

Original Article

# Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird

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Dispersal behavior is key to population dynamics, yet little is known about the temporal, spatial, and social factors affecting natal dispersal. We studied natal dispersal behavior by intensively tracking a pair-breeding resident bird, the red-bellied woodpecker (*Melanerpes carolinus*), from fledging until permanent departure from the natal territory. Juveniles used a centrally based foray prospecting strategy. Woodpeckers made repeated forays into the surrounding landscape with subsequent daily returns to the natal area to roost. Prospecting individuals preferentially chose foray paths with greater forest cover. Woodpeckers eventually dispersed after repeated forays, and foray direction predicted dispersal direction. Birds that fledged earlier in the season and individuals from larger broods dispersed at a younger age than birds fledging later in the year and those from smaller broods. Females and smaller individuals dispersed farther than males and larger birds, but we identified no sex bias in dispersal direction. Prospecting and dispersal areas had more forest cover than areas beyond dispersal locations, indicating that fragmented landscapes may serve as barriers to dispersal. We provide evidence that juvenile birds used repeated forays to inform decisions about dispersal prior to permanent departure from the natal area. Intrinsic and social factors affected the distance and the age of dispersal, whereas habitat configuration affected direction of movement. *Key words*: Brownian bridges, corridors, dispersal age, foray, habitat connectivity, *Melanerpes carolinus*, natal dispersal, prospecting, red-bellied woodpecker, sex-biased dispersal. [*Behav Ecol*]

## INTRODUCTION

Movements and decisions made by dispersing individuals underpin broader population-level patterns and processes. Dispersal movements 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). In order to properly model dispersal, ecologists must consider causes of variation in behavior during all 3 stages of dispersal: departure, transience, and settlement (Clobert et al. 2009). However, studies of dispersal largely include only reports of dispersal outcomes, and little is known about the factors affecting the movement behaviors of dispersing individuals. Few have intensively tracked movement during all 3 stages of natal dispersal and even fewer attempted to evaluate variation among individual dispersers (but see Selonen and Hanski 2006; Kesler et al. 2010).

Dispersal movements differ among individuals, populations, and species; however, the factors driving this variation are unclear. Reed et al. (1999) outlined conceptual models of exploratory movement patterns (prospecting) used during the transient stage of avian dispersal and proposed that prospecting behaviors were associated with the mating system of the species. Although these models were

developed for birds, they could also be applied to other taxa. The “cooperative breeder” model was defined as a centrally based foraging behavior, which 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 and other family living species, in which juveniles remain on the natal territory past parental independence (Komdeur and Ekman 2010). The “floater” model prescribes that birds make one permanent departure from the natal area, whereupon they move among potential breeding territories until a vacancy is encountered. Floater behavior has been described in many pair-breeding species and may be preceded by aggression from parents that causes an abrupt departure from the natal site (Holleback 1974; Gayou 1986; Tarwater and Brawn 2010). The “colonial breeder” model was described for birds that monitor potential settlement colonies before settling, but without using the natal colony as a home base.

Proximate factors can influence the movement behavior of individual animals employing any of the informed dispersal models. The effect of habitat configuration on disperser decisions has been evidenced in mammals (Revilla et al. 2004; Selonen and Hanski 2006; Proctor et al. 2012), birds (Kesler and Walters 2012), and amphibians (Rittenhouse and Semlitsch 2006) when movements were directionally biased by habitat features. Animals may choose to move within features that resemble natal habitats (i.e., a breeding territory; Selonen and Hanski 2006; Kesler and Walters 2012), reduce predation risk (Miller et al. 1997), or otherwise facilitate movement (e.g., prevailing winds, Delgado et al. 2010; stream flow, Congdon 1994).

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Dispersal distance, age, and direction can also vary among individuals, and differential dispersal patterns can lend insight into the tradeoffs associated with dispersal decisions. Longer ranging animals may have an increased susceptibility to predation and lower reproductive success, whereas philopatric animals may risk decreased gene flow (Gaines and McClenaghan 1980; Béchon et al. 1996). Individuals that remain on the natal territory longer may benefit from increased survival and/or reproductive success (Ekman et al. 1999; Tarwater and Brawn 2010; Sparkman et al. 2011), whereas those departing earlier may have first access to quality vacant territories (Waser 1985). Sex-biased dispersal is often apparent in dispersal distance (Pusey 1987; Clarke et al. 1997), age (Middleton and Green 2008), and direction (Congdon 1994; Poole 1997). Body condition (Ferrer 1993; Belthoff and Dufty 1998; Lens and Dhondt 1994; Pasinelli and Walters 2002), phenology (Mulder 1995; Spear et al. 1998; Pasinelli et al. 2004; Tarwater and Brawn 2010), sibling competition (Belthoff and Dufty 1998; Pasinelli and Walters 2002), and habitat quality (Lens and Dhondt 1994; Long et al. 2005) can also affect dispersal distances and/or dispersal age.

