

NATAL DISPERSAL AND SURVIVAL OF RED-BELLIED WOODPECKERS IN A
FRAGMENTED LANDSCAPE

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In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
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The undersigned, appointed by the dean of the Graduate School, have examined the
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NATAL DISPERSAL AND SURVIVAL OF RED-BELLIED WOODPECKERS IN A
FRAGMENTED LANDSCAPE

presented by Allison S. Cox,

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**NATAL DISPERSAL AND SURVIVAL OF RED-BELLIED WOODPECKERS IN
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ABSTRACT

The juvenile life stage has been shown to be critical to population persistence in birds. Movements during this phase determine gene flow between populations, allow for colonization of vacant habitats, reduce inbreeding risks, and maintain optimal population densities. Despite its importance, the post-fledging period is the least studied stage of the avian life cycle. Biologists have outlined theoretical models of movement behavior to predict how birds make dispersal decisions and respond to the surrounding landscape, but empirical tests of these models are lacking. Further, it has been assumed that risks associated with exploring novel habitats make natal dispersal costly. Although previous estimates of post-fledging survival are correspondingly low, it is unclear how much dispersal behavior contributes to high mortality rates in young birds. My thesis research investigates movement and survival of a resident bird during natal dispersal. Specifically, I aimed to (1) identify the model of prospecting used by dispersing Red-bellied Woodpeckers (*Melanerpes carolinus*), (2) investigate landscape effects on individual movement as the birds departed their natal home range, (3) explore the impact of unforested habitats on dispersal, (4) test factors that may influence dispersal age and dispersal distance, and (5) provide post-fledging survival estimates for Red-bellied

Woodpeckers and investigate the relative influence of factors with the potential to affect juvenile survival.

In 2009 and 2010, we radio-tagged 52 Red-bellied Woodpecker nestlings and intensively tracked birds after they fledged. Our study site was located in central Missouri in areas of fragmented forest in the Mark Twain National Forest and within the primarily contiguous hardwood forest of the adjacent Baskett Wildlife Research and Education Area. When woodpeckers were observed making prospecting movements outside of their natal home range, we recorded movement paths and compared land cover within the movement path to random available paths. We estimated survival using known fate models and an information theoretic framework to compare factors potentially affecting survival.

Juveniles used a foray prospecting strategy by making repeated exploratory movements into the surrounding area between returns to the natal home range to roost. Prospecting individuals traveled in paths containing higher forest cover than was randomly available in the area and prospecting direction predicted dispersal settlement direction. Areas used by woodpeckers as they dispersed also had significantly higher forest cover than areas beyond their settlement location. Birds fledging earlier in the season dispersed from the natal area at a younger age than birds fledging later in the year and females dispersed farther than males. Red-bellied Woodpeckers were most vulnerable during the first few weeks after fledging and then showed relatively high rates of survival for the remainder of the study and throughout periods of prospecting and dispersal.

Red-bellied Woodpeckers demonstrated a foray prospecting behavior previously associated with cooperative breeders and contrary to the floater pattern predicted by theoretical models for pair-breeding birds. The centrally-based foray pattern may allow birds to participate in the potentially risky behavior of exploring novel habitats while benefiting from familiarity and nepotistic benefits of remaining on the natal territory. In addition, birds traveled through forested areas and avoided more open habitats, underscoring the importance of forest habitat connectivity to resident birds during natal dispersal. Thus, landscape configuration has the potential to guide woodpecker movement and gene flow between populations. Finally, our results revealed that the dispersal process was not costly in our population, as we observed no mortalities during periods of prospecting and dispersal. Repeated forays into potential breeding habitats from the natal territory combined with preferential use of forested habitat during their movements may ameliorate the costs of dispersal in this species.

We present a unique contribution to our understanding of the natal dispersal process by linking dispersal behavior, the effect of landscape connectivity on movement, and post-fledging survival. We provide a refined mechanistic understanding of how animals make decisions during natal dispersal and the costs associated with this life stage. This information will improve our ability to create realistic models of movement when attempting to manage and conserve intact populations.

THESIS FORMAT

The chapters of this thesis were written as independent manuscripts prepared for submission to peer-reviewed journals. As a result, some essential introductory and methodological materials are repeated, and a separate literature cited section follows each chapter. In addition, I use the plural noun “we” rather than “I” throughout each chapter.

CHAPTER 1

PROSPECTING BEHAVIOR AND THE INFLUENCE OF FOREST COVER ON NATAL DISPERSAL IN A RESIDENT BIRD

ABSTRACT

An understanding of dispersal behavior is key to landscape scale conservation management and maintaining healthy metapopulations. Despite the importance of this stage in the avian life cycle, very little is known about the temporal, spatial, and social factors affecting dispersal. We intensively tracked Red-bellied Woodpeckers, a pair-breeding resident bird, from fledging to dispersal from the natal home range. Juveniles used a centrally-based foray prospecting strategy previously only associated with cooperatively breeding birds. Birds repeatedly forayed between returns to the natal home range to roost. Prospecting individuals traveled along paths containing higher forest cover than was randomly available in the area and prospecting direction predicted dispersal settlement direction. Areas used by woodpeckers as they dispersed also had significantly higher forest cover than areas beyond their settlement location. Birds fledging earlier in the season dispersed from the natal area at a younger age than birds fledging later in the year and females dispersed farther than males. We provide evidence of juvenile birds making exploratory movements to make informed decisions about dispersal prior to permanent departure from the natal area. In addition, we demonstrate the value of landscape habitat connectivity to a dispersing resident forest bird.

INTRODUCTION

Dispersal movements are critical to population dynamics as they determine gene flow between populations (Whitlock 2001), allow for colonization of vacant habitats (Pulliam and Danielson 1991, Hanski 1998, Cooper and Walters 2002), reduce inbreeding risks (Johnson and Gaines 1990), and maintain optimal population densities (Hamilton and May 1977, Adriaensen et al. 1998). Despite the importance of the dispersal stage in the avian life cycle, a mechanistic understanding of movement behavior during the dispersal process is lacking. Previous investigations attempted to infer movement patterns by comparing natal and settlement territories (Cadahía et al. 2005, Stenzel et al. 2007, Sternalski et al. 2008, Studds et al. 2008) or modeled dispersal using random walk simulations or other theoretical patterns (Turchin 1996, Zollner and Lima 1999). However, few have investigated movement behavior of birds during the dispersal process (*but see* Forsman et al. 2002, Kesler and Haig 2007, Martín et al. 2008, Kesler et al. 2010). Detailed information on individual behavior during the dispersal process is necessary for the development of realistic models of movement (Morales and Ellner 2002).

Reed et al. (1999) suggested that young birds make informed decisions during natal dispersal through exploratory movements they termed “prospecting” and outlined conceptual models of prospecting movement and behavior. Reed et al. (1999) described three specific variations of prospecting behaviors theorized to characterize bird movements. The “cooperative breeder pattern” is a centrally-based foraging behavior that includes young birds using the natal area as a home base from which they make

repeated forays into the surrounding landscape. This prospecting strategy may be particularly suited to cooperative breeders, as adults are tolerant of juveniles remaining on the natal territory past parental independence (Komdeur and Ekman 2010). The second form, the “floater pattern,” prescribes that birds depart from the natal area and move among potential breeding territories until a vacancy is encountered (Reed et al. 1999) and do not return to the natal area after they enter the floater movement stage. Floater behavior has been described in many pair-breeding species, and may also include an abrupt departure from the natal site following aggression from adults (Holleback 1974, Gayou 1986, Tarwater and Brawn 2010). The last variant of informed prospecting behavior described by Reed et al. (1999) is the “colonial breeder pattern,” which allows birds to move between and monitor several colonies before settling, with the possibility of choosing the natal site for settlement. The colonial pattern is used exclusively by colonial nesters, as many individuals can occupy the same breeding territory. The models presented by Reed et al. provide theoretical guidelines for understanding bird prospecting behavior, but few empirical tests of these models exist, and movements and behaviors which lead to dispersal remain poorly understood (Walters 2000, Liu and Zhang 2008).

The lack of spatially-detailed information collected during dispersal movement also precludes researchers from determining the impact of proximate factors on dispersal, such as habitat heterogeneity. Previous studies concluded that gene flow in birds is significantly reduced in areas of higher habitat fragmentation (Delaney et al. 2010). However, the mechanisms hindering gene flow are unclear because the impact of landscape configuration on individual movement during natal dispersal remains almost

entirely unstudied for avian species. The lack of information is dually surprising, given that it is essential for conservation reserve design (Simberloff et al. 1992, Beier and Noss 1998, Van Dyck and Baguette 2005). For example, in a review by Beier et al. (2008), only four of 24 studies that produced maps of habitat linkages to guide conservation decisions included birds, and none used data on dispersal movements of the focal species to create their model.

Several homing experiments demonstrate how adult birds use corridors and respond to different habitat matrices when returning to their territories after translocation (Bélisle et al. 2001, Gobeil and Villard 2002, Castellón and Sieving 2006, Gillies and St. Clair 2008). However, it is unclear if results from experimental translocations predict movement patterns during natural dispersal events as homing and dispersal movement behaviors differ within several taxa (Zollner and Lima 1999). Additionally, homing birds are likely to move in a single direction – toward the home territory – whereas dispersers can potentially travel in any direction. Animals forced to emigrate may also behave differently than animals that depart an area voluntarily (Lin and Batzli 2004), and juvenile animals may exhibit vastly different movement patterns and habitat preferences than their adult counterparts (Anders et al. 1998, Rittenhouse and Semlitsch 2006). Thus, evidence of landscape effects during natal dispersal is necessary when managing for population connectivity, especially in resident species where the most drastic and important dispersal movement occurs during the juvenile life stage (Greenwood and Harvey 1982).

Temporal dispersal strategies are also important to population dynamics. Although dispersal initiation can potentially begin immediately following parental

independence, asynchronous dispersal has been found to theoretically stabilize populations (Doebeli 1995). Dispersal timing can vary greatly within species, populations and even broods (Ekman et al. 2002, Pasinelli and Walters 2002, Tarwater and Brawn 2010) and may be influenced by a variety of intrinsic, environmental, and social factors. Age at dispersal is sex-biased in American Dippers (*Cinclus mexicanus*) and females disperse earlier than males (Middleton and Green 2008). Body condition has also been observed to affect dispersal timing in several species; however, the reported trends vary by species. Larger Eastern Screech Owls (*Megascops asio*; Belthoff and Dufty 1998) and Crested Tits (*Lophophanes cristatus*; Lens and Dhondt 1994) disperse at a younger age, whereas Red-cockaded Woodpecker (*Picoides borealis*) males that disperse as juveniles are smaller when compared to males that remain on the natal site as helpers (Pasinelli and Walters 2002). Social influences, such as sibling competition have also been suspected to affect dispersal age (Belthoff and Dufty 1998, Pasinelli and Walters 2002). When hatch date varies within a population, seasonal effects on dispersal age may also be apparent. Individuals fledging earlier in the year correlated with earlier dispersal ages in Western Slaty-antshrikes (*Thamnophilus atrinucha*; Tarwater and Brawn 2010) and timing may be tied to the parents laying a second clutch. Finally, habitat quality may influence dispersal age (Lens and Dhondt 1994).

