

NESTING ECOLOGY OF RED-HEADED WOODPECKERS (*MELANERPES
ERYTHROCEPHALUS*) IN CENTRAL MINNESOTA

A THESIS
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

BRITTNEY YOHANNES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

ADVISER: DR. TODD W. ARNOLD

DEC 2017

© Brittney Yohannes 2017

Acknowledgements

I am grateful to my adviser, Dr. Todd Arnold, for his guidance on this project and insight on how to get the most out of graduate school. I also acknowledge my other committee members, Dr. Robert Blair and Dr. Francesca Cuthbert, for their thoughtful input and advice on this study, and for being excellent educators.

Above all I recognize my supportive husband, Abdiwak Yohannes, for all his encouragement and enthusiasm about this project. He was always first to celebrate even my smallest successes, and he helped reinvigorate my commitment to research through my challenges. I also appreciate my family, Scott Larson, Tami Larson, and Cameron Larson, for their support over the years as I developed my passion for avian conservation.

This project would not have been possible without Chet Meyers, James Howitz, Siah St. Clair, and Red-headed Woodpecker Recovery; their assistance and enthusiasm for this study made me feel as if I had my own personal cheerleaders. Additionally, I extend a special thank you to Mary Spivey and Cedar Creek Ecosystem Science Reserve for their resources and permission to access the study site. I am also grateful to David Luneau for provision of camera equipment, as well as assistance troubleshooting it when help was needed. Finally, I recognize and thank my two field assistants, Laura Jaskiewicz and Brittany Turner, who helped with data collection and provided keen birding eyes. They were also the reason I look back so fondly on our two summers of data collection.

Funding for my research was provided by the University of Minnesota's Department of Fisheries, Wildlife and Conservation Biology, the Wally Dayton Wildlife Fund, the Minneapolis Audubon Society, Red-headed Woodpecker Recovery, and Patagonia clothing company.

Dedication

This thesis is dedicated to my grandparents, Lee and Joann Titus, and William and Shirley Larson, for inspiring my love of nature, and my obsession with birds.

Abstract

The nesting ecology of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) has not been well studied anywhere in the species' range, and the few studies that have addressed nest success have not monitored nests through the entirety of the nesting cycle. The objectives of my study include estimating nest success, documenting the extent and timing of brood reduction, and detailing developmental milestones of Red-headed Woodpeckers in central Minnesota. Using a cavity camera, I monitored 61 nests throughout the nesting cycle in 2014 and 2015 and estimated nest success (from initiation to fledging) was 78.0% with logistic exposure modeling. Daily nest survival rate was higher for nests initiated earlier in the season and for nests in cavities in dead branches, as supported by lowest Akaike information criterion (AIC) scores among candidate models. Of nests found during the egg laying stage, 100% experienced some amount of brood reduction. On average, nest contents were reduced by 48.1% between egg laying and fledging with reduction occurring at all points in the nesting cycle. I documented the ages at which nestlings reach developmental milestones, which had previously been lacking from the literature, and included images of nestlings at various ages in Appendix 1 so that future investigators can determine approximate nestling ages based on visual inspections.

Adult Red-headed Woodpeckers on the study site were color banded, and using Program MARK, I analyzed mark-resighting data using a Cormack-Jolly-Seber (CJS) model to estimate annual apparent survival and detection probability. In the most parsimonious model, apparent survival varied by year and detection probability differed by sex. Annual apparent survival ranged from 0.38-0.70 among years, and averaged lower than other apparent survival studies. Estimated detection rates were high, and averaged 0.72 for females and 1.00 for males. A small sample size of banded pairs was used to analyze mate-fidelity across breeding seasons and I found a positive association between individuals pairing with new mates and failed nesting during the previous breeding season (Fisher exact test: $p = 0.095$). Although Red-headed Woodpecker populations have declined for decades, my study is one of the few to measure both fecundity and survival.

Table of Contents

Acknowledgements	i
Dedication	ii
Abstract	iii
Table of Contents	iv
List of Tables	v
List of Figures	vi
Preface	1
Chapter 1: ESTIMATING RED-HEADED WOODPECKER NEST SUCCESS, BROOD REDUCTION, AND DEVELOPMENTAL MILESTONES USING A CAVITY CAMERA	2
Methods.....	6
Results.....	9
Discussion	12
Chapter 2: APPARENT SURVIVAL AND MATE FIDELITY IN A RED-HEADED WOODPECKER POPULATION	20
Methods.....	22
Results.....	24
Discussion	25
Literature Cited	31
Appendix 1: Clutch Development Photos	37

List of Tables

Table 1.1	Summary of Red-headed Woodpecker nest success rates reported in the literature.	15
Table 1.2	Step-wise multivariate analysis of logistic exposure modeling of daily survival rate of Red-headed Woodpeckers nesting at Cedar Creek Ecosystem Science Reserve, East Bethel, MN in 2014 and 2015. Parameters included year, nest initiation date, tree height, height of nest cavity entrance from the ground, diameter at breast height of nest tree, presence of other holes of similar size to the entrance hole on nest tree, status of tree (dead or alive), status of branch (dead or alive), age of nest, and presence of eggs or nestlings in nest.	16
Table 2.1	Summary of body measurements of adult Red-headed Woodpeckers at time of banding.	28
Table 2.2	Candidate model results from Program MARK used to estimate apparent survival during the breeding seasons from 2012 to 2015 for banded adult Red-headed Woodpeckers at Cedar Creek Ecosystem Science Reserve, Minnesota, USA.	29
Table 2.3	Mate fidelity of adult Red-headed Woodpeckers with known mates and known nest fates from previous year. There is a positive association between individuals pairing with new mates and failed nesting during the previous breeding season (Fisher exact test: $p = 0.095$).	30

List of Figures

Fig. 1.1	Map of study area. Map depicts the south east corner of Cedar Creek Ecosystem Science Reserve, East Bethel, MN.	17
Fig. 1.2	Error! Reference source not found.	18
Fig. 1.3	Cumulative nest survival as a function of branch status (dead and alive) of Red-headed Woodpeckers nesting at Cedar Creek Ecosystem Science Reserve, East Bethel, MN in 2014 and 2015. Error bars show 85% CI. The parameter estimate in the final model is -0.98 (SE = 0.61, p = 0.11).	19
Fig. A.1	Prior to egg laying woodchips are visible on the bottom of the cavity.	37
Fig. A.2	Two eggs in the nest.	38
Fig. A.3	Three eggs in the nest.	38
Fig. A.4	Six eggs in the nest.	39
Fig. A.5	Adult Red-headed Woodpecker investigating the camera.	39
Fig. A.6	Six eggs in the nest.	40
Fig. A.7	15 days after the first egg was laid the eggs begin to hatch. Photo shows two newly hatched chicks, four unhatched eggs, and eggshell remnants. Nestlings are altricial.	41
Fig. A.8	Five days after hatching, three nestlings are visible with at least one unhatched egg still in the nest.	42
Fig. A.9	Nine days after hatching, brood reduction has decreased the original six eggs to just two nestlings. Nestlings begin to show pin feathers. Eyes are beginning to open as slits. Begging calls are easily heard from a few meters distant from base of nest tree.	44
Fig. A.10	12 days after hatching, pin feathers continue to grow. Eyes are open.	44
Fig. A.11	14 days after hatching, feather color is apparent. Nestlings begin to change behavior from begging to hunkering when the camera enters the nest.	45
Fig. A.12	16 days after hatching, eyes are wide open.	46
Fig. A.13	19 days after hatching, feather tracts have disappeared. Nestlings are seen climbing on each other and on the sides of the cavity.	47

Fig. A.14	21 days after hatching, gape flanges are disappearing.	48
Fig. A.15	23 days after hatching, nestlings are crowded in the nest cavity.	48
Fig. A.16	26 days after hatching, nestlings easily climb up toward the cavity entrance.	49
Fig. A.17	28 days after hatching, 43 days after nest initiation, nestlings are ready to fledge. 28 days after hatching, 43 days after nest initiation, nestlings are ready to fledge.	49

Preface

Volunteers from Minneapolis Audubon's Red-headed Woodpecker Recovery team began locating Red-headed Woodpecker nests at Cedar Creek Ecosystem Science Reserve (hereafter Cedar Creek) in central Minnesota in 2008, initiated banding adult birds in 2011, and began monitoring nest success in 2012. Arianna Waldstein, a graduate student at the University of Minnesota, used cavity cameras to monitor Red-headed Woodpecker nests (Waldstein 2012a). She also studied territory and nest site selection within the Cedar Creek population in 2010-2011 (Waldstein 2012b). I built on that work by utilizing a similar nest camera protocol to monitor Red-headed Woodpecker nests at Cedar Creek in 2014 and 2015. The broad goal of my thesis is to contribute to the sparse literature regarding the nesting ecology of Red-headed Woodpeckers. Ultimately this work may inform future conservation strategies for this declining species.

In Chapter 1, formatted for the *Journal of Field Ornithology*, I evaluated nest success and investigated the extent brood reduction is reducing fledgling production at Cedar Creek. Only a handful of studies have estimated nest success of Red-headed Woodpeckers, and none have thoroughly examined how partial clutch and brood reduction affects the number of fledglings produced. The nest camera allowed me to count eggs and nestlings beginning at the egg laying stage, ultimately providing data to quantify the differences between initial clutch sizes and the actual number of young that fledged from each nest. To assist in future nesting studies, information is also included about the ages at which nestlings reach developmental milestones, and images of nestlings at various ages are included in Appendix 1.

