation by avian predators such as: common ravens (*Corvus corax*) and California gulls (*Larus californicus*), and river otters (*Lontra canadensis*; Warren et al. 2014). I did not find a relationship between distance to upland and fate in high-water years, which indicates that placement of nests is not as important in high-water years, or there may be a threshold distance in high-water years where it may be easier to be far from upland. The lack of a similar relationship with distance to upland in high-water years is due to the secondary Hot Spot that is located on the northwest shore of Lower Red Rock Lake in an area that contains many small ephemeral ponds. In high-water years an increased amount of water on the landscape caused many of these small ponds to become inundated making access to nesting areas more difficult for terrestrial predators. The trend of successful nests being located farther from upland at the Refuge is consistent with the finding that composition of predators at a local site and the distance predators had to travel from their dens to the nests was influential to nest fate (Larivière and Messier 1998). In low-water years predators may have greater access to core nesting areas farther from upland, which could explain why the pattern was less pronounced in low-water years. The nearest wooded area is located directly to the south of Lower Red Rock Lake, which influences the composition, timing, and distance needed to travel by terrestrial predators to nesting locations, and may partially explain why Cold Spots for nest fate tended to be located near the southern fringe of Lower Red Rock Lake.

In both high and low-water level years, clusters of nests initiated later in the season coincided with Hot Spots for nest fate (i.e., high-quality habitat patches, clusters of successful nests), whereas areas that tended to be selected for first, evidenced by clusters of nests initiated earlier, tended to overlap with clusters of Cold Spots for nest fate. In low-

water years, successful nests (1153 m) were located 22.0% farther from upland than unsuccessful nests (944 m). Successful nests were located 21.0% and 23.0% (i.e., 49 and 50 m) closer to conspecific nests than unsuccessful nests in low and high-water levels, respectively. Although nest success was not significantly different between high and low-water level years, the locations of Hot Spots and Cold Spots were affected by the differences in water levels. Another study conducted on the refuge found that found that nest daily survival rate was strongly correlated with nest age (Pokley 2014). Therefore, management actions focused on survival and reproductive success of scaup should consider managing water levels and habitat for later nesting scaup to increase survival and recruitment.

Literature Cited

Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. Auk 101:255-265.

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: A retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management: 65:781-796.

Allen, G. T., D. F. Caithamer, and M. Otto. 1999. A review of the status of greater and lesser scaup in North America. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Arlington, Virginia, USA.

Anderson, M. G., R. B. Emery, and T. W. Arnold. 1997. Reproductive success and female survival affect local population density of canvasbacks. Journal of Wildlife Management 61:1174-1191.

Arnold, T, W., M. G. Anderson, M. D. Sorenson, and R. B. Emery. 2002. Survival and philopatry of female redheads breeding in southwestern Manitoba. Journal of Wildlife Management 66:162-169.

Austin, J. E., C. M. Custer, and A. D. Afton. 1998. Lesser scaup (Aythya affinis). In The Birds of North America, no. 47 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Bethke, R. W. 1993. Geographical patterns of persistence in duck guilds. Oecologia 93:102-108.

Campomizzi, A. J., J. A. Butcher, S. L. Farrell, A. G. Snelgrove, B. A. Collier, K. J. Gutzwiller, M. L. Morrison, and R. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. Journal of Wildlife Management 72:331-336.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80:272-287.

Cowardin, L. M., D. S. Gilmer, and C. W. Shaffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92:1-37.

Cowardin, L. M., T. L. Shaffer, and P. M. Arnold. 1995. Evaluations of duck habitat and estimation of duck population sizes with a remote-sensing-based system. U.S. Fish

and Wildlife Service, National Biological Survey, Washington, USA. Biological Science Report 2.

Danchin, É., L.-A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487-491.

Dawson, R. D., and R. G. Clark. 1996. Effects of variation in egg size and hatching date on survival of lesser scaup *Aythya affinis* ducklings. Ibis 138:693-699.

Dawson, R. D., and R. G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. Condor 102:930-935.

Doligez, B., C. Cadet, E. Danchin, and T. Boulinier. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Animal Behaviour 66:973-988.

Emery, R. B., D. W. Howerter, L. M. Armstrong, M. G. Anderson, J. H. Devries, and B. L. Joynt. 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian prairies. Journal of Wildlife Management 69:1181-1193.

ESRI. ArcGIS 10.2. 2013. Environmental Systems Research Institute, Inc., Redlands, California.

Flint, P. L., J. B. Grand, T. F. Fondell, and J. A. Morse. 2006. Population dynamics of greater scaup breeding on the Yukon-Kuskokwim Delta, Alaska. Wildlife Monographs 162:1-22.

Fournier, M. A., and J. E. Hines. 2001. Breeding ecology of sympatric greater and lesser scaup (*Aythya marila* and *Aythya affinis*) in the subarctic Northwest Territories. Arctic 54:444-456.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gurney, K., R. Clark, S. Slattery, N. Smith-Downey, J. Walker, L. Armstrong, S. Stephens, M. Petrula, R. Corcoran, and K. Martin. 2011. Time constraints in temperate-breeding species: influence of growing season length on reproductive strategies. Ecography 34:628-636.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883-900.

Horn, D. J., M. L. Phillips, R. R. Koford, W. R. Clark, M. A. Sovada, and R. J. Greenwood. 2005. Landscape composition, patch size, and distance to edges: interactions affecting duck reproductive success. Ecological Applications 15:1367-1376.

Jamieson, L., and S. Brooks. 2004. Density dependence in North American ducks. Animal Biodiversity and Conservation 27:113-128.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.

Johnson, D. H., and J. W. Grier. 1988. Determinants of breeding distributions of ducks. Wildlife Monographs 100:1-37.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557-562.

Koons, D. N., J. J. Rotella, D. W. Willey, M. Taper, R. G. Clark, S. Slattery, R. W. Brook, R. M. Corcoran, and J. R. Lovvorn. 2006. Lesser scaup population dynamics: what can be learned from available data? Avian Conservation and Ecology 1(3):6. URL: http://www.ace-eco.org/vol1/iss3/art6/

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox, Jr. 2006. Mallard brood movements, wetland use, and duckling survival during and following a prairie drought. Journal of Wildlife Management 70:1436-1444.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150:650-661.

Larivière, S., and F. Messier. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? Oikos 83:12-20.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150:650-661.

Newton, I. 1994. The role of nest sites in limiting the number of hole-nesting birds: a review. Biological Conservation 70:265-276.

Newton, I. 1998. Population limitation in birds. Academic Press, London, UK.

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

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Piorkowski, M. D., and T. J. O'Connell. 2010. Spatial pattern of summer bat mortality from collisions with wind turbines in mixed-grass prairie. American Midland Naturalist 164:260-269.

Pokley, K. J. 2014. Testing Competing Hypotheses for the Seasonal Variation in Nesting Success of a Late-Nesting Waterfowl. Thesis. Montana State University. Bozeman, USA.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:50-66.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/.

Ringelman, K. M., J. M. Eadie, and J. T. Ackerman. 2012. Density-dependent nest predation in waterfowl: the relative importance of nest density versus nest dispersion. Oecologia 169:695-702.

SAS Institute. 1988. SAS/STAT user's guide. Release 6.03. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American breeding bird survey, results and analysis 1966–2003. USGS Patuxent Wildlife Research Center Laurel, MD.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474-480.

Sheaffer, S. E. 1998. Recruitment models for mallards in eastern North America. Auk 115:988-997.

Stamps, J., and V. Krishnan. 2005. Nonintuitive cue use in habitat selection. Ecology 86:2860-2867.

Trauger, D. L. 1974. Eye color of female lesser scaup in relation to age. Auk 91:243-254.

U.S. Fish and Wildlife Service. 2014. Waterfowl population status, 2014. U.S. Department of the Interior, Washington, D.C., USA.

Verhulst, S., J. Å. Nilsson, S. Verhulst, and J. Å. Nilsson. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B: Biological Sciences 363:399-410.

Viljugrein, H., N. C. Stenseth, G. W. Smith, and G. H. Steinbakk. 2005. Density dependence in North American ducks. Ecology 86:245-254.

Walker, J., M. S. Lindberg, M. C. MacCluskie, M. J. Petrula, and J. S. Sedinger. 2005. Nest survival of scaup and other ducks in the boreal forest of Alaska. Journal of Wildlife Management 69:582-591.

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

Weller, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20:111-113. (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006) (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006) (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006) (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006) (Bethke 1993, Newton 1998, Sheaffer 1998, Krapu et al. 2006)

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliff, New Jersey.

Tables

Table 2.1. Dates for all nest-searching periods used in lesser scaup nest-site selection analyses from 2006-2013 at Red Rock Lake National Wildlife Refuge, USA.

Year	Nest Searching
2006	May22-July 20
2007	June 16-July 19
2008	June 7-July 24
2009	June 3-July 10
2010	June 1-July 16
2011	June 6-July 22
2012	May 20-July 18
2013	May 30-July 15

Figures

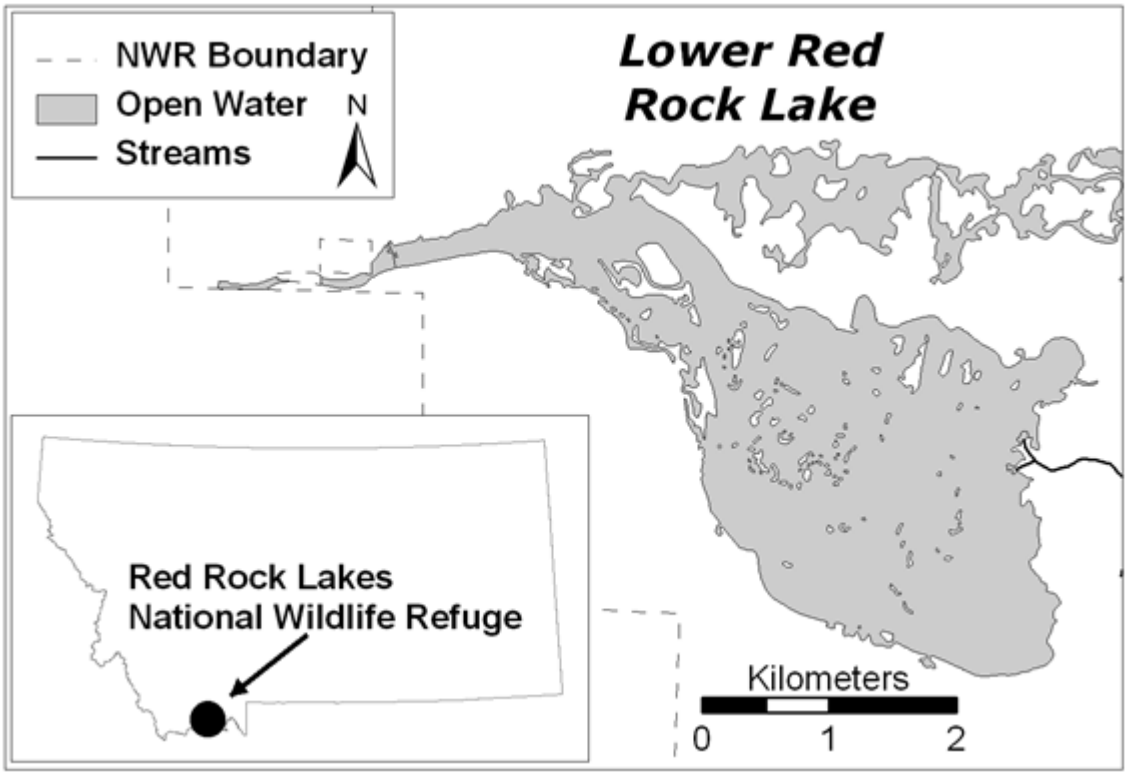

Figure 2.1. Lower Red Rock Lake and River Marsh study site on Red Rock Lakes National Wildlife Refuge (NWR), Montana, USA. Inset shows location of Red Rock Lakes NWR within Montana.

