

REEVALUATING THE COST OF NATAL DISPERSAL: POST-FLEDGING SURVIVAL OF RED-BELLIED WOODPECKERS

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Abstract. Accurate estimates of juvenile survival are critical to understanding population processes. However, information about post-fledging vital rates is lacking for most avian species because of the difficulty of following individuals after they leave the nest. We radio-tagged 43 Red-bellied Woodpeckers (*Melanerpes carolinus*) as nestlings. We tracked the birds for 5 months after fledging, during exploratory forays and after natal dispersal. We modeled the influence of intrinsic, temporal, social, and landscape factors with the potential to affect survival during the post-fledging period. Estimates of post-fledging survival were best explained by fledging age. Predictions of weekly survival rates were 0.94 for birds 1 week after fledging, then quickly increased to over 0.99 for birds 7–22 weeks after fledging. We calculated period survival for the entire 5 months as 0.80 (95% CI: 0.65–0.90). We observed no mortalities after the birds departed natal territories, suggesting that exploratory and dispersal behaviors are not costly in this species.

Key words: *demography, foray, juvenile survival, Melanerpes carolinus, population modeling, prospecting.*

Reevaluando el Costo de la Dispersión Natal: Supervivencia Posterior al Emplumamiento en *Melanerpes carolinus*

Resumen. Los estimados precisos de la supervivencia juvenil son críticos para entender los procesos poblacionales. Sin embargo, falta información de tasas vitales posteriores al emplumamiento para la mayoría de las especies de aves debido a la dificultad de seguir a los individuos luego de que dejan el nido. Colocamos radio transmisores a 43 individuos de *Melanerpes carolinus* en el nido y seguimos a las aves por cinco meses posteriores al emplumamiento durante la dependencia de los volantes y las incursiones exploratorias y luego de la dispersión natal. Modelamos la influencia de factores intrínsecos, temporales, sociales y del paisaje con el potencial de afectar la supervivencia durante el período posterior al emplumamiento. Los estimados de la supervivencia posterior al emplumamiento fueron mejor explicados por la edad del volantón. Las predicciones de las tasas de supervivencia semanal fueron de 0.94 para las aves una semana después de emplumar y luego incrementaron rápidamente a más de 0.99 para aves de 7–22 semanas posteriores al emplumamiento. Calculamos la supervivencia del periodo para los cinco meses completos como de 0.80 (95% IC: 0.65–0.90). No observamos mortalidad luego de que las aves partieron de sus territorios natales, lo que sugiere que los comportamientos exploratorios y de dispersión no son costosos en esta especie.

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, Kesler et al. 2012). Among birds, however, estimates of post-fledging survival have been hindered by difficulties associated with tracking birds after they leave the nest. Researchers assume that the juvenile life stage is inherently risky, which has been supported by radio-telemetry data from a small number of avian species (Anders et al. 1997, White 2005, Davies and Restani 2006, Suedkamp Wells et al. 2007). However, estimates of post-fledging survival are completely lacking for entire suites of birds, with studies of raptors and passerines nesting in open

cups dominating the literature. Estimates of juvenile survival have been calculated indirectly from band returns (Thomson et al. 1999) or as a fraction of adult survival (Ricklefs 1973), but these estimates can be biased by dispersal beyond study areas and assumptions about differences between juvenile and adult survival (Baker et al. 1995, Cooper et al. 2008).