Natal dispersal distance has been calculated for a wide range of bird species using mark and recapture techniques. However, the high probability of birds dispersing outside of the study area may skew results (Koenig et al. 1996, Cooper et al. 2008). Nonetheless, a number of factors have been identified to affect how far juveniles settle from their natal territory. Sex-biased dispersal has been reported in an overwhelming number of bird

species with the trends most often skewed toward females dispersing farther (for review see Clarke et al. 1997). However, sex does not account for all variation in dispersal distance in avian species. Ferrer (1993) concluded that more fit Spanish Imperial Eagles (*Aquila adalberti*) traveled farther from the natal site. A seasonal effect has been documented in a number of species (Mulder 1995), but the trend may be a positive correlation where birds hatching earlier in the year disperse shorter distances (Ferrer 1993, Spear et al. 1998) or the trend may differ by sex (Nilsson 1989). In Red-cockaded Woodpeckers, the timing of the dispersal event may affect dispersal distance as birds that delayed dispersal, settled closer to the natal territory (Pasinelli et al. 2004).

We investigated movement of Red-bellied Woodpeckers (*Melanerpes carolinus*) during natal dispersal in study areas of fragmented forest in central Missouri. The Red-bellied Woodpecker is a pair-breeding bird that holds year-round territories and shows high site fidelity (Kilham 1961, Boone 1963, Ingold 1991). Consequently, natal dispersal of the woodpecker is integral to metapopulation dynamics as it is almost solely responsible for the persistence of subpopulations and preservation of genetic diversity. The life-history traits, abundance, and size of the Red-bellied Woodpecker make it an ideal study species to intensively track individuals from fledging to settlement and obtain detailed movement and behavior data during natal dispersal of a resident bird.

We aimed to identify which model of prospecting is used in a dispersing resident bird. The conceptual prospecting models of Reed et al. (1999) predict that Red-bellied Woodpeckers, a pair-breeding bird, would use a floater prospecting strategy in which individuals would make abrupt and direct movements from the natal area, followed by movements between and among potential breeding habitats. In addition, we investigated

landscape effects on individual movement as the birds departed their natal home range. Once the birds settled in a new area, we explored the impact of unforested habitats on settlement locations and tested the relationship between prospecting movements and dispersal settlement. Although the theory behind prospecting assumes that the behavior is used to make informed dispersal decisions, few studies have linked individual prospecting movements to settlement locations. Finally, we tested for intrinsic, social, and environmental factors that may influence dispersal age and dispersal distance.

METHODS

Study site and field techniques

We conducted the study in the 6,677 ha Mark Twain National Forest's Cedar Creek Unit in central Missouri (38°46'N, 092°07'W) and in the adjacent 917 ha Baskett Wildlife Research and Education Area (38°46'N, 092°15'W). Work was conducted from March through November during 2009 and 2010. The national forest study area was composed of privately owned residential and agricultural inholdings interspersed within federally administered property. The Cedar Creek Unit of the Mark Twain National Forest is additionally fragmented by federal pastures. The Baskett Wildlife Research and Education Area is primarily contiguous hardwood forest. By including both of these areas in the study site, we were able to increase our gradient of forest cover.

We searched for Red-bellied Woodpecker nests and used a wireless cavity viewer (Huebner and Hurteau 2007) to assess nest stage and determine nestling age. At approximately 20 days post-hatch, we ascended to nests using a guyed extension ladder (Rohwer 1988) and retrieved nestlings with the hole-saw method (Ibarzabal and

Tremblay 2006). We banded each bird with three colored, plastic leg bands and one numbered, aluminum band (USGS Patuxent Bird Banding Laboratory). We also weighed nestlings and attached radio transmitters (2.6g; model A1060; Advanced Telemetry Systems, Isanti, MN). A modified leg harness (Kesler 2011) was used to mount transmitters on four birds in 2009; however, woodpeckers were able to break the weak link before battery life expired. Thereafter, we used a permanent leg harness (Rappole and Tipton 1991). Transmitters weighed 3-4% of body mass and had a battery life of 4-6 months. Blood or feather samples were taken from each bird for molecular genetic sex determination (Avian Biotech International, Tallahassee, FL). Nestlings were then returned to the cavity and monitored daily until fledging (2 – 8 days after tagging). In 2009, heavy nest predation limited our sample size of fledged birds available for tracking, so we fitted nest trees with snake excluder devices (Neal et al. 1998) in 2010.

Forty-three radio-marked juvenile Red-bellied Woodpeckers successfully fledged from 18 nests. After fledging, radio-marked Red-bellied Woodpeckers were tracked daily in 2009 and 2-3 days per week in 2010. To avoid temporal activity biases (Kernohan et al. 2001) we used a rotating schedule of bird order. We located birds using the homing method (White and Garrott 1990) with model R-1000 Communications Specialists (Orange, CA) receivers and three-element Yagi antennas. Geographic locations (Universal Transverse Mercator coordinate system, UTM) were recorded for each individual with a global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, KS) after visually confirming individual color band combinations.

We recorded behavioral data during 10-minute focal watches (Altmann 1974) after locating each bird. We noted the individual's state (foraging, begging, resting,

preening) for each minute of observation time and all interactions with conspecifics (begging from adults, fed by adults, aggression from adults or siblings, aggression toward adults or siblings). We remained near the birds for a minimum of 30 minutes to identify if study subjects made prospecting movements during that time.

We intensively tracked the birds for two hours or until they returned to the natal area if individuals made putative prospecting movements, which included quick, long, solitary movements away from the natal area as per Baker (1969) or when birds were initially located off of the natal area. During intensive tracks, we recorded geographic locations whenever the bird moved more than 10 meters. If an individual remained off of the natal area for the two hour tracking session, the bird was located before dawn the following day to determine whether or not it roosted off of the natal home range. We considered that a bird had dispersed when it roosted off of the natal home range and thereafter obtained weekly locations for the remainder of the study period. This distinction proved to be accurate as no birds were located back on the natal home range after roosting away. The locations of dispersers were then revisited during the following breeding season to verify residency at dispersal destinations using playbacks of Red-bellied Woodpecker calls and recording the location of banded individuals that responded.

Birds occasionally moved onto private property where access was not granted. We obtained directional bearings and used triangulation methods (LOAS, Ecological Software Solutions LLC. Hegymagas, Hungary; Version 4.0) to remotely estimate bird locations when homing was not possible. We excluded locations with error ellipses greater than ten percent of the mean natal home range.

Prospecting

Prospecting patterns

To classify departures from the natal area, we first derived natal home range utilization distributions (UDs) with KernelHR (Version 4.27; Seaman et al. 1998), using locations obtained within the area where birds were observed interacting with their parents. A fixed kernel density estimator and least-square cross-validation was used to calculate the home range. We defined the natal home range boundary as the 95% isopleth of the utilization distribution and the home range center was identified as the centroid of the polygon encircled by the 5% isopleth. We overlaid home range probability distributions and point data obtained during movement tracking in a geographic information system (ArcGIS 9.3, ESRI, Redlands, CA). We defined a movement as a prospecting movement when a bird traveled farther than the radius of a mean natal home range (240 m) outside of its natal home range boundary (i.e., birds that traveled far enough to, on average, enter the center of an adjacent territory were considered prospectors). These prospecting movements were then classified as forays if the bird returned to the natal home range to roost. Once birds roosted off of the natal home range, we calculated the settlement area as 95% of home range use of post-dispersal locations using KernelHR. We then compared settlement home range areas to natal home range areas using a two-tailed t-test (proc TTEST; SAS Institute Inc. 2008) to determine if birds were settling to a single territory or floating between several territories.

Prospecting direction

Many Red-bellied Woodpeckers made repeated prospecting movements away from the natal home range on multiple days. We tested whether birds were more likely to prospect in a single direction by comparing prospecting orientations with random orientations. For each prospecting movement, we calculated the orientation of the farthest recorded bird location from the natal home range centroid. An identical number of random orientations were produced for each bird by generating random numbers between 1 and 360 from a uniform distribution. To account for individual differences in direction of movement, we calculated the mean prospecting orientation for each individual (mean angle; pages 599-600; Zar 1999) and then used the difference of each prospecting orientation from the corresponding mean as our metric for analysis. We compared absolute values from observed and random datasets using a Wilcoxon-Mann-Whitney test (proc NPAR1WAY; SAS Institute Inc. 2008).

Landscape effects on prospecting movements

We tested for an effect of landscape configuration on Red-bellied Woodpecker prospecting movements by comparing habitat composition in areas used during prospecting to areas that were available. To account for location uncertainty caused by birds moving faster than observers, we modeled occurrence probabilities with Brownian bridge methods (Horne et al. 2007). Brownian bridges incorporate time between observations, distance between locations, location error, and a variance related to the animal's mobility to create probability distributions of temporally correlated spatial data. We used an error of 3 m for all observations based on the 95% circular error probability

of our GPS units (Garmin International Inc. 2007). For locations obtained by triangulation methods, we calculated the radius of a circle equal to the area of the 95% error ellipse obtained from LOAS. We used Animal Space Use (version 1.3; Horne and Garton 2009) to derive utilization distributions and considered landscape areas encompassed by the isopleth encircling 95% of the probability distribution. We intersected Brownian bridge probability distributions with land cover maps (Missouri Land Use Land Cover Data, Columbia, MO: Missouri Spatial Data Information Service, 2005) to calculate weighted habitat use values for prospecting birds. We considered forested habitats and non-forested habitats in the analysis. Forests included areas coded as deciduous forest, evergreen forest, deciduous woody/herbaceous, and woody-dominated wetland within land cover maps. Non-forested areas included urban, impervious, cropland, grassland, herbaceous-dominated wetland, and open water.

We compared the proportion of forest cover weighted by probability of occurrence within each used and five matched available areas. The available areas were identified by rotating each Brownian bridge utilization grid around the individual's home range center to random orientations. By doing so, we maintained movement sinuosity and travel distances (Fig. 1). Comparisons were made with a generalized linear mixed model (proc GLIMMIX, SAS Institute Inc. 2008), which can be used to fit a binomial response (used, available) and simultaneously account for repeated measures (individuals; Kleinbaum et al. 2008).

Dispersal

Relationship between prospecting and settlement

We tested for a circular correlation of the mean prospecting direction and mean dispersal direction for each bird by calculating the coefficient r_t (Fisher and Lee 1983) based on 100 permutations using a SAS macro (Kölliker and Richner 2004, SAS Institute Inc. 2008) following circular statistical methods outlined by Fisher (1993).

