

Research Article

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Variation in individual autumn migration and winter paths of Great Lakes red-headed woodpeckers (*Melanerpes erythrocephalus*)

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Abstract: Migratory movements of facultative migrants are poorly understood due to their irregular and often unpredictable occurrence. However, tracking such movements is important for understanding population dynamics, informing annual cycle conservation plans, and identifying possible cues of facultative migration. We used pinpoint GPS tags to track autumn and winter movements of migratory red-headed woodpeckers (*Melanerpes erythrocephalus*) to better understand migration frequency, timing, and routes for birds breeding in managed oak savanna systems in the North American Great Lakes region. Proportions of individuals migrating differed between the two sites, with 72% of the Ohio population migrating, while no individuals in the Minnesota population migrated. Of the Ohio birds that migrated, their movements were highly variable in distance and direction but generally occurred south of the breeding site. Wintering sites ranged from 111 – 218 km from the breeding site. Cover types occupied during migration and wintering were almost exclusively small patches of closed-canopy hardwood forest within agricultural matrices. We documented one-time movements in migratory and non-migratory individuals during the year that have not previously been described in facultative migrants. We found no evidence of a harness or marker effect on proportions of individuals migrating, migration return rates, or annual survival regardless of migration.

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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 considered to have a genetic basis [1, 2] and variation in one or a few genes can explain differences in migration behavior in some species [3]. Due to the irregularity of facultative migration, little is known about the intrinsic and extrinsic factors controlling this behavior [1, 4]. In general, facultative migration occurs in populations that experience seasonally fluctuating, but year-round, presence of food on the breeding site [5], but can occur due to other factors such as weather events [6, 7]. Facultative migrants are often characterized by varying proportions of the population migrating annually. Furthermore, this migration tends to be highly variable among individuals with regard to timing, distances, and direction compared to obligate migration [1]. The inherent variability in individuals' migration behaviors in populations of facultative migrants presents challenges when attempting to study 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 begin their breeding season in May [8, 9] and young may not fledge until the late August or September [10]. Clutches range in size from 4-7 eggs and both sexes incubate [11]. Nest cavities are primarily excavated in dead trees or dead sections

of live trees, and as such, red-headed woodpeckers are commonly associated with oak savanna ecosystems and other open forest systems [12, 13]. These open forest systems have nearly been lost due to land use changes since European settlement [14]. Over the past 50 years the red-headed woodpecker has declined by nearly 70% across its breeding range [15], 75% within Ohio [16], and subsequently is listed as Near Threatened by the IUCN [17]. Many explanations have been hypothesized for this decline, including increased rates of predation due to elevated *Accipiter* populations [18, 19], loss of habitat and the clearing of dead trees which are used for nesting and roosting [12], increased competition for cavities from introduced species such as European starlings (*Sturnus vulgaris*) [20], and vehicle collisions due to the species' low aerial foraging behavior [21]. All of these hypotheses are primarily 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 [22] and is critical for land management efforts aimed at conserving red-headed woodpeckers and other oak savanna specialists. Wintering habitat of red-headed woodpeckers varies throughout the range, with northern populations found in mature hardwood forests [23, 24] and southern populations favoring bottomlands and pine-oak forests [25, 26].

The migration strategies of red-headed woodpeckers have been described as semi-migratory [27], nomadic [28], and short-distance [29]. Knowledge related to autumn movements of red-headed woodpeckers has largely been anecdotal [12] 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 [30] [28, 31]. However, at our site that has been under long-term monitoring there has been no apparent relationship between oak mast and migration occurrence (J. Howitz, per. comm. 2019). Banding records from the early to mid-twentieth century indicate that fall migration occurs on scales not previously quantified through individual tracking, but these records are uncommon (<10 since 1927) and do not provide meaningful spatial or temporal resolution [32]. One study included radio-marked red-headed woodpeckers during autumn migration in South Carolina and found annual variation in the proportion of the population that migrated, and noted variation in migration distance with 71% of birds migrating beyond the 30-km limitation of their monitoring capabilities [33].

To our knowledge, there have been no other efforts to track red-headed woodpecker movements outside of the breeding period. Similar to other woodpecker species, migration in red-headed woodpeckers is under-studied and relatively unknown. Newly developed lightweight GPS tags have been useful for identifying nonbreeding season movements in other avian species [34-36] 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, 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. We hypothesized that migration would vary between our two study sites, whether in the proportion of individuals migrating, the distance or duration of the migration itself, or the timing of migratory movements. 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 speculate about migration timing, routes, distance, or habitat used outside the breeding period.