Fewer studies have aimed at identifying factors that influence juvenile survival, and their conclusions vary about which factors have the greatest effect. Starvation and depredation are the two primary causes of avian mortality across life stages (Newton 1998), and younger birds may be more susceptible than older, experienced birds. Indeed, studies of post-fledging survival often report survival to be lowest immediately after fledging (Anders et al. 1997, Dreitz et al. 2004, King et al. 2006, Yackel

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Adams et al. 2006, Berkeley et al. 2007, Gruebler and Naef-Daenzer 2008, Kershner et al. 2009). This age-influenced effect may also be quadratic, as juveniles of resident species may experience another decrease in survival during dispersal from the natal territory (Wiens et al. 2006). In addition, birds with greater mass may be in better condition to survive the transition from parental dependence to independence, as post-fledging survival of heavier chicks is higher in some species (Naef-Daenzer et al. 2001, Suedkamp Wells et al. 2007, Greño et al. 2008). However, intrinsic qualities do not explain differences in post-fledging survival in all avian species. Gruebler and Naef-Daenzer (2008) reported a positive relationship between duration of parental care and survival of juvenile Barn Swallows (*Hirundo rustica*), and Styrsky et al. (2005) found that brood size predicted post-fledging survival in the Spotted Antbird (*Hylophylax naevioides*), which emphasizes the influence of sibling competition and parental investment beyond the nest stage.

Post-fledging survival may also vary temporally with annual or seasonal changes in food availability and predator abundance (Dreitz et al. 2004, Yackel Adams et al. 2006, Schmidt et al. 2008). When nesting is asynchronous, survival may vary within a year, and deviation from optimal nest-initiation dates can have long-lasting consequences for survival (Perrins 1970). Specifically, in some forest birds, seasonal patterns in juvenile survival have been associated with date of fledging (Naef-Daenzer et al. 2001, Sunde 2005, Gruebler 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).

Landscape-level change has been widely studied, and increased habitat fragmentation can result in higher rates of nest predation (Robinson et al. 1995). However, with the exception of a few studies of grassland birds (King et al. 2006, Berkeley et al. 2007), the effects of habitat composition and configuration on young birds after they leave the nest remain largely unstudied. Higher densities of nest predators have been documented in fragmented habitats (Rosenberg and Raphael 1986, Robinson et al. 1995, Dijak and Thompson 2000), and these same predation pressures may also affect juvenile survival after the nestling stage.

A clear need for studies of post-fledging survival aimed at birds from a wider range of taxonomic groups and life histories is apparent. 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*), and the first direct estimates of avian survival throughout periods of prospecting and after settlement. Furthermore, we investigated the relative influence of social, temporal, and landscape factors with the potential to affect survival during early life stages.

Although no previous studies of juvenile survival have detected differences in survival between the sexes, Kilgo and Vukovich (2012) found survival estimates of females of the congeneric Red-headed Woodpecker (*M. erythrocephalus*) to be lower than those of males. We therefore tested whether juvenile female woodpeckers were at a higher risk of mortality than were males. We predicted elevated mortality in smaller birds with fewer nutrient reserves and in younger birds that were likely less mobile and adept at foraging. However, we also expected survival to decrease once birds started dispersing, as mortality is high during dispersal in other taxa (Harrison 1992, Carr and Fahrig 2001, Kramer-Schadt et al. 2004). We predicted that birds fledging earlier should have greater survival rates and hypothesized that birds from smaller broods should be more likely to experience increased parental care and thus suffer decreased mortality. We hypothesized that although the Red-bellied Woodpecker is highly adapted to human-influenced landscapes, reduced forest cover might provide lower-quality habitat and thus result in decreased survival from increased exposure to predators such as rat snakes (*Elaphe* spp.), which have been found to depredate adult *Melanerpes* woodpeckers (Stickel 1963, Kilgo and Vukovich 2012) and are increasingly influential nest predators as landscapes become more fragmented (Cox 2011).

METHODS

STUDY SITE AND FIELD TECHNIQUES

Our study site included the Mark Twain National Forest's Cedar Creek Unit in central Missouri (38° 46' N, 92° 07' W) and the adjacent Baskett Wildlife Research and Education Area (38° 46' N, 92° 15' W). The study site and surrounding areas are composed of privately owned residential and agricultural inholdings interspersed within the managed properties and additionally fragmented by pastures for cattle grazing on the federal land. Our field work extended from March through November 2009 and 2010.