Landscape barriers to dispersal

We investigated landscape barriers to dispersal by comparing forest cover in the area the bird potentially used to disperse and the area beyond the settlement location. To represent the area that the birds used during dispersal, we designated a pie-shaped polygon originating at the natal home range center and terminating at the farthest dispersal location (Fig. 2). We used the average range of exploration during prospecting movements (~ 40 degrees) to estimate the range of area that the bird likely used (or angle of the pie piece). We identified the unused area by extending the pie shape 1.3 km beyond the farthest dispersal location. We chose 1.3 km as this represented the mean distance of a prospecting movement, birds were therefore capable of exploring at this distance. We then compared the proportion of forest cover in the area used to the area beyond the dispersal destination using a paired one-tailed t-test (proc TTEST; SAS Institute Inc. 2008) and differences were considered statistically significant at $\alpha < 0.05$.

Dispersal timing

We tested for effects on the timing of dispersal in Red-bellied Woodpeckers with a generalized linear mixed model (proc GLIMMIX; SAS Institute Inc. 2008), which can

be used to model binomial responses and include random effects. We included individual and nest of origin as random effect variables (random intercepts) to account for repeated measures of individuals and the possibility that siblings did not act independently. Each week of observation was coded with a response of “0” if the bird remained on the natal home range and “1” if it dispersed, and fit the data with a logistic regression model. We censored study individuals after mortality, when telemetry batteries began to fail, or if the radio harness fell off the study individual. With one exception, all censored birds were either confirmed dead, resighted after radio or harness failure, or had a documented gradual decrease in radio signal strength prior to non-detection. Birds were therefore only removed from the study due to mortality or equipment failure, and not movement outside of the study area.

We considered ecologically plausible models to test for the effects of year, fledge date, mass, brood size, and habitat composition on dispersal age. Body mass, as an index of body condition, was measured at the time of radio-tagging (between 19 and 23 days). No relationship was detected between age at measurement and body mass ($r^2 = 0.049$), and growth models indicated that chick mass stabilized at 19 days post-hatch (Stickel 1963). Thus, mass was not adjusted for measurement age.

We used two metrics to model the influence of habitat quality on dispersal timing. First, we calculated the proportion of forest cover within the natal home range. We intersected the 95% isopleth natal home range polygon with the land cover map to calculate the proportion of forest cover within the natal home range. Second, we measured the proportion of forest cover outside of the natal home range to determine if birds would delay dispersal if the surrounding area was of poor quality. We buffered

each home range center by a radius of 1.3 km (mean prospecting distance) and then excluded the natal home range from this buffered area. We again intersected the buffered area with the land cover map to calculate the proportion of forest cover outside of the natal home range, but within the probable area of exploration.

We also considered the ratio between proportion of forest cover within the natal home range and the area surrounding the natal home range to test if relative habitat quality change affected dispersal age. Finally, we examined several biologically plausible combinations of variables. The pseudolikelihood framework of proc GLIMMIX, when modeling with random effects, precludes comparisons of candidate models with an information criteria approach (SAS Institute Inc. 2008). Therefore, we present means \pm SE, F- and P-values to evaluate which factors significantly affect dispersal age.

Dispersal distance

Dispersal distance was measured as the maximum distance a bird was located from the natal home range center after dispersal. We tested possible factors contributing to dispersal distance including sex, mass, fledge date, dispersal date (measured as ordinal date), and biologically plausible combinations based on the literature. We used a mixed model (proc MIXED; SAS Institute Inc. 2008) and assigned nest of origin as a random effect (random intercept) to account for a possible genetic component as several species have demonstrated that dispersal distance is correlated in siblings (Greenwood et al. 1979, Forero et al. 2002, Pasinelli et al. 2004). Distance was log transformed to meet the assumptions of normality. We used an adjusted Akaike's information criteria (AIC_c) to

identify the best model(s) by considering all models within 0-2 ΔAIC_c (Burnham and Anderson 2002). Model support was evaluated with Akaike weights (ω_i ; Burnham and Anderson 2002). For all other analyses, we considered differences statistically significant at $\alpha < 0.05$ throughout, and we present confidence intervals (CI) wherever appropriate.

RESULTS

Prospecting

Red-bellied Woodpeckers were observed using a centrally-based foray prospecting strategy. We identified a total of 102 foray events from 26 different birds. Individuals made long, quick, directed, solo movements away from their natal area, foraged and interacted with conspecifics in the foray destination, and then returned to the natal home range to roost. Both sexes were observed making foray movements (16 males, 10 females). The median foray distance (maximum recorded distance from natal home range center) was 1.07 km (range: 0.35 – 4.23 km). Birds usually made their first prospecting movements roughly one month after fledging (median: 36 days; range: 22 – 114 days) and then made repeated forays over a median span of 22 days (range: 2 – 78 days). Multiple forays were observed in 18 woodpeckers, and were directionally clustered for each individual ($P < 0.0001$; Fig. 3). The average difference from the mean orientation was 19 degrees (CI: 14 – 23 degrees). This predicted an average range of exploratory movement of 38 degrees (19 degrees on either side of the mean).

When prospecting, Red-bellied Woodpeckers moved through areas of higher forest cover than was randomly available in the area. We obtained movement paths (forays during which we recorded multiple locations) on 62 forays from 24 birds during

the study period. Used paths contained higher forest cover than available paths ($P = 0.046$). Mean proportion of forest cover in all used and available paths was 0.57. A ten percent increase in forest cover from the mean resulted in an 11% increase in probability of woodpecker occurrence during foray movements (odds ratio estimate: 1.11; CI: 1.00 – 1.22; Fig. 4).

Dispersal

We recorded 18 dispersals made by juvenile Red-bellied Woodpeckers. Eight birds died prior to dispersal and 16 woodpeckers were resighted after premature radio-tag failure before dispersal. One bird was censored without a confirmed resight and was last observed on the natal area. Due to the relatively short distance that our dispersing birds travelled, we deduced that it was unlikely that the single missing bird dispersed outside of the detectible area. Thus, we were confident that we observed the range of behaviors exhibited by our radio-marked birds.

Mean settlement home range for dispersed birds was 26.6 ha (CI: 14.0 - 39.3). The mean settlement area was not significantly different from the mean natal home range (18.3 ha; CI: 12.3 - 24.2; $P = 0.16$). Therefore, we concluded that birds settled in a single new territory and were not exhibiting floating behavior (Fig. 5). In addition, six birds were resighted during the following breeding season in the same home range they occupied in November of the previous year.

Prospecting direction was correlated with dispersal settlement direction. We observed prospecting movements and dispersal events for 16 individuals. Comparisons

between the mean prospecting direction and the mean dispersal direction showed a strong positive correlation ($r_t = 0.766$; $P < 0.0001$; Fig. 6).

Forest cover in the area used during dispersal movements was significantly higher than the area beyond the farthest dispersal location ($P = 0.0005$). Fifteen out of 18 birds had a higher proportion of forest in the used area than the area 1.3 km beyond the settlement location (Fig. 7). Model estimates revealed that areas leading up to the settlement location were 12% more forested than areas beyond dispersal settlement location (estimate: 0.12; CI: 0.05 – 0.13).

Nest initiation date was associated with dispersal timing. The single variable model of fledge date was the only model to significantly correlate with dispersal age (Table 1). The model predicted that juveniles fledging earlier in the year would disperse at a younger age than those fledging later in the year (Fig. 8). Parameter estimates predicted that a bird fledging on May 29 would only have a 20% probability of remaining on the natal territory five months after fledging, whereas a bird fledging on June 28 would have a 74% chance of remaining on the natal area five months after fledging. Mean dispersal age for those that dispersed during the study period was $9 (\pm 1)$ weeks.

Red-bellied Woodpecker natal dispersal distance was sex-dependent (Table 2). The model with a sex indicator variable received 73% of model weight and indicated that females dispersed significantly farther than males ($P = 0.0092$; Fig. 9). Model estimates predicted females dispersed a mean of 2.9 km from the natal home range center (CI: 2.2 – 3.8) and males dispersed at a mean distance of 1.8 km (CI: 1.4 – 2.3). Mass ranked 2.4 ΔAIC_c points below the top model and indicated that dispersal distance increased as

nestling mass decreased ($\beta_{\text{mass}} = -0.02$; 95% CI = $-0.05 - 0.00$). However, this model only received 22% of model weight (Table 2).

DISCUSSION

Contrary to predictions based on the literature and previous conceptual models, Red-bellied Woodpeckers used a centrally-based foraging prospecting behavior during natal dispersal. The behavior was much more complex than patterns previously described in pair-breeders, as individuals made repeated movements into the surrounding landscape, followed by returns back to the natal home range. This foray behavior was similar to that previously observed only in cooperatively breeding birds, including Florida Scrub-Jays (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1977), Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig et al. 1996), Micronesian Kingfishers (*Todiramphus cinnamominus*; Kesler and Haig 2007), and Red-cockaded Woodpeckers (Kesler et al. 2010).

The complexity of the centrally-based foray pattern in cooperatively breeding species has been thought to be driven by resource limitations where adaptive learning during repeated explorations of the surrounding landscape would be necessary for species with few options for settlement (Kesler and Haig 2007). However, our results indicate that extreme resource limitations (as those that drive cooperative-breeding systems) are not required to promote foray prospecting behavior during natal dispersal. The centrally-based foray pattern may allow birds to participate in the potentially risky behavior of exploring novel habitats (Yoder et al. 2004) while benefiting from familiarity and nepotistic benefits of remaining on the natal territory (Ekman and Griesser 2002). The

cooperative breeder foray model defined by Reed et al. (1999) is particularly well suited to species with helpers at the nest because adults are tolerant of juveniles remaining on the natal territory after parental independence. However, our research indicates that the strategy may be more widespread among a variety of mating systems, and the benefits of increasing the potential of an offspring's successful dispersal may outweigh the costs of allowing another individual to remain on the natal territory.

During prospecting, Red-bellied Woodpeckers were observed repeatedly exploring in the same general direction. The fitness benefits of familiarity have been documented in several species (Yoder et al. 2004, Brown et al. 2008), and the costs of dispersing may be reduced if the bird continues to explore in the same direction each time it departs the natal territory. In contrast, birds may choose a certain direction of travel and then continue searching in the same direction if the habitat is deemed suitable (adequate food resources and lack of aggression from competitors). However, aggression from conspecifics on non-natal territories was repeatedly observed while juveniles were prospecting and the birds continued to prospect in the same direction despite this aggression. In addition, the direction of the prospecting movements predicted the final dispersal settlement direction, which supports the idea that prospecting birds can use repeated forays to gather information about potential breeding territories before making a final settlement decision.