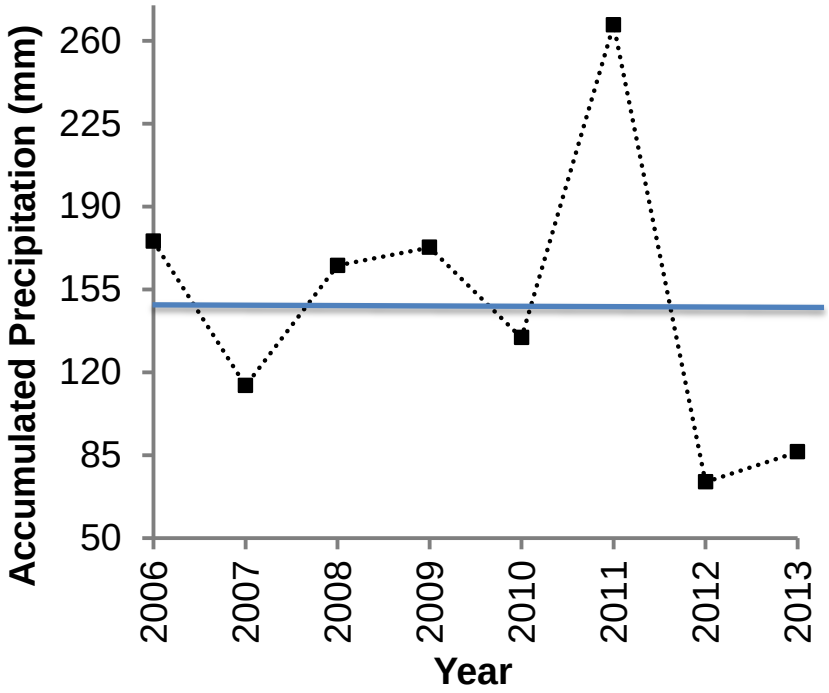

Figure 2.2. Accumulated precipitation (mm) from the first day a nest was initiated (22 May, 2006) to 35 days after (25 August, 2011) the last day a lesser scaup nest was initiated (21 July, 2011) on Lower Red Rock, Red Rock Lakes National Wildlife Refuge, Montana 2006-2013. The blue bar represents the separation between precipitation in high and low-water years, with points above the blue bar categorized as years with above-average precipitation, and points below categorized as years with below-average precipitation.

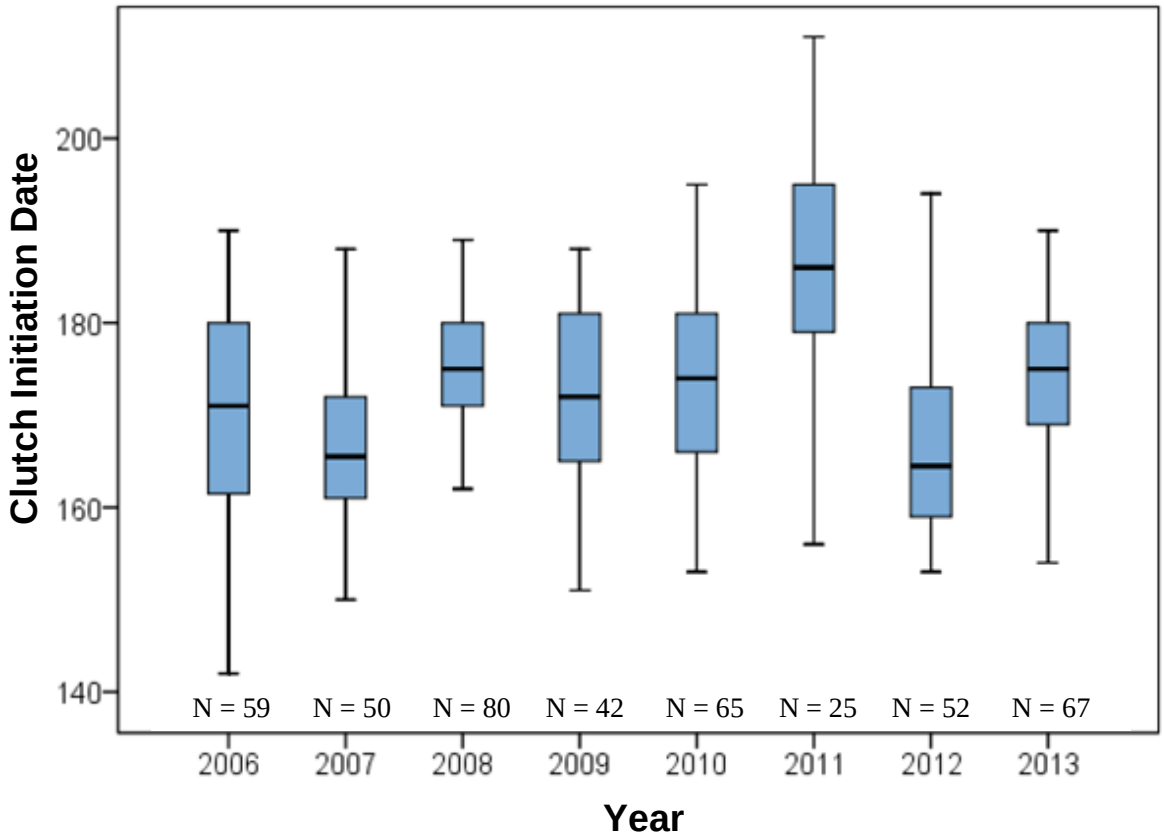

Figure 2.3. Box plots representing clutch initiation date of lesser scaup during the 2006-2013 nesting seasons at Red Rock Lakes National Wildlife Refuge, Montana, USA. Each box contains 50% of the data points (first to third quartile range), the bold line represents the median, and the top and bottom lines show the maximum and minimum values.

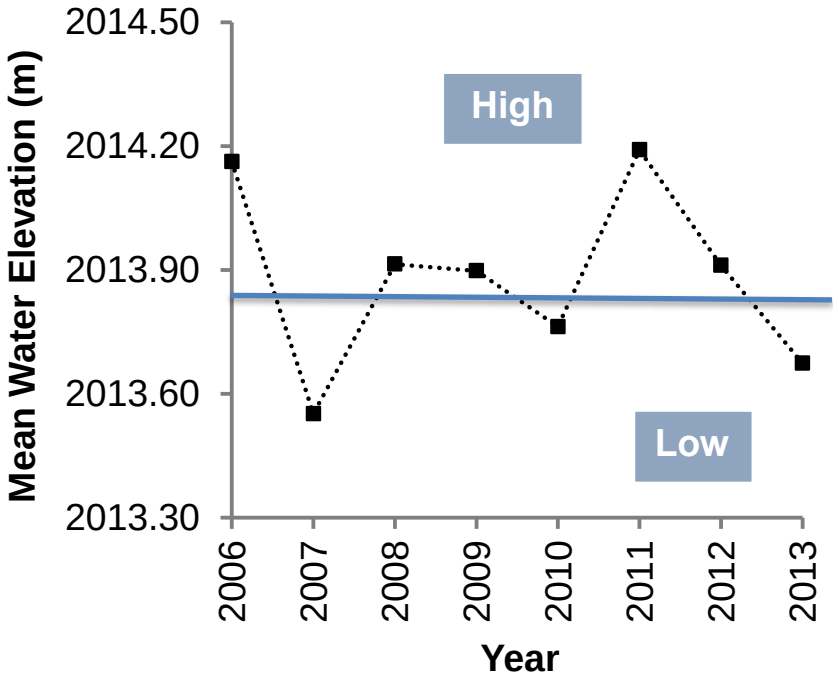

Figure 2.4. Mean water elevation (m) from the first day a nest was initiated (22 May, 2006) to 35 days after (25 August, 2011) the last day a lesser scaup nest was initiated (21 July, 2011) on Lower Red Rock, Red Rock Lakes National Wildlife Refuge, Montana, USA, 2006-2013. The blue bar represents the separation between high and low-water years, with points above categorized as high-water levels, and points below categorized as low-water levels.

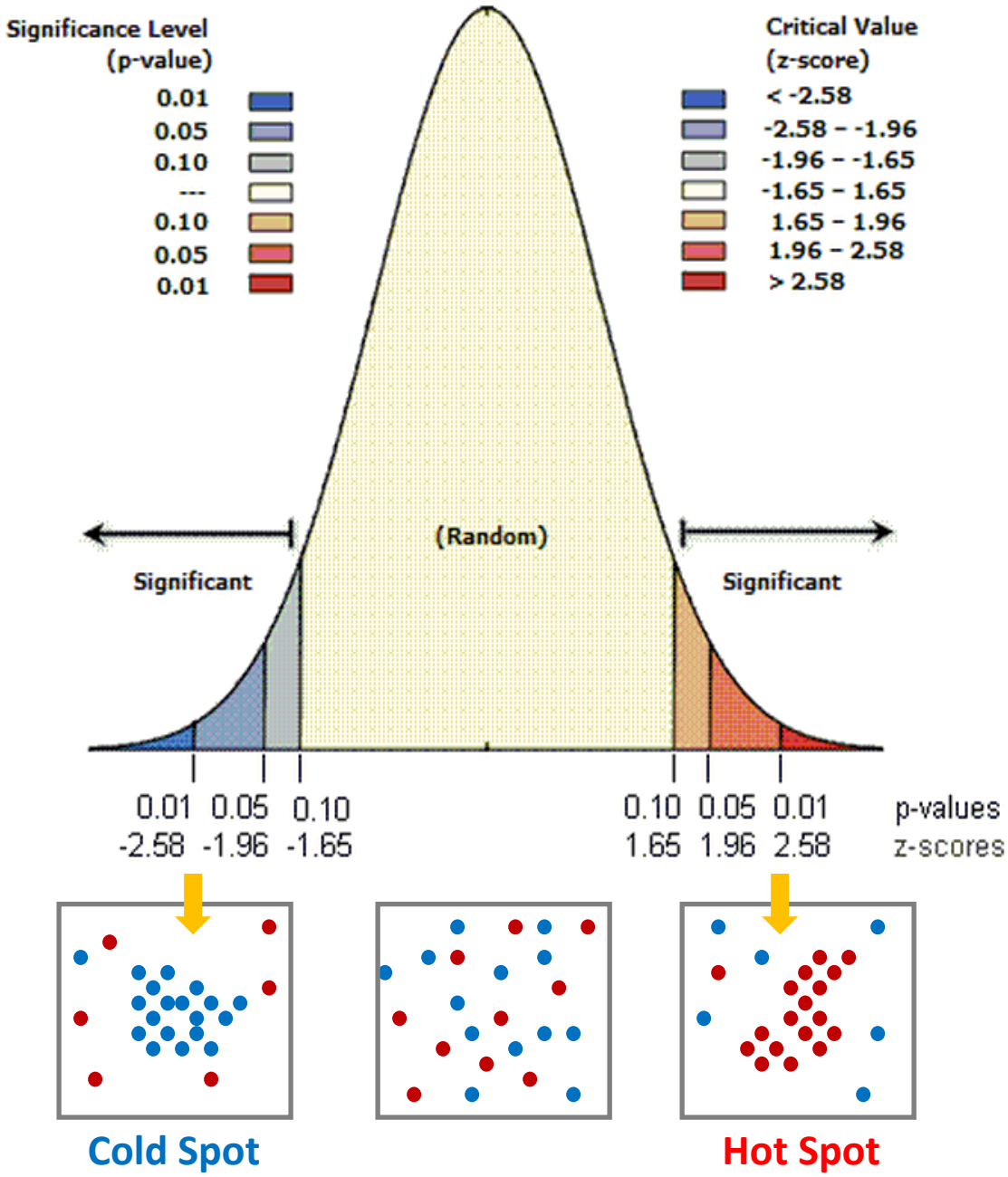

Figure 2.5. This pattern analysis tool was used to identify spatial clusters of high values (Hot Spots) and spatial clusters of low values (Cold Spots) using the Getis ord Gi* statistic. Features in the ± 3 bins reflect statistical significance with a 99 percent confidence level; features in the ± 2 bins reflect a 95 percent confidence level; features in the ± 1 bins reflect a 90 percent confidence level; and the clustering for features in bin 0 is not statistically significant. Very high (positive) or very low (negative) Z-scores, associated with very small P-values indicate the Hot Spot and the Cold Spot, respectively (ESRI 2013).

