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entitled

Annual Cycle Demography, Habitat Associations, and Migration Ecology in Red-headed

Woodpeckers (Melanerpes erythrocephalus)

by

R. Kyle Pagel III

Submitted to the Graduate Faculty as partial fulfillment of the requirements for the

Master of Science Degree in

Biology

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An Abstract of

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In vertebrate ecology, a majority of studies focus on the breeding season of the respective study population (Marra et al. 2015). In avian ecology in particular, more is known about the ecology of birds during the nesting season than during any other portion of their life cycle (Harrison et al. 2011). The season season comprises only one proportion of an individual's full annual cycle, which also includes the post-fledging period (from nesting to autumn migration), migration to wintering grounds, non-breeding season, and the migration back to the breeding grounds. These relatively understudied portions of the annual cycle likely have similar, or even greater, importance with regards to individual population-level ecology (Harrison et al. 2011). Even when events outside the nesting season don't contribute directly to mortality, they may influence individuals in a non-lethal manner during a subsequent portion of the annual cycle, a process known as carry-over effects (Norris 2005). In nearly all migratory birds, there is a lack of knowledge about migration and the non-breeding season, but for many species there also remains a gap in knowledge about the post-fledging period, which is arguable the relatively "low-hanging fruit" of the annual cycle outside of nesting ecology. In species that are of conservation concern, gaining knowledge about the full annual cycle could illuminate factors expediting population declines that would otherwise be unknowable.

Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are charismatic cavity-nesters that breed in open forest systems across the eastern and midwestern United States and southern portions of central and eastern Canada. Red-headed Woodpeckers are closely associated with oak savanna ecosystems throughout the midwestern United States because of the open canopies and low understories for aerial foraging and abundance of dead limbs and trees for cavity-nesting (Brawn 2006, Frei et al. 2015). Once common throughout their range, a range-wide population decline of 70% has been seen in the past 50 years (Sauer et al. 2013). Many factors have been hypothesized to contribute to this decline including, but not limited to, the loss of open forest systems and the removal of dead trees that could be potential nesting habitat (Smith 1986), increased rates of predation due to elevated accipiter populations (Koenig et al. 2017), increased competition for nesting cavities from introduced species such as starlings (Graber et al. 1977), and mortalities resulting from vehicle collisions while aerially foraging (Eifrig 1937). A combination of some or all of these hypotheses is most likely responsible. Despite their charismatic appearance, Red-headed Woodpeckers are an under-studied species with a lack of understanding about several key stages of their full annual cycle including migration (Smith et al. 2000) and the post-fledging period (Frei et al. 2015).

Migration is a behavior found throughout the natural world that allows individuals or populations to avoid potential negative effects and take advantage of seasonal changes in resources. Migration comprises two portions of the annual cycle (Marra et al. 2015). Migration is typically divided into two categories: obligate migration, which occurs regularly and is considered "hard-wired" (Berthold 2001, Newton 2012); and facultative which occurs irregularly and is considered to be "optional" (Berthold 2001). This irregularity of facultative migration presents unique problems when attempting to study the behavior, and as such, little is known about the intrinsic and extrinsic factors controlling facultative migration (Berthold 2001).

Facultative migration has been observed most notably in avian species, including the Common Crane (Alonso et al. 1994), Yellow-rumped Warblers (Terrill & Ohmart 1984), and

Great Bustards (Streichet al. 2006), but occurs in insects including melon aphids (Kring 1959) and cotton bullworms (Zheng & Zhang 2000). Current understanding of facultative migration suggests that variation in resource availability and seasonality are the cues (i.e., they underlie the triggering) for facultative migration. In Red-headed Woodpeckers, facultative migration has primarily been described anecdotally (Smith et al. 2000) with few banding records indicating that fall migration occurs at varying spatio-temporal scales (USGS 2019). Most empirical data regarding Red-headed Woodpecker migration has been a result of a single study in South Carolina, which used radio telemetry to track the migration routes of short distance migration (<30 km) and monitor the proportion of the breeding population that migrated each fall (Vukovich & Kilgo 2013). Otherwise, Red-headed Woodpecker migration has not been empirically studied on an extent larger than 30 km. To better understand this unknown portion of the Red-headed Woodpecker's annual cycle and add to the limited existing knowledge of facultative migration, we used GPS tags to study proportions of individuals migrating, migration routes, wintering sites, and the timing associated with migration in two breeding populations of Red-headed Woodpeckers in the Midwestern United States. The addition of migration knowledge in this species in a different part of its breeding distribution can help better understand its annual cycle and habitat requirements to inform conservation plans designed to prevent further population declines.

The post-fledging period of the breeding season is another understudied section of the full annual cycle in migratory birds (Streby et al. 2014). However, many bird populations, including those of waterfowl (Amundson et al. 2013) and songbirds (Streby & Andersen 2011), are more susceptible to variations in fledgling survival during the brood rearing phase rather than variation in nest success. Before recent technological advances of radio telemetry, fledgling survival was calculated using mark-recapture or re-sighting individual fledglings, which can be unreliable when attempting to determine the fate or movement of individual fledglings.

Radio telemetry has been used on adult Red-headed Woodpeckers (Vukovich & Kilgo 2009), but fledglings have not been tracked, and as such there is a lack of reliable fledgling survival rate estimates. Nest success and nest productivity has also been studied in Red-headed Woodpeckers (Frei et al.2015, Ingold 1989, Jackson 1976), but once nestlings fledge, little is known about their subsequent fate and movements. As with many other species, knowledge of the post-fledging period in Red-headed Woodpeckers is needed to better inform population models and to inform ongoing landscape management practices intended to benefit this declining species (Frei et al. 2015). To provide the first fledgling survival rate estimates for Red-headed Woodpeckers and quantify fledgling movements and cover-type associations, we used radio telemetry to track individual fledglings at two breeding populations of Red-headed Woodpeckers in the midwestern United States.

This thesis focuses on two aspects of the annual cycle of Red-headed Woodpeckers that are relatively understudied, facultative migration and post-fledging ecology. Knowledge of these two unique stages of the Red-headed Woodpecker's lifecycle can potentially inform management and conservation practices to better understand and address this species' population declines. My research addresses (1) facultative migration timing, movements, survival, and proportions of populations migrating in adult Red-headed Woodpeckers and; (2) post-fledging survival, cover-type associations, and movements of fledgling Red-headed Woodpeckers.

Dedicated to my parents. Without your support and love, this wouldn't have been

possible.

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Survival, Cover-type Selection, and Movement Patterns of Fledgling Red-headed Woodpeckers in Managed Oak Savannas of the Midwestern United States

1.1 Introduction

When developing population models for a species of conservation concern, it is important to study all stages of the species' life cycle to better understand when factors contributing to population declines may be occurring. Research focused on movements and survival of fledglings during the post-fledging period (i.e., the period after young leave the nest, but before they are fully independent from adult care) is sparse when compared to adult movement and survival during the breeding season (Anders et al. 1997). By studying the post-fledging period, we can improve population models with more accurate estimates of reproductive success and recruitment (Anders et al. 2017, Streby and Andersen 2011), and in turn, better estimate population trends (Streby and Andersen 2011, Shipley et al. 2013). Intensive study of the post-fledging period also allows us to understand how fledglings use various cover types in heterogenous landscapes (King et al. 2006, Streby and Andersen 2013a). These cover-type associations and fledgling around and within various cover types can influence fledgling survival rates (Cohen and Lindell 2004, Streby and Andersen 2013a, Vitz and Rodewald 2010, Streby

et al. 2016). Knowledge of these landscape-demography interactions can be used to better inform landscape management to optimize multiple demographic parameters rather than maximizing one to the potential detriment of overall population growth (Streby et al. 2014, Peterson 2014, Streby et al. 2013a).