We searched for Red-bellied Woodpecker nests by using parental cues. We used a wireless cavity viewer (Huebner and Hurteau 2007) to assess a nest's stage and determine nestlings' age. At approximately 20 days after hatching, we ascended to nests by means of a guyed extension ladder (Rohwer 1988) and retrieved nestlings by the hole-saw method (Ibarzabal and Tremblay 2006). We banded each bird with three colored plastic leg bands and one numbered aluminum band (U.S. Geological Survey Patuxent Bird Banding Laboratory). We also weighed nestlings and attached radio transmitters (model A1060; Advanced Telemetry Systems, Isanti, MN) with leg harnesses (Rappole and Tipton 1991, Kesler 2011). Transmitters weighed 2.6 g, an average of 3.7% (range 3.2–4.7%; recommended <5%; Fair et al. 2010) of body mass at time of tagging (range 55–82 g), and had a battery life of 4–6 months. We obtained blood or feather samples from each bird

for molecular-genetic sex determination (Avian Biotech International, Tallahassee, FL). We returned nestlings to the cavity and monitored them daily until they fledged (within 5 days of extraction). In 2009, nest predation limited our ability to track fledged birds, so in 2010 we fitted nest trees with snake-excluding devices (Neal et al. 1998).

We tracked radio-marked Red-bellied Woodpeckers 2 or 3 days each week for the first 22 weeks after fledging. We used the homing method (White and Garrott 1990) to locate birds with telemetry receivers (model R-1000; Communications Specialists, Orange, CA) and three-element Yagi antennas. We recorded each individual's coordinates (Universal Transverse Mercator system) with a global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, KS) after determining survival and visually confirming the individual's color-band combination. We confirmed mortality from 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 (LOAS, version 4.0; Ecological Software Solutions LLC, Hegymagas, Hungary) to remotely estimate birds' locations when homing was not possible. We confirmed survival with changes in radio signals, which indicated movements, and with differences in location among observation periods.

FACTORS INFLUENCING SURVIVAL

We identified factors with the potential to influence post-fledging survival of Red-bellied Woodpeckers, including body mass, sex, age, year, date of fledging, brood size, and forest cover of the landscape. We measured body mass, as an index of body condition, at the time of radio-tagging (between 19 and 23 days). There was no relationship between a nestling's age at measurement and body mass ($r^2 = 0.049$), and growth models indicated that chick mass stabilized at 19 days after hatching (Stickel 1963). Therefore, we did not adjust mass for differences in nestling age at measurement. To model the effects of fledglings' age on survival, we used the number of weeks after fledging. We determined brood size at time of radio-tagging.

To assess habitat effects on juvenile survival, we calculated the proportion of forest cover in the area 240 m around each telemetry location within the natal area, the approximate radius of a natal home range (Cox and Kesler 2012). We used a geographic information system (ArcView 9.2, ESRI, Redlands, CA) to buffer each natal location by 240 m 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 forest within the merged polygon.

STATISTICAL ANALYSIS

We estimated post-fledging survival of Red-bellied Woodpeckers with the known-fate option in program MARK (White and

Burnham 1999), which uses a Kaplan–Meier approach. The Kaplan–Meier procedure evaluates survival on the basis of a series of occasions, and estimates of survival for each occasion are based on the number of individuals at risk at the beginning of each interval (Kaplan and Meier 1958). We considered each week after fledging 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 independence of siblings' survival 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 was independent ($\chi^2_{13} = 6.696, P = 0.917$).

Our data also meet the Kaplan–Meier procedure's assumption that censoring of study animals is independent of biological phenomena (Pollock et al. 1989). We censored individuals beginning when weak radio transmission from battery failure prevented us from tracking the individual effectively or if the radio harness fell off. For those individuals, we continued censoring for the duration of the study. Except for one individual, all censored birds were either resighted after radio or harness failure or their radio signal weakened gradually prior to nondetection. Therefore, we concluded that these birds had been removed from the study because of equipment failure and not movement outside of the study area or death. Because of the relatively short distance that our dispersing birds traveled, we deduced that it was unlikely that the missing bird traveled outside of the area in which it could be detected and had an equal chance of carrying a faulty transmitter or a transmitter damaged during predation.