The direction of prospecting movement was influenced by the habitat composition of the landscape. Birds traveled in directions with more forest cover than was available in other random directions. Red-bellied Woodpeckers are capable of crossing large gaps of unforested areas (personal observation). However, juveniles prospecting away from

their natal home range moved through forested areas rather than open areas comprised of cropland, grassland, and residential property. This phenomenon may be a result of differences in behaviors and habitat preferences of adults and juveniles (Anders et al. 1998), or a difference between movement behaviors exhibited during prospecting and home ranging (Van Dyck and Baguette 2005). The preference for forested areas by juveniles during prospecting demonstrates the importance of forested corridors during the most drastic movement phase of a resident bird when behavior is focused on net displacement. Although Red-bellied Woodpeckers were still able to cross landscapes without forest cover, the forested corridors have the potential to guide woodpecker movement and influence demographic and genetic population connectivity at a landscape scale. The value of connectivity takes on additional importance in the face of global climate change. A review by Heller and Zavaleta (2009) listed “increase connectivity” as the most cited recommendation for biodiversity management in response to climate change. Thus, habitat connectivity may be especially key to population persistence as climates change and habitats respond. Although flight increases individual vagility between habitats, we provide evidence that small-scale landscape connectivity affects bird movement during dispersal. The configuration of the forested areas influences direction of dispersal and increased forest composition allows for additional movement options.

Settlement location was also affected by landscape composition as juvenile Red-bellied Woodpeckers moved through areas with higher forest cover during prospecting, and then settled at dispersal destinations before moving into areas of lower forest cover. This information suggests that there may be a threshold proportion of forest cover needed

to facilitate dispersal movement. Desrochers and Hannon (1997) found that several bird species were less likely to cross large gaps (>100 m) than similar distances within the forest when responding to mob calls. Although dispersing Red-bellied Woodpeckers appear to have a higher gap crossing threshold than many species studied by Desrochers and Hannon (1997) based on movements observed in this study, vast expanses of grassland or cropland may induce them to discontinue further prospecting and choose a settlement location. Calculations of possible barriers to dispersal lend further insight into the effects of forest fragmentation on individual bird movement by elucidating the impacts of forest gaps.

Red-bellied Woodpeckers fledging earlier in the year dispersed at younger ages than those fledging later in the season. Early departure may be especially advantageous for birds fledging earlier in the season, as there is likely decreased competition for vacant territories. Alternatively, birds fledging earlier may have been produced by more fit parents on higher quality territories (Price et al. 1988) and increased fitness may allow birds to be better prepared to compete for territories at a younger age. Social factors may also influence the seasonal trend. Natal departure in Western Slaty-antsrikes often occurred in conjunction with the production of a second brood by the parents (Tarwater and Brawn 2010). Therefore, birds fledging later in the year would be allowed to remain on the natal territory longer as it would be too late for the parents to attempt a subsequent brood. Double-brooding was not observed in our population, however, adults were not intensively tracked after study subjects fledged and evidence of double brooding in Red-bellied Woodpeckers has been observed in the southern extent of their range (Breitwisch 1977).

Although we observed aggression between siblings, we identified no association between brood size and dispersal age. Our population demonstrated brood-splitting within a few days after fledging. Therefore the pressure of sibling competition may have been reduced as the entire brood rarely occupied the same natal home range or depended on the same parent. Forest cover on the natal home range and in the surrounding area also did not appear to affect timing of dispersal. Lens and Dhondt (1994) found that birds from smaller habitat fragments dispersed at an older age. However, they also found that birds in fragmented plots had lower body mass so the proximate factor was unclear. Our population did not show an effect of body mass, potentially due to delayed fledging of smaller siblings.

Female Red-bellied Woodpeckers dispersed farther than males, a sex-biased phenomenon widely reported in birds (Clarke et al. 1997). The ultimate causes of female-biased dispersal have been debated, although most agree that the pattern is driven by a skewed cost of dispersal (Pusey 1987). One well-cited theory suggests that monogamous mating systems where males defend territories would display female-biased dispersal because males would benefit from settling near the natal territory where resources were more familiar and females would benefit from departing until she located a sufficient mate (Pusey 1987, Whitfield et al. 2009, Gienapp and Merilä 2010). Red-bellied Woodpeckers fit this model well as males defend territories (Kilham 1961) and show shorter dispersal distances than females. In contrast, male Great Bustards (*Otis tarda*; Martín et al. 2008) and males of several Anatidae species (Coleman and Minton 1979, Lessells 1985, Baillie and Milne 1989) do not defend territories and show male-biased dispersal.

Our analysis revealed some support for an effect of mass on dispersal distance. The model predicted smaller birds would disperse farther regardless of sex. Dispersal theory dictates that juveniles should attempt to minimize movement away from the natal territory due to the costs associated with dispersal (Murray 1967). Therefore, smaller juveniles may be outcompeted and forced to disperse farther.

Individual-based models of movement are becoming increasingly popular and are useful tools for predicting dispersal of animals. However, these models must include empirical behavioral information in order to provide accurate predictions (Bélisle and Desrochers 2002). Here, we provide a holistic study of the dispersal process in a pair-breeding resident bird. We present the first example of a pair-breeding bird using a centrally-based foray strategy that included substantial individual investment in information gathering prior to making dispersal decisions. This discovery may be due to the lack of studies that intensively track birds during natal dispersal, and thus the behavior may be prevalent in other species as well. We also found that the direction of movement during prospecting was affected by forest configuration, a result supporting the long-standing assertion that habitat connectivity is key to conservation planning. Additional empirical evidence of how birds prospect for breeding territories and make dispersal decisions, as well as the influence of the landscape during dispersal, will allow for a refined mechanistic understanding of animal movement and will improve our ability to create realistic models of movement when attempting to manage and conserve intact populations.

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FIGURES

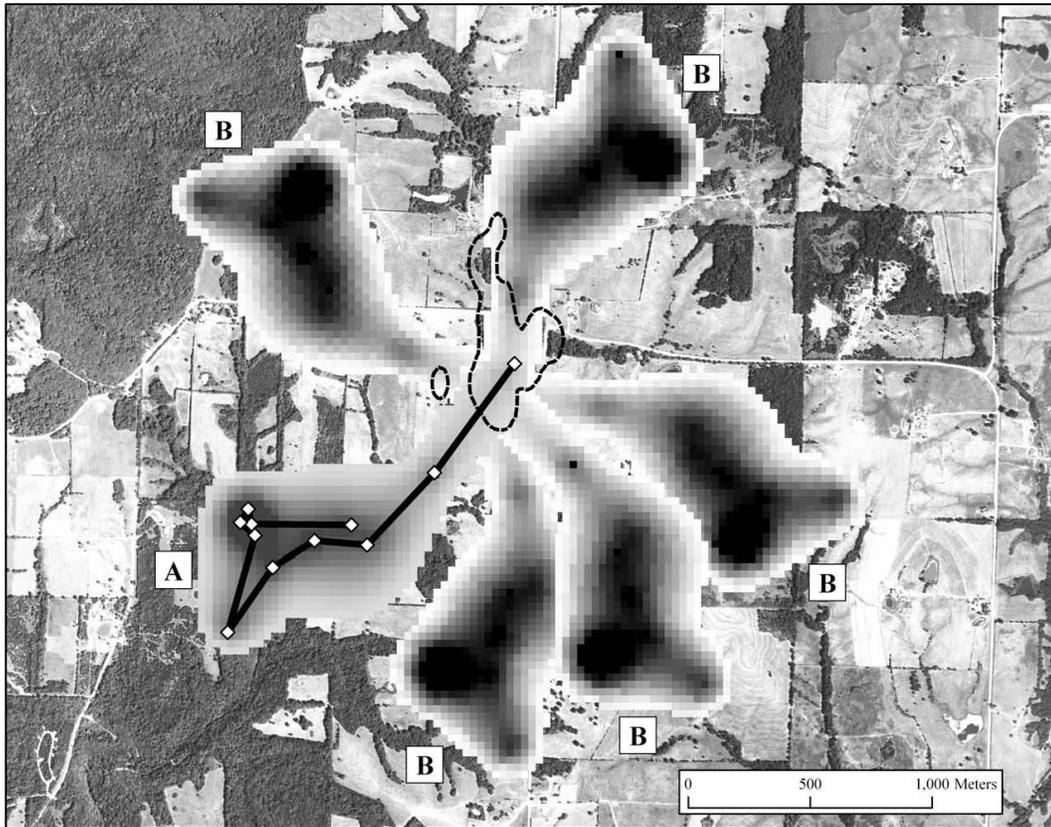


Figure 1. An example of a Red-bellied Woodpecker prospecting movement. Locations (represented by white diamonds) are connected with a solid black line to indicate the order of observation. Dotted line indicates 95% kernel natal home range boundary. Brownian bridge distribution (A) of the observed prospecting movement was used to account for uncertainty in bird location between observations. Five available prospecting areas (B) were created by rotating the observed utilization grid in random orientations around the natal home range center. Darker areas on grids indicate a higher probability of occurrence.

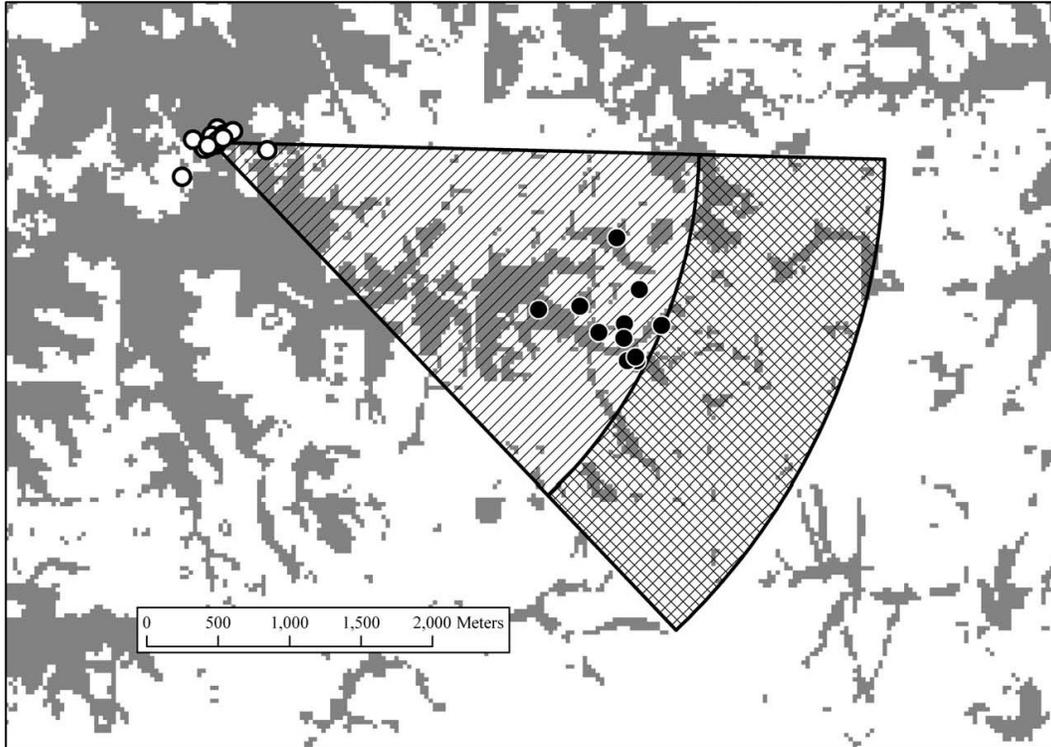


Figure 2. Example of spatial data used to test for barriers to dispersal. The used area (striped) originates at the natal home range center and terminates at the farthest location recorded after dispersal. The angle of the arc used for all birds was 40 degrees (mean range of exploratory movements). Unused habitats (cross-hatched) are designated as the area 1.3 km beyond the farthest dispersal location. Bird locations on the natal home range are indicated with white circles and locations after natal dispersal are indicated with black circles. Forested areas are shaded in gray.