In Chapter 2, formatted for *The Condor*, I used banding and resighting data from Cedar Creek to estimate site fidelity and apparent survival. Limited previous research has explored survival in this species, despite the fact that declining population levels could likely benefit from this information. Mate fidelity was also studied using banding data to record another undocumented aspect of this species' breeding ecology.

Chapter 1: ESTIMATING RED-HEADED WOODPECKER NEST SUCCESS, BROOD REDUCTION, AND DEVELOPMENTAL MILESTONES USING A CAVITY CAMERA

The need for a broader understanding of factors affecting Red-headed Woodpecker (*Melanerpes erythrocephalus*, hereafter RHWO) breeding productivity continues to grow as their population declines. The Breeding Bird Survey reports a 2.5% annual decrease in RHWO populations survey-wide since 1966 (Sauer et al. 2014) and the International Union for Conservation of Nature (IUCN) lists them as a near-threatened species (BirdLife International 2017). Although habitat loss is thought to be a major cause of this decline (Pulich 1988; Ehrlich et al. 1992; Melcher 1998), nest success varies greatly in different regions and low reproductive success may be the limiting factor to overall population growth (Berl et al. 2014). In particular, populations at the periphery of the range may be more likely to be sinks (Frei et al. 2015a). The first objective of my study was to provide nest success estimates for one of the largest breeding populations in Minnesota, near the northern limit of its range. Logistic exposure was used to estimate nest success, and step-wise multivariate analysis using backward elimination was employed to evaluate which explanatory variables contributed most to nest success.

The second objective of my study was to document the extent of clutch and brood reduction within nests (hereafter “brood reduction”). Brood reduction had not been thoroughly documented in RHWO populations prior to my study. Brood reduction was measured using the maximum and minimum clutch or brood size of each nest, and then calculating the percentage of eggs and/or nestlings the nest lost during the nesting period. The Birds of North America account for RHWO (Frei et al. 2015b) states that there is “surprisingly little information” about RHWO growth and development, so my final objective was to provide detailed information regarding this aspect of their natural history. An appendix of photographs of nestling development has been included so that future investigators can more readily determine ages of nestlings (Appendix 1). Analysis of nesting ecology, including success and phenology, is important to broaden

understanding of this species and identify strategies to bolster conservation efforts.

Breeding habitat— RHWO breed in a variety of semi-open habitats with dead trees present, including oak savanna and open woodlots (Grundel and Pavlovic 2007; King et al. 2007; Frei et al. 2015a) and even golf courses (Rodewald et al. 2005). These areas are hypothesized to be attractive because they allow woodpeckers space for flycatching (Conner 1976) and for a variety of other foraging methods (Vierling et al. 2009). However, Adkins Giese and Cuthbert (2003) found that RHWO will nest in closed canopy forest and that the nest tree itself is more significant for determining nest site selection than the surrounding habitat. The presence of dead trees and dead limbs within the nest territory or as a feature of the nest tree has been well documented (Rodewald et al. 2005; Waldstein 2012b; Frei et al. 2013; Hudson and Bollinger 2013; Kilgo and Vukovich 2014). A threshold of decadent trees needed for an area to be suitable breeding habitat may also exist (King et al. 2007). However, dead trees are not always required and RHWO have also been documented nesting in utility poles (Jackson 1976; Ingold 1991; Atterberry-Jones and Peer 2010). Pre-existing cavities are also a preferred feature for RHWO because they are weak excavators (Ingold 1994b; Gentry and Vierling 2008). For example, RHWO have been documented usurping nest cavities of Mountain Bluebirds (*Sialia currucoides*), Hairy Woodpeckers (*Leuconotopicus villosus*), Northern Flickers (*Colaptes auratus*; Kronland 2007), Downy Woodpeckers (*Picoides pubescens*; Schwab 1959), Red-bellied Woodpeckers (*Melanerpes carolinus*; Ingold 1989), and Red-cockaded Woodpeckers (*Leuconotopicus borealis*; LaBranche and Walters 1994), and pairs that usurp nest cavities initiate nesting earlier in the season (Kronland 2007). Although habitat loss has been suggested as a major contributor to their population decline, RHWO can thrive in oak savanna habitat restored by prescribed burns (Brawn 2006), in areas with increased snag densities created through tree girdling (Kilgo and Vukovich 2014), and in forested areas opened by disturbance (Graber and Graber 1979).

Nest success— Rates of nest success in RHWO vary greatly, ranging from 32-68%

among studies using exposure-based methods (Mayfield 1961, 1975; Shaffer 2004) (Table 1.1). Some studies have found that RHWOs have greater nest success in taller (Frei et al. 2013; Hudson and Bollinger 2013) and larger diameter trees (Frei et al. 2013). In a site with low nest success (32%), greater nest concealment and greater vegetative structure immediately around the nest tree were positively correlated to nest success (Berl et al. 2014). Other studies have indicated that RHWOs may be vulnerable to ecological traps. For example, Frei et al. (2013) found that RHWOs nested more abundantly in open areas where flycatching is easier, but birds in these areas had lower nest success than those nesting in closed canopy areas. Hudson and Bollinger (2013) documented another ecological trap, finding that RHWOs prefer nesting in shorter trees, but nesting in shorter trees was correlated with decreased nest success.

Brood reduction— Brood reduction occurs when part of the clutch or brood is lost prior to fledging. As opposed to predation, nest tree collapse, or other factors that typically lead to destruction of the entire nest contents, brood reduction affects only a portion of the clutch or brood. Koenig's (1986) meta-analysis evaluating 133 bird species found that on average 10% of eggs surviving to the end of incubation never hatch. Other sources of partial clutch loss can include partial predation events, where a predator removes only part of the clutch (Ackerman et al. 2003). Losses may continue to occur after hatch, especially through direct or indirect sibling competition. Morandini and Ferrer (2015) reviewed literature on sibling competition and its relationship to brood reduction. In their review, hypotheses attempting to explain brood reduction caused by sibling competition ranged across a variety of reproductive strategies including: overproduction of offspring to hedge bets or select the fittest offspring; parental favoritism affecting competition among siblings; sibling aggression based on food availability, food size, and food quality; extra eggs as insurance to offset potential hatching failure; tradeoffs between producing few, quality offspring versus many, lower-quality offspring; hormonal differences; brood size effect on sibling competition; hatching asynchrony; and the influence of ectoparasites on food distribution. These

hypotheses are not mutually exclusive, thus, several may act in concert to produce observed patterns of brood reduction.

Brood reduction is more prevalent in natural cavity nests than in open nests or in artificial nest boxes. Nilsson's (1986) meta-analysis, which included six cavity nesting species and ten open nesting species, found an average of 24% loss from clutch size to brood size in natural cavity nests compared to 13% loss in open nests. Nilsson suspected that ectoparasites may find refuge in cavities, contributing to increased occurrences of partial brood loss. LaBranche and Walters (1994) reported that brood reduction occurred in 27% of Red-cockaded Woodpecker nests after incubation began. There was no correlation between mean clutch size and the number of nestlings, nor fledglings, suggesting some limiting factor to the number of offspring that could be raised to fledging age. Three days after the clutches began hatching, 5-7% of eggs were unhatched, and 1.1% of eggs were runts. Most of the remaining brood reduction occurred within six days of hatching (LaBranche and Walters 1994).

RHWO clutches average 4.82 eggs (SD = 0.80, n = 71, Koenig 1986) with 4-7 eggs being most common (Frei et al. 2015b). There has been little documentation of brood reduction in RHWO since most published studies have not recorded clutch size and number of fledglings. Ingold (1989) found that among successful nests approximately 50% of RHWO eggs resulted in fledglings, however his study did not distinguish how much of the reduction resulted from total versus partial loss, or if the loss occurred while the nest contained eggs or nestlings. Frei et al. (2015a) found that out of 21 successful nests monitored in New York and Ontario with a nest cavity camera, clutch size ranged from 3-6 eggs, with an average of 4.6, but only 59% of eggs hatched. Among successful nests, 39% of eggs laid resulted in fledglings, with successful nests averaging 1.7 fledglings. The high percentage of unhatched eggs could be due to incomplete incubation or mortality of asynchronously hatching offspring. The presence of runt eggs may also contribute to partially unhatched clutches; however, runt eggs were found infrequently among RHWO museum eggs, at a rate of <1% of eggs (5 out of 731 eggs) (Koenig 1980). The incidence of runt eggs may be even less than museum collections suggest

since unusual eggs may have been more prized as museum additions because of their uniqueness (Rothstein 1973). One recent study removed a nest from the data analysis due to the suspicion that all eggs were infertile (Frei et al. 2015c).

By estimating nest success, documenting nestling development, and measuring brood reduction, my study will fill in gaps in the literature. This knowledge will help inform future conservation efforts for RHWO.

Methods

Study area— My study area was approximately 5 km² and was situated within Cedar Creek Ecosystem Science Reserve (45.41° N, 93.20° W) in central Minnesota, USA. The area lies on the Anoka Sand Plain and is made up primarily of sand prairie, savanna, small wetlands, and forest ecosystems mainly comprised of northern pin oak (*Quercus ellipsoidalis*) and bur oak (*Quercus macrocarpa*) (Peterson and Reich 2001). The study site is bordered by Hellen Allison Savanna Scientific and Natural Area to the south, a residential area to the east, 134 ha Fish Lake to the north (Minnesota Department of Natural Resources 1998), and closed-canopy forest to the west (Fig. 1.1). The area surveyed for nests included 22 land units which are burned every 1-5 years to maintain oak savanna habitat, as well as surrounding area that is burned every 8 to 20 years (Parmelee 1983; Davis et al. 2000).