One species that is reliant upon a managed ecosystem is the Red-headed Woodpecker (*Melanerpes erythrocephalus*). A cavity-nester and aerial forager, the Red-headed Woodpecker in the Midwestern United States is closely associated with oak savanna ecosystems with their open canopies, low understory, and abundance of dead limbs and trees (Brawn 2006, Frei et al. 2013). Once widespread throughout the region, less than 1% of pre-settlement oak savanna remains intact and un-encroached by denser forest types (Nuzzo 1986). Unknown amounts of oak savanna remain in varying states of woody encroachment due to fire suppression, wetland drainage, and lack of other disturbance that historically maintained oak savannas (Nielsen et al. 2003). The close association with oak savanna and similar open forest systems has been hypothesized as a primary cause of the sharp decline of Red-headed Woodpeckers across their range (Brawn 2006, Koenig et al. 2017). In recent decades, efforts have accelerated across the Midwest to restore oak savannas in places where they historically occurred (Abella et al. 2001). Although many management efforts have succeeded in producing oak savannas that are structurally and aesthetically consistent with historical savannas, the demographic responses of local wildlife populations remain largely unknown. We studied fledgling survival, movements, and cover-type selection in two managed oak savanna ecosystems within the Midwestern United States. Previous studies of Red-headed Woodpeckers have focused on nesting success and nest productivity (Jackson

1976, Ingold 1989, Frei et al. 2015), which is generally high and may not be limiting population growth. Relatively little is known about the post-fledging period in Red-headed Woodpeckers (Frei et al.2015), which is the case for most avian species (Cox et al. 2014). To quantify fledgling survival rates and investigate post-fledging cover-type associations in Red-headed Woodpeckers, we used radio telemetry to monitor movements and fates of fledglings from nests in various cover types within two managed oak savanna systems. Fledgling survival is expected to be greater in species with relatively long nestling period and advanced developmental stage at fledging (Martin 2014). We therefore hypothesized that moderate to low fledgling survival might be a factor contributing to ongoing population declines in Red-headed Woodpeckers. Because Red-headed Woodpeckers are historically associated with oak savanna in our study region, we hypothesized that fledglings from nests in oak savanna would remain in oak savanna and experience the highest survival rates, while fledglings from nests in other cover types would move into oak savanna and potentially experience lower survival before reaching oak savanna.

1.2 Methods

1.2.1 Study Area

We studied Red-headed Woodpeckers at Oak Openings Preserve Metropark, Lucas County, Ohio (hereafter Ohio) and Cedar Creek Ecosystem Science Reserve, Anoka County, Minnesota. The Ohio study site is approximately 20 km^2 comprised of oak savanna (*Quercus alba, Q. velutina, and Q. rubra*), tallgrass prairie (*Schizachyrium scoparium, Andropogon gerardii,* and *Sorghastrum nutans*), mesic upland forest (*Q. bicolor, Q. palustris,* and *Acer rubrum*), and pine-spruce plantations (*Pinus resinosa, P. strobus, P. banksiana,* and *Picea abies*).

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The Minnesota site is approximately 22 km^2 comprised of oak savanna (*Q. macrocarpa* and *Q. ellipsoidalis*), tallgrass prairie (*Schizachyrium scoparium, Andropogon gerardii,* and *Sorghastrum nutans*), mesic upland forest (*A. Saccharum, Tilia americana, Q. rubra, Q. alba, Betula papyrifera,* and *A. rubrum*), and mixed conifer-hardwood forest (*P. strobus, P. resinosa, Q. rubra, Populus grandidentata,* and *A. rubrum*). Both sites are actively managed for oak savanna ecosystems and are located within a matrix of successional forest, forested and open wetlands, agriculture, and rural housing.

1.2.2 Nest Monitoring and Nestling Marking

During the 2017 and 2018 breeding seasons, we studied fledgling Red-headed Woodpeckers from nests we monitored at each site. Nests were located in a variety of cover-types including oak savanna, upland conifer, mesic hardwoods, and mixed deciduous-conifer forests. After discovering nests by watching adult behavior, we monitored nesting cavities using a low-light mini-camera mounted on a 9-m extendable pole modified from previous cavity monitoring designs (Proudfoot et al. 1996, Huebner and Hurteau 2007). Approximately every 3 days, we inserted the camera into each nest cavity to monitor contents and nestling development to predict fledging dates. When nestlings had developed flight feathers but were still predicted to be >3 days from fledging, we accessed cavities using a 12-m free-standing extendable ladder, secured in place using climbing ropes as guy wires attached to surrounding live trees, a method previously described by Rohwer (1988). We removed nestlings from each nest cavity using a modified mechanics tool grabber (Richardson et al. 1999.). We then transported nestlings in a soft cloth bag from the nest cavity to a nearby processing station, usually in a field vehicle.

1.2.3 Nestling Sampling and Radio Transmitter Attachment

We banded each nestling with an aluminum U.S. Geological Survey band and a single plastic color band, recorded mass and wing chord, and collected blood samples to use in genetic analysis to determine the sex of each nestling. We fitted each nestling with a radio transmitter

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(Blackburn Inc., Nacogdoches, Texas) using a modified figure-eight harness design made from elastic jewelry cord (Stretch Magic; Pepperell Braiding Company, Pepperell, Maryland) (Rappole and Tipton 1991, Streby et al. 2015). The 2.41-g transmitters were designed to produce a radio signal for up to 13 months and were ~3.5% of mean nestling mass, a percentage of body mass shown to have no apparent effects on Red-headed Woodpecker behavior (Vukovich and Kilgo 2009). We observed no apparent effects of transmitter attachment on fledglings in comparison to observed unmarked fledglings. Once marking and sampling were completed, we returned all nestlings to the nest cavity and monitored the cavity from the ground for ~30 minutes to note whether force-fledging (i.e., leaving the nest due to our handling activities) occurred.

1.2.4 Fledgling Tracking and Data Collection

Following sampling, we monitored nestlings daily until they fledged from the nest. We located fledglings once daily using ground-based telemetry from late June until mid-August. Following mid-August, we tracked fledglings once weekly until September or until the radio signal was lost, which we assumed to indicate that winter migration or dispersal had likely occurred. During each monitoring event, visual confirmation of each individual was attempted and individuals that we could not see (e.g., occupying dense canopy and not moving) were assumed to be alive until we tracked a bird to the same location for >3 days or signs of predation were apparent (i.e., feathers on the ground, transmitters found with damage, etc.,). When an unseen bird remained in the same location for 3 days, we assumed mortality occurred on the first day at that location. We recorded the date, time, and location of each fledgling observation using a handheld global positioning system (GPS) unit. We also recorded the length of each observation, cover type occupied, behavior (e.g., foraging, perched, vocalizing), foraging technique (e.g., sallying, gleaning), diet (e.g., insects, acorns), perching substrate (e.g., dead tree, species of live tree, branch, main trunk), perch height, and conspecific interactions at each fledgling location.

1.2.5 Survival Rates and Logistic Exposure Models

Using fledgling fates from telemetry data, we modeled dependent fledgling survival, the rate of survival during the period when fledglings are dependent upon parental care, which was ~28 days based on our observations of fledgling-parent interactions. We built logistic exposure models (Shaffer 2004) in R (R Core Team 2018) to estimate fledgling daily survival rates. We considered multiple variables including year, site, age (i.e., days since fledging occurred), fledge date, precipitation events (binary; days where rainfall > 1.27 cm), and nest cover types (savanna or other; Table 1). All models included a random effect of brood to account for non-independence of siblings. Models were then ranked using ΔAICc compared to the best supported model.

1.2.6 Cover-type Selection

To assess whether fledglings demonstrated selection for the cover-type in which their respective nests were located, hereafter "nest cover-type", we recorded the cover-type occupied by fledglings throughout the monitoring period and plotted daily locations in QGIS (QGIS Development Team 2019). We determined cover types at each study site using state land cover classification maps (Minnesota DNR 2019) and cover-type maps we hand digitized from aerial imagery (ESRI 2011) and our own ground-truthing. We created a buffer of 800 m around each nest representing 95% of the maximum distance from the nest any fledgling traveled in the first 28 days after fledging. Within each buffer, we calculated the area of the nest cover type and all other cover types combined, hereafter "non-nest cover type". The number of fledgling locations in the nest cover type and non-nest cover type categories was then tallied for the dependent post-fledging period. We created a selection index using Manly's α (Manly et al. 2007) and compared the use of the two cover-type categories relative to their availability. A larger area of the landscape could have been available for use by each fledgling if we considered cumulative daily distances moved throughout the monitoring period, and the available area likely increased with fledgling development (Streby & Andersen 2013a). However, we limited available space to a

biologically reasonable area after we observed apparent restrictions (i.e., some level of home-range maintenance) on fledgling movements, presumably driven by parental behavior. In Manly's index, α values range from 0-1 with an α value greater than 0.5 indicating selection for a resource (in this case cover type), an α value less than 0.5 indicating selection against, and an α value equal to 0.5 indicating use of a resource in accordance with availability. We calculated cover-type selection for each site, both sites combined, fledglings from nests in oak savanna, and those from nests in cover types other than oak savanna for 2017, 2018, and both years combined.