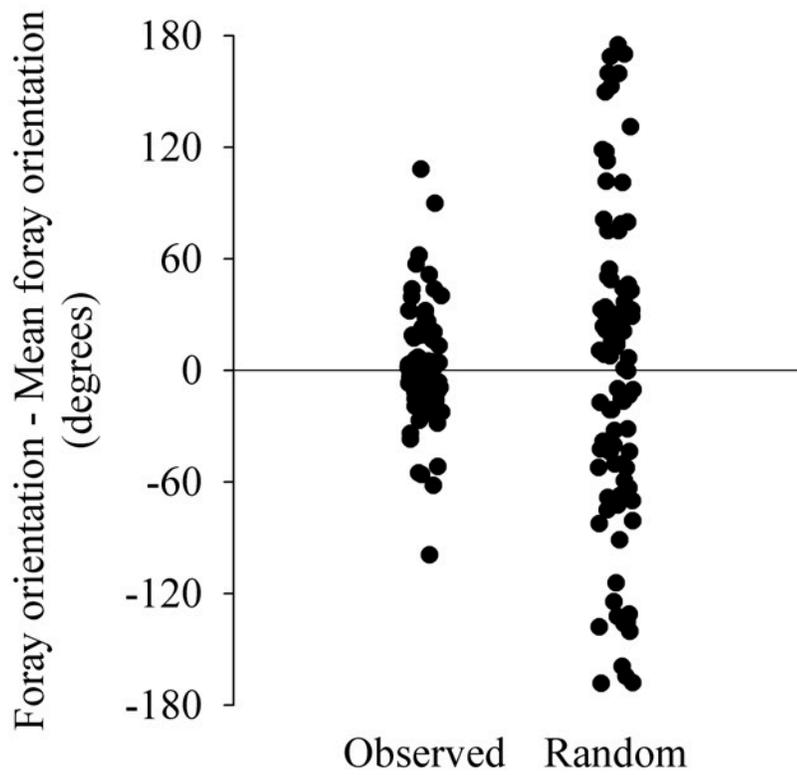


Figure 3. Directions recorded for repeated prospecting movements of juvenile Red-bellied Woodpeckers and random directions. Zero on the Y-axis has been standardized to represent the mean prospecting orientation for each bird. Difference in orientation for each prospecting movement from the mean are presented for both observed and randomly generated orientations.

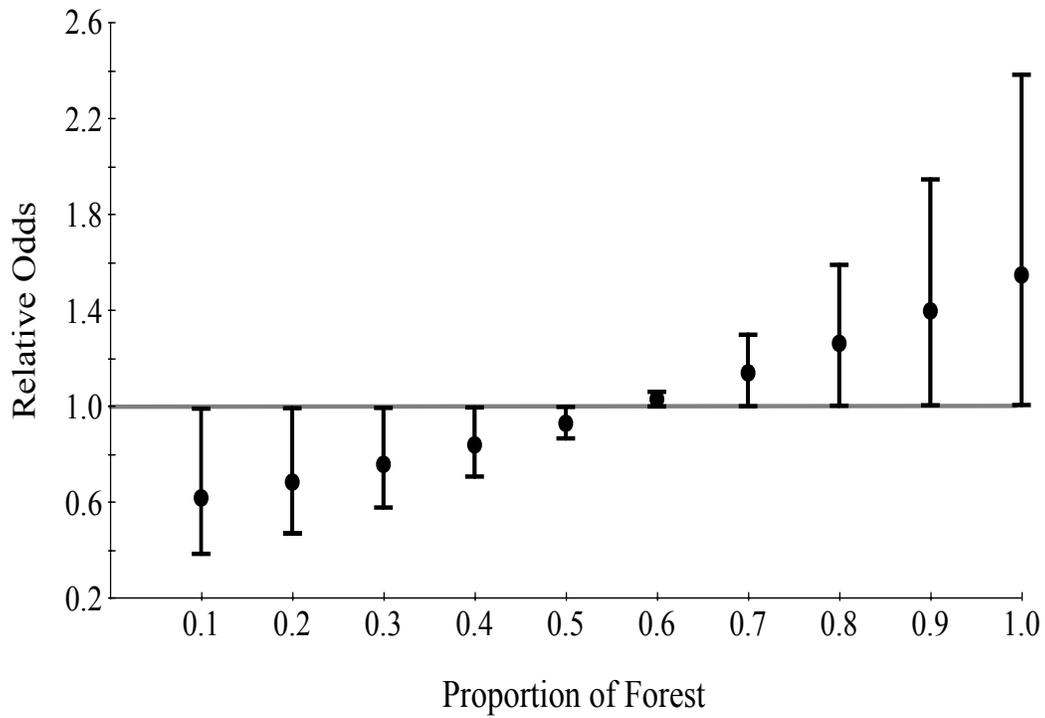


Figure 4. Predicted relative odds of Red-bellied Woodpecker use during prospecting movements for a range of forest cover when compared to the mean forest cover in the study site (0.57).

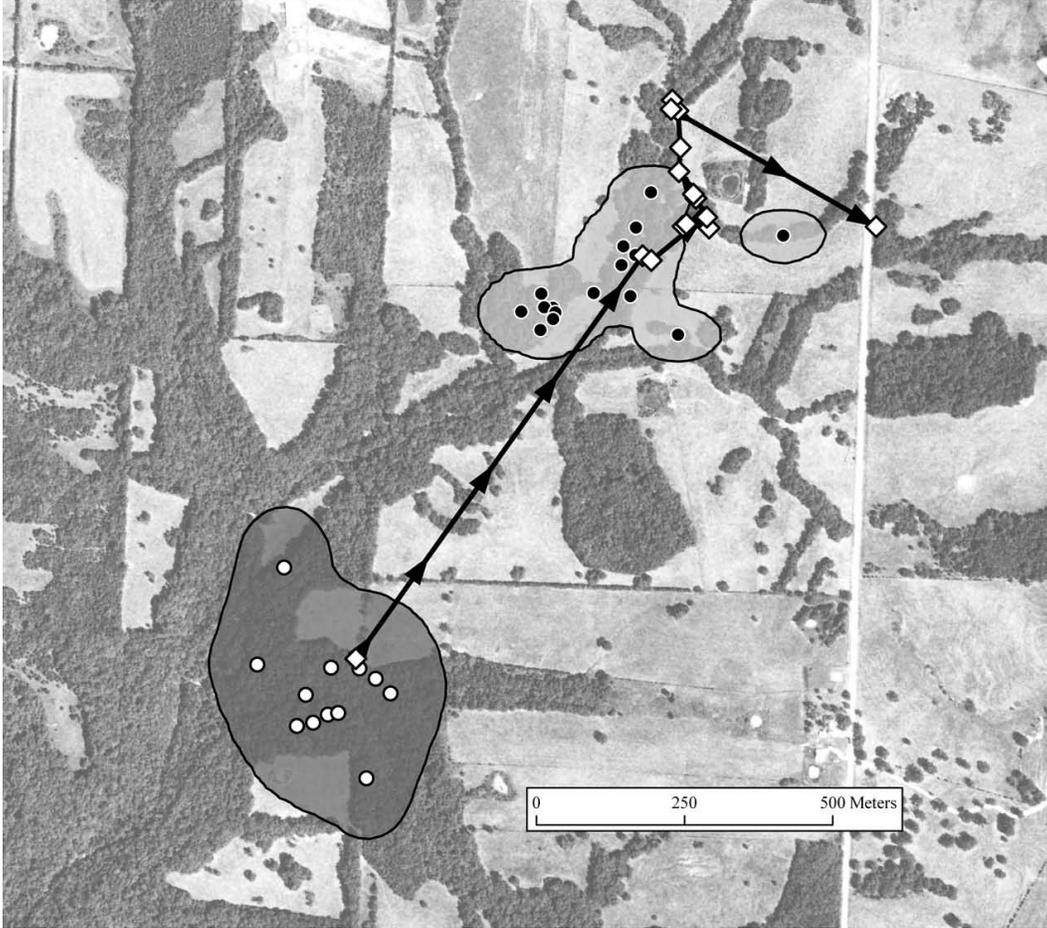


Figure 5. An example of a Red-bellied Woodpecker natal home range (shaded in dark gray), a prospecting movement (locations marked by white diamonds and connected with an arrowed line to represent location order), and a settlement home range (shaded in light gray). Home ranges are represented by a kernel utilization distribution (95% contour by volume). Bird locations on the natal home range are represented by white dots and bird locations after dispersal are represented by black dots.