Despite the contributions of studies investigating dispersal outcomes and theoretical models of dispersal, understandings of the dispersal process have stagnated because of a lack of animal-based evidence from movement studies (Walters 2000; Liu and Zhang 2008). Theoretical models provide a strong conceptual foundation for prospecting behaviors, and they have indeed predicted the outcomes of dispersal based on mating systems (Gayou 1986; Koenig et al. 1996; Kesler and Haig 2007; Tarwater and Brawn 2010). However, the Reed et al. (1999) models of informed dispersal relate directly to fine-scale animal movements made before settlement, and few study the dispersal process at the spatio-temporal resolution necessary to validate these models. Extremely little is known, for any species, about the daily foray movements that precede permanent dispersal from the natal site or about the connection between forays and dispersal.

We studied the full natal dispersal process in red-bellied woodpeckers (*Melanerpes carolinus*) to identify factors affecting departure, transience, and settlement stages. 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, the most drastic movement for this resident species occurs during the juvenile life stage (Greenwood and Harvey 1982). We studied the daily foray movements of the woodpeckers throughout the dispersal process. We identified which prospecting model(s) best represented juvenile red-bellied woodpecker movement behavior during natal dispersal. We predicted that the woodpecker, which is not a family-living species, would use a floater prospecting strategy, in which individuals make abrupt and direct movements from the natal area followed by movements among potential breeding habitats before dispersal settlement (Reed et al. 1999). We also investigated factors affecting prospecting and dispersal directions and predicted that foraging birds would prospect in directions with higher forest cover because animals may select foraging habitats similar to breeding habitats (Selonen and Hanski 2006; Kesler and Walters 2012). Finally, we tested for intrinsic, social, and environmental factors that may influence permanent departure age and dispersal distance.

## METHODS

### Study site and field techniques

We conducted our study in the 6677-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) from March through November during 2009 and 2010. The study site included hardwood forests, pastures, private agricultural and residential inholdings, and spanned a gradient of forest fragmentation (natal areas spanned 18–100% forest cover; Cox and Kesler 2012).

We radio-tagged and banded nestling red-bellied woodpeckers (see Cox and Kesler 2012 for detailed methods). We tracked radio-marked birds daily in 2009 and 2–3 days each 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) where we followed the strength of the signal until we observed the bird and recorded geographic locations for each individual with a global positioning system. We used triangulation (LOAS Version 4.0; Ecological Software Solutions, Hegymagas, Hungary) to remotely estimate bird locations when birds were inaccessible, but excluded triangulated locations with error ellipses greater than 1.8 ha (approximately 10% of mean natal home-range size). We remained near each individual for a minimum of 30 min, noted interactions with conspecifics (e.g., begging, feeding, aggression), and identified if study subjects made forays from the natal area during that time.

We intensively tracked birds if a putative prospecting movement (i.e., a quick, long, solitary movement away from the natal area; Baker 1969) was detected or if the initial location was outside the natal area. Intensive tracking sessions lasted 2 h or until a return to the natal area. During intensive tracks, we recorded geographic locations when birds moved >10 m. If an individual remained off the natal area >2 h, the bird was located the following day before dawn to determine whether it roosted on or off the natal area. We classified individuals as dispersers once they roosted off the natal territory and collected weekly locations thereafter. No bird returned to the natal territory after roosting elsewhere, and subsequent visits to dispersal locations during the following breeding season verified that at least 6 birds remained at dispersal destinations throughout the winter (Cox 2011).

### Prospecting

We derived natal home-range utilization distributions (UDs) with KernelHR (Version 4.27; Seaman et al. 1998), using locations obtained within the area where we observed birds interacting with their parents. We used a fixed kernel density estimator and least-square cross-validation to calculate the home range. We defined the natal home-range boundary as the 95% isopleth of the UD and identified the home-range center as the centroid of the polygon encircled by the 5% isopleth. Our estimates of natal home range were likely conservative as we limited it to the area where we observed birds interacting with parents (begging, being fed) to ensure that we were indeed measuring parental territory. We compared putative prospecting movements to natal home-range boundaries and reclassified movements as forays when birds traveled farther than the radius of a mean natal home range (240 m) outside of their natal home-range boundary. This conservative measurement ensured that the birds traveled far enough to, on average, enter the center of an adjacent territory and thus be well beyond their parent's territories before they were considered prospectors.

We tested whether birds that made multiple forays were more likely to prospect in a single direction each time they left the natal territory by comparing foray orientations with a random data set. For each foray, we calculated the orientation from the natal home-range centroid to the farthest location

recorded. We calculated the absolute difference between each foray orientation and the mean prospecting orientation for that individual (mean angle; Zar 1999:599–600). We compared observed and random data sets using a Wilcoxon–Mann–Whitney test (proc NPARIWAY; SAS Institute Inc. 2008).