Nest searching— Since 2008 RHWO nests on this site have been identified by Red-headed Woodpecker Recovery, a committee of the Audubon Chapter of Minneapolis. In 2011 they began banding adults using colored leg bands, allowing individuals to be identified. The following year they began monitoring the nests and banded pairs. For my research, I conducted detailed nest monitoring with a nest cavity camera in 2014 and 2015. Teams of volunteers were each assigned a portion of the study area to locate potential nest cavities and monitor them for evidence of nesting activity. Depending upon the size of the assigned area, searching was conducted by walking around the perimeter or through the interior, ensuring the entirety of the area could be thoroughly searched.

Visual cues of nesting activity included cavity excavation, adults entering or peering into a cavity, and adults feeding nestlings. Recordings with RHWO calls were occasionally used to utilize territorial responses as a means for finding additional breeding pairs. Areas were searched at least biweekly from May through August by the volunteers or the primary researchers. Potential nest trees were marked with colored tape around the base of the tree and the location was recorded in a portable GPS unit. The color banded birds allowed me to determine if a nest was a renesting attempt by an individual or pair.

Nest monitoring— A color and infrared nest cavity camera (ibwo.org) mounted on top of a 15-meter telescoping pole (Crain product, manufactured by Seco Tools, Fagersta, Sweden) was used to monitor all potential and active nest cavities. Real-time images from the camera could be displayed on a wireless screen and saved as photographs or video.

Nest monitoring took place in 2014 and 2015 for the full duration of the nesting season: 10 May – 15 August. Active nests were monitored three times per week, weather permitting. Photo and video documentation of the inside of each nest was collected at each visit. Nest visits were completed in 10 minutes or less to minimize disturbance. I attempted to obtain a photographic count of eggs and nestlings during each visit; however adult birds within the cavity or the positioning of the nestlings in the cavity sometimes inhibited complete counts. When obstructions limited ability to positively determine the nest contents using the camera, ground level observations were made to determine if the nest was still active until the next quality camera image allowed a complete count. If the nest cavity was inaccessible or reliable images could not be obtained, ground level observations were made to try to determine if the nest was still active, and if the nest was in the egg laying, egg incubation, or nestling rearing stage. Such nests were used only in appropriate portions of the analysis.

Once fledglings left the nest, they were counted by observing adult feeding behavior. Any nearby fledgling being fed by an individual adult was assumed to be its offspring and was considered a fledgling from the adult's respective nest. Color banding

of adults allowed me to determine which nest offspring fledged from. Searching attempted to account for all fledglings that were presumed to fledge from a nest based on the most recent count of nestlings observed using the cavity camera. There were two cases where no fledglings could be found from nests with offspring old enough to have fledged. Since, in both cases, the adults were found and observed for 30-90 minutes multiple times within the first week of recording the nest as empty with no signs of interactions with fledglings, these two nests were assumed to have failed before any offspring left the nest. Pairs would occasionally produce two clutches per breeding season. Each nest attempt was treated as a separate nest and they were counted separately in the results unless noted.

Nest tree data— At the end of each season I collected nest tree characteristics to be used as covariates for nest success. I measured tree height and the height of the cavity from the ground using the telescoping pole, or the combination of a clinometer and laser range finder. Tree girth was measured using diameter at breast height (DBH). Cavities were described as being in a dead tree, a living part of a living tree, or a dead part of a living tree. The presence of other cavities and holes of comparable size to the nest entrance hole were also noted.

Statistical analysis— All statistical analyses were conducted using Program R version 3.1.2. Logistic exposure modeling was used to estimate the probability of a nest on the site fledging at least one young and to determine which parameters were affecting daily nest survival (Shaffer 2004; M. Herzog, U.S. Geological Survey, unpubl.). Although our methods of data collection attempted to record data for each nest three times a week, weather occasionally caused 5-7 day intervals between nest checks. The logistic exposure method was therefore the most appropriate method for analysis since it does not require knowledge of the exact date a nest failed. The explanatory variables tested to determine influence on daily nest survival included nest initiation date, tree height, height of the cavity entrance, DBH, whether the tree had other holes of

comparable size to the nest cavity, whether the tree was dead or alive, whether the portion of the tree containing the nest was dead or alive, nest age, and nest stage (eggs vs. nestlings). A step-wise multivariate analysis using backward elimination was used to fit the most parsimonious model based on minimal values of Akaike information criterion (AIC). Standard errors (SE) for predicted daily survival rates at different covariate values were calculated using the delta method (Powell 2007). Because daily nest survival did not vary by nest age (see Results), confidence intervals for cumulative nest survival over the entire 45-day nesting period were obtained by finding the upper and lower 85% CI for each daily survival rate, and raising those values to the 45th power to represent the total nesting period.

Brood reduction was calculated using the maximum and minimum clutch or brood size of each nest, and then calculating the percentage of eggs and/or nestlings the nest lost during the nesting period. Only nests that were found during the egg laying stage and those that did not experience total clutch or brood loss were included in the brood reduction analysis. All nests found after egg laying was completed were excluded from brood reduction calculations because it was impossible to know if any eggs had been lost prior to the discovery of the nest.

Results

I located 67 RHWO nests; 35 in 2014 and 32 in 2015. Six nests could not be monitored due to physical or visual inaccessibility of the cavity, leaving 61 nests that were monitored consistently and used for all parts of the analysis. The six obstructed nests were still monitored for activity from the ground and were included in appropriate portions of the analysis.

Five of 28 woodpecker pairs (17.9%) produced a second clutch in 2014 and 3 of 29 pairs (10.3%) laid a second clutch in 2015. Of the pairs that laid second clutches, four had successful first broods, all of which were among the earliest initiated nests of the seasons. The other four pairs that had second clutches did so after their first clutch failed. In one case a pair began laying the second clutch less than a week after the first clutch

was depredated.

Most nests (46 of 61; 75.4%) were found in dead trees. An additional six nests were in a dead branch of a living tree. Only nine nests (14.8%) were found in a living part of a living tree. About half the nests (34 of 61; 55.7%) were in trees with additional holes comparable to the nest cavity. Although some pairs have been observed to nest in the same cavity year after year, 35 of 61 nests (57.4%) were in trees that had not been identified as being utilized for nesting by a RHWO in previous years since record keeping began in 2008. In these cases, they either excavated new cavities or utilized cavities that were previously unoccupied or used by another species.

Based on nests where incubation and rearing lengths could be estimated to within two days, the time between the last egg laid and the first hatching averaged 14.8 days (SD = 1.8, n = 29) and the time between the first egg hatching and the first nestling fledging was 28.8 days (SD = 1.9, n = 35). The total nesting period from first egg laid to first nestling fledged averaged 44.7 days (SD = 1.7, n = 27). Clutch size averaged 4.8 (SD = 1.0) at the 46 nests with complete clutches, including 2 nests with 2 eggs, 1 nest with 3 eggs, 12 nests with 4 eggs, 23 nests with 5 eggs, 7 nests with 6 eggs, 0 nests with 7 eggs, and 1 nest with 8 eggs. Successful nests averaged 2.6 fledglings (SD = 0.80, n = 46).

For nests with unknown initiation dates, initiation dates were estimated using the average nesting period, the average rearing period, and/or the average incubation period for known nests in my study. Mean nest initiation date was 27 May (SE 2.9 days), the earliest was 13 May and the latest was 11 July. Mean fledging date was 9 July (SE 2.4 days), the earliest was 27 June and the latest was 13 August.

Nestling growth and development—Newly-hatched RHWO chicks were altricial and typically laid on their bellies, but would often reach up and beg, neck outstretched, heads waving, mouths gaping, in response to the camera entering the nest cavity. Begging behavior would stop within seconds, but could be stimulated again by bumping the camera against the side of the cavity entrance. Nestlings about nine days old would beg more consistently and could be heard a few meters away from the base of the nest tree.

Pin feathers were visible 10 days (SD = 1.8) after hatching, at which point nestlings also began to open their eyes. Eye opening began as small slits with eyes fully opening a few days later. Once the nestlings opened their eyes, they were generally less likely to beg when the camera entered the cavity, and instead often would sit motionless. As they developed, they began to cling to the sides of the cavity in a stacked manner with some nestlings closer to the cavity entrance and some further below. Nestlings were also seen standing on top of each other. Feathers began to grow longer and feather tracts were no longer visible on the head at 18 days (SD = 2.3) after hatching. Prior to fledging the nestlings would climb close to the cavity entrance and would occasionally peck at the camera if within reach.

Nest success— Of the 67 nests found during 2014-2015, 21 nests failed before fledging, including 3 nests that failed due to storm-induced toppling of trees or branches. Additionally, another tree fell down just after two nestlings fledged but the last remaining nestling died inside the cavity. Three clutches of eggs remained unhatched well over the average incubation length, ranging from 19-30 days of egg incubation. These clutches were either abandoned, were entirely infertile, or experienced embryo death. Since the cause of these unhatched clutches could not be determined, they were considered to be failed nests after they surpassed the average length of egg incubation. The rest of the failures were assumed to be predation. Depredated nests were usually characterized by complete disappearance of the nest contents and almost never had evidence as to the type of predator. A bullsnake (*Pituophis catenifer sayi*) was observed eating eggs from one nest and bullsnakes have been observed climbing trees and looking into empty tree cavities on two other occasions (Yohannes and Howitz, in press).