2 Methods

2.1 Study area

We studied red-headed woodpecker breeding populations at two study sites (Fig. 1), 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 to maintain oak savanna and are home to breeding and wintering populations of red-headed woodpeckers. Despite being located approximately 850 km apart, timing of the breeding season is similar between the two sites. 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. ellipsoidalis*; *Q. spp.*). Both sites originated from glacial sandplains and are located within a matrix of closed-canopy forest, wetlands, agriculture, and rural housing.

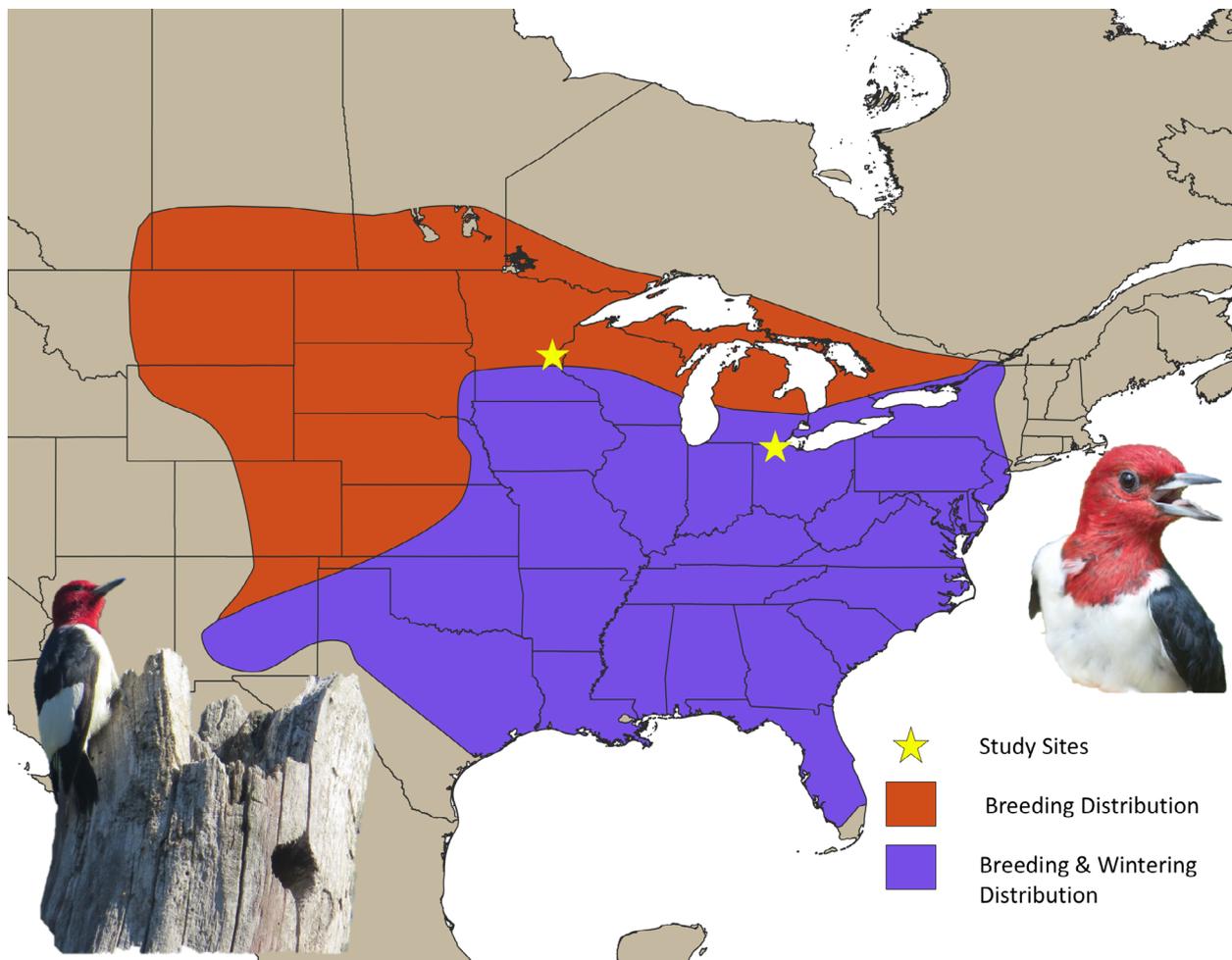


Fig. 1 Breeding and wintering distributions of red-headed woodpeckers. Study sites are denoted with gold stars. Photo credit: Henry Streby.