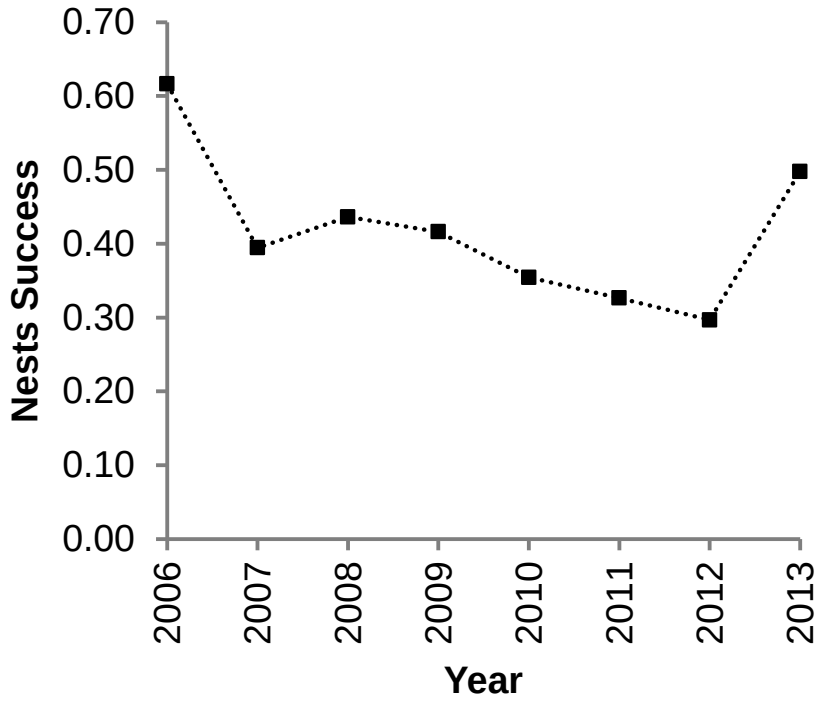

Figure 2.6. Maximum likelihood estimates of lesser scaup nest success from 2006-2013 on Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA.

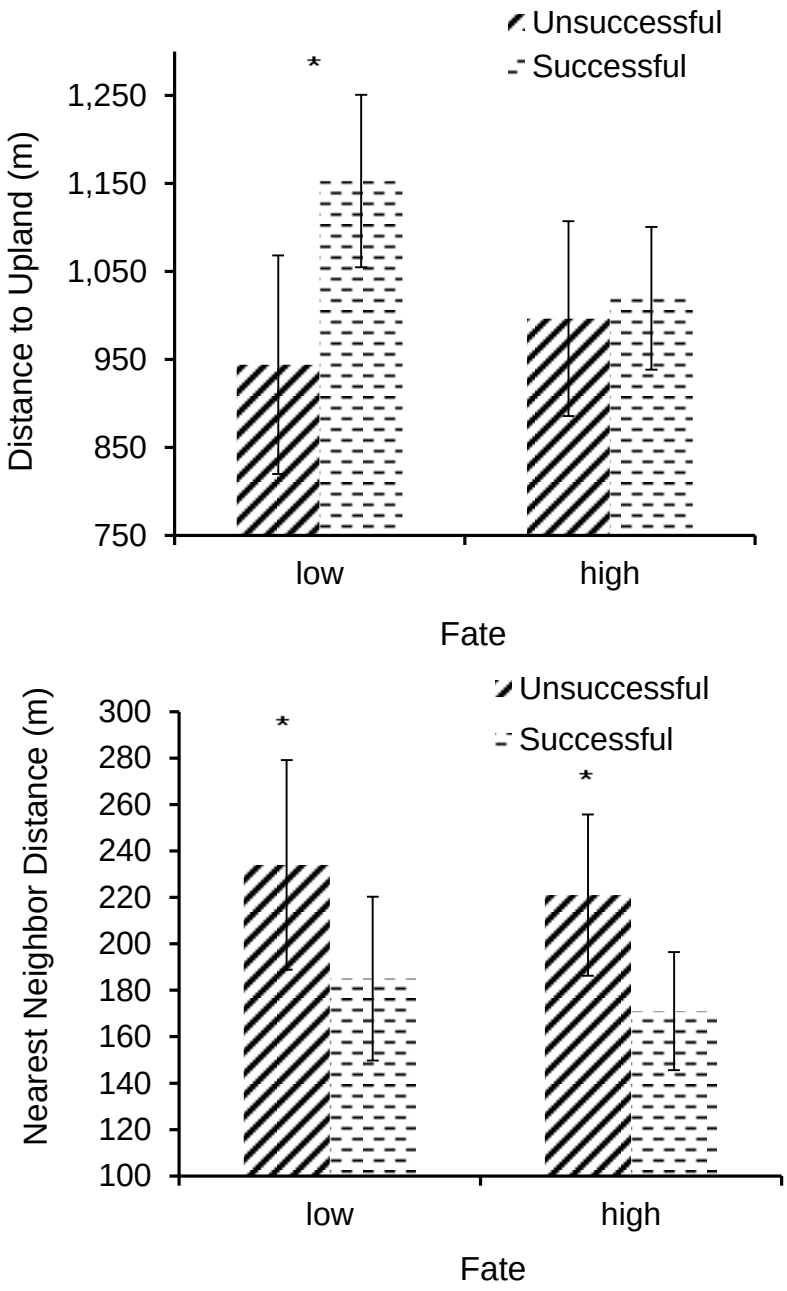

Figure 2.7. Relationship between fate of lesser scaup nests with mean distance to upland and mean Nearest Neighbor Distance (error bars represent ± SE) in high and low-water years at Red Rock Lakes National Wildlife Refuge, Montana, USA. Asterisk represents significant difference ($P < 0.05$).

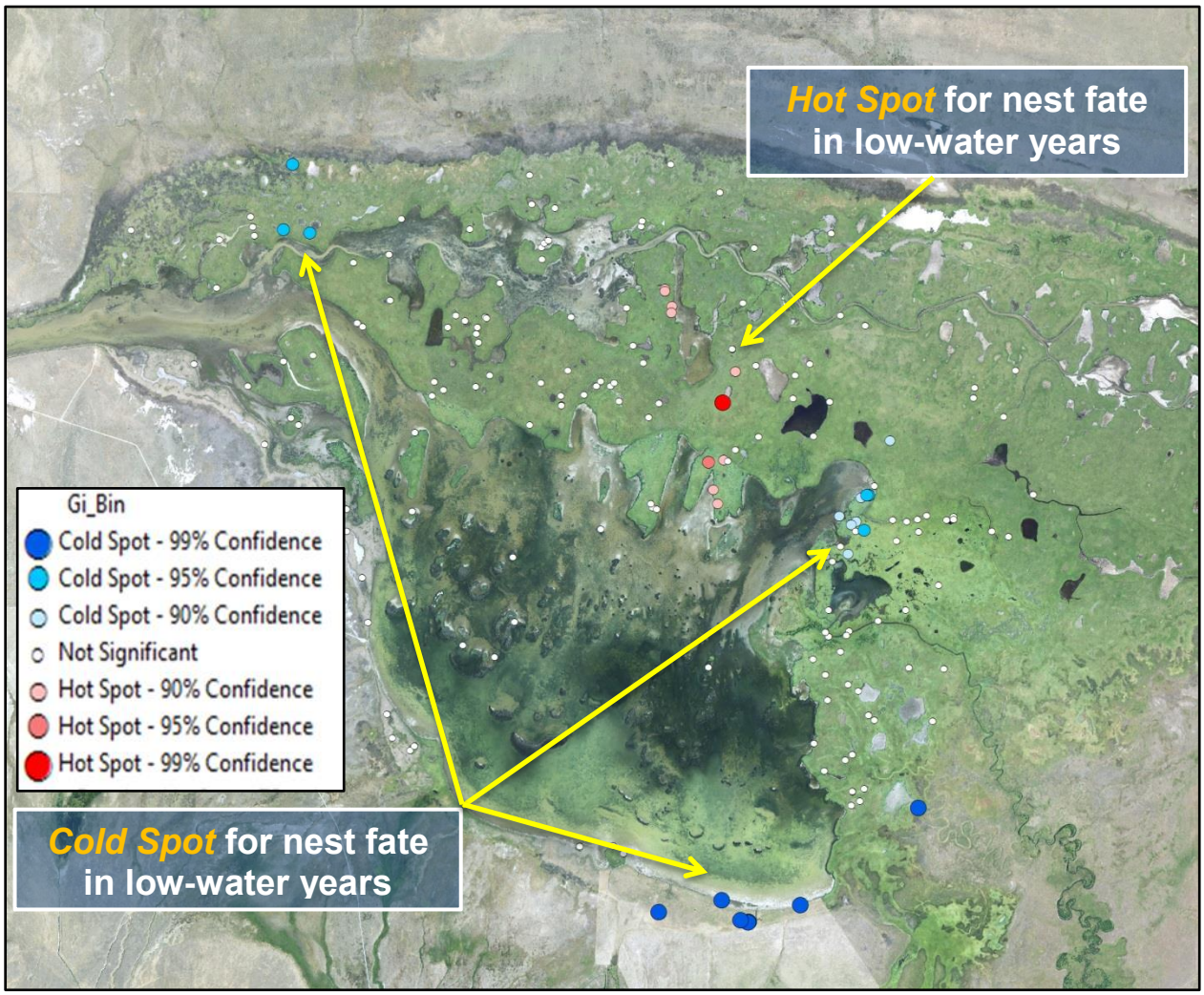

Figure 2.8. Distribution of Hot (red; successful) and Cold (blue; unsuccessful) Spots based on nest fate of lesser scaup in low-water years combined (2007, 2010, and 2013) displayed on orthoimagery of Lower Red Rock Lake, Red Rock Lake National Wildlife Refuge, Montana, USA. Each nest point is color coded by the Z-score and the P-value as shown in the legend. The top blue circle and lowest red circle represent Z-scores ± 3 standard deviations of the mean ($P < 0.01$), and the second blue and red circles represent Z-scores ± 2 standard deviations of the mean ($P < 0.05$), respectively.