Daily survival rate was influenced by nest initiation date and the status of the branch or trunk containing the nest (dead or alive) (Table 1.2). Daily nest survival rate was higher for nests initiated earlier in the season (Fig. 1.2) and for nests in dead branches, but the latter relationship was not statistically significant ($p = 0.11$, Fig. 1.3). Daily survival rate on the mean initiation date (27 May) for nests in dead branches was

0.9945 (SE = 0.0019, which yields 78.3% nest success when raised to the 45th power).

Brood reduction occurred in 100% of the successful nests where camera monitoring began during the egg laying stage (n = 25). On average, nests retained just over half their original clutch by the time of fledging, with an average brood reduction of 48.1%. Nests started with an average of 5 eggs (SE 0.19) but fledged an average of 2.56 fledglings (SE 0.16). Brood reduction took place during all stages of the nesting cycle. In both years 5.0% of the reduction was due to egg disappearance during incubation, and 25.0% occurred because of eggs that were incubated to term but failed to hatch. In most cases the unhatched eggs disappeared between a couple of days and a week after the rest of the clutch hatched. Additionally, 31.7% of the brood reduction occurred during a time frame when it could not be determined if an egg disappeared from the nest prior to hatching or a nestling had disappeared within a couple of days after hatching. Nestlings disappearing or dying in the nest accounted for the remaining 38.3% of brood reduction.

Discussion

The 78.0% rate of Mayfield nest success in my study for the Cedar Creek population of RHWO is at the high end of nest success estimates reported in the literature (Table 1.1). I found that nests initiated earlier in the season and in dead branches had higher rates of nest success, although branch status was not as important as initiation date. AIC values for candidate models showed that a model containing only initiation date was competitive with the best model (Table 1.2). In other studies, height of the cavity entrance above the ground was positively correlated to nest success (Hudson and Bollinger 2013), but no significant relationship was found in my study. I found that the likelihood of nest failure increased for nests initiated late in the nesting season. This is contrary to the relationship documented by Frei et al. (2015c), who found that nest success improved later in the season. However, Frei et al. suggested that interactions with European Starlings (*Sturnus vulgaris*) on their study site were driving this trend, but European Starlings were rarely observed on my study site.

Brood reduction affected 100% of 25 successful nests found during the egg laying

stage. Brood reduction occurred during all stages of the nesting cycle, indicating that there were likely multiple causes. Among successful nests found in my study during the egg laying stage, approximately 30% of eggs failed to hatch, disappeared, or the newly hatched offspring disappeared so quickly they were never observed. This was lower than the 41% rate of unhatched eggs reported by Frei et al. (2015a). Some eggs that failed to hatch appeared to be lighter in color, perhaps indicating lack of embryo development.

Losses that occurred in the nestling stage were likely due to sibling competition, either in the form of direct aggression or indirect competition for food. After their eyes were open, nestlings were often motionless and fixated on the nest camera during the times of observation, yet occasionally chicks were observed pecking each other. As the nestlings developed and grew in size, they climbed the sides of the nest cavity, standing above or below their siblings. The nestlings standing at the top of the stack took up so much of the cavity it was sometimes difficult to see the nestlings below. It seems quite possible that the parents would have similar difficulty seeing and accessing the lower nestlings to feed them. In some instances, dead nestlings were visible at the bottom of the cavity and not removed by the parents, perhaps because they could not access the cavity floor. It is possible that larger nest cavities or greater food resources may lessen the effects of sibling competition.

Mock and Parker (1986) explored brood reduction among asynchronously hatching herons and egrets. They demonstrated that breeding pairs can benefit by producing more eggs than are usually fledged because of two components adding to reproductive value: “extra reproductive value” which is not contingent upon the survival of older siblings, and “insurance reproductive value” in which a younger sibling survives after an older sibling dies. Lamey et al. (1996) built on this idea by dividing the insurance component into two categories: “substitute offspring” which serve as replacements of senior siblings that die, or as “lottery offspring” which survive random mortality. Because most RHWO nests in my study experienced extreme brood reduction affecting more than one egg or chick per nest, it seems most likely that large clutch sizes at Cedar Creek represent extra reproductive value that was not realized during my study, perhaps because food

availability was inadequate to raise more than 2-3 chicks to fledging age.

Because small, portable cameras are a relatively new technology that has only very recently been applied to cavity nest studies, little historical information exists about brood reduction in woodpeckers. Ingold (1989) used a light and mirror to count RHWO eggs and nestlings in accessible nests. He also found only approximately half of eggs laid resulted in fledglings. The findings from my study were remarkably similar, with 52.0% of the total number of eggs laid resulting in fledglings. Future studies might consider mounting video cameras inside nest cavities to continuously record undisturbed activity, which may shed light on the mechanism of brood reduction (e.g., incomplete incubation, direct sibling attacks, starvation). Quantifying reproductive value, as was done in the Mock and Parker (1986) study, might also provide a better understanding of how brood reduction influences reproductive success of the adults. Observing how food abundance may affect brood reduction would also provide insight as to whether food is a limiting factor for the number of offspring able to successfully fledge from a nest. This could be accomplished observationally with a breeding population by estimating food abundance and number of fledged offspring over time, or experimentally through supplemental feeding for a portion of the population.

My study also provides data on the timing of major developmental milestones, contributing information to help better understand RHWO growth and development, the second highest research priority for the species as listed by *The Birds of North America* (Frei et al. 2015b). Timing and detail of nestling development ought to be replicated in future studies to compare among populations across their breeding range. Future work might also explore the significant variation in nest success among populations to determine which factors might be driving these differences. Finally, more work is needed to determine the mechanism of brood reduction and to further consider how it may or may not impact overall population demographics and trends. If certain circumstances (e.g. abundant food resources; larger nest cavities) could lower brood reduction, there may be potential to increase the number of fledglings produced per nest. This information could ultimately be an important key to RHWO conservation.

Table 1.1 Summary of Red-headed Woodpecker nest success rates reported in the literature.

Location	Rate	Method	Reference
New York	0.32	Mayfield 1961	Berl et al. 2014
South Dakota	0.47	Logistic exposure Shaffer et al. 2004	Vierling and Lentile 2006
Illinois	0.56	Logistic exposure Shaffer et al. 2004	Hudson and Bollinger 2013
Ontario	0.68	Logistic exposure Shaffer 2004	Frei et al. 2015c
Mississippi - late	0.69	Apparent nest success	Ingold 1989
Ohio	0.77	Apparent nest success	Rodewald et al. 2005
Minnesota	0.78	Logistic exposure Shaffer 2004	My study
Mississippi - early	0.83	Apparent nest success	Ingold 1989

Table 1.2 Step-wise multivariate analysis of logistic exposure modeling of daily survival rate of Red-headed Woodpeckers nesting at Cedar Creek Ecosystem Science Reserve, East Bethel, MN in 2014 and 2015. Parameters included year, nest initiation date, tree height, height of nest cavity entrance from the ground, diameter at breast height of nest tree, presence of other holes of similar size to the entrance hole on nest tree, status of tree (dead or alive), status of branch (dead or alive), age of nest, and presence of eggs or nestlings in nest.

Model Parameters	Parameter removed between steps	AIC
Year + Initiation Date + Tree Height + Hole Height + DBH + Mult Holes + Tree Status + Branch Status + Age + Stage ^a		162.01
Year + Initiation Date + Tree Height + Hole Height + DBH + Mult Holes + Tree Status + Branch Status + Stage	Age	160.02
Year + Initiation Date + Tree Height + Hole Height + DBH + Tree Status + Branch Status + Stage	Mult Holes	158.03
Initiation Date + Tree Height + Hole Height + DBH + Tree Status + Branch Status + Stage	Year	156.07
Initiation Date + Tree Height + Hole Height + DBH + Branch Status + Stage	Tree Status	154.27
Initiation Date + Tree Height + Hole Height + DBH + Branch Status	Stage	152.66
Initiation Date + Tree Height + DBH + Branch Status	Hole Height	151.24
Initiation Date + Tree Height + Branch Status	DBH	149.38
Initiation Date + Branch Status^b	Tree Height	148.39
Initiation Date	Branch Status	148.66
(Null model)		175.61