Using an information-theoretic approach, we fitted survival data to eight models. Given the low number of mortalities, we considered only single-variable models and a constant-survival model (null model). We considered ecologically plausible models to test for the effects on survival of year, age, date of fledging, mass, brood size, and habitat composition. We used second-order Akaike's information criteria (AIC_c) to identify competing models, which included those within $2 \Delta AIC_c$ (Burnham and Anderson 2002, Symonds and Moussalli 2011). We evaluated models' support with Akaike weights (w_i ; Burnham and Anderson 2002). We also report parameter estimates and 95% confidence intervals (95% CI) for variables included in models with more support than the null model.

RESULTS

We radio-tagged 52 nestling Red-bellied Woodpeckers from 19 nests. Of these, 43 birds from 18 nests successfully fledged with radios and thus were included in our analysis of post-fledging survival (2009: 5 males, 5 females; 2010: 17 males, 16 females). We confirmed the fate of all but one individual and obtained locations in every sampling period until death or

censoring because of a confirmed failure of the transmitter or harness. We documented eight mortalities from seven different nests. All mortalities occurred within 7 weeks of fledging. Four mortalities occurred in the first 2 weeks after fledging, and one death occurred each week thereafter (with the exception of week 5). No birds died outside of the natal home range, even though we observed 18 dispersing to settlement areas and 26 making prospecting forays into the surrounding landscape (Cox and Kesler 2012).

Results showed a strong association between age and survival (Table 1). The age model received >95% of w_i . The top-ranked model indicated an increasing probability of survival with age ($\beta_{age} = 0.31$; 95% CI 0.06, 0.55; Fig. 1). For example, the model predicts that the weekly survival rate is 0.94 at 1 week after fledging and increases to 0.99 by 7 weeks after fledging. Although the model with date of fledging also ranked above the null model, it contained only 1% of the w_i and showed a weaker effect; its confidence intervals bounded zero ($\beta_{fledge} = -0.05$; 95% CI $-0.10, 0.01$). From the product of all weekly estimates, we estimated period survival for the 22 weeks after fledging as 0.80 (95% CI 0.65, 0.90).

DISCUSSION

Age of the bird was the key predictor of survival for Red-bellied Woodpeckers in the first 5 months after fledging. The young woodpeckers were most vulnerable during their first few weeks, then survived at relatively high rates for the remainder of the study. The causes of age-related vulnerability during the first several weeks after fledging are not entirely clear. Greater mortality in younger birds may be due to an increased risk of predation, as all mortalities showed evidence of being partially consumed or tooth marks or scrape marks on the transmitter. Young birds may be more vulnerable to predators because of a lack of experience and an associated inability to identify threats (Rajala et al. 2003) or may not be able to avoid approaching predators because of reduced flight

TABLE 1. Ranking of competing models explaining survival (φ) of Red-bellied Woodpeckers for the first 22 weeks after fledging in central Missouri. K , number of estimated parameters; AIC_c , second-order Akaike's information criterion; w_i , Akaike weight (model probability given the set of candidate models).

Model	K	ΔAIC_c^a	w_i	Deviance
$\varphi(\text{age})$	2	0.00	0.96	73.29
$\varphi(\text{fledge date})$	2	8.71	0.01	82.00
$\varphi(\cdot)$	1	9.72	0.01	85.03
$\varphi(\text{year})$	2	10.73	0.00	84.02
$\varphi(\text{sex})$	2	10.97	0.00	84.26
$\varphi(\text{brood size})$	2	11.17	0.00	84.46
$\varphi(\text{forest cover})$	2	11.37	0.00	84.66
$\varphi(\text{mass})$	2	11.72	0.00	85.01

^aThe AIC_c value for the top model was 77.31.