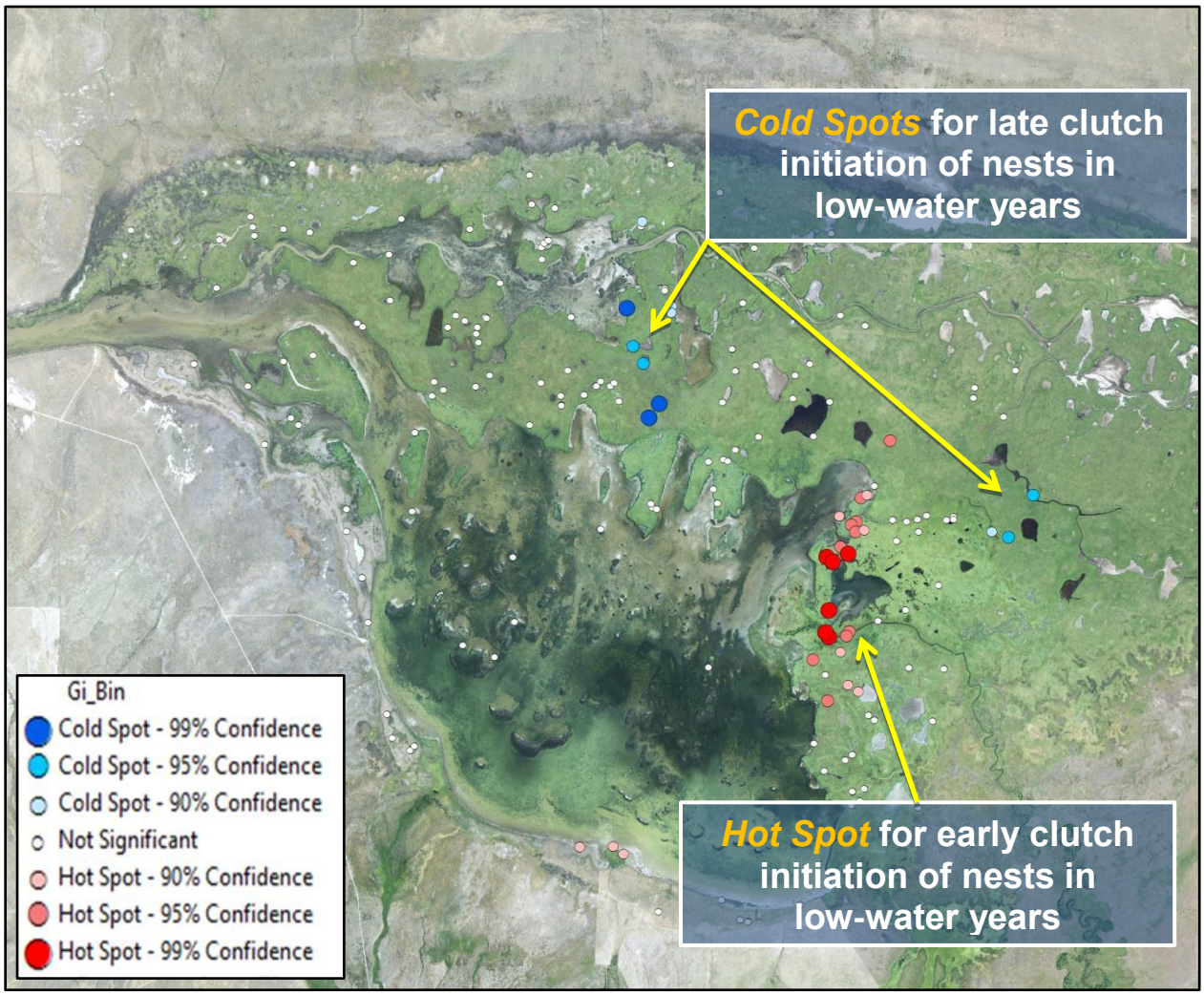

Figure 2.9. Distribution of lesser scaup nest-site selection based on timing of clutch initiation in low-water years combined (2007, 2010, and 2013) displayed on orthoimagery of Lower Red Rock Lake, Red Rock Lake National Wildlife Refuge, Montana, USA. Early (red) and late (blue) clutch initiation are color coded by the Z-score and P-values, as shown in the Gi_Bin legend. The top blue circle and lowest red circle represent Z-scores ± 3 standard deviations of the mean ($P < 0.01$), and the second blue and red circles represent Z-scores ± 2 standard deviations of the mean ($P < 0.05$), respectively.

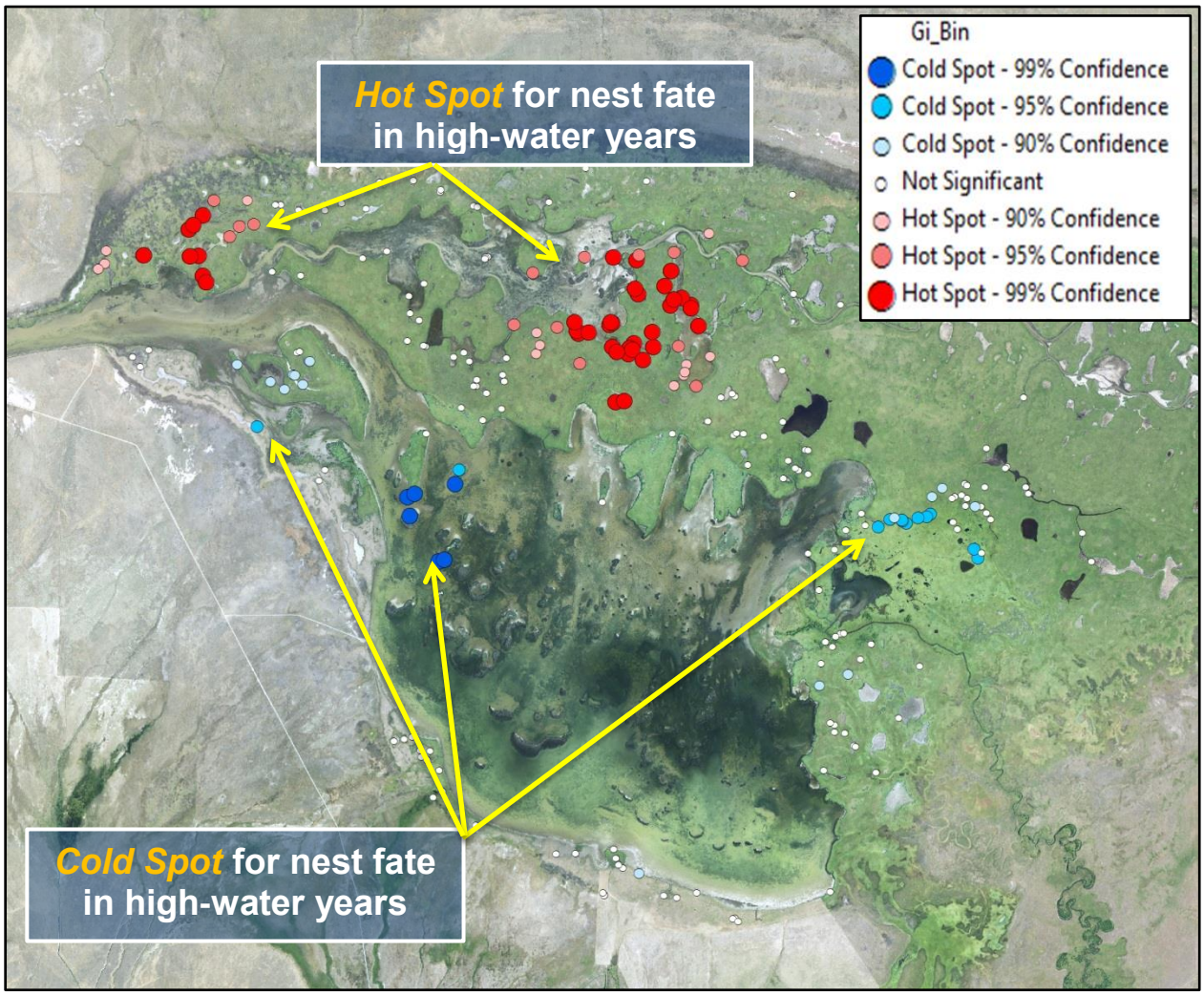

Figure 2.10. Distribution of Hot (red; successful) and Cold (blue; unsuccessful) Spots based on nest fate of lesser scaup in high-water years combined (2006, 2008, 2009, 2011, and 2012) displayed on orthoimagery of Lower Red Rock Lake, Red Rock Lake National Wildlife Refuge, Montana, USA. Each nest point is color coded by the Z-score and the P-value as shown in the Gi_Bin legend. The top blue circle and lowest red circle represent Z-scores ± 3 standard deviations of the mean ($P < 0.01$), and the second blue and red circles represent Z-scores ± 2 standard deviations of the mean ($P < 0.05$), respectively.

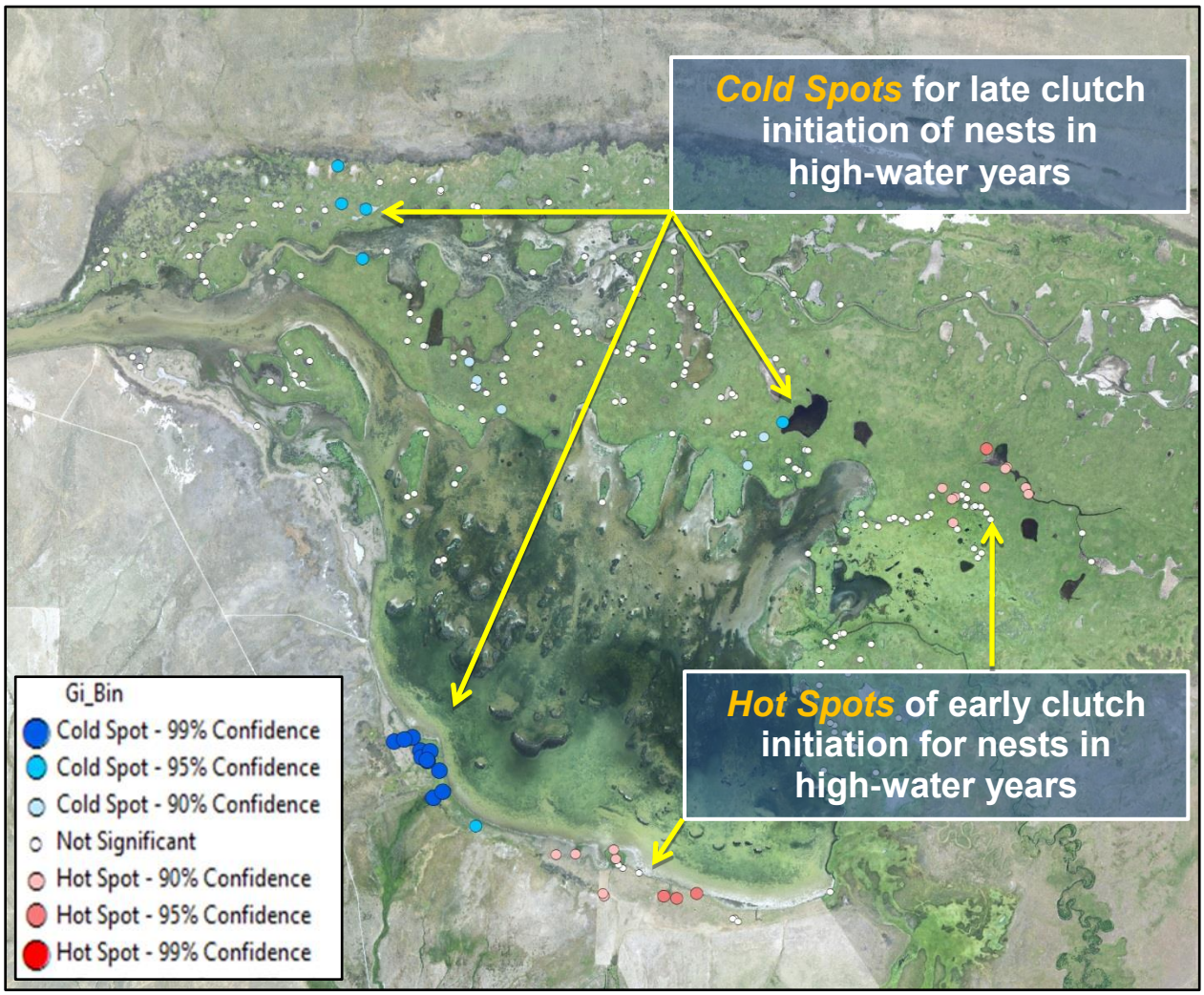

Figure 2.11. Distribution of lesser scaup nest-site selection based on timing of clutch initiation in high-water years combined (2006, 2008, 2009, 2011, and 2012) displayed on orthoimagery of Lower Red Rock Lake, Red Rock Lake National Wildlife Refuge, Montana, USA. Early (red) and late (blue) clutch initiation are color coded by the Z-score and P-values, as shown in the Gi_Bin legend. The top blue circle and lowest red circle represent Z-scores ± 3 standard deviations of the mean ($P < 0.01$), and the second blue and red circles represent Z-scores ± 2 standard deviations of the mean ($P < 0.05$), respectively.