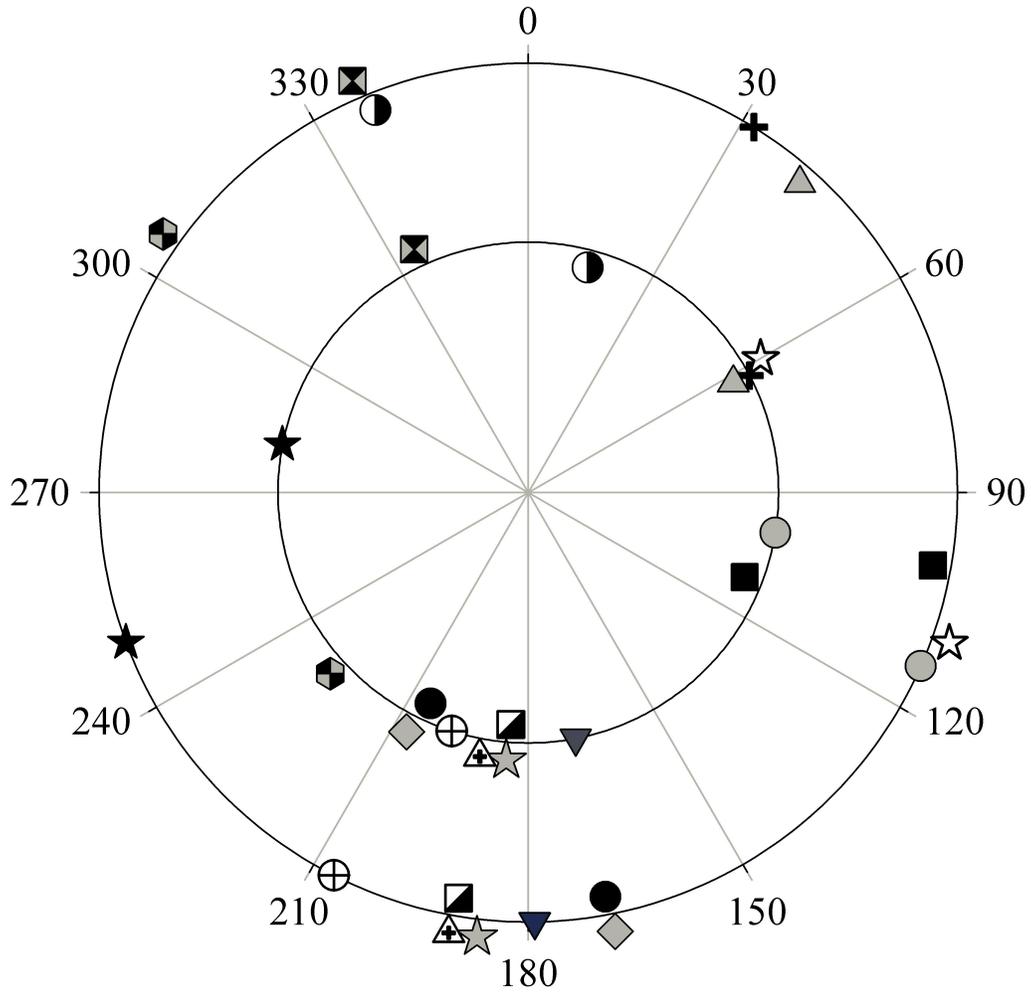


Figure 6. Polar plot of mean prospecting direction (inner ring) and mean dispersal direction (outer ring) of 16 Red-bellied Woodpeckers in central Missouri, illustrating correlation between prospecting and dispersal direction. Each symbol represents a different individual.

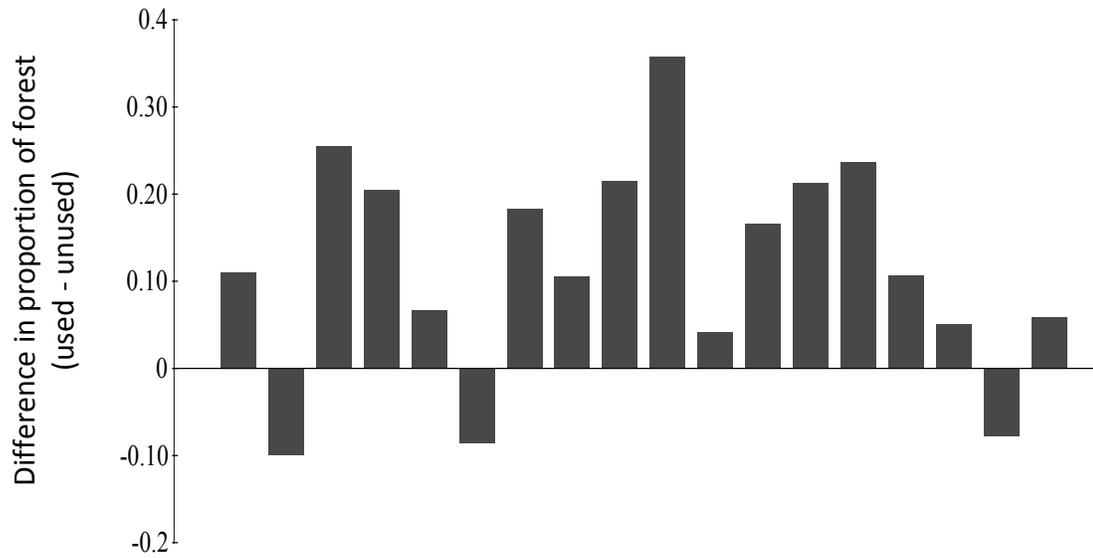


Figure 7. Difference in proportion of forest cover within areas potentially used during dispersal and unused areas beyond the settlement area. Each bar represents a different individual.

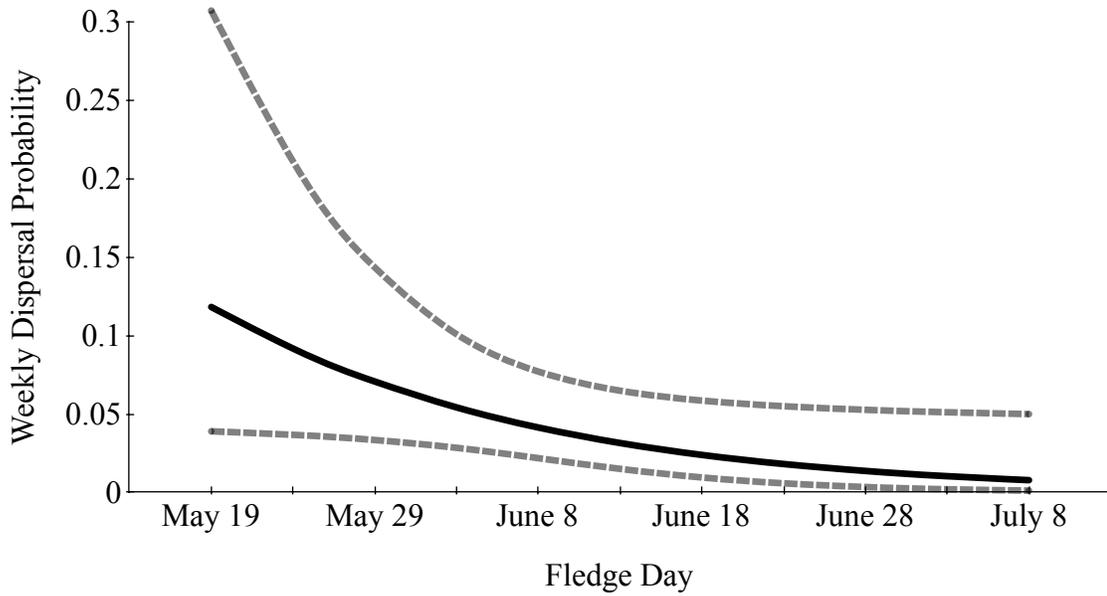


Figure 8. Predicted estimates of weekly dispersal probabilities for juvenile Red-bellied Woodpeckers in central Missouri (solid line) with 95% confidence intervals (dotted lines).

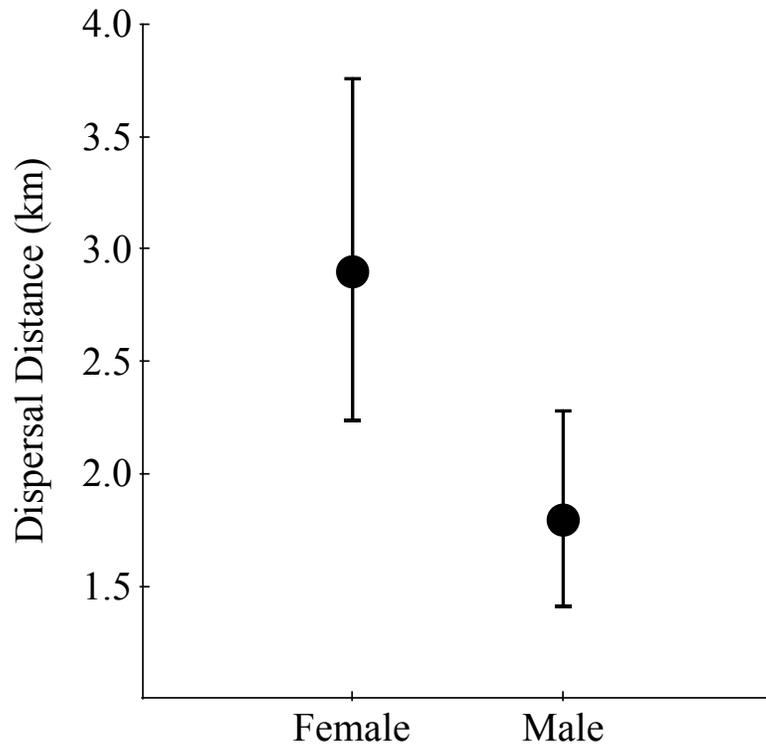


Figure 9. Predicted mean natal dispersal distance for male and female Red-bellied Woodpeckers in central Missouri. Error bars represent 95% confidence intervals.

TABLES

Table 1. Estimates of fixed parameters with associated standard errors (SE), F-values (calculated from Type III sums of squares) and P-values for hypothesized models explaining dispersal age in Red-bellied Woodpeckers in central Missouri. For models including sex, estimates are reported for females.

Model	Parameter Estimate ± SE	F Value	P Value
Fledge date	-0.057 ± 0.028	3.97	0.047
Brood size * sex	-1.101 ± 0.702	2.46	0.117
Brood size	0.541 ± 0.396	1.87	0.172
Mass	0.063 ± 0.050	1.57	0.210
Forest cover ratio	-0.725 ± 0.653	1.23	0.267
Mass * brood size	0.090 ± 0.107	0.71	0.400
Surrounding forest cover	1.545 ± 2.012	0.59	0.443
Fledge date * sex	-0.028 ± 0.037	0.55	0.457
Sex	-0.306 ± 0.435	0.49	0.482
Natal forest cover	-0.407 ± 1.300	0.10	0.755

Table 2. Ordered ranking of dispersal distance models in Red-bellied Woodpeckers in central Missouri; K is the number of estimated parameters, AIC_c is the second-order Akaike Information Criteria, and ω_i is the Akaike weight (model probability given the set of candidate models).

Model	Log-likelihood	K	AIC_c	ΔAIC_c	ω_i
Sex	-11.7	2	-6.8	0	0.73
Mass	-6.7	2	-4.4	2.4	0.22
Mass + sex	-6.1	3	-1.1	5.7	0.04
Fledge date	0.2	2	2.5	9.3	0.01
Fledge date + sex	-2.6	3	2.4	9.2	0.01
Dispersal date + sex	-0.4	3	4.6	11.4	0.00
Dispersal date	2.3	2	4.6	11.4	0.00

CHAPTER 2

POST-FLEDGING SURVIVAL IN RED-BELLIED WOODPECKERS

ABSTRACT

Juvenile survival parameters are critical to accurately modeling population growth. However, information about post-fledging vital rates is lacking for most avian species due to the difficulty of following individuals after they leave the nest. We assessed the influence of several intrinsic, temporal, social and landscape factors with the potential to affect survival during the post-fledging period in Red-bellied Woodpeckers. We radio-tagged woodpeckers in the nest and tracked the birds for five months and through periods of parental dependence, exploratory forays and natal dispersal. Estimates of post-fledging survival were best explained by fledgling age. Predictions of weekly survival rates were 0.94 for birds one week after fledging and then quickly increased to over 0.99 for birds 7 - 22 weeks after fledging. Period survival for the entire five months was calculated as 0.80 (CI: 0.65 - 0.90). No birds perished after departing the natal territory, suggesting that exploratory and dispersal behaviors are not costly in this species. These findings reveal the necessity to investigate age-specific patterns of survival in order to effectively predict population changes.