^a Full model with all tested parameters

^b Reduced model with minimum AIC

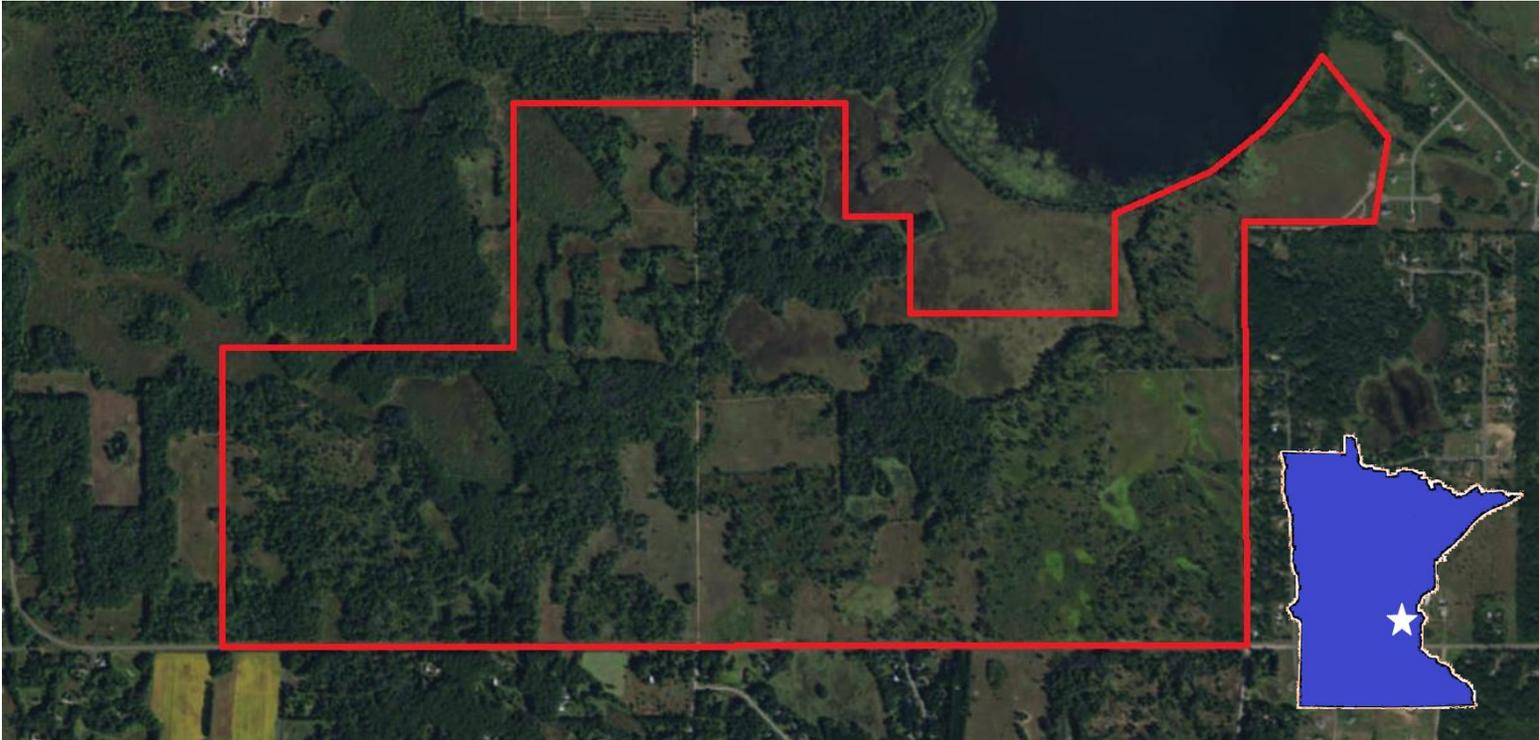


Figure 1.1 Map of study area. Map depicts the south east corner of Cedar Creek Ecosystem Science Reserve, East Bethel, MN.

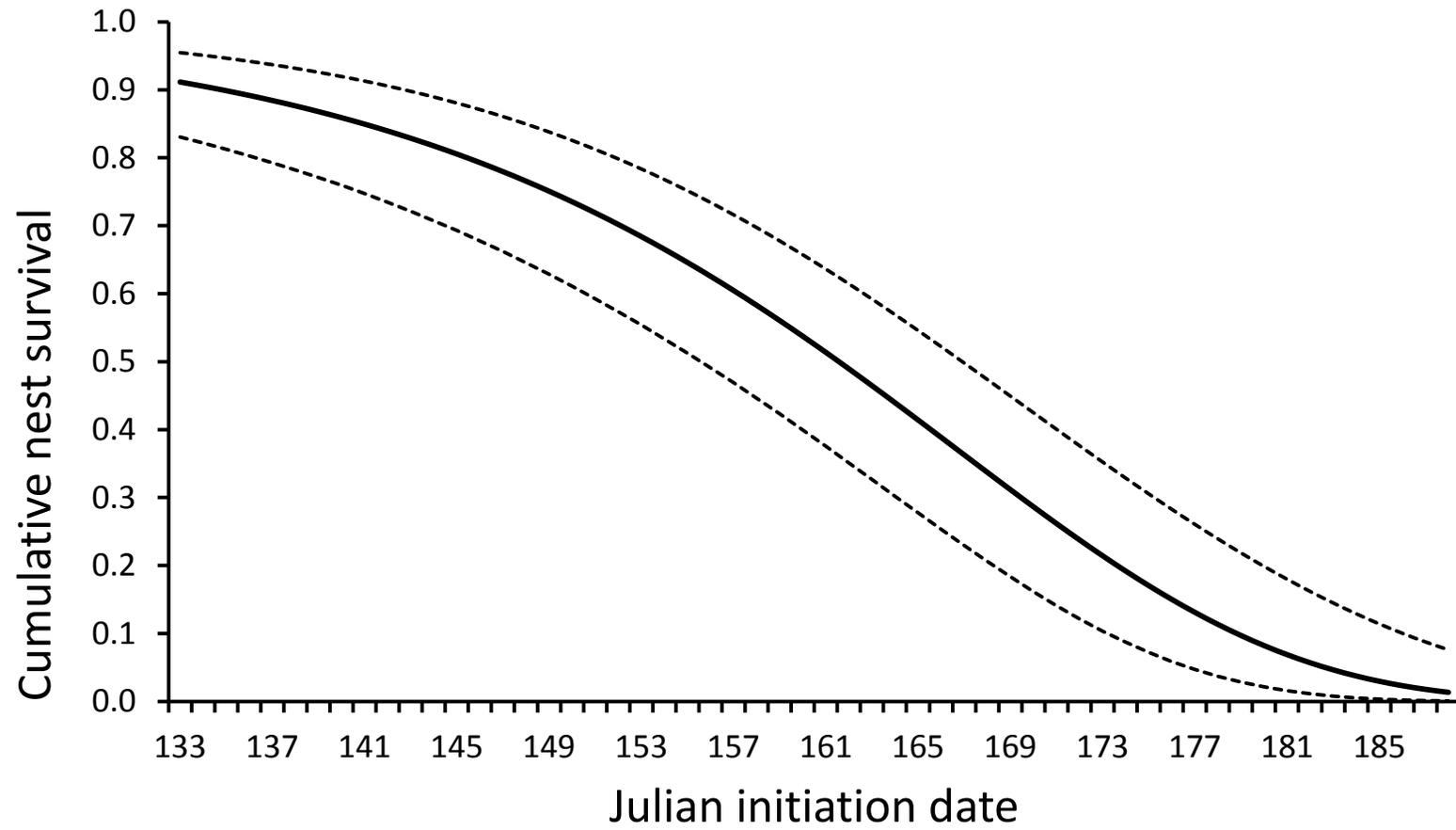


Figure 1.2 **Error! Reference source not found.**

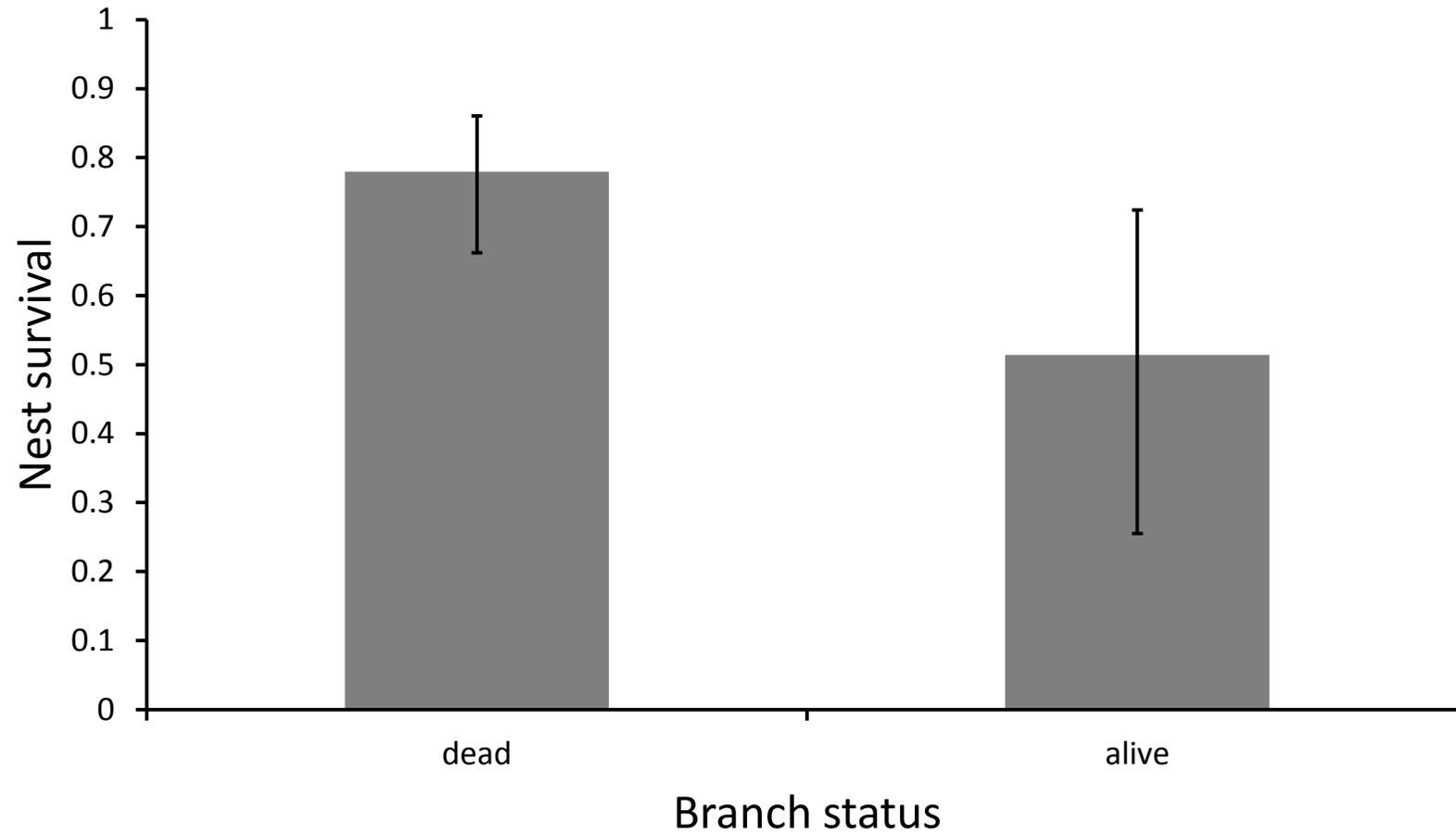


Figure 1.3 Cumulative nest survival as a function of branch status (dead and alive) of Red-headed Woodpeckers nesting at Cedar Creek Ecosystem Science Reserve, East Bethel, MN in 2014 and 2015. Error bars show 85% CI. The parameter estimate in the final model is -0.98 ($SE = 0.61$, $p = 0.11$).