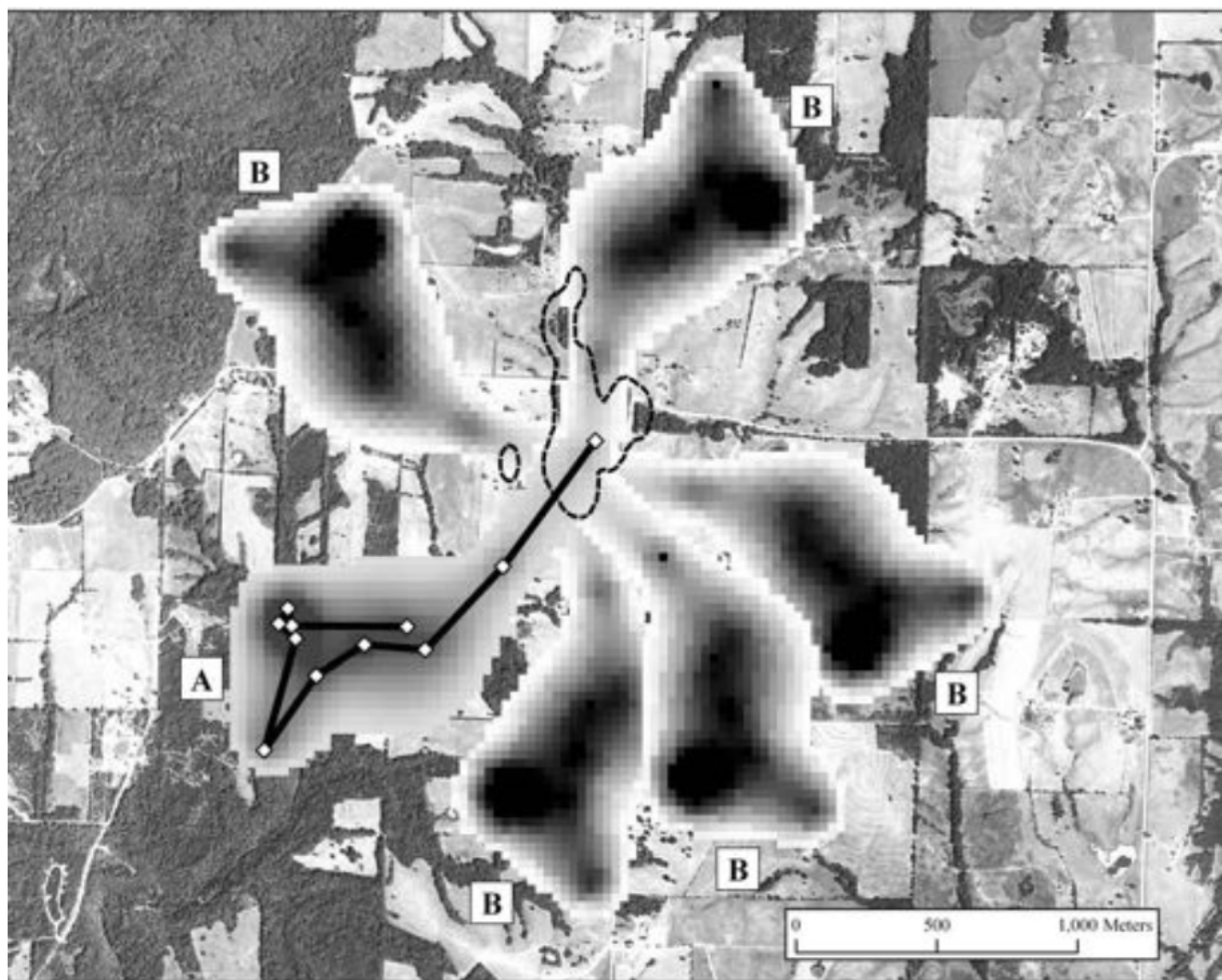
We tested for an effect of landscape configuration on red-bellied woodpecker forays by comparing habitat composition (forest versus nonforest) in areas used during prospecting to other areas that were available to the woodpecker. We modeled occurrence probabilities for forays with Brownian bridge methods (Horne et al. 2007), which create probability distributions of temporally correlated spatial data. We used Animal Space Use (version 1.3; Horne and Garton 2009) to derive probability distributions and considered landscape areas encompassed by the isopleth encircling 95% of the 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 compared the proportion of forest cover, weighted by probability of bird occurrence, in used areas to 5 matched available areas. We identified the available areas by randomly rotating each Brownian bridge utilization grid around the

individual's home-range center to maintain movement sinuosity and travel distances (Figure 1). We compared forest cover in actual and random paths with a generalized, linear mixed model (proc GLIMMIX; SAS Institute Inc. 2008) with a binomial response (actual, random) and included random effects for individual and nest to account for a potential lack of independence within individuals and among siblings (Kleinbaum et al. 2008).