Abstract – Blood Parasite Prevalence

Blood parasites, *per se*, do not lead to direct mortality, but instead reduce the health of individual birds, which may ultimately lead to decreased reproductive success. Evidence has shown that presence of blood parasites can reduce fitness, body condition, and reproductive success of waterfowl. For many avian species, the cost of reproduction is manifested as a negative relationship between female breeding effort and breeding season survival, with trade-offs occurring when these adaptive choices become detrimental to future reproductive performance. Blood was drawn for parasite load determination from 112 individual adult scaup captured from 2011 to 2012 via spotlighting and drive-trapping. Parasite prevalence was determined through blood assays that were created using a two-slide wedge technique. Relationships among seasonal heterophile:lymphocyte ratio (a proxy for health), body mass at time of capture (throughout pre-, during, and post-breeding periods), breeding status (females only), and Julian date of capture (date of capture) of capture with parasite prevalence were analyzed using linear (lm) regression models in R 2.15.2. The blood parasite infection rate was 5.0%, with prevalence differing by gender with 33.3% of males positive for blood parasites compared to 1.0% of females. The presence of blood parasites did not affect health, fitness, or breeding status of scaup. A quadratic relationship was found with body mass and date of capture, indicating that body mass increased from pre-breeding period to the breeding period and decreased significantly at the end of the summer during molt. A negative relationship between the heterophile:lymphocyte ratio of female scaup and date of capture (i.e., the health of scaup females was greatest during the pre-breeding period after which it consistently decreased until the molting period). A strong negative correlation between heterophile:lymphocyte ratio and body mass was found in both genders, which indicated that scaup in poor body condition were also in poor health at the end of the breeding season.

Chapter 3 - Effects of Blood Parasite Prevalence on Body Mass, Breeding Status, and Health of Lesser Scaup at Red Rock Lakes National Wildlife Refuge

Introduction

Life history strategies are evolutionary responses by organisms that optimize survival and reproduction. Trade-offs occur when these adaptations to specific cues choices become detrimental to future reproductive performance (Schlaepfer et al. 2002). For many avian species, the cost of reproduction is manifested as a negative relationship between female breeding effort and breeding season survival (Rigby and Haukos 2012). Underlying causes for this relationship have been demonstrated by the physical demands of nesting and brood rearing resulting in females becoming more vulnerable to predation (Sargeant and Raveling 1992) and susceptible to Haematozoa infections, or commonly known as blood parasites (hereafter, blood parasites; Gustafsson et al. 1996). The presence of blood parasites has been found to reduce body condition (Marzal et al. 2008), reproductive success (Gustafsson et al. 1996, Marzal et al. 2005), and survival (Nordling et al. 1998, Valkiunas 2004). For example, a study on great tits (*Parus major*) found that individuals who invested more in reproduction and greater total pre-fledging weight demonstrated a relationship between severity of heterophile:lymphocyte ratios (a proxy for stress) and blood concentration levels of *Haemoproteus* (Ots and Hõrak 1996). This negative relationship highlights the importance of trade-offs between health maintenance and resources invested in reproduction. However, limited data have quantified a trade-off between health maintenance and reproduction in waterfowl species, and further investigation is warranted to determine if host-parasite interactions are resulting in detrimental effects on the fitness and species life histories (Loiseau et al. 2012).

Bood parasites, *per se*, do not lead to direct mortality, but instead reduces the health of individual birds, which may ultimately lead to decreased reproductive success (Sheldon and Verhulst 1996, Ots and Hõrak 1998). The three most common blood parasites encountered in North American waterfowl (*Haemoproteus* spp., *Leucocytozoon* spp., and *Plasmodium* spp.*)* can cause trade-offs between relationships of an individual's health,

reproductive effort, and parasite defense (Bennett et al. 1975, Richner et al. 1995). The three blood parasites are intracellular sporozoan parasites that require two host species: a bird and an invertebrate host. The bird is needed for schizogony (asexual replication) and the invertebrate host is required for sporogony (sexual replication; Wobeser 1997). Blood parasites are transmitted to avian hosts by members of the order Diptera, such as midges (*Culicodies* spp.), mosquitoes (*Anopheles* spp.), and blackflies (*Simulium* spp.; Ots and Horak 1996). Presence and prevalence of blood parasites have been shown to vary by vertical stratification of nest site location at a local scale (Greiner et al. 1975), by gender (Dey 2008), temporally (Loven et al. 1980), and at different points of the migration route in the same species (Bennett et al. 1982, Fedynich and Pence 1994, Forrester et al. 2001). A positive relationship of blood parasite prevalence and mortality rate was noted in a review of studies conducted on waterfowl noted (Sorci and Møller 1997). Negative effects of parasites in avian hosts; when treated for reduction in parasites, were experimentally demonstrated in individuals that invested fewer resources in parasite defense and had greater reproductive success (Merino et al. 2000, Tomas et al. 2006). The warming of climate is associated with a global increase of these infectious parasites, and this effect can be detrimental in areas of short growing seasons and low parasitemia prevalence. Avian *Plasmodium* transmission was first documented by a study conducted in the North American Arctic as high as latitude 64°N, which they concluded that the effects of climate change and the potential impacts of the emergence of vector-borne parasites at higher latitudes and altitudes is of growing concern (Loiseau et al. 2012).

To further investigate influences on health maintenance and resources invested in an individual's health fitness, I addressed the effects of blood parasite prevalence on body mass, breeding status, and health in a bird species of conservation concern. According to the annual Breeding Population Survey (BPOP) lesser scaup (*Aythya affinis*; hereafter, scaup) reached an all-time low in 2005 of 37% below the 1955-2005 average (Fig. 3.1; U.S. Fish and Wildlife Service 2014; hereafter USFWS), with the species failing to respond to favorable breeding conditions across the core breeding area of the western boreal forest (; Afton and Anderson 2001). The scaup population in the traditional survey area (i.e., central Canada, north-central United States, and Alaska) steadily increased from 2006 to 2014, and currently remains ~ one and a half million birds below the North American Waterfowl

Management Plan goal of 6.3 million birds. Contemporary estimates of adult survival, breeding status, and reproductive success are crucial to furthering our knowledge and understanding of scaup population dynamics (Austin et al. 2006). Factors thought to influence these vital rates, including reduced spring body condition upon arrival to the breeding grounds and health issues due to effects of blood parasites, need to be investigated at multiple scales and study sites to improve understanding of the spatio-temporal covariation in vital rate estimates (Austin et al. 2009, Devink and Slattery 2013). The variation in presence, potential negative effects, varying level of blood parasite prevalence, and lack of knowledge of these relationships in relation to body mass, health, and breeding status in scaup deserve more attention.

The goal of this study was to provide baseline information on the effects of blood parasite prevalence in relation to body mass, breeding status, and health in lesser scaup (hereafter, scaup). I predicted that scaup infected with blood parasites would have reduced body mass than scaup and greater Heterophile:Lymphocyte ratio values than uninfected birds. I predicted that prevalence of blood parasites would differ between males and females due to females investing more in reproduction than males. Last, I predicted blood parasite presence would negatively affect breeding propensity (i.e., proportion of birds that attempt to nest) in female scaup.

Study Area

This study was conducted at Lower Red Rock Lake, a 2,332 ha palustrine montane wetland complex, consisting of a mixture of clear open water, submerged aquatic vegetation (SAV), interspersed islands of hardstem bulrush (*Schoenoplectus acutus*), and other emergent vegetation (Fig. 3.2). Lower Red Rock Lake was within Red Rock Lakes National Wildlife Refuge (hereafter, Refuge) located in the high-elevation Centennial Valley in southwest Montana (MT; 44° 37' N, 111° 50' W). The Refuge encompasses ~ 10,000 ha of natural and created montane wetlands, providing breeding habitat for a variety of waterbirds (Cutting et al. 2011).

The climate and high elevation (2,014 m above mean sea level) of Lower Red Rock Lake provides a narrow window of breeding opportunity for the local population of scaup. The Refuge experienced late thaws and early freezes, which resulted in a short growing

season, comparable to that of areas in the Western Boreal Forest, (e.g., Minto Flats State Game Refuge located in Alaska, latitude 65°; Gurney et al. 2011). However, the Refuge supports one of the highest density, stable breeding populations of scaup in North America >7.7 pairs/km^2 (Cutting 2010). The Refuge is near the southern portion of their breeding range, yet scaup experience some of the harshest conditions during the breeding season resulting in a unique area to investigate how different environmental conditions effect scaup demography and may help explain conflicting differences from other studies across the breeding range of scaup (Gurney et al. 2011).

Methods

Data Collection

Scaup were captured over 4-6 nights during prebreeding (30 May - 2 June in 2011) and breeding (27 June - 5 July in 2011 and 17-23 June in 2012) periods via spotlighting during the new moon phase each month. Scaup were also captured during molt (13-17 August and 4-8 September in 2012) via drive-trapping. Capture for this study occurred over 22 days in both 2011 and 2012 combined. We measured body mass (nearest 5 g) using a Pesola spring scale, flattened wing using a wing board (±1 mm), head length (±0.1 mm), and tarso-metatarsus (±0.1 mm) lengths using calipers. Birds were banded with a U.S. Geological Survey numbered aluminum leg band from the Bird Banding Lab. Additionally, each female was marked with a uniquely identifiable nasal marker (Lokemoen and Sharp 1985) to allow estimation of seasonal survival.

We determined breeding status by palpating the oviduct to determine if an egg was present. Females with an egg present represented known breeders, and females without an egg present represented unknown breeders. A blood sample (≤1.5 ml) was collected from each individual's brachial vein of the wing (Bennett 1970), stored in a heparin-treated Vacutainer tube and placed on ice to minimize the chance of clotting. Three blood smears were prepared shortly after collection (<10 hrs) for each specimen using the two-slide wedge technique (Campbell 1995). Smears were allowed to air-dry, then packaged and sent in for blood assays to be conducted by the Avian and Exotic Animal Clinical Pathology Laboratory, in Wilmington, Ohio, USA.

Slides were stained with a Romanowsky staining procedure (Campbell and Ellis 2013). Blood assays were read and reviewed by two separate observers to insure accuracy. Data collected from the slides included estimated white blood cell count (WBC), blood parasites per oil field and type if present, polychromasia (color changes in the red blood cells and sign of bone marrow stress), anisocytosis (size of the red blood cells, common in anemia), heavy metal changes, presence or absence of thrombus, and the blood differential, which measures the percentage of WBCs or leukocytes (heterophils, lymphocytes, basophils, eosinophils, monocytes). Each individual's health was estimated using the heterophile:lymphocyte ratio, which was derived by taking the ratio of percent heterophile by percent lymphocyte. This study was conducted under the Federal Bird Banding permit: 06266, and was approved through Northern Prairie Wildlife Research Center's Animal Care and Use Permit project number: 3210APN.