INTRODUCTION

Population models often reveal the key role of juvenile survival to population persistence in short-lived vertebrates (Gaillard et al. 1998, Wisdom et al. 2000). Among birds, however, estimates of post-fledging survival have been hindered by the difficulties

associated with tracking birds after they leave the nest. Researchers assume that the juvenile life stage is inherently risky and this assumption has been supported by radio-telemetry data collected on a small number of avian species (Anders et al. 1997, White 2005, Davies and Restani 2006, Suedkamp Wells et al. 2007). However, post-fledging survival estimates for entire suites of birds are completely lacking, with studies of raptors and open-cup nesting passerines dominating the literature. While estimates of juvenile survival have been calculated indirectly from mark-recapture band returns (Thomson et al. 1999) or as a fraction of adult survival (Ricklefs 1973), these estimates can be biased low by dispersal beyond study areas and assumptions about relative differences in juvenile and adult survival (Baker et al. 1995, Cooper et al. 2008).

Even fewer studies include covariates that could influence juvenile survival and those that do vary greatly in conclusions about which factors have the greatest effect. Starvation and depredation are the two main causes of avian mortality across life stages (Newton 1998) and younger birds may be more susceptible than older, experienced birds. Indeed, post-fledging survival studies often report the lowest survival estimates immediately after fledging (Anders et al. 1997, Dreitz et al. 2004, King et al. 2006, Yackel Adams et al. 2006, Berkeley et al. 2007, Gruebler and Naef-Daenzer 2008, Kershner et al. 2009). In addition, birds with greater mass may be in better condition to survive the transition from parental dependence to independence as heavier chicks had higher post-fledging survival in some species (Naef-Daenzer et al. 2001, Suedkamp Wells et al. 2007, Greño et al. 2008). However, these intrinsic qualities do not explain differences in post-fledging survival in all avian species. Barn Swallow (*Hirundo rustica*) juveniles also showed a positive relationship between duration of parental care

and survival (Grüebler and Naef-Daenzer 2008) while brood size predicted post-fledging survival in Spotted Antbirds (*Hylophylax naevioides*; Styrsky et al. 2005). These findings emphasize the influence of sibling competition and parental investment beyond the nest stage.

Post-fledging survival also seems likely to vary temporally. Yearly or seasonal changes in food availability and predator abundance have been noted to affect juvenile survival (Dreitz et al. 2004, Yackel Adams et al. 2006, Schmidt et al. 2008). Within-year differences in survival may also occur when nesting is asynchronous and deviation from optimal nest initiation dates can have long-lasting survival consequences (Perrins 1970). Specifically, seasonal patterns in juvenile survival have been associated with fledge date in some forest birds (Naef-Daenzer et al. 2001, Sunde 2005, Grüebler and Naef-Daenzer 2008). The phenomenon has been attributed to a host of causes including higher overall fitness of early breeding parents, fluctuations in food abundance, and peaks in predation pressures (Verhulst and Nilsson 2008).

The effect of landscape-level habitat fragmentation on nest survival has been widely studied, and increased fragmentation can result in higher nest predation rates (Robinson et al. 1995). However, the effect of habitat composition and configuration on young birds after they leave the nest remains largely unstudied (but see King et al. 2006, Berkeley et al. 2007 for habitat effects on grassland birds). Densities of nest predators have been documented to be higher in fragmented habitats (Rosenberg and Raphael 1986, Robinson et al. 1995, Dijak and Thompson III 2000) and these same predation pressures may also affect juvenile survival after the nestling stage.

There is a clear need for post-fledging survival studies aimed at birds from a wider range of taxonomic groups and life histories. An expanded knowledge of juvenile survival will help elucidate the factors driving life-history strategies and their influence on population demography. We provide the first estimates of post-fledging survival in a North American cavity excavator, the Red-bellied Woodpecker (*Melanerpes carolinus*). Further, we investigate the relative influence of social, temporal, and landscape factors with the potential to affect survival during early life stages.

METHODS

Study site and field techniques

We conducted our study in the Mark Twain National Forest's Cedar Creek Unit in central Missouri (38°46'N, 092°07'W) and the adjacent Baskett Wildlife Research and Education Area (38°46'N, 092°15'W). Work was conducted from March through November 2009 and 2010. The national forest areas are composed of privately owned residential and agricultural inholdings interspersed within the federally administered property. This portion of the national forest is additionally fragmented by pastures for cattle grazing on the federal land. The Baskett Wildlife Research and Education area is primarily contiguous hardwood forest. By including both of these areas in the study site, we were able to increase our gradient of forest cover.

We searched for Red-bellied Woodpecker nests in each study area. Once nest locations were identified, we used a wireless cavity viewer (Huebner and Hurteau 2007) to assess nest stage and determine nestling age. At approximately 20 days post-hatch, we ascended to nests using a guyed extension ladder (Rohwer 1988) and retrieved nestlings

with the hole-saw method (Ibarzabal and Tremblay 2006). We banded each bird with three colored, plastic leg bands and one numbered, aluminum band (USGS Patuxent Bird Banding Laboratory). We also weighed nestlings and attached radio transmitters (2.6g; model A1060; Advanced Telemetry Systems, Isanti, MN) with a leg-harness (Rappole and Tipton 1991). Transmitters weighed 3-4% of body mass and had a battery life of 4-6 months. Nestlings were returned to the cavity and monitored daily until fledging (within five days of extraction). In 2009, heavy nest predation limited our ability to track fledged birds, so we fitted nest trees with snake excluder devices (Neal et al. 1998) in 2010.

Radio-marked Red-bellied Woodpeckers were tracked 2-3 days per week for the first 22 weeks post-fledging. We located birds using the homing method (White and Garrott 1990) with model R-1000 Communications Specialists receivers and three-element Yagi antennas. Location coordinates (Universal Transverse Mercator coordinate system, UTM) were recorded for each individual with a global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, KS) after determining survival and visually confirming individual color band combinations. We confirmed mortality based on post-mortem remains, tooth marks or scrape marks on the transmitter, or blood on the harness material.

Birds occasionally moved onto private property where access was not granted. We used triangulation methods (LOAS, Ecological Software Solutions LLC. Hegymagas, Hungary; Version 4.0) to remotely estimate bird locations when homing was not possible. We confirmed survival with changes in radio signals, which indicated individual movements, and with among-observation period differences in location.

Factors influencing survival

We identified factors with the potential to influence post-fledging survival in Red-bellied Woodpeckers, including body mass, age, year, fledge date, brood size, and landscape forest cover. Body mass, as an index of body condition, was measured at the time of radio-tagging (between 19 and 23 days). No relationship was detected between age at measurement and body mass ($r^2 = 0.049$), and growth models indicated that chick mass stabilized at 19 days post-hatch (Stickel 1963). Thus, mass was not adjusted for measurement age. We used the number of weeks after fledging as a measure of age. We predicted elevated mortality in smaller birds with fewer nutrient reserves and in younger birds that were likely less mobile and adept at foraging. We measured within-season temporal effects as a function of fledge date, as previous work indicated earlier fledging birds might have higher survival (Verhulst and Nilsson 2008). We determined brood size at time of radio-tagging and we hypothesized that birds from smaller broods would be more likely to experience elevated parental care and thus suffer lower mortality.

To assess habitat effects on juvenile survival, we calculated the proportion of forest cover in the area 240 meters around each location on the natal area, the approximate radius of a natal home range (see Chapter 1). We used a Geographic Information System (GIS; ArcView 9.2, ESRI, Redlands, CA) to buffer each natal location by 240 meters and dissolved all polygons into a single area of habitat influence for each bird. We then used land cover maps (Missouri Land Use Land Cover Data, Columbia, MO: Missouri Spatial Data Information Service, 2005) to quantify the proportion of forested area within the natal area. We did not investigate habitat influences of birds moving outside of the natal home range once it was determined that

no birds perished while outside of the natal area. We predicted that reduced forest cover would result in lower survival from increased exposure to predators.

Data analysis

We estimated post-fledging survival in Red-bellied Woodpeckers with the known-fate option in program MARK (White and Burnham 1999), which uses a Kaplan-Meier approach (Kaplan and Meier 1958). We considered each week to be an encounter occasion. The Kaplan-Meier procedure assumes that an individual's probability of survival is independent from that of all other individuals in the study (Pollock et al. 1989). By radio-marking siblings, we risked violating this assumption. Therefore, we tested for sibling survival independence with a goodness of fit test of the summation of partial χ^2 values calculated for each possible outcome of mortalities, given all possible brood sizes (see Wiens et al. 2006). Results indicated that the survival of siblings acted independently ($\chi^2 = 6.696$, $df = 13$, $P = 0.9171$).

Our data also meet the Kaplan-Meier procedure assumption that censoring of study animals is independent of biological phenomenon (Pollock et al. 1989). We censored study individuals beginning when poor radio transmission strength prevented us from effectively tracking the individual or if the radio harness fell off the study individual, and continued censoring for the duration of the study for those individuals. With the exception of one individual, all censored birds were either resighted after radio or harness failure, or had a documented gradual decrease in radio signal strength prior to non-detection. Therefore, it was apparent that these birds had been removed from the study due to equipment failure and not movement outside of the study area or death. Due

to the relatively short distance that our dispersing birds traveled, we deduced that it was unlikely that the single missing bird travelled outside of the detectible area and had an equal chance of carrying a faulty transmitter or a transmitter damaged during a predation event.

We fitted survival data to eight models using an information theoretic approach. Given the low number of mortalities encountered, we only considered single variable models and a constant survival model. We considered ecologically plausible models to test for the effects on survival of year, age, fledge date, mass, brood size, and habitat composition. We used an adjusted Akaike's information criteria (AIC_c) to identify the best model(s) by considering all models within 0-2 ΔAIC_c (Burnham and Anderson 2002). Model support was evaluated with Akaike weights (ω_i ; Burnham and Anderson 2002). We also report parameter estimates and 95% confidence intervals (95% CI) for variables included in the model candidate set.

RESULTS

We radio-tagged 52 nestling Red-bellied Woodpeckers from 19 nests. Of these, 43 birds from 18 nests successfully fledged with radios, and those were included in our post-fledging survival analysis. We confirmed the fate of all but one individual and obtained locations at every sampling period until death or censoring due to a confirmed transmitter or harness failure. We documented eight mortalities from seven different nests during the study period. All mortalities occurred within seven weeks of fledging. Four mortalities occurred in the first two weeks after fledging and one mortality occurred each week thereafter (with the exception of week five). No birds died outside of the natal

home range, even though 18 individuals dispersed during the study period and 26 birds were observed making forays into the surrounding landscape (see Chapter 1).