Chapter 2: APPARENT SURVIVAL AND MATE FIDELITY IN A RED-HEADED WOODPECKER POPULATION

Thorough documentation of Red-headed Woodpecker (*Melanerpes erythrocephalus*, hereafter RHWO) survival is needed to better understand population dynamics and potential conservation strategies. RHWO were on the Partners in Flight Watch List due to widespread declines with no known cause (Rich et al. 2004). Across North America, the Breeding Bird Survey has documented a 2.5% annual decline in RHWO between 1966 and 2014 (Sauer et al. 2014), and they are listed as a near-threatened species by the International Union for Conservation of Nature (BirdLife International 2017). Kilgo and Vukovich (2011) estimated adult survival during the breeding season using radio telemetry in South Carolina, but survival studies have not been conducted elsewhere in their range, perhaps due to their unpredictable migration patterns and a lack of large scale marking efforts. My study analyzed four years of mark-recapture data from adult RHWO in central Minnesota and represents one of the first estimates of apparent survival for RHWO anywhere in their range.

Adult survival— RHWO are partial migrants, remaining on their breeding territories year round when mast crops are favorable, otherwise migrating to alternative wintering areas (Bock et al. 1971; Smith 1986; Smith and Scarlett 1987; Zimmerman 1993). RHWO erratic seasonal movements can make individuals difficult to follow over time. A color marked individual may not return to the breeding site between years, but it is not known if the individual died or is alive at a different location. When true survival and site fidelity cannot be differentiated, they can be estimated together as apparent survival (Pollock et al. 1990; Sandercock 2006).

Very few studies have provided information about survival RHWO. Ingold (1991) banded 45 adult RHWO in Mississippi and observed 15 returning adults the following year. Because the fate of the non-returning birds was not known, his study provides evidence that RHWO are at least somewhat site faithful, although little can be drawn

from this small sample about survival. Martin (1995), citing unpublished data from Ingold (1989), quotes a 0.62 annual survival rate for RHWO, but information about timing, sample sizes and methodology are not provided. Kilgo and Vukovich (2011) estimated that breeding season survival was 0.72, with sex and the abundance of cover affecting survival. Because radio transmitters were used, the fates of all but two individuals were known, making this the only published study of true rather than apparent RHWO survival. Transmitters have been documented to negatively affect survival (Barron et al. 2010), however, the authors considered their estimate to be accurate since there was no evidence that a smaller body mass to transmitter mass ratio negatively impacted survival, nor was there any observed behavior change among birds wearing transmitters (Vukovich and Kilgo 2009; Kilgo and Vukovich 2011).

Additionally, there are only a handful of documented cases of known cause of death of adult RHWO. Among the 20 cases of mortality in the radio telemetry study, 17 were due to *Accipiter* predation, two were attributed to gray rat snakes (*Elaphe obsoleta*), and one cause was unknown (Kilgo and Vukovich 2011). Collisions with cars have also been cited as a cause of adult mortality (Eifrig 1937 and 1938, as cited in Graber et al. 1977). An adult and two juvenile RHWO, among other species, died of apparent exposure during severe winter weather (Graber and Graber 1979).

Adult mate fidelity— Information about RHWO mate fidelity between breeding seasons is nearly nonexistent in the literature. One study of a marked population recorded two cases of RHWO pairs who remained together and used the same nest cavity in consecutive years, but since not all adults in this study were banded there is no estimation of the proportion of the population that remained with their previous mate (Ingold 1991). The only large marking effort did not publish and evaluate breeding and mate selection (Kilgo and Vukovich 2011). There is no information listed about pair formation in *Birds of North America* (Frei et al. 2015b). There is great diversity in pair formation among other *Melanerpes* species, ranging from long term permanent pairing of Lewis's Woodpeckers (*Melanerpes lewis*; Bock 1970) and year-round pairing of Golden-fronted

Woodpeckers (*Melanerpes gurifons*; Husak and Maxwell 1998) to lack of year-round pairing of Red-bellied Woodpeckers (*Melanerpes carolinus*; Kilham 1958).

Methods

Capture and banding—Banding took place at Cedar Creek Ecosystem Science Reserve (45.41° N, 93.20° W) in central Minnesota, USA during 2012-2015. Banding took place throughout the year, but most often during May-August. Mist nets and Potter traps were used to capture birds for banding. Typically, the net or trap was positioned in a territory where the target individual could be caught with minimum interference from other birds. When targeting a bird using a mist net, recorded RHWO calls and a decoy woodpecker were used to lure the target individual near the net. If set up within a bird's territory, most adults responded quickly to the recording and decoy and would approach with territorial behavior. Potter traps baited with peanuts or other nuts were used on top of simple feeding platforms mounted on a post 1 to 1.5 m off the ground. A short habituation process was often used to entice the birds to enter the Potter traps. First, nuts were placed on the platform with no trap. Once the target individual used the platform repeatedly without the trap, an open arch made of chicken wire was added over the top and sides of the platform to habituate the bird to walking inside a metal structure while feeding. Once the target individual consistently fed inside the arch, it was replaced with a Potter trap. When the target individual was observed entering the trap, the trap was manually closed from a distance using a long cord attached to the trap door.

Once captured, individuals were weighed, measured (Table 2.1), and banded using a unique combination of three colored leg bands (size 2; Avinet, Portland, ME) and one metal USFWS band. Five breast feathers were removed for sex determination via DNA analysis (Avian Biotech International, Tallahassee, FL). After banding, each bird was released where it had been caught. Banded individuals were monitored throughout the breeding season using binoculars and telephoto images. Sightings of banded individuals, including locations and other associated individuals, were recorded and later converted to

encounter histories for mark-recapture analysis. All banding was done under a US Federal Bird Banding and Marking Permit assigned to James Howitz (Red-headed Woodpecker Recovery) and the University of Minnesota Institutional Animal Care and Use Committee protocol 1406-31581A.

Data analysis— I analyzed mark-resighting data using a Cormack-Jolly-Seber (CJS) model, as implemented in Program MARK (White and Burnham 1999). CJS models were used to estimate annual apparent survival (ϕ) and detection (p) probabilities in relation to year, sex, and capture weight. I treated sex as a covariate with values 0 for females, 1 for males. I considered models where apparent survival and resighting potentially varied by year, sex, weight, or combinations thereof. I began by modeling resighting rates while modeling apparent survival with a general model that included both sex and year effects. After finding the best supported model structure for resighting, I held this portion of the model constant and applied the same approach to apparent survival (Lebreton et al. 1992). Akaike's information criterion corrected for small sample size (AIC_C) was used to determine the most parsimonious model of apparent survival and detection probability (Anderson et al. 1994).

Mate fidelity analysis— Mate fidelity was evaluated by determining if a marked adult remained with the same marked mate as the previous year, conditional on both birds surviving and being re-observed. Although the total banded population included 125 birds, the rigorous criteria for birds to be used for mate fidelity analysis resulted in a small subset. Birds with an unbanded mate one year and a banded mate the next year were excluded since it was unknown if the mate was the same as the year before. Three distinct mate-fidelity options were possible for breeding adults surviving multiple years. The first is mate faithfulness, in which case a breeding adult remains with the same mate as the previous breeding season. The second is mate divorce, in which case a breeding adult takes a new mate even though the mate from the previous season has survived and has returned to the breeding site. The third is a mate change resulting from the death or emigration of the previous year's mate.

Results

From 2012 to 2015, 125 banded birds were observed 1096 times during the breeding seasons (including many birds with multiple observations per breeding season). Although males were slightly larger than females (Table 2.1), there was too much overlap to use body measurements to discriminate sex.

In the most parsimonious mark-recapture model, apparent survival (ϕ) varied among years and detection probability (p) differed by sex. This model received nearly three times as much support as the next best model (Table 2.2). Estimated apparent survival from the top-supported model was 0.38 (SE = 0.07) between 2012-2013, 0.70 (SE = 0.09) between 2013-2014, and 0.55 (SE = 0.09) between 2014-2015. Estimated detection probability was 0.72 (SE = 0.13) for females and 1.00 for males.

I observed mortality of three banded adults during my study. Two birds (one male, one female) were found dead by the side of the road in 2012, presumably hit by vehicles. In 2014 one male was killed inside the cavity he had defended with his mate and his partially consumed remains were found with the nest cavity camera. The female repaired with another male and laid eggs in the cavity within two days after her mate's remains were discovered.

Among the 30 banded woodpeckers with banded mates the previous year, 10 previously successful nesters remained with their previous mate, 8 birds divorced their previous mate (including 3 successful nesters, 2 failed nesters, and 3 birds with unknown nesting histories), and 12 birds were observed with new mates, but their previous mate was not observed and may have died, emigrated, or simply not been seen (Table 2.3). Conditioning on the 15 birds where their previous mate was known to be alive and their previous breeding history was known, there was some evidence for a positive association between divorce and failed nesting during the previous breeding season (Fisher exact test: $p = 0.095$).