Data Analysis

Relationships among seasonal health of an individual, body mass at time of capture (throughout pre-, during, and post-breeding periods), breeding status (females only), and blood parasite prevalence were analyzed with linear (lm) regression models in R 2.15.2 (R Development Core Team 2012). Body mass was used as an index of relative body condition of individuals. Independent variables were male and female body mass, breeding status (presence/absence of an egg), and Julian date of capture. The dependent variable for all of the regression analyses was health (i.e., heterophile:lymphocyte ratio). I also tested for a difference between the health and breeding status, health and presences/absence of blood parasites using a Welch Two-Sample *t*-test and analysis of variance tests. Standard model validation graphs were used to generate a plot of residuals vs fitted values to check homogeneity, and histograms to verify normality of the residuals.

Results

Blood was drawn from 112 individual scaup (15 males and 97 females); only six (5%) had blood parasites (Table 3.1). Blood parasite prevalence differed by gender with 33.3% of males five of 15 positive for blood parasites compared to 1.0% of females one of 97 (t_{14} = -2.56, P = 0.02). Four males had *Leukocytozoon* infections, with the fifth male having both *Plasmodium* and *Haemoproteus* present. The single female was infected by a

Leukocytozoon in 2012.

Slight anisocytosis and polychromasia were noted among the erythrocytes. Four different leukocyte types were found during the blood assays: heterophils, lymphocytes, basophils, and eosinophils. Thrombosis or signs of clotting were evident in all of the samples. Red blood cells evaluated contained adequate mature hemoglobin content. There were no signs of metal toxicity or other toxins.

Relationships between scaup body mass and heterophile:lymphocyte ratio were consistent between genders. A negative relationship between heterophile:lymphocyte ratio and body mass for male scaup was found in 2011 (Table 3.2), indicating individuals with poor body mass were also in poor health (Fig. 3.3). When data were pooled across both years for females, it resulted in a negative relationship between female body mass and heterophile:lymphocyte ratio (Table 3.2), indicating a similar relationship to that of males (Fig. 3.3). A positive relationship was found between female scaup heterophile:lymphocyte ratio and date of capture ($\hat{\beta}$ = 0.008, 95% CI: 0.004 to 0.012). This relationship showed that health decreased (i.e., heterophile:lymphocyte ratio increased) from early spring through the breeding season to molt. Further investigation revealed a difference between heterophile:lymphocyte ratio in two of the three different capture periods when pooled across both years of the study. Scaup female heterophile:lymphocyte ratios during the pre-breeding season were 0.25 (± 0.51, 95% CI) less than females during the breeding season; however, the difference was not statistically significant (t_{94} = -0.95, P = 0.343). Scaup female heterophile:lymphocyte ratios during molt were 0.65 (± 0.30, 95% CI) greater than females during the breeding season (t_{94} = 4.30, P < 0.001). Average female heterophile:lymphocyte ratio did not differ (t_{48} = -1.48, P = 0.146) during the breeding seasons of 2011 $\bar{x}$ = 0.98 (± 0.51, 95% CI) and 2012 $\bar{x}$ = 1.19 (± 0.08, 95% CI).

Body mass varied among the three different capture periods when pooled across both years of the study. A quadratic relationship was found with body mass and capture date (Fig. 3.4), indicating that body mass increased from pre-breeding period to the breeding period and decreased significantly at the end of the summer during molt. Scaup female body mass during the pre-breeding season was on average 65 (± 47.87, 95% CI) grams less than females during the breeding season (t_{94} = -2.61, P = 0.010). Scaup female body mass during the molt season was 190 (± 27.79, 95% CI) grams less than females

during the breeding season (t_{94} = -13.32, P < 0.001). Average female body mass differed during the breeding seasons (t_{48} = -2.02, P = 0.049) of 2011 ($\bar{x}$ = 730 ± 61.00, 95% CI) and 2012 ($\bar{x}$ = 760 ± 0.10, 95% CI).

Female scaup with an egg were 45 grams heavier than individuals without eggs present in the oviduct across both years ($\bar{x}$ = 765 ± 14.56 95% CI, $\bar{x}$ = 720 ± 74.10 95% CI, respectively, t_{48} = -2.93, P = 0.005). I did not find a significant association between individuals with and without an egg present in the oviduct between years (t_{54} = 1.39, P = 0.171). Breeding status of females was not related to heterophile:lymphocyte ratio, with average heterophile:lymphocyte ratio of females with an egg ($\bar{x}$ = 1.09 ± 0.32, 95% CI) and without an egg ($\bar{x}$ = -1.07 ± 0.35, 95% CI) present in the oviduct (t_{35} = -0.10, P = 0.921).

The presence of a blood parasite was not related to heterophile:lymphocyte ratio in scaup captured during the time period this study was conducted (t_7 = -0.69, P = 0.513). I found no difference between the average heterophile:lymphocyte ratio of males with and without a blood parasite present (t_{12} = -0.12, P = 0.914). The average body mass of all scaup captured for this study did not differ between those that had a blood parasite and those that did not have a blood parasite (t_6 = -1.21, P = 0.274). I found no difference between male scaup average body mass with or without a blood parasite present (t_8 = 1.10, P = 0.306). Relationships between body mass, breeding status, and heterophile:lymphocyte ratio with and without a blood parasite present for females could not be tested because only one of 97 females captured was positive for a blood parasite.

Discussion

The Spring Condition Hypothesis states that female scaup reproductive success has declined due to females arriving on the breeding grounds in reduced body condition (Austin et al. 2000, Afton and Anderson 2001, Anteau and Afton 2004). Anteau and Afton (2004) showed that scaup females are not acquiring sufficient levels of nutrient reserves because of depleted food resources on wintering grounds and staging areas. After arriving on the breeding grounds, losses in body mass (e.g., fat stores) from migration need to replenished before breeding (Afton 1984, Martin 2007). Across many bird species, females are often faced with a trade-off of postponing timing of reproduction until a sufficient level of reserves are met to produce a larger clutch, or breeding earlier with lower energy stores and

potentially producing fewer but higher quality young (Drent and Daan 1980, Rohwer 1992). Presence of blood parasites has been linked to reductions in body condition, fitness, and parental investment in other avian species (Dawson and Bortolotti 2000, Merino et al. 2000, Tomas et al. 2006). Therefore, I measured the impact of blood parasites on health, body mass, and breeding status in scaup on the breeding grounds to determine if their presence was contributing to reductions in body mass and/or health in scaup.

My results did not find supporting evidence of blood parasites having a negative effect on body mass in scaup nesting at this Refuge. A possible explanation for this study finding just a few infected individuals (n = 6) could be the two-slide wedge technique that was used in this study. Although this method is common in mammalian medicine, it is not a widely accepted technique used for avian blood smears (Hume 1995). Overall, body mass was not related to presence of blood parasites in this study, which conflicts with studies that have found presence of blood parasites to reduce body condition in their avian hosts (Dawson and Bortolotti 2000, Merino et al. 2000, Schrader et al. 2003, Marzal et al. 2012). However, my study's findings are consistent with others that also found no negative effects of blood parasites on body condition in gadwalls and mallards (Shutler et al. 1999) and passeriforms (Bennett et al. 1988).

The observed rate of infection (5%) in this study was much lower than other studies. For example, 39% (n = 180) of scaup were infected with three types of blood parasites (*Leucocytozoon simondi*, *Haemoproteus nettionis*, and *Plasmodium circumflexum*) over a two-year study in a wintering population in Texas (Loven et al. 1980). In contrast, an investigation of blood parasite prevalence in Michigan waterfowl found similar rates of blood parasite prevalence (7%) during summer and fall trapping combined (n = 345), with no differences among age, species, or sex detected. These findings as well as many others, demonstrate considerable spatial and temporal variation in prevalence of blood parasite patterns, which could be due to differences in favorable conditions of certain vectors in different areas. One of the primary vectors of *Leucocytozoon* spp., the black fly (*Simulium rugglesi*), has commonly been found feeding on waterfowl within 15 m of shoreline (Bennett 1960), which lead to my hypothesis that blood parasite prevalence would be greater in females due to spending more time in or near vegetation for the purpose of nesting. Contrary to this prediction, my data showed that blood parasites were more

prevalent in males. This result supported findings from another study that found prevalence was greater in male than in female waterfowl (Dey 2008).

The dominant species of infection found in this study was classified to the genus level as *Leukocytozoon* spp., which was consistent with the dominant species found in similar studies in waterfowl (Loven et al. 1980, Bennett et al. 1982). Dey et al. (2008) found that *Leucocytozoon simondi* was only in 5.3% of ducks, whereas *Leucocytozoon caulleryi* was found in 54.7% of ducks. Previous research on this Refuge found that the majority of male scaup spend a protracted amount of time at the Refuge than that of females, and migrate farther north to molt (Warren et al. 2014). I found low prevalence of female infection in both years throughout three different capture periods. It is possible that males may be arriving on the breeding grounds already infected. It is evident that vector-borne infectious disease is not an issue at this Refuge. I conclude that other factors that occur prior to arrival to the Refuge, or factors not investigated during this study account for differences in parasite prevalence between genders.

Investigation of the interactions between blood parasites and possible detrimental effects to bird health determined that heterophile:lymphocyte ratio of scaup infected by blood parasites did not differ from that of uninfected birds. This finding was inconsistent with a study that found the presence of blood parasites were related to elevated levels of heterophile:lymphocyte ratios (Ots and Hõrak 1998). The lack of a difference in heterophile:lymphocyte ratio and body mass of infected birds in this study could be attributed to the small number of birds actually infected by blood parasites, or sick birds were not encountered. Studies suggest that farther migration distances could weaken a birds' immune system by exposing them to a greater number and diversity of parasites (Figuerola and Green 2000, Smith et al. 2004). Due to the location of my study site, which in the southwestern extent of the breeding range, scaup experience a much shorter migration distance compared to conspecifics that migrate father north. For example, band recoveries from the Refuge have shown that scaup winter in San Francisco Bay and Salton Sea, California (USFWS unpublished), which may partially help explain the lack of prevalence found and why scaup females were not experiencing any trade-offs between parasite defense with body mass, health, or breeding status.

Body condition and health are important factors that influence reproductive success (Blums et al. 2002, Devries et al. 2008). A study on tufted ducks (*Aythya fuligula*), a close relative to scaup, found strong support for higher survival in earlier hatched young by females that had greater size-adjusted body conditions (Blums et al. 2002). My study found a weak positive relationship between the health of female scaup and date of capture with the heterophile:lymphocyte of scaup females being lowest during the pre-breeding period after which it consistently increased until the molting period (Fig. 3.4). These data also demonstrated a strong negative relationship between heterophile:lymphocyte ratio and body mass in both genders, which indicated that scaup in poor body mass were also in poor health at the end of the breeding season. I found no difference in heterophile:lymphocyte between the breeding and non-breeding season for female scaup at the Refuge during this study, which is inconsistent with the hypothesis that better conditioned and healthier females will be more likely to invest in reproduction than females that need to increase somatic lipid reserves to a desired threshold before initiating breeding. Body mass is crucial to the reproductive success of birds during the breeding season, and in a late-nesting species (e.g., lesser scaup) much of these somatic reserves may be acquired on the breeding grounds (Afton 1984, Esler et al. 2001). Previous research on this Refuge found that locally acquired resources during pre-breeding, comprised a large portion of lipid reserves used by females during breeding season for clutch formation (Warren and Cutting 2011, Cutting et al. 2013). My data supports these studies in that scaup female body mass increased from pre-breeding to breeding period and then decreased dramatically during molt. The initial increase demonstrates that females are relying on locally acquired resources to replenish body mass reserves prior to breeding, which is consistent with most capital breeders (Alisauskas and Ankney 1992).