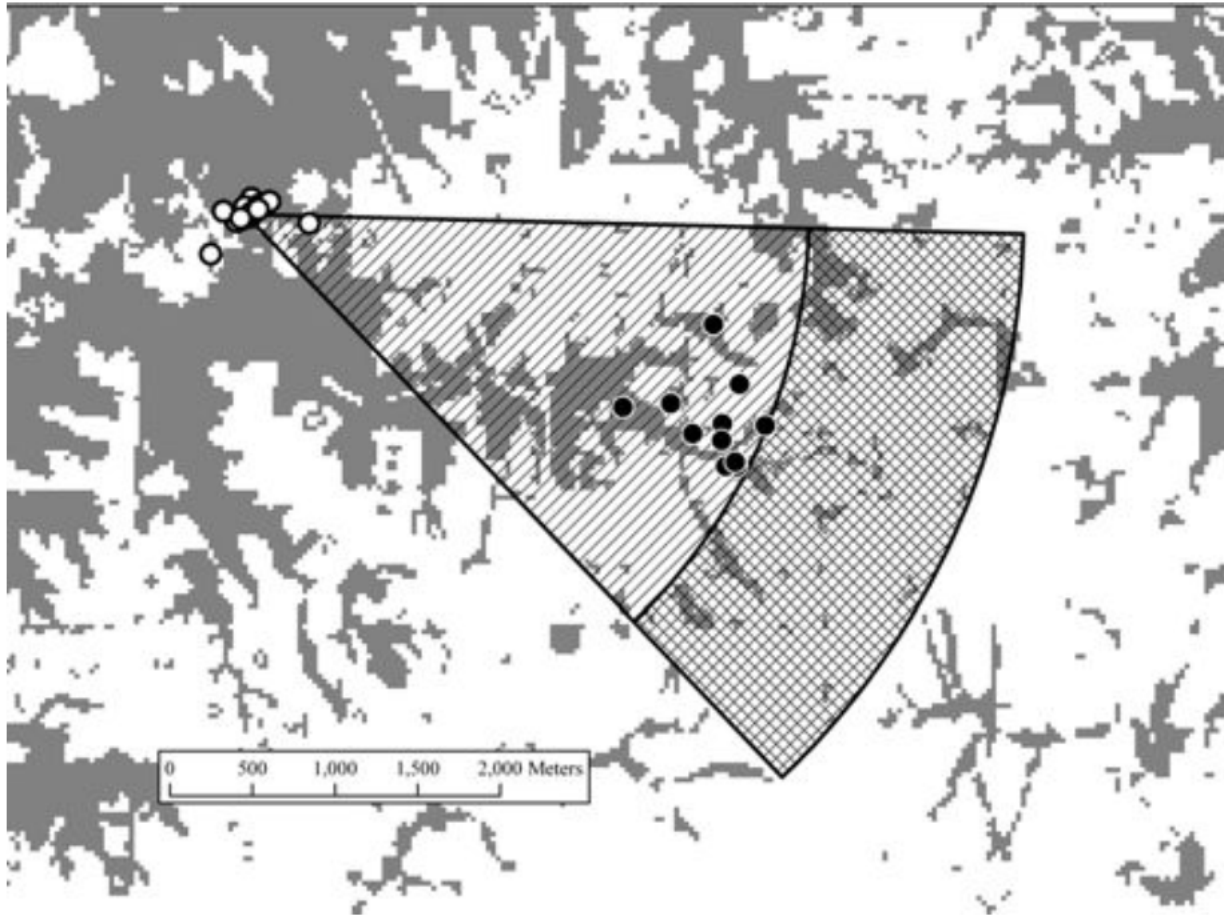
### Dispersal

We used weekly locations from dispersed birds to estimate postdispersal range sizes and compared them to natal home-range sizes with a 2-tailed *t*-test. We tested for an association between the mean foray direction and the mean dispersal direction for each bird using a circular correlation test (Fisher and Lee 1983; Kölliker and Richner 2004). We then tested for a sex bias in dispersal direction with a Watson–Williams 2-sample test for circular distributions (Zar 1999:625; Kölliker and Richner 2004).

We tested for landscape barriers to dispersal by comparing forest cover in areas used during dispersal with landscape cover in areas beyond dispersal locations. We represented the



**Figure 1**  
Example of a juvenile red-bellied woodpecker prospecting movement. Observed locations (white diamonds) are connected with a solid black line to indicate the order of observation. The dotted line indicates the natal home-range boundary. The 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 to 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. 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  $40^\circ$  (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.

area that a bird used during dispersal as a pie-shaped polygon with a  $40^\circ$  internal angle (the average range of exploration movements during forays; see results) originating at the natal home-range center and terminating at the farthest dispersal location (Figure 2). We identified the potential barrier as the area 1.3 km (the mean distance of a prospecting movement) beyond the used area. We then compared the proportion of forest cover in the used area to forest cover in the area beyond the dispersal destination with a paired 1-tailed *t*-test.

We evaluated the effects of sex, fledge date, mass, brood size, and habitat composition on dispersal age with a generalized, linear mixed model (proc GLIMMIX) with nest of origin as a random effect and a binary response variable to represent if a bird dispersed (1) or not (0) within a given week (with week 1 being the first week after fledging), so our results would not be biased toward birds dispersing earlier (during the study period). We censored study individuals after mortality, when telemetry batteries began to fail, or if the radio harness fell off the study individual. We measured body mass at the time of radio-tagging (19–23 days old). 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 posthatch (Stickel 1963), so we did not adjust mass for measurement age. We tested whether habitat composition (percent forest) within the natal territory influenced dispersal age by intersecting the 95% isopleth natal

home-range polygon with the land cover map to calculate the proportion of forest within the natal home range. We tested whether habitat composition outside the natal territory influenced dispersal by calculating the forest cover within a radius of 1.3 km (mean bird prospecting distance) while excluding the natal home range. 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. We assessed predictor variables for correlation (Pearson's  $r > |0.7|$ ). We were only able to include single variable models and the null because of our small number of events (18 dispersals) and our necessity to account for an additional random effects variable (nest). This limitation also prevented us from assessing goodness of fit on a fully parameterized model. Therefore, we calculated Pearson  $\chi^2/df$  to evaluate goodness of fit for each single-variable model. We ranked models by calculating Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ), as well as the difference between the top model and other candidate models ( $\Delta AIC_c$ ; Burnham and Anderson 2002). We considered all models within 0–2  $\Delta AIC_c$  as having substantial support and evaluated model support with Akaike weights ( $w_i$ ; Burnham and Anderson 2002).