Discussion

Linear measurements and mass of adult birds documented in my study contribute to formal description of this species. According to the Birds of North America account, no data have been published on differences in weight between sexes (Frei et al. 2015b). The heaviest female I encountered was 85.1g, while the heaviest male was 97.2, suggesting birds weighing in the upper 80s or 90s g may reliably be considered male without DNA sexing. However, only 17% of the males I encountered weighed more than 85g. The presence of overlap among the ranges of all physical measurements between males and females in my study justify the use of DNA analysis for sexing.

My analysis indicated that apparent survival fluctuated substantially among the three years of my study. With mark-resighting survey designs, it is unknown if unobserved birds are dead or have emigrated from the study site, making it impossible to tease true survival apart from site fidelity. The fluctuations of apparent survival across time could be due to changes in food availability year to year, which could affect both true survival and site fidelity, or may be correlated with competition for suitable territories, or whether an individual was able to successfully reproduce the year before, both of which could affect site fidelity. The estimated detection rate was high, especially for males, suggesting that Red-headed Woodpecker Recovery volunteers and their methods for resighting banded birds are working well to provide fairly complete records of which birds are on the study site.

My estimate of apparent survival averaged across the three study years was 0.55, which is lower than Martin's (1995) estimate of 0.62 based unknown methods, and also lower than Kilgo and Vukovich's (2011) 0.72 estimate of breeding season survival; however, their estimate only considered mortality during the 18-week breeding season. My findings of lower apparent survival could suggest that mortality or emigration during migration could be more significant than previously thought, or that there could be regional differences affecting apparent survival.

The three cases of observed mortality suggest that vehicle collisions may be an important source of mortality for RHW. Adults were often observed leaving their nest

territory to feed alongside roads and from bird feeders in nearby residential neighborhoods. These features may be attractive for foraging, and in fact could be an important food source, but may also be putting adults at risk. While my study site was located in a relatively rural area bordered on only two sides by roads and not heavily trafficked, this is certainly not always the case among areas where RHWOs are known to nest. Future studies in areas with higher road traffic may shed light on whether vehicle collisions are a substantial cause of mortality. In Chapter 1, of the 67 nests monitored for nest survival, 15 failed due to apparent predation, yet I found only one adult that was dead inside of a nest cavity. Due to the very small cavity openings and depth of the nest, I suspect it would be very difficult for a predator reaching into a nest, such as a raccoon, to remove an adult, dead or alive, from a cavity. The single instance of adult mortality within the nest compared to 15 instances of nest predation could signify that nest predators are not a significant threat to adults, or that any adults killed by nest predators were eaten in the nest by predators fully entering the cavity, such as snakes or weasels. Cameras mounted inside nest cavities could reveal how great a threat nest predators are to adults.

No previous study has investigated the relationship between past reproductive success and mate fidelity of RHWOs. Among the 18 cases where both banded members of a previous pair returned to the site, 10 demonstrated mate-fidelity and 8 demonstrated switching of partners. Although instances of individuals choosing to pair with their previous mate occur more frequently than if mates were randomly chosen, the relatively equal number of pairs switching partners suggests this species is not highly mate-faithful. The sample size of pairs demonstrating observable mate-fidelity that also had known nest fates for the previous year was even smaller. Although the sample size was limited, the evidence suggests that unsuccessful breeding attempts are correlated with mate divorce the following year. Because the banded population of birds on the study site is substantial and added to yearly, it may be possible to increase the sample size in the coming years to better analyze the effects of reproductive success on mate fidelity.

There is potential to continue these analyses with the same population as more data

are acquired in coming years. Of particular interest may be incorporation of winter encounter histories into the apparent survival analysis. This would not only increase the number of times individuals were observed, but may also provide insights of the seasonal survival and movement of these birds. Estimating breeding-season apparent survival would also have the added benefit of allowing more direct comparison with the breeding-season survival rate by Kilgo and Vukovich's (2011). Larger sample sizes would enable additional analysis of the impacts breeding success and fecundity have on mate fidelity the following year.

This is among the first studies to document RHWO apparent survival and mate fidelity. The result that apparent survival varies by year suggests conservation efforts would do well to further investigate what mechanism is driving this fluctuation, and how it might potentially be manipulated to provide greater stability and higher rates of apparent survival. While much work has been done to document the survival and fecundity of this particular population, the conclusions to be drawn regarding potential conservation strategies are limited until similarly comprehensive work is done with other populations across the geographic range of the species. Geographic factors such as food availability, abundance of suitable habitat, severe weather, competing species, predators, and migration distance may all play significant roles in the challenges these populations face. The methods of resighting yielded high detection rates and can serve as a template for future apparent survival studies. RHWO have been on a decline for decades, and there is a clear need for additional studies across their range which can inform conservation efforts, particularly those focused on population dynamics, reducing mortality, and increasing fecundity.

Table 2.1 Summary of body measurements of adult Red-headed Woodpeckers at time of banding.

Measurement	Average for females		Range for females	Average for males		Range for males	Average for sexes combined	
Weight (g)	74.08	n = 55	64.5 – 85.1	79.26	n = 70	67 – 97.2	76.98	n = 125
Wing chord length (mm)	135.74	n = 55	130 – 145	138.61	n = 69	131 – 149	137.34	n = 124
Tail length (mm)	80.25	n = 55	66 – 90	81.85	n = 71	70 – 91	81.15	n = 126
Tongue length (mm)	11.59	n = 41	10.5 – 14	12.23	n = 60	11 – 14.5	11.97	n = 101

Table 2.2 Candidate model results from Program MARK used to estimate apparent survival during the breeding seasons from 2012 to 2015 for banded adult Red-headed Woodpeckers at Cedar Creek Ecosystem Science Reserve, Minnesota, USA.

Model	AIC _c ^a	ΔAIC _c ^b	AIC _c Weight	Number of parameters
$\varphi(t),p(\text{sex})$	187.73	0.00	0.658	4
$\varphi(t+\text{mass}),p(\text{sex})$	189.88	2.15	0.225	5
$\varphi(t),p(t)$	193.26	5.53	0.042	5
$\varphi(t),p(\cdot)$	194.12	6.39	0.027	4
$\varphi(\cdot),p(t)$	194.56	6.82	0.022	4
$\varphi(t+\text{sex}),p(\cdot)$	195.00	7.27	0.017	5
$\varphi(\cdot),p(\cdot)$	196.35	8.62	0.009	2

^aAkaike's Information Criterion corrected for small sample size

^bChange in AIC_c value between ranked models. A ΔAIC_c = 0.00 is interpreted as the best fit model among the models tested.

Table 2.3 Mate fidelity of adult Red-headed Woodpeckers with known mates and known nest fates from previous year. There is a positive association between individuals pairing with new mates and failed nesting during the previous breeding season (Fisher exact test: $p = 0.095$).

Nest fate the previous year	Mate faithful	Mate divorce	Mate change due to mortality or immigration
Successful	10	3	10
Unsuccessful	0	2	1
Unknown	0	3	1
Total	10	8	12

Literature Cited

- ACKERMAN, J. T., J. M. EADIE, D. L. LOUGHMAN, G. S. YARRIS, AND M. R. MCLANDRESS. 2003. The influence of partial clutch depredation on duckling production. *The Journal of Wildlife Management* 67:576-587.
- ADKINS GIESE, C. L., AND F. J. CUTHBERT. 2003. Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the upper midwest, USA. *Forest Ecology and Management* 179:523-534.
- ANDERSON, D. R., K. P. BURNHAM, AND G.C. WHITE. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780-1793.
- ATTERBERRY-JONES, M. R., AND B. D. PEER. 2010. Cooperative breeding by Red-headed Woodpeckers. *The Wilson Journal of Ornithology* 122(1):160-162.
- BARRON, D. G., J. D. BRAWN, AND P. J. WEATHERHEAD. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1:180-187.
- BERL, J. L., J. W. EDWARDS, J. S. BOLSINGER, AND T. E. KATZNER. 2014. Survival of Red-headed Woodpeckers' (*Melanerpes erythrocephalus*) nests in northern New York 126:700-707.
- BIRDLIFE INTERNATIONAL. 2017. *Melanerpes erythrocephalus*. (amended version published online in) The IUCN Red List of Threatened Species 2017.
- BOCK, C. E. 1970. The ecology and behavior of the Lewis Woodpecker (*Asyndesmus lewis*). University of California Press.
- BOCK, C. E., H. H. HADOW, AND P. SOMERS. 1971. Relations Between Lewis' and Red-headed Woodpeckers in Southeastern Colorado. *The Wilson Bulletin* 83:237-248.
- BRAWN J. D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460-469.
- CONNER, R. N. 1976. Nesting habitat for red-headed woodpeckers in southwestern Virginia. *Bird-Banding* 47:40-43.
- DAVIS, M. A., D. W. PETERSON, P. B. REICH, M. CROZIER, T. QUERY, E. MITCHELL, J. HUNTINGTON, AND P. BAZAKAS. 2000. Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* 8:30-40.