2.2 Woodpecker capture and pinpoint GPS deployment

From May to 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 (Minnesota only), and hoop nets at roosting and nesting cavities [37]. 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 archival 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) [38, 39]. Archival GPS tags store data collected throughout their deployment and must be recovered in order to download locations. 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: $N = 35$), fitted only with leg bands, comprised the control group to test for possible marker effects on migration behavior and survival. All birds were aged based on plumage [40]. 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 ($N > 1$ 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 conducted a mark-control comparison of migration rates (i.e., proportion that migrated) 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.

2.3 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 [41]. 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 that even “low quality” 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 [42]. 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 site 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 [43]. We estimated departure date to be the midpoint 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 at least two consecutive GPS locations were recorded, indicating the individual had settled for a period greater than one week.

3 Results

We conducted our analyses with a total 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 at the breeding site ($N = 1$ 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 an artifact of capture before breeding territories were established.

Table 1. Autumn migration movements by red-headed woodpeckers breeding in Ohio.

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

^adistances are minimum distances measured between GPS locations during autumn migration

3.1 Migration and return proportions

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%; $\chi^2 = 0.005$, $p = 0.94$). 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 meaningful statistical comparison. 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 ($\chi^2 = 0.9$, $p = 0.34$) though we note that these sample sizes are small.

3.2 Migration timing and movements

During spring and 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, 3 GPS tags, all from Ohio, included data indicating that migration had occurred during the prior year. All three migratory individuals had been aged during their capture in 2017 as ASY, or “after second year”, birds. 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 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. Average distance travelled between 3-day locations varied by individual, with the longest averaging 200 km and the shortest averaging only 57 km between locations. Distance between locations ranged from 247 km to 2 km. 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), closed-canopy hardwood forest patches within landscapes dominated by agricultural fields. Of the 33 locations recorded during autumn migration and the wintering season, 32 (97%) were in closed-canopy hardwood forest patches and the single remaining location was in 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 location recorded away from the winter site with both the preceding and following locations on respective wintering sites) during the winter (Table 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 closed-canopy 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 accurate and not the result of GPS error.

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

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.

3.3 Apparent survival between breeding seasons

We re-sighted 60% (15/25) of previously-captured 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 either site (Ohio tagged = 57%, Ohio control = 64%, $\chi^2 = 0.108$, $p = 0.74$; Minnesota tagged = 53%, Minnesota control = 54%, $\chi^2 = 0.008$, $p = 0.92$). 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, which were statistically similar ($\chi^2 = 0.325$, $p = 0.568$).

4 Discussion

4.1 Migration and return proportions

Facultative and other non-regular migratory movements are relatively understudied, primarily because of their variability and unpredictability in timing and proportions of animals in a population that migrate at any one time. Our study exemplifies these drawbacks, with our sample size of migratory red-headed woodpeckers limited primarily by marking birds in a year of relatively low migratory activity. Nonetheless, we documented autumn migratory movements, wintering sites, one-time movements away from wintering sites, and proof of concept for using GPS tags to track this species with no apparent deleterious effects. 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. This variation in proportions of red-headed woodpeckers migrating both among years and among populations has previously been observed range-wide through Christmas Bird Count data and using mark-recapture methods at breeding sites [28, 33]. Long-term monitoring at our Minnesota study site indicates that annual migration proportions range from nearly 0% to nearly 100% with no apparent relationship to oak mast (J. Howitz, pers. comm. 2019). This difference in migration behavior between the two populations suggests that extrinsic factors that influence whether migration occurs were at the landscape-level and that migration in red-headed woodpeckers is possibly determined at the landscape scale.

Fifty percent ($N=9$) of individuals that migrated returned to the breeding site the following spring, a percentage similar to the survival rate of birds that remained on the breeding site for the entire year (58%; $N=59$). It is unknown if migratory 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 [44]. Breeding site fidelity in red-headed woodpeckers has been disputed with some suggesting no population is resident to a specific area [12]. 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 [33]. 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 the 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 including our study species.