We measured dispersal distance 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, and age, but we were unable to consider additive models because of limited sample size. We used a mixed model (proc MIXED; SAS Institute Inc. 2008) and assigned nest of origin as a random effect to account for nonindependence among siblings. We log-transformed distance to meet the assumptions of normality. We investigated variable correlation, assessed goodness of fit, and compared models using  $AIC_c$  with methods identical to those used in our dispersal age analysis. For all other analyses, we considered differences statistically significant at  $\alpha < 0.05$ , and we present 95% confidence intervals (CI) whenever appropriate.

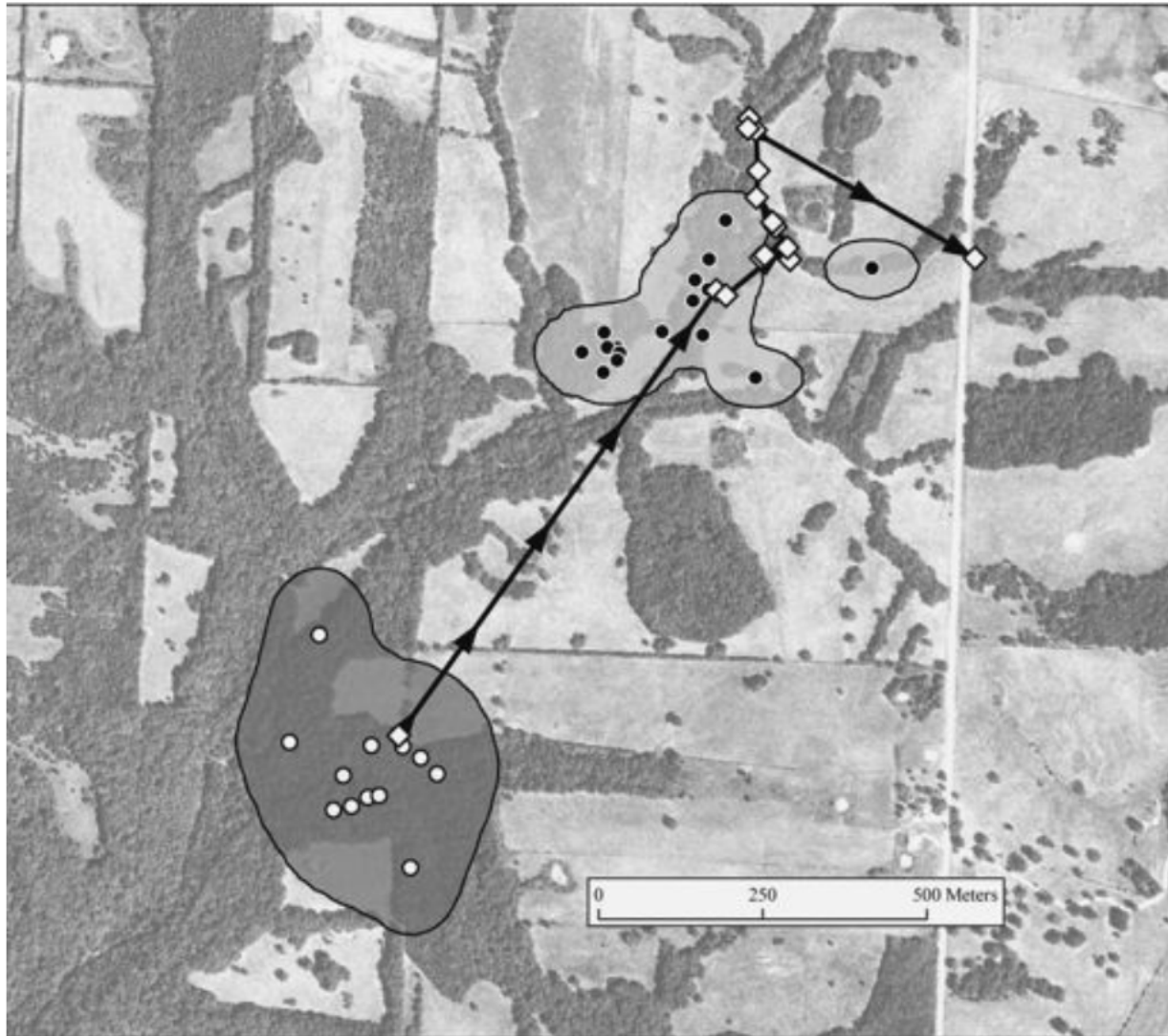
## RESULTS

### Prospecting phase

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 analyses.

We identified 102 forays by 26 birds. These repeated forays and returns to natal areas were consistent with a centrally based foray prospecting strategy. Both sexes were observed making foray movements (16 males, 10 females). The median foray distance was 1.07 km (mean: 1.3 km; range: 0.35–4.23 km). Typically, birds made their first foray movement roughly 1 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). We observed multiple forays in 18 woodpeckers, and they were directionally clustered for each individual ( $P < 0.001$ ). The average difference from the mean orientation was  $19^\circ$  (CI:  $14$ – $23^\circ$ ). This predicted an average range of exploratory movement of  $38^\circ$  ( $19^\circ$  on either side of the mean).