1.2.7 Movement Patterns and Directionality

We determined distance from nest and minimum daily distance traveled for each daily fledgling location using QGIS (QGIS Development Team 2019). To test for circular uniformity and directionality of fledgling movements during the first 28 days post-fledging, we performed Kuiper's test and Rayleigh's test using the "CircStats" package in R (R Core Team 2018) as these tests have valuable applications in ecology (Fisher & Lee 1992, Mutwiri et al. 2016). Kuiper's test compares the distribution of directional data to a theoretical uniform distribution while Rayleigh's test determines whether directional data are uniformly or unimodally (i.e., are concentrated around one direction) distributed (Batschelet 1981).

1.3 Results

1.3.1 Fledgling Survival

We deployed 55 radio transmitters on fledgling Red-headed Woodpeckers during the 2017 (OH: $n = 9$, MN: $n = 15$) and 2018 (OH: $n = 17$, MN: $n = 14$) breeding seasons from 32 nests (OH: $n = 12$, MN: $n = 20$). In 2017, dependent fledgling survival was 0.60 in Minnesota and 0.56 in Ohio. In 2018, dependent fledgling survival was 0.64 in both Minnesota and Ohio. Of the 21 recorded mortalities, 86% occurred due to predation and 14% occurred due to exposure. Fledglings that force-fledged ($n = 6$; due to underestimation of nestling development) had high survival, similar to the rest of the sample.

Daily survival rates were lowest in the first 5 days post-fledging at ~0.98 and increased to >0.99 at 12 days after fledging, well within the parental dependent phase, with no mortalities observed past 50 days (Fig. 1-1). The logistic exposure model including only a random effect for brood and a quadratic effect for age was the best supported model of fledgling daily survival. All other models performed relatively poorly (Table 1-1).

1.3.2 Cover-type Selection

Using 826 daily locations for 53 fledglings during the first 28 days post-fledging, selection indices and Manley's α showed that fledglings select for their respective nest cover-types and select against non-nesting cover-types (Table 1-2). This selection was consistent between sites, years, and regardless of whether fledglings were from nests in oak savanna or other cover types.

1.3.3 Movement Characteristics

Using 1,042 locations for 53 fledglings following 74 days post-fledgling, fledgling distance from nest was increased with age both during the parental dependent phase (1Q: 50 m, median: 85 m, 3Q: 136 m) and once fledglings were independent (1Q: 61 m, median: 129 m, 3Q: 412 m). Similarly, minimum daily distance traveled increased with age both during the parental dependent phase (1Q: 26 m, median: 57 m, 3Q: 102 m) and once fledglings were independent (1Q: 19 m, median: 64 m, 3Q: 145 m). These trends were consistent between sites and years (Fig. 1-2). Overall, mean distance from nest was greater in Minnesota than Ohio, with mean distance from nest increasing up to 1600-m around day 53 and in comparison, the maximum mean distance from nest in Ohio was just below 400-m around day 34.

We used angular data to create rose plots showing the distribution and frequency of fledgling movements (Fig. 1-3). The distribution of turning angles of fledgling locations did not differ from a uniform distribution between sites, years, and with all of the locations combined (Kuiper's tests: all $p > 0.15$). Fledglings turning angles did not indicate any particular direction of

movements, with all sites and years failing to reject the null hypothesis (Rayleigh tests: all $p >$ 0.05).

1.4 Discussion

1.4.1 Fledgling Survival

Red-headed woodpecker fledgling survival rates were consistent between sites and years, averaging 0.62 for the period of adult care. Daily survival was high compared to most published estimates of fledgling songbirds (Anders et al. 1997, King et al. 2006, Ricklefs 1968) and woodpeckers (Cox & Kesler 2012, Robles et al. 2007), with the lowest rate of survival occurring during the first few days post-fledging, consistent with many fledgling studies (Anders et al. 1997, Berkeley 2007, Ricklefs 1968). This high fledgling survival is consistent with predictions based on the long nestling development period of the species (Martin 2014). Nest cover type was not a meaningful predictor of fledgling survival, indicating that fledgling survival is consistent from nests across our study sites. High fledgling survival, combined with the high rates of nest success at our study sites (E. West and R. Pagel, unpublished data), either indicates that regional population declines are due to factors outside of the breeding season, or may explain why the populations at our study sites are apparently stable in recent years despite broader-scale declines. Research on nesting and post-fledging ecology at additional sites, and study of non-breeding factors in our study populations, will be necessary to clarify which of those is true.

1.4.2 Cover-type Selection

Fledglings selected their respective nest cover-types over non-nesting cover-types during the first 28 days post-fledging despite nesting cover-types not being consistent among nesting pairs. Even fledglings from nests located in non-savanna cover-types demonstrated selection for their nest cover-type and did not select for savanna. This may be a byproduct of parental care as parental home ranges may keep fledglings close to the nest due to parental dependence or it may be due to fledgling familiarity with the nest cover-type. Red-headed Woodpeckers are often

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associated with savannas, but our results suggest that fledglings can be successfully raised to independence in cover types that are not savanna and fledgling cover-type preference may be plastic or inherited.

1.4.3 Movement Characteristics

Fledgling movement, measured in terms of minimum daily distance and daily distance from the nest, increased with age, a trend that is common throughout passerines and near-passerines (del Mar Delgado 2009, Peterson 2014). This pattern was consistent between sites and years. The small extent of these daily movements during the dependent post-fledging period suggests that Red-headed Woodpeckers may have a true all-purpose breeding home range for nesting and raising of fledglings. During 2018 in Minnesota, several fledglings from different broods moved >2.5 km away from their respective nests across the study site. These movements occurred greater than 55 days post-fledging, indicating that independent dispersal may be occurring. Dispersal of fledglings following the parental dependence period at this scale could indicate that small patches of oak savanna may not be adequate to retain fledglings that originate from a population following dispersal.

Kuiper's and Rayleigh's tests indicated that fledgling movements during the first 28 days post-fledging were uniformly distributed because the null hypothesis (that each distribution was uniform) was not rejected with either test (Table 1-3). This uniform distribution may be a byproduct of parental care, as fledglings are dependent upon their parents during the first 28 days post-fledging and have no need to make continuous directed movements (i.e., go somewhere other than the established parental home range). Similar behavior has been seen in owlets (del Mar Delgado et al. 2009), however, directional movement has been seen in fledgling songbirds during the dependent phase (Peterson 2014). This difference may be attributable to duration of territoriality, with some birds seeming to dissolve territorial boundaries immediately after nesting (Streby & Andersen 2013b; Vitz & Rodewald 2010), while others maintain all-purpose territories