Overall, the first blood parasite study conducted on scaup in Montana to my knowledge, revealed scaup were not experiencing any trade-offs between immune response to blood parasites and reproduction. No direct connections were identified linking their presence to diminishing effects on body mass, breeding status, or health of scaup using this Refuge. The lack of any relationships found in this study could be due to a small sample size of birds infected with blood parasites, or suggest that there are more complex processes

than presence of blood parasites that underlay any trade-offs between reductions in immune function, body mass, and reproductive effort that may be experienced by scaup.

Literature Cited

Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. Auk 101:255-265.

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management: 65:781-796.

Afton, A. D., R. H. Hier, and S. L. Paulus. 1991. Lesser scaup diets during migration and winter in the Mississippi flyway. Canadian Journal of Zoology 69:328-333.

Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 109-127 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney,D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Anteau, M. J., and A. D. Afton. 2004. Nutrient reserves of lesser scaup (*Aythya affinis*) during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. Auk 121:917-929.

Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and J. K. Ringelman. 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin 28:254-263.

Austin, J. E., M. J. Anteau, J. S. Barclay, G. S. Boomer, F. C. Rohwer, and S. M. Slattery. 2006. Declining scaup populations: reassessment of the issues, hypotheses, and research directions. Consensus report from the second scaup workshop, 17-19 January 2006, Bismarck, ND, USA.

Austin, J.E., G. S. Boomer, M. Koneff, and J. Lyons. 2009. Applying the concepts of structured decision-making to the development of a comprehensive scaup conservation model. Extended abstract, Plenary Session Linking Habitat, Harvest and Human Dimensions, North American Duck Symposium, 20 August 2009, Toronto, Ontario, Canada.

Bennett, G. F. 1960. On some ornithophilic blood-sucking diptera in Algonquin Park, Ontario, Canada. Canadian Journal of Zoology 38:377-389.

Bennett, G. F. 1970. Simple techniques for making avian blood smears. Canadian Journal of Zoology 48:585.

Bennett, G., A. Smith, W. Whitman, and M. Cameron. 1975. Hematozoa of the Anatidae of the Atlantic Flyway. II. The Maritime Provinces of Canada. Journal of Wildlife Diseases 11:280-289.

Bennett, G., D. Nieman, B. Turner, E. Kuyt, M. Whiteway, and E. Greiner. 1982. Blood parasites of prairie anatids and their implication in waterfowl management in Alberta and Saskatchewan. Journal of Wildlife Diseases 18:287-296.

Blums, P., R. G. Clark, and A. Mednis. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. Journal of Animal Ecology 71:280-295.

Campbell, T. W. 1995. Avian hematology and cytology. 2nd Edition. Iowa State University Press, Ames, USA.

Campbell, T. W., and C. K. Ellis. 2013. Avian and exotic animal hematology and cytology. John Wiley & Sons, New York, New York, USA.

Cutting, K. A. 2010. Nutrient allocation to egg formation of lesser scaup. Dissertation. Montana State University. Bozeman, USA.

Cutting, K. A., K. A. Hobson, J. J. Rotella, J. M. Warren, S. E. Wainwright-de la Cruz, and J. Y. Takekawa. 2011. Endogenous contributions to egg protein formation in lesser scaup (*Aythya affinis)*. Journal of Avian Biology 45:505-513.

Cutting, K. A., K. A. Hobson, J. J. Rotella, J. M. Warren, J. Y. Takekawa, S. E. De La Cruz, and M. Parker. 2014. Relative contribution of lipid sources to eggs of lesser scaup. Journal of Avian Biology 45:197-201.

Dawson, R. D., and G. R. Bortolotti. 2000. Effects of hematozoan parasites on condition and return rates of American kestrels. Auk 117:373-380.

Devink, J. M., and S. S. Slattery. 2013. The Great Scaup Mystery. Retrieved 02-December-13 http://www.ducks.org/conservation/waterfowl-biology/the-great-scaup-mystery

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618-628.

Dey, A. R., N. Begum, A. Anisuzzaman, M. A. H. N. A. Khan, and M. M. H. Mondal. 2008. Haemoprotozoan infection in ducks: prevalence and pathology. Bangladesh Journal of Veterinary Medicine 6:53-58.

Dirschl, H. J. 1969. Foods of lesser scaup and blue-winged teal in the Saskatchewan River delta. Journal of Wildlife Management 33:77-87.

Drent, R. H., and S.Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-52.

Esler, D., J.B. Grand, and A.D Afton. 2001. Intraspecific variation in nutrient reserve use during clutch formation by lesser scaup. Condor 103:810-820.

Fedynich, A. M., and D. B. Pence. 1994. Hemosporid parasitism of mallards at the southern periphery of their breeding range. Avian Diseases 38:885-886.

Figuerola, J., and A. J. Green. 2000. Haematozoan parasites and migratory behaviour in waterfowl. Evolutionary Ecology 14:143-153.

Forrester, D. J., G. W. Foster, and J. E. Thul. 2001. Blood parasites of the ring-necked duck (*Aythya collaris*) on its wintering range in Florida, USA. Comparative Parasitology 68: 173-176.

Greiner, E. C., G. F. Bennett, E. M. White, and R. F. Coombs. 1975. Distribution of the avian hematozoa of North America. Canadian Journal of Zoology 53:1762-1787.

Gurney, K., R. Clark, S. Slattery, N. Smith-Downey, J. Walker, L. Armstrong, S. Stephens, M. Petrula, R. Corcoran, and K. Martin. 2011. Time constraints in temperate-breeding species: influence of growing season length on reproductive strategies. Ecography 34:628-636.

Gustafsson, L., D. Nordling, M. Andersson, B. Sheldon, and A. Qvarnström. 1996. Infectious diseases, reproductive effort and the cost of reproduction in birds. In Infection, Polymorphism and Evolution. Proceedings of the Royal Society of London B 346: 53-61.

Hume, A. 1995: Practical avian haematology. Proceedings of the Australian Committee of the Association of Avian Veterinarians, Annual Conference Proceedings. Dubbo, Australia: 163-181.

Lokemoen, J. T., and D. E. Sharp. 1985. Assessment of nasal marker materials and designs used on dabbling ducks. Wildlife Society Bulletin 13:53-56.

Figuerola, J., and A. J. Green. 2000. Haematozoan parasites and migratory behaviour in waterfowl. Evolutionary Ecology 14:143-153.

Greiner, E. C., G. F. Bennett, E. M. White, and R. F. Coombs. 1975. Distribution of the avian hematozoa of North America. Canadian Journal of Zoology 53:1762-1787.

Loiseau, C., R. J. Harrigan, A. J. Cornel, S. L. Guers, M. Dodge, T. Marzec, J. S. Carlson, B. Seppi, and R. N. M. Sehgal. 2012. First evidence and predictions of plasmodium transmission in Alaskan bird populations. PLoS One 7: e44729.

Loven, J., E. Bolen, and B. Cain. 1980. Blood parasitemia in a south Texas wintering waterfowl population. Journal of Wildlife Diseases 16:25-28.

Martin, K.H. 2007. Breeding ecology and fasting tolerance of scaup and other ducks in the boreal forest of Alaska. Masters, University of Alaska Fairbanks, Fairbanks, USA.

Marzal, A., F. d. Lope, C. Navarro, and A. P. Møller. 2005. Malarial parasites decrease reproductive success: an experimental study in a passerine bird. Oecologia 142:541-545.

Marzal, A., S. Bensch, M. Reviriego, J. Balbontin, and F. De Lope. 2008. Effects of malaria double infection in birds: one plus one is not two. Journal of Evolutionary Biology 21:979-987.

Marzal, A., M. Reviriego, I. G. Hermosell, J. Balbontín, S. Bensch, C. Relinque, L. Rodríguez, L. Garcia-Longoria, and F. de Lope. 2012. Malaria infection and feather growth rate predict reproductive success in house martins. Oecologia 171:853-861.

Merino, S., J. Moreno, J. José Sanz, and E. Arriero. 2000. Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). Proceedings of the Royal Society of London, B: 267:2507-2510.

Nordling, D., M. Andersson, S. Zohari, and G. Lars. 1998. Reproductive effort reduces specific immune response and parasite resistance. Proceedings of the Royal Society of London B: 265:1291-1298.

Ots, I., and P. Hõrak. 1996. Great tits (*Parus major*) trade health for reproduction. Proceedings of the Royal Society of London, B: 263:1443-1447.

Ots, I., and P. Hõrak. 1998. Health impact of blood parasites in breeding great tits. Oecologia 116:441-448.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/.

Richner, H., P. Christe, and A. Oppliger. 1995. Paternal investment affects prevalence of malaria. Proceedings of the National Academy of Sciences 92:1192-1194.

Rigby, E. A., and D. A. Haukos. 2012. Breeding season survival and breeding incidence of female mottled ducks on the upper Texas Gulf Coast. Waterbirds 35:260-269.

Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 485-539 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney,D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Sargeant, A. B., and D. G. Raveling. 1992. Mortality during the breeding season. Pages 396-422 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney,D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474-480.

Schrader, M. S., E. L. Walters, F. C. James, E. C. Greiner, and T. Grubb. 2003. Seasonal prevalence of a haematozoan parasite of red-bellied woodpeckers (*Melanerpes carolinus*) and its association with host condition and overwinter survival. Auk 120:130-137.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155-163.

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecology and Evolution 11:317-321.

Shutler, D., R. Clark, S. T. Rutherford, and A. Mullie. 1999. Blood parasites, clutch volume, and condition of gadwalls and mallards. Journal of Avian Biology 30:295-301.

Smith, R. B., E. C. Greiner, B. O. Wolf, and K. Steenhof. 2004. Migratory movements of sharp-shinned hawks (*Accipiter striatus*) captured in New Mexico in relation to prevalence, intensity, and biogeography of avian hematozoa. Auk 121:837-846.

Sorci, G., and A. Møller. 1997. Comparative evidence for a positive correlation between haematozoan prevalence and mortality in waterfowl. Journal of Evolutionary Biology 10:731-741.

Tomas, G., S. Merino, J. Moreno, J. Morales, and J. Martinez-De La Puente. 2006. Impact of blood parasites on immunoglobulin level and parental effort: a medication field experiment on a wild passerine. Functional Ecology 21:125-133.

U.S. Fish and Wildlife Service. 2014. Waterfowl population status, 2014. U.S. Department of the Interior, Washington, D.C., USA.

Valkiunas, G. 2004. Avian malaria parasites and other haemosporidia. RC Press, Boca Raton, FL, USA.

Walker, J., and M. S. Lindberg. 2005. Survival of scaup ducklings in the boreal forest of Alaska. Journal of Wildlife Management 69:592-600.

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

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

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

Wobeser, G. A. 1997. Diseases of wild waterfowl. Plenum Press, New York, USA.

Tables

Table 3.1. Lesser scaup capture results during summer of 2011 and 2012, Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA. Blood samples (≤1.5 ml) were taken from each individual for blood assays to determine general health and test for blood parasite prevalence. Males were only captured in 2011.

	Capture Session							
	2011				2012			
	Pre-breeding[a]		Breeding[b]		Breeding[b]		Molt[c]	
	Total	BPP[d]	Total	BPP[d]	Total	BPP[d]	Total	BPP[d]
F[e]	8	0	27	0	29	1	34	0
M[f]	11	3	4	2	N/A	N/A	N/A	N/A

[a] Spotlighting capture dates during pre-breeding season May - 2 June 2011.
[b] Spotlighting capture dates during breeding season 27 June - 5 July 2011.
[c] Drive-trapping capture dates during molting season 13-17 August & 4-8 September 2012.
[d] Blood parasites present
[e] Female lesser scaup
[f] Male lesser scaup

Table 3.2. Results from regression models for male and female lesser scaup health index (heterophile:lymphocyte ratio) as a function of body mass in 2011 and 2012 at Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA. Males were only captured in 2011.