Prospecting individuals preferentially chose foray paths with greater forest cover. We obtained movement paths (forays during which we recorded multiple locations) on 62 forays from 24 birds. Used paths contained higher forest cover than available paths (used: mean = 0.63; available: mean = 0.55;  $P = 0.046$ ). Mean proportion of forest cover



**Figure 3** A red-bellied woodpecker natal home range (shaded in dark gray), a prospecting movement (observations represented by white diamonds and connected with an arrowed line to represent location order), and a post-dispersal home range (shaded in light gray). Home ranges are represented by a kernel UD (95% isopleth by volume). Bird locations on the natal home range are represented by white dots and bird locations after dispersal are represented by black dots.

**Table 1**  
**Ordered ranking of models explaining dispersal age in red-bellied woodpeckers in Missouri, 2009–2010**

Model	Log-likelihood	<i>K</i>	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	<i>ω</i> <sub><i>i</i></sub>
Fledge	146.07	3	152.13	0	0.42
Brood	147.93	3	153.99	1.86	0.17
Null	150.42	2	154.48	2.35	0.13
Forest ratio	149.07	3	155.13	3.00	0.09
Mass	149.51	3	155.57	3.44	0.08
Surrounding forest	149.80	3	155.86	3.73	0.06
Sex	150.22	3	156.28	4.15	0.05
Natal forest	150.33	3	156.39	4.26	0.05

A random variable for nest was included in all models to account for a lack of independence between siblings. *K* is the number of estimated parameters, AIC<sub>c</sub> is the second-order Akaike's Information Criterion, and *ω*<sub>*i*</sub> is the Akaike weight.

in all used and available paths was 0.57. Together, these indicated that a 10% increase in forest cover over the mean resulted in an 11% increase in probability of woodpecker use during foray movements (odds ratio estimate: 1.11; CI: 1.00–1.22).

### Dispersal

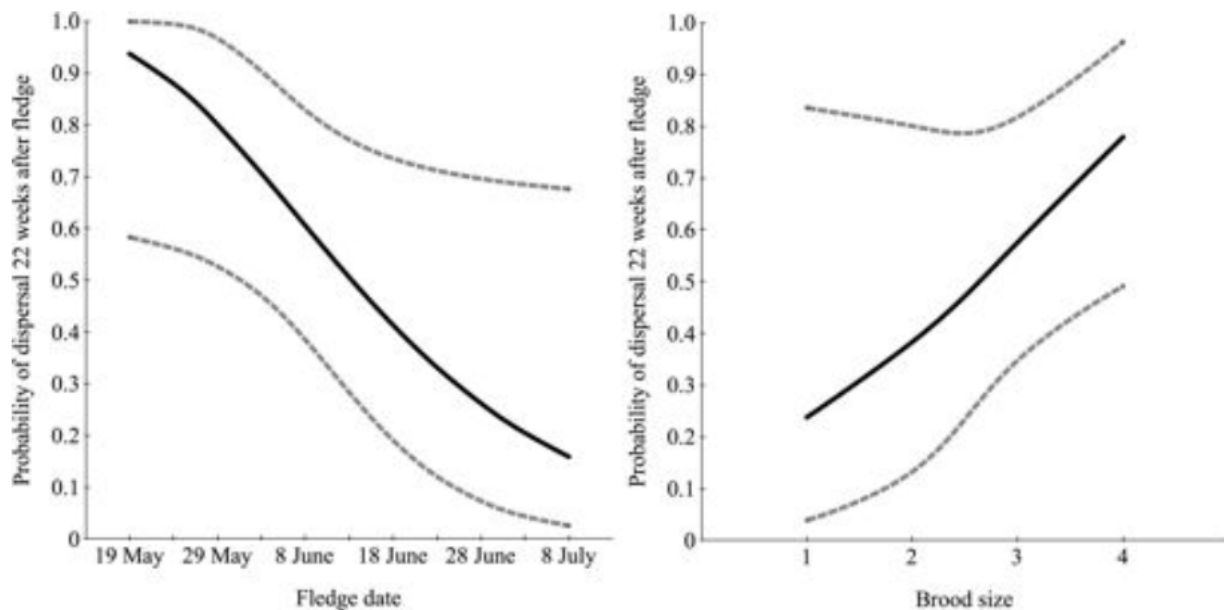
We recorded 18 dispersals made by juvenile red-bellied woodpeckers. Eight birds died on natal territories prior to dispersal and 17 woodpeckers remained on natal sites when they were censored because of transmitter or harness failure. Mean postdispersal home range was 26.6 ha (CI: 14.0–39.3 ha), which did not differ from the mean natal home range (18.3 ha; CI: 12.3–24.2 ha; *P* = 0.16). Thus, birds did not exhibit wide-ranging floating behavior after dispersal (Figure 3).