throughout the breeding season (Krebs & Kacelnik 1983). The woodpecker movements we observed seem to fall somewhere between these extremes, with the maintenance of a home range and association with nesting cover type, but movements that overlapped with other fledglings and extended well beyond neighboring nest locations.
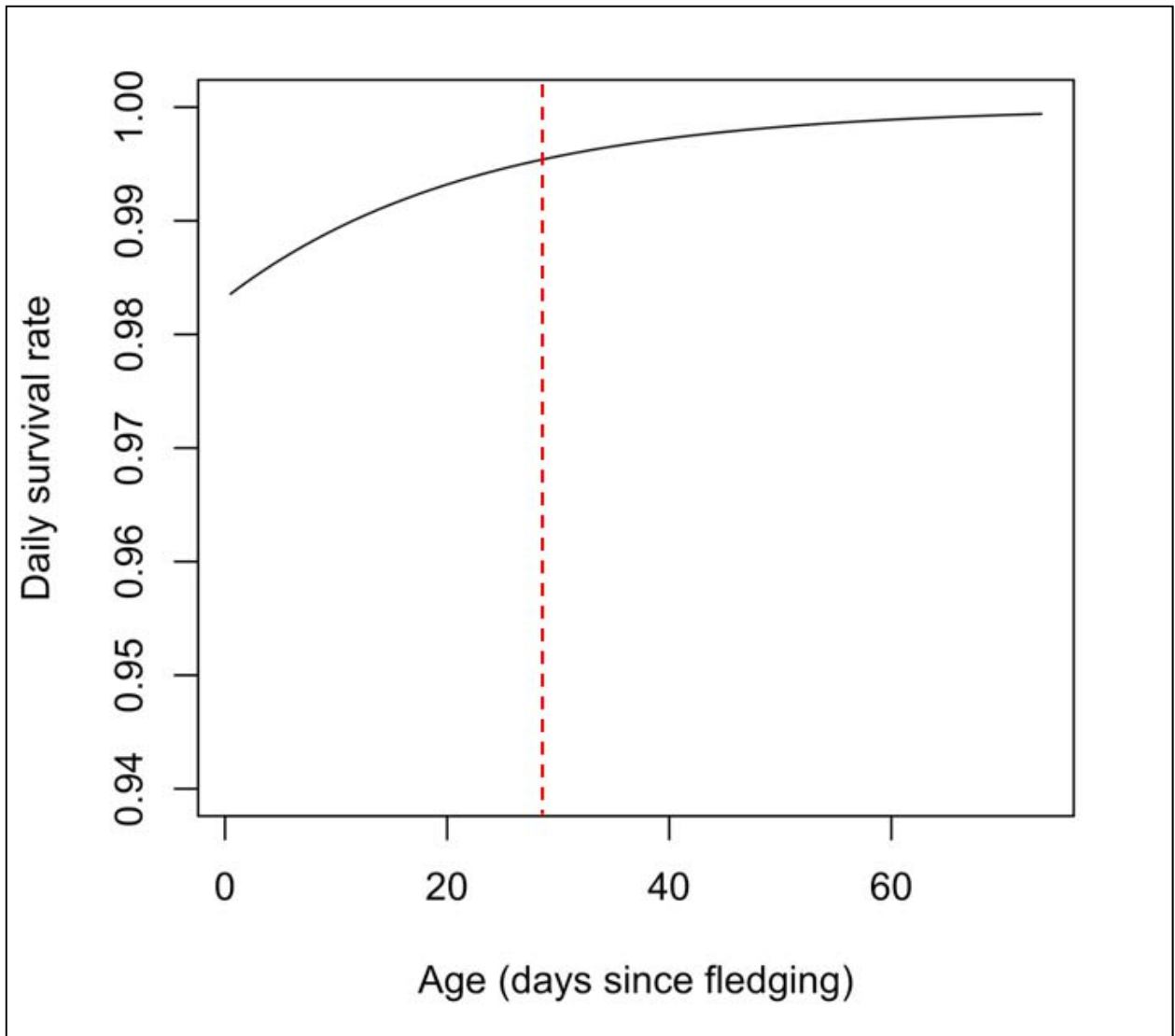
Figure 1-1 Daily survival rate curve for fledgling Red-headed Woodpeckers during the 2017
and 2018 breeding seasons in Ohio and Minnesota. Estimates produced from the
best-supported logistic exposure model which included a random effect for brood
and a quadratic age term. Dotted red line indicates end of the parental dependence
phase and beginning of the independent phase at day 28.
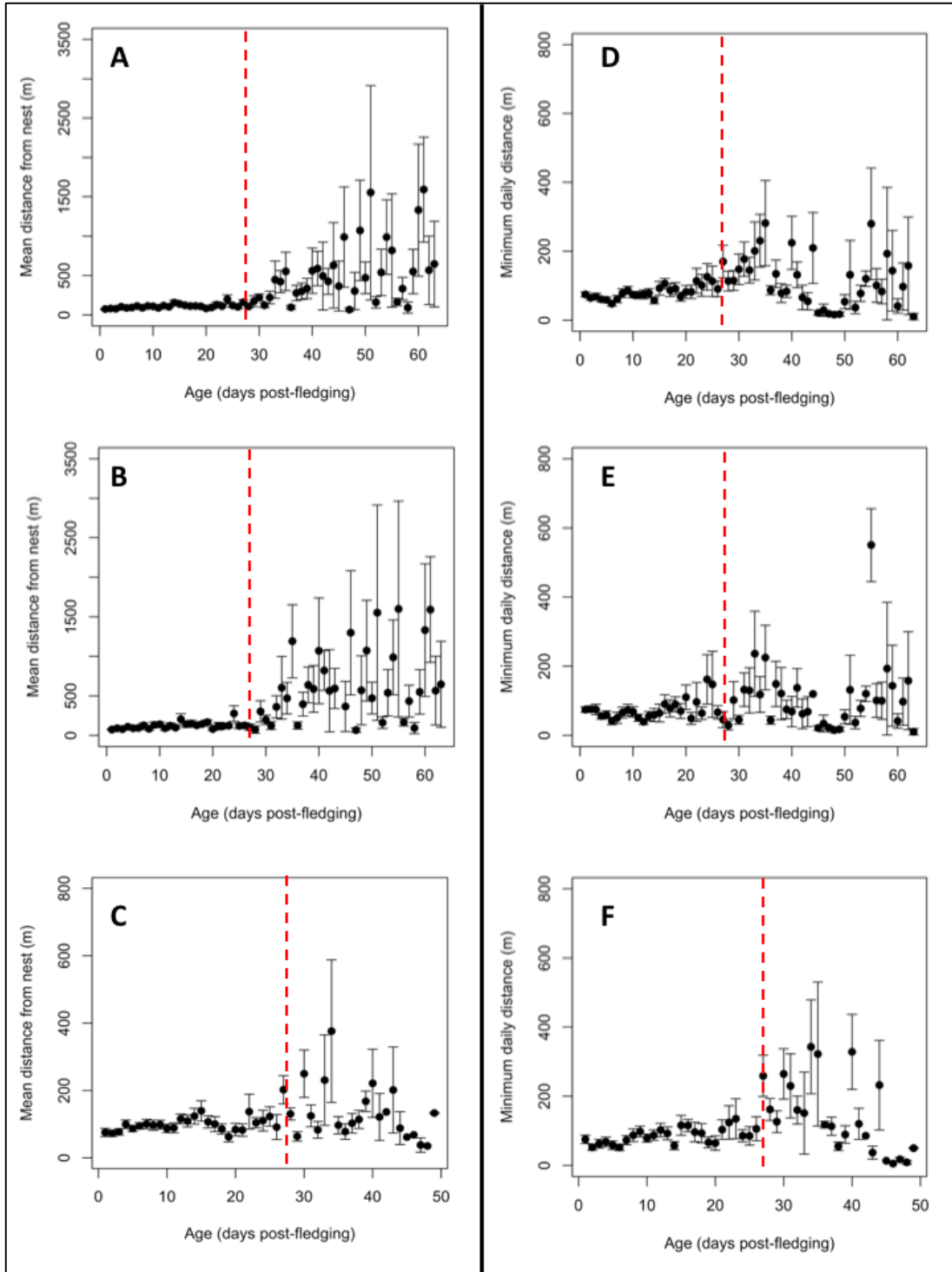
Figure 1-2   Mean distance from nest for Red-headed Woodpecker fledglings in 2017 and 2018 at both study sites (A), Minnesota (B), and Ohio (C). Minimum daily distance from last location for fledglings at both study sites (D), Minnesota (E), and Ohio (F). Dotted red line indicates end of the parental dependence phase and beginning of the independent phase at day 28.