Gender	Parameter	$\hat{\beta}$	SE	P ≤
Male	Intercept	8.407	2.093	0.001
	Body Mass	-0.009	0.003	0.005
Female	Intercept	2.312	0.482	0.001
	Body Mass	-0.002	0.001	0.034

Figures

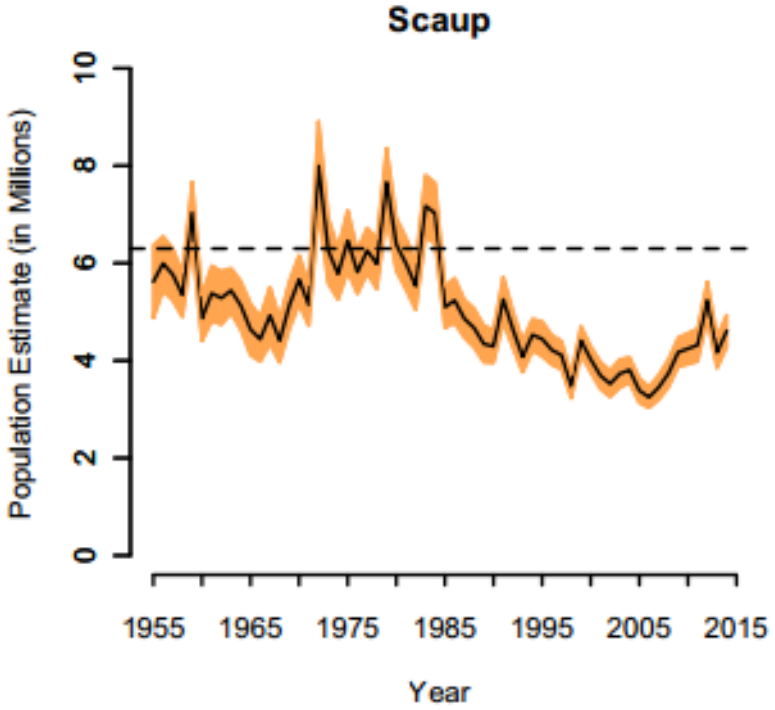

Figure 3.1. Breeding population estimates, 95% confidence intervals, and North American Waterfowl Management Plan population goal (dashed line) for selected species in the traditional survey area (strata 1-18, 20-50, 75-77) for scaup (U.S. Fish and Wildlife Service 2014).

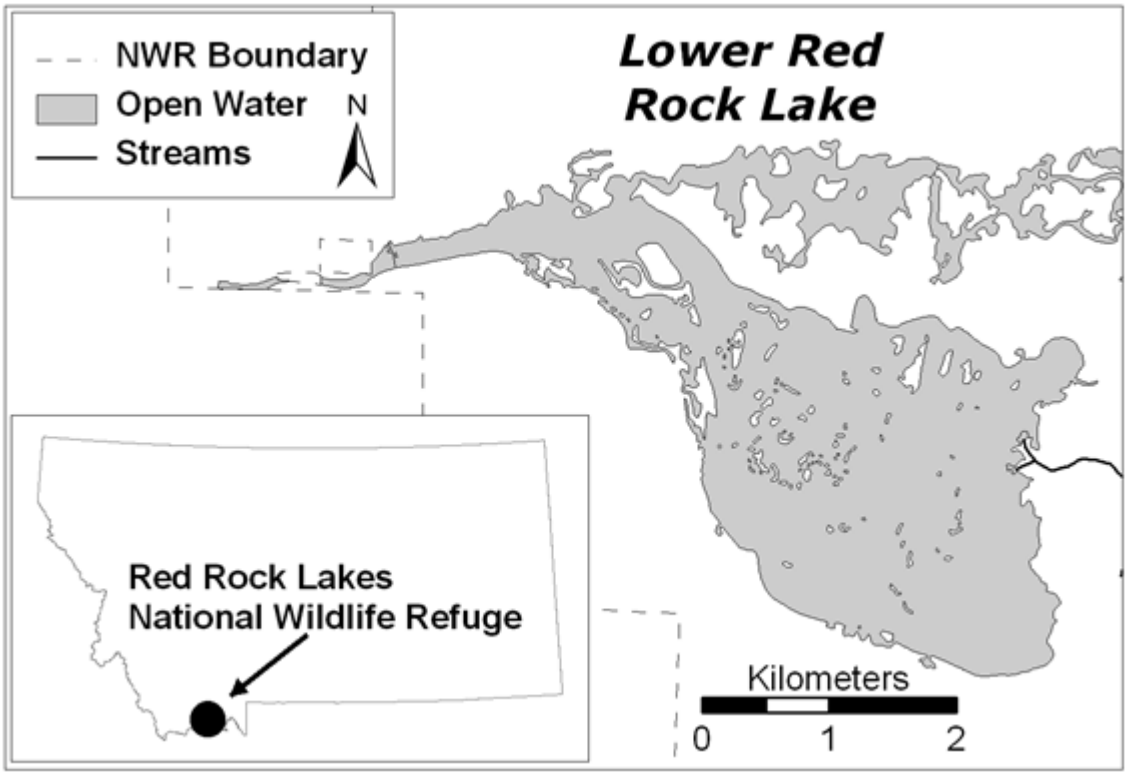

Figure 3.2. Lower Red Rock Lake and River Marsh study site on Red Rock Lakes National Wildlife Refuge, Montana USA. Inset shows location of Red Rock Lakes NWR within Montana.

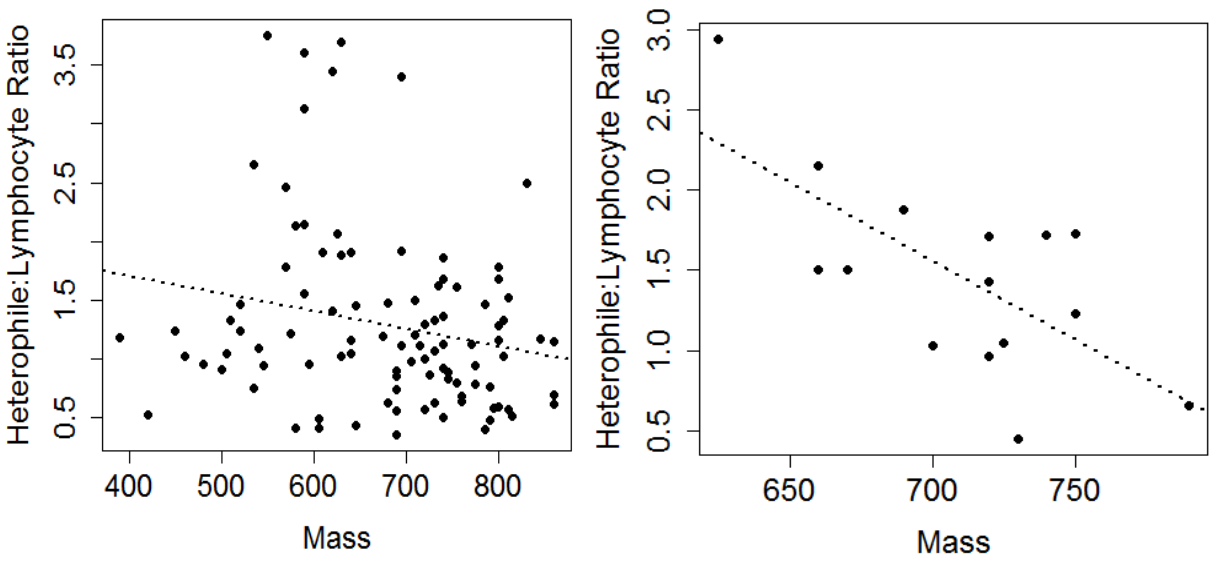

Figure 3.3. Relationship between female (left) and male (right) lesser scaup heterophile:lymphocyte ratio, a proxy for an individual's health, and mass on Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA, between 30 May and 5 July 2011. Dashed line represents the slope of the relationships for female (Adjusted $R^2 = 0.03$, $F_{1,95} = 4.62$, $P = 0.034$) and male (Adjusted $R^2 = 0.42$, $F_{1,13} = 11.05$, $P < 0.005$).

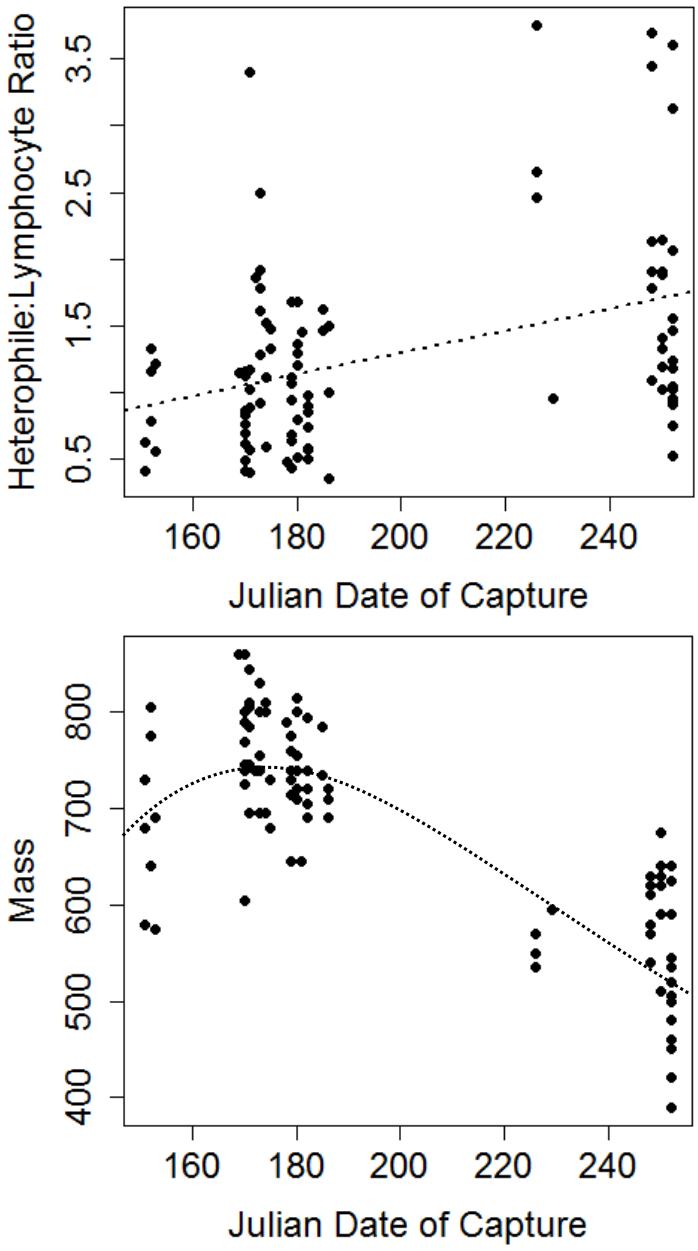

Figure 3.4. Relationship between female lesser scaup heterophile:lymphocyte ratio (left), a proxy for an individual's health, and mass (right) with Julian date of capture on Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, USA, 2011-2012. Dashed line represents the slope of the relationship for heterophile:lymphocyte ratio (Adjusted R^2 = 0.17, $F_{1,94}$ = 11.08, P = 0.001) and mass (Adjusted R^2 = 0.67, $F_{1,94}$ = 195, P < 0.001).