- EHRlich, P. R., D. S. DOBKIN, AND D. WHEYE. 1992. *Birds in jeopardy*. Stanford University Press, Stanford, CA.
- FREI B., J. W. FYLES, J. J. NOCERA. 2013. Maladaptive habitat use of a North American woodpecker in population decline. *Ethology* 119:377-388.
- FREI, B., J. W. FYLES, J. L. BERL, J. W. EDWARDS, AND J. J. NOCERA. 2015a. Low fecundity of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) at the northern edge of the range. *The Wilson Journal of Ornithology* 127:639-645.
- FREI, B., K. G. SMITH, J. H. WITHGOTT, AND P. G. RODEWALD. 2015b. Red-headed Woodpecker, *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online database: <http://bna.birds.cornell.edu/bna/>
- FREI B., J. J. NOCERA, AND J. W. FRYLES. 2015c. Interspecific competition and nest survival of the threatened Red-headed Woodpecker. *Journal of Ornithology* 156:743-753.
- GENTRY D. J., AND K. T. VIERTLING. 2008. Reuse of woodpecker cavities in the breeding and non-breeding seasons in old burn habitats in the Black Hills, South Dakota. *American Midland Naturalist* 160:413-429.
- GRABER, J. W., R. R. GRABER, AND E. L. KIRK. 1977. Illinois Birds: Picidae. *Biological Notes* 102.
- GRABER, J. W., AND R. R. GRABER. 1979. Severe winter weather and bird populations in southern Illinois. *Wilson Bulletin* 91:88-103.
- GRUNDEL, R., AND N. B. PAVLOVIC. 2007. Distinctiveness, use, and value of midwestern oak savannas and woodlands as avian habitats. *Auk* 124:969-985.
- HUDSON, N. C., AND E. K. BOLLINGER. 2013. Nest success and nest site selection of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) in east-central Illinois. *American Midland Naturalist* 170:86-94.
- HUSAK, M. S., AND T. C. MAXWELL. 1998. Golden-fronted Woodpecker. *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online database: <http://bna.birds.cornell.edu/bna/>
- INGOLD, D. J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings. *Auk* 106:209-217.

- INGOLD D. J. 1991. Nest-site fidelity in Red-headed and Red-bellied Woodpeckers. *The Wilson Bulletin* 103:118-122.
- INGOLD D. J. 1994b. Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. *Ohio Journal of Science* 94:2-7.
- JACKSON, J. A. 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. *The Condor* 78:67-76.
- KILGO, J., AND M. VUKOVICH. 2011. Factors affecting breeding season survival of Red-Headed Woodpeckers in South Carolina. *Journal of Wildlife Management* 76:328-335.
- KILGO, J. C., AND M. A. VUKOVICH. 2014. Can snag creation benefit a primary cavity nester: Response to an experimental pulse in snag abundance. *Biological Conservation* 171:21-28.
- KILHAM, L. 1958. Pair formation, mutual tapping, and nest hole selection of Red-bellied Woodpeckers. *Auk* 75:318-328.
- KING, R. S., K. E. BRASHEAR, M. REIMAN. 2007. Red-headed Woodpecker nest-habitat thresholds in restored savannas. *The Journal of Wildlife Management* 71:30-35.
- KOENIG, W. D. 1980. The incidence of runt eggs in woodpeckers. *The Wilson Bulletin* 92:169-176.
- KOENIG, W. D. 1986. Geographical ecology of clutch size variation in North American woodpeckers. *Condor* 88:499-504.
- KRONLAND, W. J. 2007. Nest usurpation by Red-headed Woodpeckers in southeastern Montana. *The Wilson Journal of Ornithology* 119:486-489.
- LAMEY, T. C., R. M. EVANS, AND J. D. HUNT. 1996. Insurance reproductive value and facultative brood reduction. *Oikos* 77: 285-290.
- LABRANCHE, M. S., AND J. R. WALTERS. 1994. Patterns of mortality in nests of Red-cockaded Woodpeckers in the Sandhills of southcentral North Carolina. *The Wilson Bulletin* 106:258-271.
- 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.

- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *The Wilson Bulletin* 73:255-261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *The Wilson Bulletin* 87:456-466.
- MELCHER, B. 1998. Red-headed Woodpecker. Pages 250-251 in Colorado breeding bird atlas. (KINGERY, H. E., Ed.) Colorado Bird Atlas Partnership and Colorado Division of Wildlife. Denver.
- MINNESOTA DEPARTMENT OF NATURAL RESOURCES. 1998. Fisheries Lake Survey, Fish Lake. <http://www.dnr.state.mn.us/lakefind/showreport.html?downum=02006500>
- MOCK, D. W., AND G. A. PARKER. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40:459-470.
- MORANDINI, V., AND M. FERRER. 2015. Sibling aggression and brood reduction: A review. *Ethology, Ecology & Evolution* 27:2-16.
- NILSSON, S. G. 1986. Evolution of hole- nesting in birds: On balancing selection pressures. *The Auk* 103: 432-435.
- PARMELEE, D. F. 1983. A progress report of the Cedar Creek Natural History Area. *Journal of the Minnesota Academy of Science* 49:1-24
- PETERSON, D. W., AND P. B. REICH. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. *Ecological Applications*, 11:914-927.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:3-97.
- POWELL, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949-954.
- PULICH, W. M. 1988. *The birds of North Central Texas*. Texas A&M Press, College Station.
- R CORE TEAM. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

- RODEWALD, P. G., M. J. SANTIAGO, AND A. D. RODEWALD. 20015. Habitat use of breeding Red-headed Woodpeckers on golf courses in Ohio. *Wildlife Society Bulletin* 33:448-453.
- ROTHSTEIN, S. I. 1973. The occurrence of unusually small eggs in three species of songbirds. *The Wilson Bulletin* 85:340-342.
- RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. IÑIGO-ELIAS, J. A. KENNEDY, A. M. MARTELL, A. O. PANJABI, D. N. PASHLEY, K. V. ROSENBERG, C. M. RUSTAY, J. S. WENDT, AND T. C. WILL. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca. Retrieved from http://www.partnersinflight.org/cont_plan/PIF2_Part1WEB.pdf
- SANDERCOCK, B. K. 2006. Estimation of demographic parameters from live-encounter data: A summary review. *Journal of Wildlife Management* 70:1504-1520.
- SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI JR., AND W. A. LINK. 2014. The North American Breeding Bird Survey, results and analysis 1966-2012 (Version 02.19.2014). USGS Patuxent Wildlife Research Center.
- SCHWAB, R. G. 1959. Strife over a nesting site between Downy and Red-headed woodpeckers. *The Wilson Bulletin* 71:190-191.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *The Auk* 121:526-540.
- SMITH, K. G. 1986. Winter population dynamics of three species of mast-eating birds in the eastern United States. *Wilson Bulletin* 98:407-418.
- SMITH, K. G., AND T. SCARLETT. 1987. Mast production and winter populations of Red-headed Woodpeckers and Blue Jays. *The Journal of Wildlife Management* 51:459-467.
- VIERLING, K., AND L. LENTILE. 2006. Red-headed Woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. *The Condor* 108:957-962.
- VIERLING, K. T., D. J. GENTRY, AND A. M. HAINES. 2009. Nest niche partitioning of Lewis's and Red-headed Woodpeckers in burned pine forests. *The Wilson Journal of Ornithology* 121:89-96.

- VUKOVICH, M., AND J. C. KILGO. 2009. Effects of radio transmitters on the behavior of Red-headed Woodpeckers. *Journal of Field Ornithology* 80:308-313.
- WALDSTEIN, A. L. 2012a. An inexpensive camera system for monitoring cavity nests. *Journal of Field Ornithology* 83:302-305.
- WALDSTEIN, A. L. 2012b. Nest-site selection and nesting ecology of Red-headed Woodpeckers. (Unpublished master's thesis). University of Minnesota.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120-S139.
- YOHANNES, B. J., AND J. L. HOWITZ. Adult Red-headed Woodpecker interaction with bullsnake after arboreal nest depredation. Manuscript submitted for publication.
- ZIMMERMAN, J. L. 1993. *The birds of Konza: the avian ecology of the tallgrass prairie*. University Press of Kansas.

Appendix 1: Clutch Development Photos

Below are photos of a typical Red-headed Woodpecker nest showing development from egg laying through fledging.



Figure A.1 Prior to egg laying woodchips are visible on the bottom of the cavity.



Figure A.2 Two eggs in the nest.



Figure A.3 Three eggs in the nest.



Figure A.4 Six eggs in the nest.



Figure A.5 Adult Red-headed Woodpecker investigating the camera.



Figure A.6 Six eggs in the nest.



Figure A.7 15 days after the first egg was laid the eggs begin to hatch. Photo shows two newly hatched chicks, four unhatched eggs, and eggshell remnants. Nestlings are altricial.



Figure A.8 Five days after hatching, three nestlings are visible with at least one unhatched egg still in the nest.



Figure A.9 Nine days after hatching, brood reduction has decreased the original six eggs to just two nestlings. Nestlings begin to show pin feathers. Eyes are beginning to open as slits. Begging calls are easily heard from a few meters distant from base of nest tree.



Figure A.10 Twelve days after hatching, pin feathers continue to grow. Eyes are open.



Figure A.11 14 days after hatching, feather color is apparent. Nestlings begin to change behavior from begging to hunkering when the camera enters the nest.



Figure A.12 16 days after hatching, eyes are wide open.



Figure A.13 19 days after hatching, feather tracts have disappeared. Nestlings are seen climbing on each other and on the sides of the cavity.



Figure A.14 21 days after hatching, gape flanges are disappearing.



Figure A.15 23 days after hatching, nestlings are crowded in the nest cavity.



Figure A.16 26 days after hatching, nestlings easily climb up toward the cavity entrance.



Figure A.17 28 days after hatching, 43 days after nest initiation, nestlings are ready to fledge.