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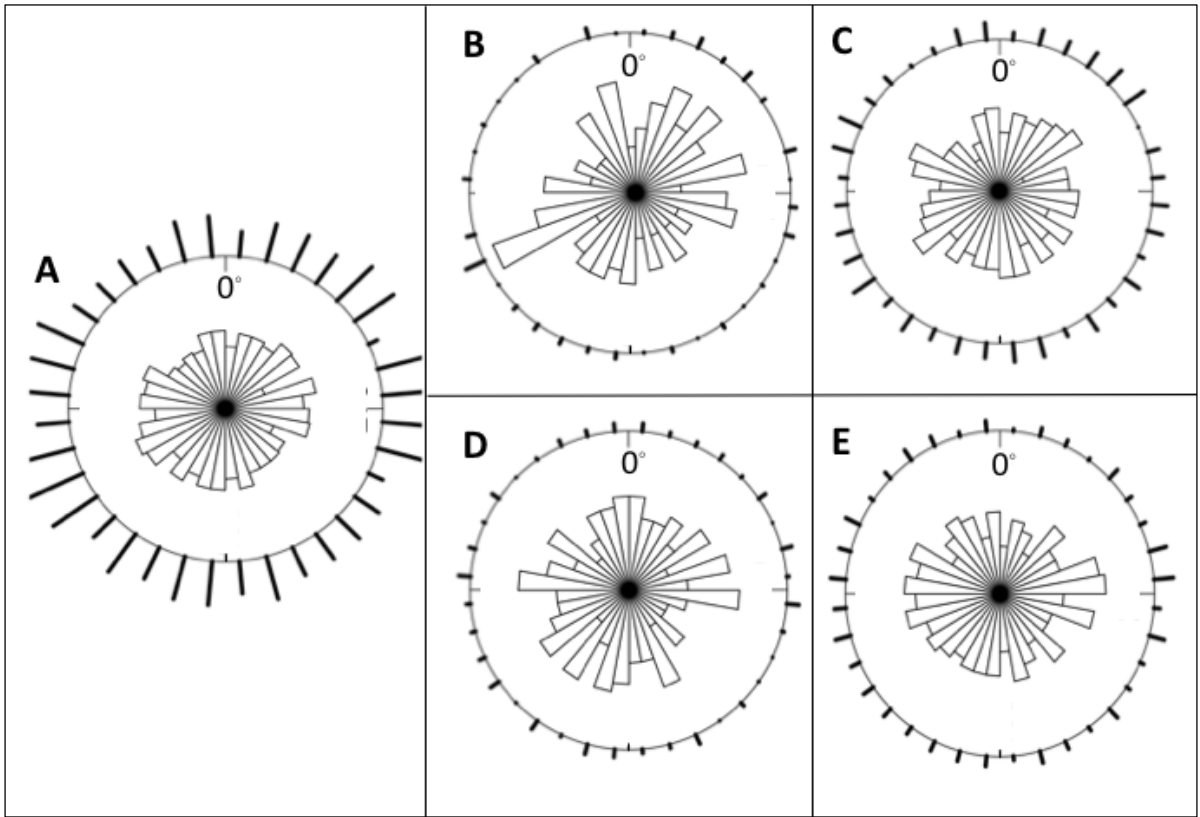
Figure 1-3 Distribution of bearings for Red-headed Woodpecker fledgling locations at all sites and years combined (A), Ohio 2017 (B), Ohio 2018 (C), Minnesota 2017 (D), Minnesota 2018 (E). Fledgling locations are during the first 28 days post-fledging.

Model	K	ΔAIC_c	ω	-2*Log-likelihood
Age[a]	3	0.00	0.54	159.8
Intercept-only[b]	2	2.81	0.13	164.6
Cover type	3	3.25	0.11	163.1
Precipitation	3	3.52	0.09	163.3
Fledge date	3	4.05	0.07	163.9
Site	3	4.80	0.05	164.6

[a]The AIC_c value for the top model was 165.84.
[b]Null model

Table 1-1   List of logistic exposure models with age as the top model.

	2017	2018	Both Years
Ohio	$\alpha = 0.83$	$\alpha = 0.89$	$\alpha = 0.87$
Minnesota	$\alpha = 0.95$	$\alpha = 0.87$	$\alpha = 0.91$
Both Sites	$\alpha = 0.91$	$\alpha = 0.88$	$\alpha = 0.89$
Savanna nest	$\alpha = 0.96$	$\alpha = 0.92$	$\alpha = 0.94$
Non-savanna nests	$\alpha = 0.70$	$\alpha = 0.83$	$\alpha = 0.81$

Table 1-2 Manly's α selection values for nesting cover-type. All values are between 0 and 1, with values > 0.5 indicating selection for and values < 0.5 indicating selection against.

	Kuiper's		Rayleigh	
	statistic	p-value	statistic	p-value
Combined	1.096	> 0.15	0.0266	0.496
Minnesota 2017	1.0178	> 0.15	0.0602	0.6286
Minnesota 2018	1.2158	> 0.15	0.0559	0.522
Ohio 2017	1.1667	> 0.15	0.0264	0.9267
Ohio 2018	1.1213	> 0.15	0.0334	0.718

Table 1-3   Circular uniformity tests performed on fledgling bearings between locations for the first 28 days post-fledging.

Chapter 2

Facultative Migratory Movements in Red-headed Woodpeckers and Consequences for Conservation

2.1 Introduction

Migration is a behavior used by individuals and populations to access resources that may be spatially or temporally limited. Migration can be classified as facultative or obligate, with facultative migration occurring intermittently and obligate migration occurring regularly. Obligate migration is thought to have a genetic basis Berthold et al. 1992, Newton 2012). Due to the irregularity of facultative migration, little is known about the intrinsic and extrinsic factors controlling this behavior (P Berthold 2001, Newton 2012). In general, facultative migration occurs in populations that experience seasonally fluctuating, but year-round, presence of food on the breeding site (Winger et al. 2018), but can occur due to other factors such as weather events (Boyle et al. 2010, Streby et al. 2015). Facultative migrants are often characterized by varying proportions of the population migrating annually. Furthermore, this migration tends to be highly variable with regard to timing, distances, and direction compared to obligate migration (Newton 2012). The inherent variability in individuals' migration behaviors in populations of facultative migrants presents challenges when attempting to identify

migration timing, distance, routes, and the location of wintering sites. This limits our ability to understand how those metrics might contribute to population trends.

One facultative migrant in eastern North America is the red-headed woodpecker (*Melanerpes erythrocephalus*). These charismatic cavity-nesters are commonly associated with oak savanna ecosystems and other open forest systems (Rodewald et al. 2005; Smith et al. 2000) which have nearly been lost due to land use changes since European settlement (Nuzzo 1986). Over the past 50 years the red-headed woodpecker has declined by 70% across its breeding range and is listed as Near Threatened by the IUCN (Sauer et al. 2013). Many explanations have been hypothesized for this decline, including increased rates of predation due to elevated *Accipiter* populations (Kilgo & Vukovich 2012, Koenig et al. 2017), loss of habitat and the clearing of dead trees which are used for nesting and roosting (Smith et al. 2000), increased competition for cavities from introduced species such as European starlings (*Sturnus vulgaris*) (Graber et al. 1977), and vehicle collisions due to the species' low aerial foraging behavior (Eifrig 1937). All of these hypotheses are generally focused on breeding season factors, and as with many migratory birds, relatively little attention has been paid to migration and wintering ecology. Determining where distinct breeding populations spend the nonbreeding portions of their annual cycle can help us understand population trends that would otherwise be unclear (Kramer et al. 2018) and is critical for land management efforts aimed at conserving red-headed woodpeckers and other oak savanna specialists.

The migration strategies of red-headed woodpeckers have been described as semi-migratory (Ingold 1991), nomadic (Smith 1986), and short-distance (Herkert 1995). Knowledge related to autumn movements of red-headed woodpeckers has largely been

anecdotal (Smith et al. 2000) and has focused on variation in food resources (i.e., annual mast production) as the primary factor hypothesized to drive whether individuals or populations leave a breeding site in autumn (Smith & Scarlett 1987). Banding records from the early to mid-twentieth century indicate that fall migration does occur on scales not previously quantified through individual tracking, but these records are uncommon (<10 since 1927) and do not provide much spatial or temporal resolution (USGS 2019). A recent radio telemetry study tracked red-headed woodpeckers during autumn migration in South Carolina and found annual variation in migration within their study population, and both short distance (<30 km) and long distance (>30 km) migration, however long distance migration was unknown past 30 km because individuals were outside of radio telemetry range (Vukovich & Kilgo 2013). To our knowledge, there have been no other efforts to track red-headed woodpecker movements outside of the breeding period. Newly developed lightweight GPS tags have been useful for identifying nonbreeding season movements in other avian species (Fraser et al. 2017, Hallworth & Marra 2015, Siegel et al. 2016), and now present an opportunity to better understand important stages in the annual cycle of declining species such as the red-headed woodpecker.

To start filling the knowledge gap regarding red-headed woodpecker migration strategies and to identify how habitat associations during the migration and the wintering season may influence populations, we used GPS tags to study proportions of individuals migrating, migration routes, wintering sites, and the timing associated with migration in two populations breeding in the Midwestern United States. Based on long-term monitoring at one of our sites, we expected anywhere from 0 to 100% of birds to leave the breeding sites in autumn (J. Howitz, pers. comm. 2019), but we had little information

on which to base hypotheses about migration timing, routes, distance, or habitat used outside the breeding period.