Results showed a strong association between age and survival (Table 1). The age model received $> 95\%$ of ω_i indicating no model uncertainty. The top-ranked model indicated an increasing probability of survival with age ($\beta_{\text{age}} = 0.31$; 95% CI = 0.06 - 0.55; Fig 1). For example, the model predicts that weekly survival is 0.94 at one week after fledging and increases to 0.99 by seven weeks after fledging. Although fledge date also ranked above constant survival, it contained only 1% of the ω_i and showed a weaker and insignificant effect size ($\beta_{\text{fledge}} = -0.05$; 95% CI = -0.10 - 0.01). We estimated period survival for the 22 weeks post-fledging as 0.80 (CI: 0.65 - 0.90) based on the product of all weekly estimates.

DISCUSSION

Age of bird was the key predictor of survival for Red-bellied Woodpeckers in the first five months after fledging. The young woodpeckers were most vulnerable during the first few weeks and then showed relatively high rates of survival for the remainder of the study. The causes of age-related vulnerability during the first several weeks post-fledging are not entirely clear. It appeared that higher mortality in younger birds in this study was due to a higher risk of predation as all mortalities showed evidence of partially consumed remains, or tooth marks or scrape marks on the transmitter. However, this distinction is often difficult to make as starving or diseased birds may also be more susceptible to predation or could have been scavenged after death from another cause. Young birds may also be more vulnerable to predators because of a lack of experience

and an associated inability to identify threats (Rajala et al. 2003). Alternatively, the young woodpeckers may not be able to avoid approaching predators because of reduced flight skills (Thompson et al. 2010).

We observed no mortalities during exploratory foray movements or after natal dispersal, even though these behaviors were seen in the first few weeks after fledging (minimum foray age = 22 days; minimum dispersal age = 34 days; see Chapter 1). Dispersal has been characterized as a costly and risky behavior with inherently lower survival (Johnson and Gaines 1990, Daniels and Walters 2000, Stamps 2001). Many studies report lower survival during dispersal due to increased anthropogenic mortality as animals encounter roads and other human-influenced landscapes, e.g., coyotes (Harrison 1992), snakes (Bonnet et al. 1999), frogs (Carr and Fahrig 2001), and lynx (Kramer-Schadt et al. 2004). In all of these cases, the danger of the habitat matrix decreased survival of dispersing terrestrial animals. The elevated survival in our population of dispersing Red-bellied Woodpeckers may be indicative of their ability to avoid unsuitable matrix habitat as they navigate away from the natal territory. Real-time tracking information investigating how birds use the surrounding landscape during dispersal would elucidate the mechanisms underlying the costs of dispersal for this class of animals.

In contrast to age effects; year, fledge date, brood size, mass, and forest cover did not provide strong evidence for an effect on juvenile survival in this population. Considering the strong age-dependent vulnerability, it seems intuitive that decreased brood size would increase the amount of parental care for any individual, and thus ameliorate the risks of inexperience. However, brood division routinely occurred in our

population, including those with only one nestling where only one parent would care for the fledgling. This behavior decreases the variability in amount of parental care after fledging, as the effective brood size during the juvenile period was either one or two fledglings per parent in almost all cases. Red-bellied Woodpeckers may also be able to reduce the effects of nestling mass on fledgling survival by allowing smaller chicks more time to develop in the nest. Four nests showed asynchronous fledging with smaller birds leaving the nest up to three days after their siblings, which could increase fitness of the smaller birds to more closely match their larger siblings once they leave the nest. The potential for effects of habitat structure on juvenile survival are less clear, but nest survival studies suggest that changes in predator density may contribute (Dijak and Thompson III 2000). However, a review by Chalfoun et al. (2002) found that changes in predator abundance in response to habitat fragmentation are predator-specific. Therefore, juvenile woodpeckers may not be vulnerable to predator guilds whose densities are affected by fragmentation. Alternatively, juvenile woodpeckers may ameliorate the risk of crossing gaps in the forest by using forested corridors when moving through a fragmented landscape (see Chapter 1).

Our juvenile Red-bellied Woodpecker survival rates were relatively high when compared to other studies of radio-tagged North American land birds tracked immediately after fledging. When survival estimates are standardized to two months after fledging for comparison, Red-bellied Woodpecker survival estimates are 8% to 52% higher than the other species (Red-bellied Woodpecker = 0.92, Snail Kite = 0.84 [*Rostrhamus sociabilis*; Dreitz et al. 2004], Northern Goshawk = 0.78 [*Accipiter gentilis*; Wiens et al. 2006], Eastern Meadowlark = 0.68 [*Sturnella magna*; Suedkamp Wells et al.

2007], Burrowing Owl = 0.57 [*Athene cunicularia*; Davies and Restani 2006], Swainson's Thrush = 0.57 [*Catharus ustulatus*; White 2005], Dickcissel = 0.55 [*Spiza americana*; Suedkamp Wells et al. 2007], and Wood Thrush = 0.40 [*Hylocichla mustelina*; Anders et al. 1997]). This disparity in juvenile survival rates could be attributed to a number of morphological or life-history differences such as size (larger animals generally have greater longevity [Lindstedt and Calder 1976]), foraging strategy, or development at fledging.

Red-bellied Woodpeckers are opportunistic generalists adapted to a variety of habitats and changes in seasonal food availability (Shackelford et al. 2000). This foraging strategy may lead to higher juvenile survival compared to other specialist bird species. Juvenile Northern Goshawks experienced a decline in survival following dispersal from the natal territory, which was most likely due to their inability to effectively capture prey in the unfamiliar habitat (Wiens et al. 2006). The opportunistic foraging style of Red-bellied Woodpeckers may be easier to master for young birds. In addition, generalists are not as susceptible to declines in abundance of particular food items (Dall and Cuthill 1997).

Another explanation for the relatively high survival rate identified in this study might be associated with the benefits of the cavity nesting life history strategy of the Red-bellied Woodpecker. Cavity nesting birds tend to have longer nestling development periods than open-cup nesters even when controlling for mass (Martin and Li 1992) and previous investigations of post-fledging survival (summarized above) focused on cup nesters. The longer nestling development phase could result in birds that are more fit at

the time of fledging. The older birds might have improved flight capacity to evade predation and be more adept at procuring food.

The juvenile life stage has been shown to be the most elastic and most variable stage in short-lived animals when modeling for population persistence (Wisdom et al. 2000). However, the resolution of our knowledge of first year survival in birds is poor. Age-related predation vulnerability has been shown in a wide range of species (Carey and Moore 1986, Iverson 1991, Lingle et al. 2008) and these transitions between a “vulnerable” state to an “invulnerable” (less vulnerable) state are integral to maintaining population balance, especially in seasonal environments (Abrams and Walters 1996). Therefore, a precise understanding of changes in survival rates throughout the juvenile stage is integral to accurately model population change. For example, in this study, Red-bellied Woodpeckers suffered higher mortality in the first few weeks after fledging, however, survival rates quickly increased to a less vulnerable state, even during the potentially risky behaviors of prospecting and dispersal. Had the lower rate of early fledgling survival been extrapolated to the entire juvenile period, first year survival would be drastically underestimated. However, juvenile Red-bellied Woodpeckers may also experience lower survival during the winter months when compared to adults. Additional future research focused on the mechanisms driving and patterns of survival in juvenile birds will expand our understanding of a neglected life-history stage and improve the accuracy of population growth models necessary for the conservation and management of birds.

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FIGURE

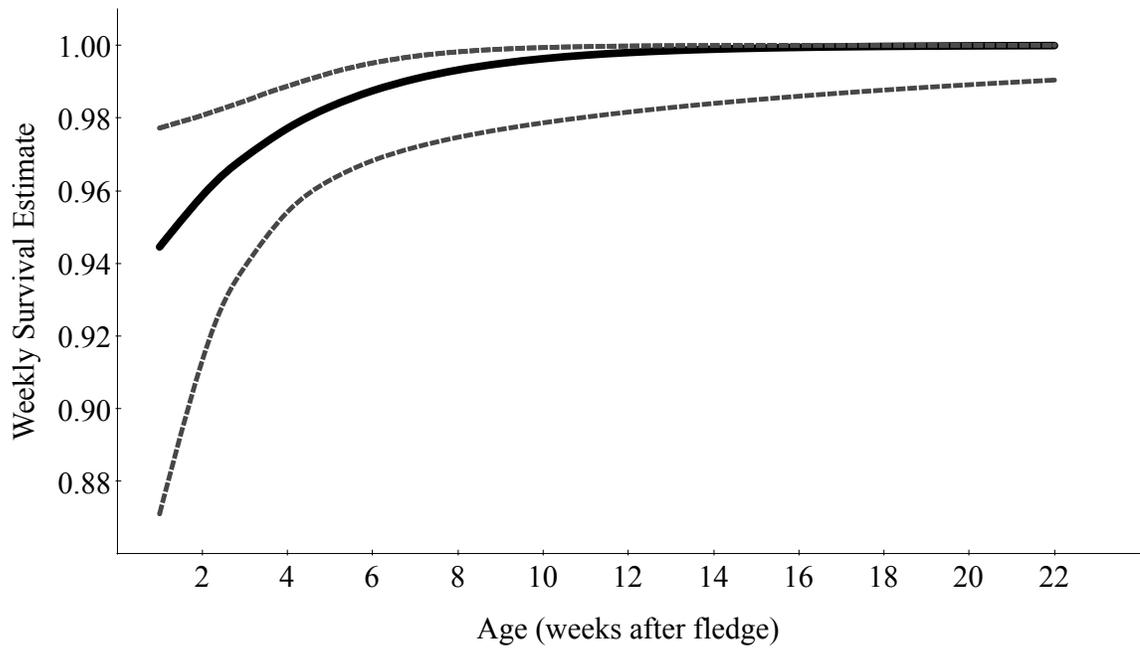


Figure 1. Estimates of weekly survival for juvenile Red-bellied Woodpeckers in central Missouri (solid line) with 95% confidence intervals (dotted lines).

TABLE

Table 1. AIC_c ranking of competing models explaining survival (\emptyset) of Red-bellied Woodpeckers for the first 22 weeks after fledging in central Missouri; K : number of estimated parameters, AIC_c: second-order Akaike Information Criteria, ω_i : Akaike weight (model probability given the set of candidate models).

Model	AIC _c	Δ AIC _c	ω_i	K	Deviance
\emptyset (age)	77.31	0.00	0.97	2	73.29
\emptyset (fledge date)	86.02	8.71	0.01	2	82.00
\emptyset (.)	87.03	9.72	0.01	1	85.03
\emptyset (year)	88.04	10.73	0.00	2	84.02
\emptyset (brood size)	88.48	11.17	0.00	2	84.46
\emptyset (forest cover)	88.68	11.37	0.00	2	84.66
\emptyset (mass)	89.03	11.72	0.00	2	85.01