4.2 Migration timing, routes, and distances

Locations of the three migratory individuals revealed similar dates of departure, with all leaving during a 16-day period in early to late September. All three individuals wintered south of the breeding site, and the first locations away from the breeding site were in a southerly direction; however, no patterns were apparent in subsequent locations relating to direction or distance (Fig. 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 [1, 3]. 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 heterospecifics 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*) [45].

We report total minimum distances traveled from the breeding site to wintering sites which exceed previous known migration distances of red-headed woodpeckers [33]. These distances also exceed known migration distances of Lewis' woodpeckers [46, 47], a close relative of red-headed woodpeckers, but are shorter distance than

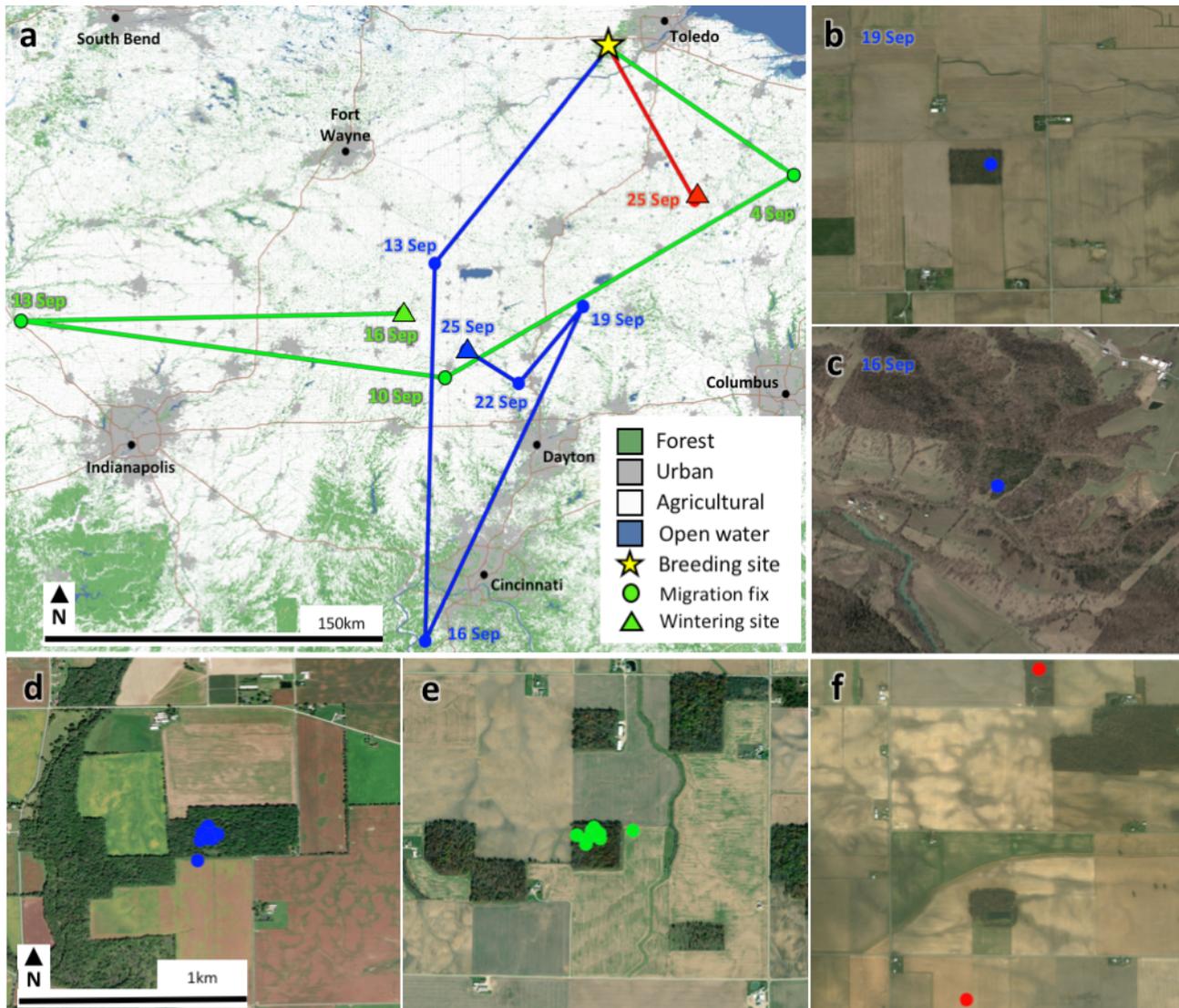


Fig. 2 Migration routes (a), migratory stopover sites (b, c), and winter sites (d, e, f) of migratory red-headed woodpeckers from a breeding population in Northwest Ohio. Colored points and connecting lines correspond to each individual. **a** Migration routes encompassed three states (OH, IN, KY). **b** A typical migratory stopover site in closed-canopy 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 closed-canopy hardwood patches surrounded by agricultural lands

known migrations of northern flickers [48]. That individual woodpeckers from the same breeding population migrated different distances is consistent with previous findings [33] and suggests that migration distance and direction in red-headed woodpeckers is a phenotypically-plastic behavior dependent upon extrinsic factors.

4.3 Wintering and migration site selection

We found that migrating red-headed woodpeckers used small patches of closed-canopy hardwood forest both during migration and for wintering sites (Fig. 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. The winter use of mature oak forests has been previously described [23, 24]. 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 closed-canopy hardwood forest in west-central Ohio (Fig. 2), suggesting that open-forest systems may not be favorable for migrating individuals during the winter. The apparent affinity for closed-canopy 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 declines in forest availability in this region continue.

4.4 One-time movements of individuals

In the Ohio population, three individuals (two sedentary and one migratory) made one-time movements from their respective breeding and wintering sites (Table 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 occur throughout 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 when some resource is scarce or conspecific densities are high enough to cue facultative migration. Landscape-scale exploratory movements have been documented in other species such as Killdeer [49] and even in other taxa such as bats [50]. 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.

4.5 Apparent survival between breeding 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 [45], 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 [51]. 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 [52, 53].

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 [54], resulting