2.2. Methods

2.2.1 Study Area

We studied red-headed woodpecker breeding populations at two study sites, Oak Openings Preserve Metropark, Swanton, Lucas County, Ohio, USA (hereafter Ohio; 41° 33'N, 83° 51'W) and Cedar Creek Ecosystem Science Reserve, Bethel, Anoka County, Minnesota, USA (hereafter Minnesota; 45° 24'N, 93° 11'W). Both sites are actively managed for oak savanna and are home to breeding and wintering populations of red-headed woodpeckers. The Ohio site is dominated by oak savanna (*Quercus bicolor* and *Q. palustris)* within a mosaic of mesic hardwoods, tallgrass prairie, and sand barrens. The Minnesota site is comprised of oak savanna (*Q. macrocarpa; Q.* spp.), sand prairie, and dry oak woodland (*Q. ellipsoidallis*; *Q.* spp.). Both sites originated from glacial sandplains and are located within a matrix of successional forest, wetlands, agriculture, and rural housing.

2.2.2 Woodpecker Capture and Pinpoint GPS Deployment

From May - August 2017, we captured 84 breeding adult red-headed woodpeckers in Ohio ($N = 32$) and Minnesota ($N = 52$) using mist-nets, potter traps baited with peanuts, and hoop nets at roosting and nesting cavities (Jackson & Parris 1991). We marked each individual with an aluminum U.S. Geological Survey band and a unique combination of 3 plastic color bands. We fitted 41 of these birds in Ohio ($N = 21$) and Minnesota ($N = 20$) with a 1.5-g GPS tag (Biotrak PinPoint-10; Wareham, UK) using a modified figure-eight harness made from elastic jewelry cord (Stretch Magic; Pepperell

Braiding Company, Pepperell, Maryland) (Rappole & Tipton 1991, Streby et al. 2015). Including the harness, markers were 3.1% of mean body mass of tagged individuals. Four individuals in Ohio ($N = 1$) and Minnesota ($N = 3$) that we observed to have lost their GPS tags during the 2017 breeding season were reclassified as control birds. In total, 47 adult woodpeckers (Ohio: $N = 12$, Minnesota: $N = 35$) comprised as the control group to test for possible marker effects on migration behavior and survival. All birds were aged based on plumage (Pyle & Howell 1995). As part of an additional study, sex of each individual was genetically determined using blood samples because this species is monomorphic to human observers. All woodpecker capture and handling methods were approved by Institutional Animal Care and Use Committee protocols at the University of Toledo (Protocol #108708) and the University of Minnesota (#1406-31581A).

We programmed GPS tags to record location estimates, hereafter "locations," once per week during the summer and winter months (May-August, December-February) and once every three days during the months in which we expected migration might occur (September-November, March-April). We conducted site-wide surveys (i.e., walked established routes through all areas at our sites known to be used by red-headed woodpeckers) during the breeding season ($N \geq 1$ survey/week during April – August) and wintering season ($N = 2$ surveys during December – February) to verify which individuals remained during the winter (i.e., did not migrate). Red-headed woodpeckers are relatively large, visually and vocally conspicuous, and occupy open forest systems at our study sites. We therefore assumed our surveys resulted in a complete or near complete census of banded birds present on our sites during breeding and wintering seasons.

We also included a mark-control comparison of migration rates and apparent survival between breeding seasons to investigate potential marker effects of pinpoint GPS tags because these markers and our marking methods are recent developments with, to our knowledge, untested application in woodpeckers.

2.2.3 Data Processing

Following recapture of GPS-tagged individuals during the breeding season in 2018, we downloaded and analyzed data using the software provided from the manufacturer. Due to substantially shorter battery life than expected in these newly developed tags, no tag lasted through the full programmed schedule and each stopped collecting data between December and February. Therefore, we did not obtain any location data during spring migration. GPS locations included an error estimate (horizontal dilution of precision, hereafter "hdop"). We excluded locations that had hdop values greater than 25 as these are considered unreliable (Langley 1999). However, breeding season locations with hdop values between 5 and 25 (i.e., purported high level of uncertainty) occurred within the normal range of breeding season movements demonstrated by locations with high accuracy (hdop < 5), suggesting these locations are likely useful for identifying general use areas (i.e., within ~100m) during migration or wintering periods. We plotted locations for each individual and determined the predominant land cover-type in QGIS 3.0 using the National Land Cover Dataset (QGIS Development Team 2019). We then determined migration status (i.e., migratory or sedentary), departure date, minimum distance traveled, sites used during migration, and wintering sites for each individual. We categorized individuals as migratory if they left the breeding site and were not observed on the study sites during winter surveys. We

categorized individuals as sedentary if they were present on the breeding site during winter surveys. We compared proportions of migrating individuals and apparent survival between tagged and control birds using a chi-square test with the 'chisq.test' function in R (R Core Team 2018). We estimated departure date to be the date between the last location taken on the breeding site and the first location away from the breeding site. We calculated minimum distance traveled as the straight-line distance between chronological points and defined migratory locations as single locations away from the breeding site. We defined wintering sites as sites away from the breeding site where multiple GPS locations were recorded, indicating the individual had settled for a period greater than one week at the site.

2.3 Results

We conducted our analyses with a sample size of 77 adult birds, comprised of 31 GPS-tagged birds (14 in Ohio and 17 in Minnesota) and 46 control birds (11 in Ohio and 35 in Minnesota). We did not include seven individuals (6 GPS-tagged and 1 control) in the migration analysis due to vehicular mortality ($N = 1$ GPS-tagged) and apparent movement outside our study site ($N = 5$ GPS-tagged and 1 control) as they did not survive, or in the case of those that apparently emigrated, could not be confirmed to have survived the breeding season or to be likely to return to our study sites in 2018 if they show breeding site fidelity. All six of the birds that apparently emigrated were captured within the first three weeks of our 2017 marking efforts, and it is unclear if this dispersal is due to a marker effect or is a byproduct of capture before breeding territories were defined.

2.3.1 Migration and Return Portions

Proportions of red-headed woodpeckers migrating differed between the two study

sites, with 72% (18 of 25) of individuals migrating from the Ohio population and 0% (0

of 52) of individuals migrating from the Minnesota population. The proportion migrating

in the Ohio population did not differ between birds with GPS tags and control birds

marked only with leg bands (tagged =71%, control = 73%; $\chi^2_{1,25}$= 0.005, p = 0.94). No

apparent differences in sex with relation to migratory status were found in Ohio with 10

males and 8 females migrating, and 2 females and 5 males remaining sedentary, but

sample sizes were too small for statistical comparison (Fig. 2-1). Of these migrating

individuals, 40% (4 of 10) of tagged birds and 63% (5 of 8) of control birds returned to

the breeding site the following spring. We found no evidence of an effect of harnesses or

markers on migration return ($\chi^2_{1,18}$= 0.9, p = 0.34) though we note that these sample sizes

are small and lack statistical power.

2.3.2 Migration Timing and Movements

During the summer of 2018, we recaptured a total of 12 tagged red-headed

woodpeckers and recovered their GPS tags (7 in Ohio and 5 in Minnesota). Five

additional individuals were regularly observed with GPS tags in 2018, but eluded

recapture despite substantial efforts. Of the 12 recaptured individuals, a total of 3 GPS

tags, all from Ohio, included data indicating that migration had occurred during the prior

year. GPS data for all 5 Minnesota individuals and the remaining 4 Ohio individuals

confirmed our observations that they remained on our study sites for the duration of the

breeding season and wintering season.

Locations from the 3 Ohio birds that migrated indicated that those individuals

departed the breeding site during the first 3 weeks of September and arrived at their

respective wintering sites within 15 days (Table 2-1). All 3 individuals departed the

breeding grounds in a generally southward direction, with a mean distance of 136 km

between locations recorded every 3 days during migration. Woodpecker locations during

migration spanned 3 states (Ohio, Indiana, and Kentucky) with wintering sites located

111 to 218 km from the breeding site. Sites occupied during migration and winter were

small (mean area = 14 ha, range = 4 - 74 ha), dense successional hardwood forest patches

within landscapes dominated by agricultural fields. Of the 33 GPS locations recorded

during autumn migration and the wintering season, 32 (97%) were in successional

hardwood forest patches and the remaining location was an area of oak savanna (180 ha)

that was used briefly during migration.