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

mean prospecting direction and the mean dispersal direction showed a strong positive relationship ( $r_t = 0.77$ ; *P* < 0.001). We found no differences in dispersal direction (*F* = 0.068; *P* = 0.900) between males and females. Areas used during prospecting and dispersal had higher forest cover than the area beyond the dispersal location (*P* < 0.001); 15 of 18 birds had a higher proportion of forest in the dispersal area than in the area 1.3 km beyond dispersal locations. Model estimates revealed that areas leading up to permanent dispersal locations were 12% (CI: 5–13%) more forested than areas beyond dispersal locations.

Mean dispersal age (weeks after fledge; ±SE) for individuals that dispersed during the study period was 9 (±1) weeks (range: 5–17 weeks). By the conclusion of the study, 4 birds remained on natal territories with functional radios (age range: 24–27 weeks). The goodness-of-fit tests for the candidate models of factors influencing dispersal age did not reveal evidence of overdispersion (all  $\chi^2/df < 1$ ). Two models were within 2 AIC<sub>c</sub> units of the top-ranked model, indicating model-selection uncertainty (Table 1). The top-ranked model garnered 42% of the *ω*<sub>*i*</sub> and predicted that juveniles fledging earlier in the year would disperse at a younger age than those fledging later (Figure 4). The second-ranked model garnered 17% of the *ω*<sub>*i*</sub> and indicated that brood size influenced dispersal age, with birds from larger broods dispersing at younger ages than birds from smaller broods (Figure 4). Fledge date and brood size were not correlated (Pearson's *r* = 0.03).

Dispersal distance ranged from 1.13–5.00 km and candidate models did not show evidence of overdispersion (all  $\chi^2/df < 1$ ). The top-ranked model for dispersal distance indicated red-bellied woodpecker natal dispersal distance was sex dependent (Table 2). The model received 50% of the *ω*<sub>*i*</sub> and predicted that females dispersed farther than males. The model-based estimate of dispersal distance for females was 2.9 km (CI: 2.2–3.8 km) from the natal home-range center and 1.8 km (CI: 1.4–2.3 km) for males. The second-ranked model was also competing (ΔAIC<sub>c</sub> = 0.9) and predicted that smaller birds traveled farther (Figure 5). Sex and mass were not correlated (Pearson's *r* = 0.22).



**Figure 4**  
 Probability that a red-bellied woodpecker dispersed from the natal territory by 22 weeks of age in Missouri, 2009–2010, as predicted by fledging date (left) and brood size (right) with 95% CIs (dotted lines).

**Table 2**  
Ordered ranking of dispersal distance models in red-bellied woodpeckers in Missouri, 2009–2010

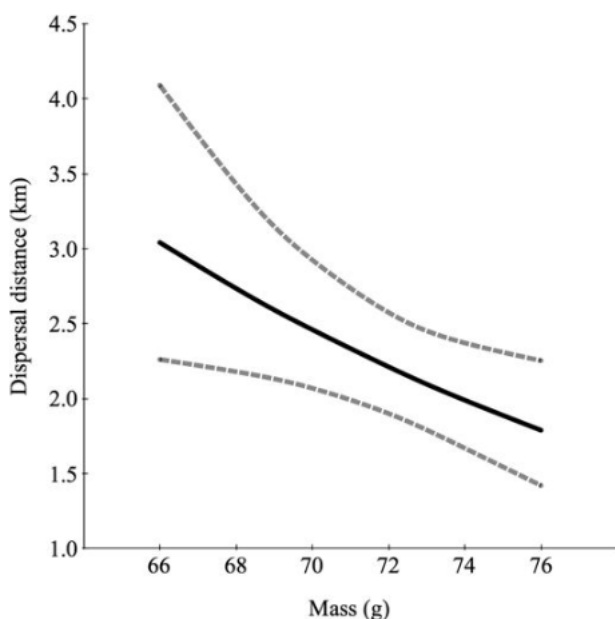
Model	Log-likelihood	$K$	$AIC_c$	$\Delta AIC_c$	$\omega_i$
Sex	-19.9	3	-12.2	0	0.50
Mass	-19.0	3	-11.3	0.9	0.32
Null	-13.9	2	-9.1	3.1	0.11
Dispersal age	-14.2	3	-6.5	5.7	0.03
Dispersal date	-14.1	3	-6.4	5.8	0.03
Fledge date	-14.0	3	-6.3	5.9	0.03

A random variable for nest was included in all models to account for a lack of independence between siblings.  $K$  is the number of estimated parameters,  $AIC_c$  is the second-order Akaike's Information Criterion, and  $\omega_i$  is the Akaike weight.

## DISCUSSION

We studied the dispersal process in juvenile red-bellied woodpeckers, which made repeated forays to potential settlement locations before permanent departure from natal areas. We provide one of the first studies identifying factors that affect animal behavior during all 3 stages of dispersal by intensively tracking individuals on the natal territory, during departure, and through periods prospecting and settlement in a new area. The configuration of landscape features affected foray direction, and by extension, landscapes influenced dispersal patterns. Dispersal distances were sex biased and affected by body condition, whereas dispersal age was affected by fledge date and brood size. Thus, a complex suite of intrinsic and extrinsic factors appears to affect the exploration and dispersal behaviors in red-bellied woodpeckers.