in positive effects on local red-headed woodpecker breeding numbers [55]. While this association with oak savanna is of importance during the breeding season, we observed individual red-headed woodpeckers using relatively small patches of closed-canopy hardwood forests, and not oak savanna, as stopover and wintering sites (Fig. 2). While our sample size of three individuals may not be representative of the entire population, if this behavior was consistent throughout all migratory individuals, it could be a contributing factor to the overall population decline seen in red-headed woodpeckers. Northwestern Ohio has remained predominately agricultural since forests were cleared for settlement [56], 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. In Northwest Ohio, nearly half of all forest patches are less than 50 acres and over 75% of forest is within 90 m (295 feet) of a non-forest edge [57, 58]. We hypothesize that this shift in wintering site availability from oak savanna to small fragments of closed-canopy 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. *Accipiter* predation of red-headed woodpeckers has been associated with increasing forest cover [18] and the close proximity to roadways may increase the probability of vehicle-related mortalities. 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. Together, if all migratory individuals exhibit similar site selection, these factors represent potential sources of winter mortality that may be exacerbated by the size and structure of wintering sites available to migratory individuals.

4.7 Future Research

Due to their relatively large size and apparent amenability to carrying GPS and other markers throughout their annual cycle, red-headed woodpeckers present a system well-suited to studying basic research questions about the intrinsic and extrinsic cues for facultative migration as well as applied questions about the drivers of population declines in a species with unique and seasonally variable habitat associations. Additional years of study could account for annual variation in migratory frequency and behavior. Ultimately, this study demonstrates the potential of pinpoint GPS tags to monitor species across

heavily-modified landscapes, thereby increasing our understanding of animal migration and conservation.

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Availability of data and materials: The datasets generated and analyzed during the current study are available in the Movebank tracking database, Movebank ID: 671681844.

Authors' contributions: RKP and HMS conceived and designed the study. RKP, HMS, and EHW carried out research in the field. All authors conducted analysis. RKP and HMS wrote the manuscript and prepared figures and tables. All authors reviewed and edited drafts of the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare they have no competing interests.

Consent for publication: Not applicable.

Ethics approval and consent to participate: Woodpeckers were captured and handled in compliance with Institutional Animal Care and Use Committee protocols at the University of Toledo (108708) and the University of Minnesota (1406-31581A), and the U.S. Geological Survey Bird Banding Permit (24072).

Data accessibility: We intend to archive our data in the Movebank repository following publication.

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