Additionally, 3 Ohio birds (two sedentary and one migratory) made one-time

movements (i.e., a single GPS location away from the winter site with both the preceding

and following GPS locations on respective wintering sites) during the winter (Table 2-2).

One-time movements occurred in all seasons for which GPS data were recorded with

both sedentary and migratory individuals exhibiting this behavior. One migratory

individual made 3 one-time movements ranging from 6 km to 80 km from the wintering

site to other successional hardwood patches and rural backyards, but preceding and

subsequent GPS locations, 7 days apart, were on the wintering site. Each of the locations

for these one-time movements had low hdop values (< 5), indicating they were all

accurate and not the result of GPS error.

2.3.3 Apparent Survival Between Seasons

We re-sighted 60% (15/25) of marked individuals in Ohio and 54% (28/52) in

Minnesota during the 2018 breeding season. Tagged birds did not differ in apparent

survival compared to control birds at both sites (Ohio tagged = 57%, Ohio control = 64%, $\chi^2_{1,25} = 0.108$, $p = 0.74$; Minnesota tagged = 53%, Minnesota control = 54%, $\chi^2_{1,52} = 0.008$, $p = 0.92$). Migratory individuals (N=18) had a wintering survival rate of 0.50 and sedentary individuals (N=59) had a wintering survival rate of 0.58 ($\chi^2_{1,77} = 0.325$, $p = 0.568$), exhibiting no significant difference.

2.4 Discussion

Facultative migration is used to access resources in a different location that may be seasonally scarce, but still present on the breeding site, during the nonbreeding season. This migration strategy is thought to be an adaptation for survival in seasonal environments (Winger et al. 2018). Like most facultative migrants, very little is known about where individual red-headed woodpeckers migrate to, and how these wintering sites may affect their survival. Here, we discuss the characteristics of facultative migration in red-headed woodpeckers, where they migrate to, and how the wintering site selection of migratory individuals may have implications on their survival.

2.4.1 Migration and Return Proportions

Proportions of red-headed woodpeckers that migrated differed between our study sites, with 72% of individuals from Ohio migrating and no individuals from Minnesota migrating. Variation in migration proportions both among years and among populations has been observed range-wide through Christmas Bird Count data and using mark-recapture methods (Smith 1986, Vukovich & Kilgo 2013). Long-term monitoring at our Minnesota study site indicates that annual migration proportions range from nearly 0% to nearly 100% (J. Howitz, pers. comm. 2019). Additional years of marking individuals

with GPS tags at both sites are needed to examine annual variation in frequency, proportions, and individual variation of migration.

Fifty percent of individuals that migrated returned to the breeding site the following spring, a percentage similar to that of birds that remained on the breeding site for the entire year. In passerines, re-sighting/recapture rates can vary strongly among populations (Martin et al. 1995) and our apparent return proportions may be low due to the variable nature of facultative migration behavior. It is unknown if tagged or control individuals that did not return to the breeding site in 2018 did not survive the winter, or if they dispersed to a different breeding site, and such unknown fates complicate efforts to determine rates of survival (Lebreton et al. 1992). Breeding site fidelity in red-headed woodpeckers has been disputed with some suggesting no population is resident to a specific area (Smith et al. 2000). However, recent studies using radio transmitters suggest that some individuals may winter short distances (< 30 km) away and return to the same breeding site the following spring (Vukovich & Kilgo 2013). Our results confirm frequent breeding site fidelity on larger spatial scales (i.e. after migrating > 200 km from their breeding site), however we are unsure of the ratio of birds in a population that exhibit this site fidelity due to the unknown fate of migratory individuals that we did not re-sight. Future research with GPS tags that enable satellite recovery of data, and therefore do not require recapture for data collection, will be of particular importance in addressing questions of dispersal in migratory birds.

2.4.2 Migration Timing, Routes, and Distances

GPS locations of the three migratory individuals revealed similar dates of departure, with all leaving during a 16-day period in early to late September. Additional

years of study would be necessary to determine whether this timing is consistent. All three individuals wintered south of the breeding site, and the first locations away from the breeding site were in a southernly direction; however, no patterns were apparent in subsequent locations relating to direction or distance (Fig. 2-2). Migratory movements appeared nomadic, with individuals likely prospecting for different wintering sites in many directions. This suggests that wintering locations are not pre-determined before migration as they tend to be for many obligate migratory birds (Newton 2012). For example, one red-headed woodpecker migrated >300 km south to northern Kentucky before returning 150 km north in a span of 6 days. Erratic and seemingly indeterminate movements before, and even after, selecting a wintering site suggest that individuals are either searching for wintering sites that meet specific criteria or may be encountering competition from conspecifics or other species with which agonistic interactions have been observed during winter such as blue jays (*Cyanocitta cristata*), white-breasted nuthatches (*Sitta carolinensis*), downy woodpeckers (*Dryobates pubescens*), or fox squirrels (*Sciurus niger*) (Doherty Jr. et al. 1996).

We report total minimum distances traveled from the breeding site to wintering sites which exceed previous known migration distances of red-headed woodpeckers (Vukovich & Kilgo 2013). That individual woodpeckers from the same breeding population migrated different distances is consistent with previous findings (Vukovich & Kilgo 2013) and suggests that migration in red-headed woodpeckers is a plastic behavior dependent upon extrinsic factors.

2.4.3 Wintering and migration site selection

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We found that migrating red-headed woodpeckers used small successional patches of hardwood forest both during migration and for wintering sites (Fig. 2-2). This may be due to a lack of available oak savanna in northwest Ohio through which individuals migrated, but it may also be indicative of different habitat requirements or associations during the migration and winter periods compared to the breeding period. One individual we tracked used a patch of oak savanna in northern Kentucky during migration before moving back north and settling at a wintering site composed of successional hardwood forest in west-central Ohio (Fig. 2-2). The apparent affinity for successional hardwood forests (97% of migratory and wintering locations) by migrating red-headed woodpeckers during migration and the wintering season could be associated with historical and potential future population declines if historic declines in forest cover in this region continue.

2.4.4 One-time Movements of Individuals

In the Ohio population, three individuals (two sedentary and one migratory) made one-time movements off their respective breeding and wintering sites (Table 2-2). These movements have not been previously described in red-headed woodpeckers and suggest that prospecting for potential wintering sites, or possibly for potential future breeding sites, may still occur during the breeding, autumn, and winter seasons. No similar movements were seen in the Minnesota population (which had no migration during our study), suggesting that these one-time movements may be exploratory flights made in years were resources are scarce enough to cue facultative migration. We are unaware of other examples of one-time movements from wintering sites in facultative migrants and

additional study of this behavior would be beneficial in understanding the drivers of migration in this species.

2.4.5 Apparent Survival Between Seasons

Our recapture and surveying efforts indicated that winter survival rates were similar between migratory and sedentary red-headed woodpeckers. There is little empirical research on survival outside of the breeding season for red-headed woodpeckers (Doherty Jr. et a. 1996), and our winter survival rates include autumn and spring migration, a time when mortality may be much higher than other periods of the annual cycle (Sillett & Holmes 2002). Additional years of study are needed to strengthen estimates of winter survival rates to account for temporal variations in migratory frequency and the potential carryover effects from a previous season of migration or extrinsic factors on the winter site (Harrison et al. 2011, Legagneux et al. 2011).

2.4.6 Conservation Implications of Wintering Site Selection

In recent decades, efforts have been made to restore oak savanna in areas where it previously existed (Abella et al. 2001), resulting in positive effects on local red-headed woodpecker breeding numbers (Brawn 2006). While this association with oak savanna is of importance during the breeding season, we observed individual red-headed woodpeckers using relatively small patches of successional hardwood forests, and not oak savanna, as stopover and wintering sites (Fig. 2-2). Northwestern Ohio has remained predominately agricultural since forests were cleared for settlement (Deines et al. 2016), a trend that may have caused individuals to shift to hardwood forests associated with agricultural areas rather than exert energy finding rare, isolated, and distant oak savanna patches. This shift in wintering site availability from oak savanna to small fragments of

successional forest may increase mortality for wintering individuals due to increased

competition for roosting cavities from European starlings, increased *Accipiter* predation,

and increased vehicle strikes due to the regular proximity of these small forest patches to

roads. In northwest Ohio, nearly half of forest land patches are less than 50 acres (Ohio

Department of Natural Resources 2010, Widmann et al. 2009). *Accipiter* predation of

red-headed woodpeckers has been associated with increasing forest cover (Koenig et al.