Contrary to our predictions that the pair-breeding red-bellied woodpecker would employ a floater dispersal model (Reed et al. 1999), juveniles used a centrally based foraging



**Figure 5**  
Estimated relationship between mean natal dispersal distance and nestling mass in red-bellied woodpeckers in Missouri, 2009–2010, with 95% CIs (dotted lines).

prospecting behavior that aligned with the “cooperative breeder” model (Reed et al. 1999). Indeed, the repeated forays we observed were similar to dispersal behaviors in cooperatively breeding 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). Foraging behavior prior to natal dispersal has also been observed in several mammal species that tolerate philopatry into the next breeding season, including snowshoe hare (*Lepus americanus*; Gillis and Krebs 1999), Siberian flying squirrel (*Pteromys volans*; Hanski and Selonen 2009), red squirrel (*Tamiasciurus hudsonicus*; Sun 1997, Haughland and Larsen 2004), European badger (*Meles meles*; Roper et al. 2003), and wolverine (*Gulo gulo*; Vangen et al. 2001).

Independent young are often tolerated on the breeding territory for extended periods in cooperatively breeding species (Stacey and Koenig 1990). Similarly, we discovered that some red-bellied woodpecker juveniles remained on natal areas for at least 27 weeks after fledging (22 weeks after the earliest dispersal age we observed). Unlike cooperatively breeding species, however, the young woodpeckers do not delay dispersal through the next breeding season. Centrally based forays allow all delayed dispersers, cooperative or not, to participate in the potentially risky behavior of exploring novel areas (Yoder et al. 2004) while benefiting from familiarity and nepotistic benefits of remaining on the natal territory (Ekman and Griesser 2002). For tolerant parents, the inclusive fitness benefits associated with an offspring's successful dispersal to a breeding site may outweigh the costs of allowing progeny to remain on the natal territory past independence. Thus, we suggest that the centrally based foray pattern may be common among nonmigrant territorial species that allow delayed dispersal, even if young disperse before the next breeding season.

During prospecting, we observed red-bellied woodpeckers repeatedly exploring in the same general direction, and the direction of the foraging movements predicted the permanent dispersal locations. These observations support the idea that prospecting birds were using repeated forays to gather information about a potential breeding territory before permanently dispersing from the natal area. 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 an individual continues to explore the same area each time it departs the natal territory. In contrast, birds may choose a 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).

Foray directionality and dispersal area choices were associated with habitat composition. Although red-bellied woodpecker adults and juveniles are capable of crossing forest gaps (Cox AS, personal observation), foraging juveniles chose forested foray paths, rather than paths characterized by cropland, grassland, and residential property. These results mirror previous reports of an aversion to gap crossing by forest birds (Desrochers and Hannon 1997) and a preference in red-cockaded woodpeckers for a matrix that resembles breeding habitats when dispersing from the natal site (Kesler and Walters 2012). Further, juvenile red-bellied woodpeckers stopped moving from the natal area before continuing on to areas with less forest cover. Together, these patterns indicated that expanses of grassland or cropland may restrict prospecting options and that there may be a threshold proportion of forest cover required to facilitate dispersal.

Forested corridors thus have the potential to guide dispersal behavior and influence demographic and genetic population connectivity at the landscape scale.

The age of dispersing red-bellied woodpeckers was associated with the date that birds fledged and with the size of the broods from which they fledged. Woodpeckers that fledged earlier in the year remained on natal areas for a shorter time period than those that fledged later. These early season birds may benefit from reduced competition for breeding vacancies if they disperse at a younger age. Alternatively, birds fledging earlier may have been produced by more fit parents on higher quality territories (Price et al. 1988), which may better prepare dispersers to compete for territories at a younger age. However, we found no association between body mass, which is often used to evaluate health, and dispersal age. Social factors may also influence the seasonal trend. Natal departure in western slaty antshrikes 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. We did not observe double brooding in our population; however, we did not intensively track adults after study subjects fledged. Evidence of double brooding in red-bellied woodpeckers has been reported in the southern extent of the range (Breitwisch 1977). We also identified an association between brood size and dispersal age. Broods were split between parents within days of fledging (Cox and Kesler 2012); however, we often observed aggression between siblings with the same caretaker parent. Therefore, the pressure of sibling competition may have contributed to an earlier age of dispersal.

Female red-bellied woodpeckers dispersed farther than males, a phenomenon widely reported in birds (Clarke et al. 1997). The ultimate causes of sex-biased dispersal have been debated, although the pattern may be driven by inbreeding avoidance or by a skewed cost of dispersal (Pusey 1987). Female-biased dispersal in territorial species may occur because males settle near the natal territory where resources are familiar and females search until they identify 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. Smaller birds dispersed farther than larger birds, yet mass was not correlated with sex. This finding potentially supports the competitive displacement hypothesis of dispersal, which predicts that individuals with a competitive disadvantage (e.g., body condition) disperse longer distances (Waser 1985).

Individual-based movement models have been shown to be useful tools for predicting dispersal of animals. However, empirical behavior information is needed to parameterize the models (Bélisle and Desrochers 2002). 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, which included substantial investment in information gathering prior to making dispersal decisions. 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 understanding of this sophisticated animal movement and will improve our ability to create realistic

models, which can be used to manage and conserve intact populations.

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