2017) and these small parcels of successional forest present a concentrated area where

Accipiter predation may occur. Vehicle strikes represent a large source of mortality at our

study sites, with 5 individuals succumbing to vehicle-related injuries over a two-year

period. Over 75 % of the forest land in northwest Ohio is within 90 m (295 feet) of the

forest edge (Ohio Department of Natural Resources 2010; Widmann et al. 2009). The

size of these small successional patches used by migratory individuals as wintering sites

may be increasing the probability of vehicle-related mortalities due to their closer

proximity to roadways than the breeding sites. Together, these factors represent potential

sources of winter mortality that may be exacerbated by the size and structure of wintering

sites available to migratory individuals.
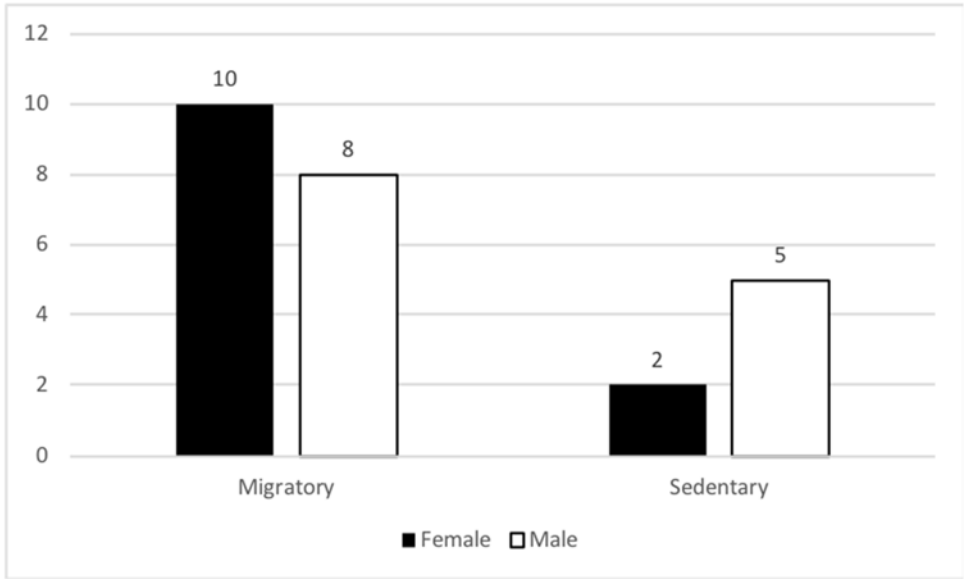
Figure 2-1 Migratory and sedentary red-headed woodpeckers between the 2017 and 2018 breeding seasons in Northwest Ohio. Minnesota birds are not included because migration did not occur in that population during our study.
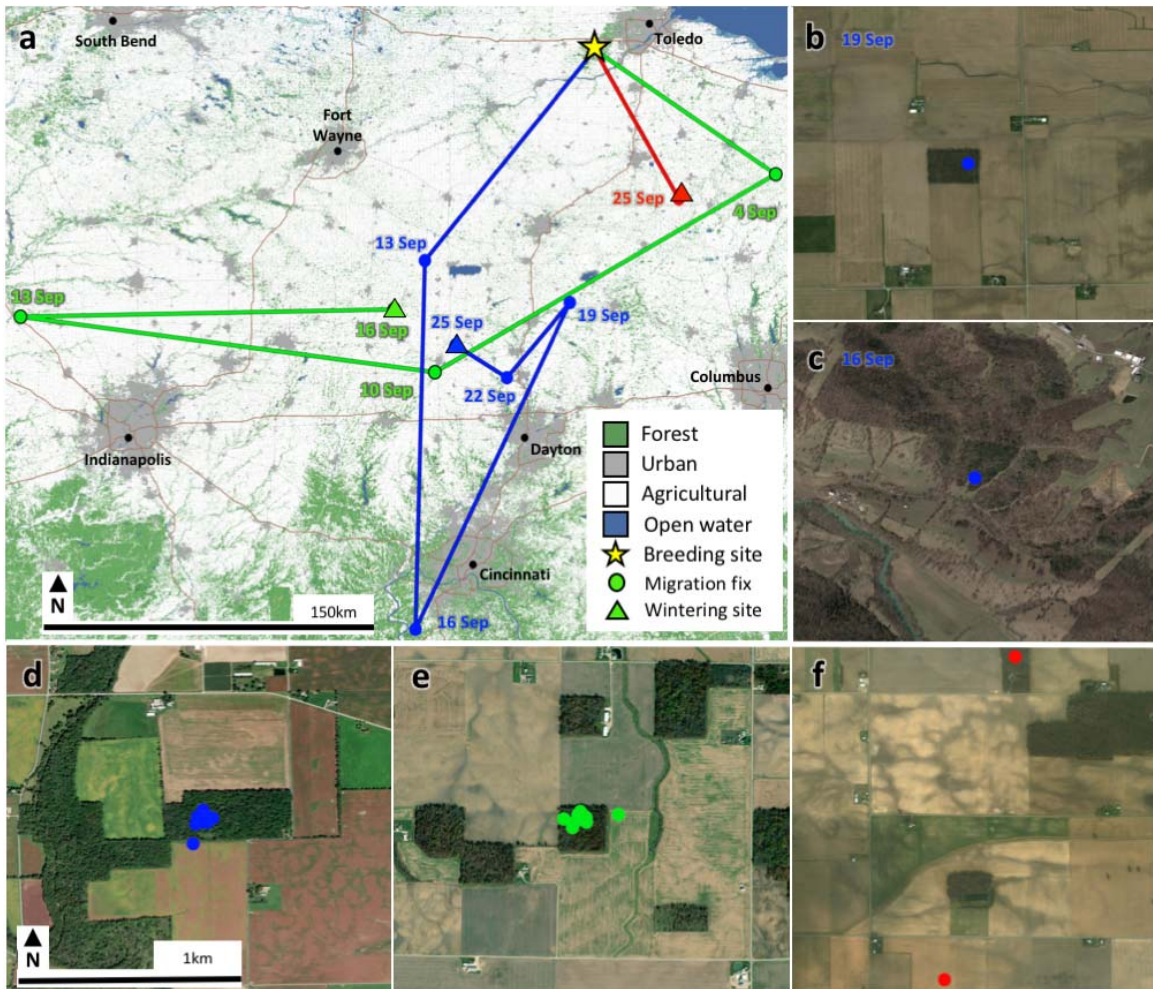
Figure 2-2 Migration routes (**a**), migratory stopover sites (**b**, **c**), and winter sites (**d**, **e**, **f**) of migratory red-headed woodpeckers from a breeding population in Northwest Ohio. Colored points and connecting lines correspond to each individual. **a** Migration routes encompassed three states (OH, IN, KY). **b** A typical migratory stopover site in successional hardwood patches surrounded by agricultural lands. **c** The only migratory stopover site located in an oak savanna/open forest cover type. **d-f** Wintering sites of three migratory individuals in successional hardwood patches surrounded by agricultural lands

Tag ID	Sex	Departure date	Arrival date	Mean 3-day distance traveled[a]	Total distance traveled[a]	Distance from wintering site to breeding site
41880	M	9/4/17	9/16/17	200 km	800 km	208 km
41892	F	9/10/17	9/25/17	150 km	663 km	214 km
41886	M	9/20/17	9/26/17	57 km	112 km	111 km

[a]distances are minimum distances measured between GPS locations during autumn migration

Table 2-1   Summary of autumn migration movements by red-headed woodpeckers breeding in Ohio.

Tag ID	Sex	Season	Date of aberrant location	Distance from wintering site	Cover type
41916	F	Breeding	8/1/17	5 km	Urban
41892	F	Autumn	10/31/17*	6 km	Forest
41892	F	Autumn	11/12/17	44 km	Forest
41892	F	Winter	12/17/17	80 km	Urban
41876	M	Winter	1/21/18	103 km	Forest

*denotes locations where previous locations were 3 days prior. All other locations were taken at 7-day intervals. The individual with Tag ID 41892 was migratory while the other two individuals were sedentary.

Table 2-2   Summary of one-time movements made by red-headed woodpeckers outside of the autumn migration period

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