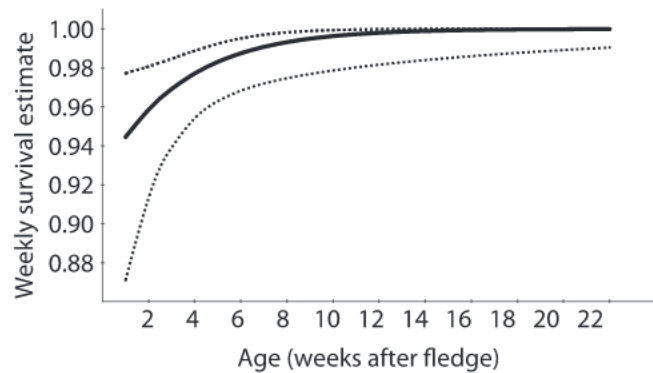


FIGURE 1. Estimates of weekly survival for juvenile Red-bellied Woodpeckers in central Missouri (solid line) with 95% confidence intervals (dotted lines).

skills (Thompson et al. 2010). Alternatively, young fledglings may be more susceptible to starvation or disease and then scavenged after death.

We observed no mortalities during exploratory forays or after natal dispersal, even though we observed these behaviors 3–5 weeks after fledging in some birds (minimum age at beginning of forays = 22 days; minimum age at dispersal = 34 days; Cox and Kesler 2012). 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 have reported decreased survival during dispersal as animals encounter roads and other human-influenced landscapes (Harrison 1992, Carr and Fahrig 2001, Kramer-Schadt et al. 2004). In all of these cases, the danger of the matrix habitat decreased survival of dispersing terrestrial animals. Dispersing Red-cockaded Woodpeckers (*Picoides borealis*) disperse widely (Kesler et al. 2010) but actively choose suitable matrix habitats (Kesler and Walters 2012) between the natal territory and ultimate settlement destination. The apparent lack of effects of dispersal on Red-bellied Woodpecker survival may indicate a similar ability to avoid unsuitable habitat as birds navigate away from the natal territory. Studies focused on real-time tracking that investigate how birds use the surrounding landscape during dispersal might elucidate the mechanisms underlying the costs of their dispersal.

In contrast to age effects, sex, year, date of fledging, brood size, mass, and forest cover did not seem to affect juveniles' survival. Although female Red-bellied Woodpeckers disperse farther than males (Cox and Kesler 2012), high survival rates during dispersal imply that females did not incur additional costs by traveling greater distances from the natal home range. We expected increased parental care of smaller broods, which might offset the risks of inexperience and elevate survival of young birds. In our population, however, adults routinely divided their broods. This behavior decreases the variability in amount of parental care after fledging, as in almost all cases the effective brood size during the fledging period was either

one or two fledglings per parent. 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. At four nests, the young fledged asynchronously, with smaller birds leaving the nest up to 3 days after their siblings, which could reduce the variation in mass at fledging. The potential for effects of habitat fragmentation on juvenile survival are less clear, but Dijk and Thompson (2000) suggested that changes in predator density might contribute to decreased nest survival in fragmented habitats. Chalfoun et al. (2002), however, found that changes in abundances of predators in response to habitat fragmentation are predator-specific. Therefore, predators (such as accipiters) whose densities are not affected by fragmentation may be more responsible for mortality of juvenile woodpeckers than are those whose densities correlate positively with forest fragmentation (e.g., rat snakes). Alternatively, juvenile woodpeckers may ameliorate the risk of crossing gaps in the forest by using forested corridors when moving through a fragmented landscape (Cox and Kesler 2012).

The survival rates we observed are higher than those reported in other studies of radio-tagged North American land birds tracked immediately after fledging. If survival estimates are standardized to 2 months after fledging, those for the Red-bellied Woodpecker are 8% to 52% higher than those for 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). The disparity in juvenile survival could be attributed to a number of morphological or life-history differences such as size (Lindstedt and Calder 1976), foraging strategy, or development at fledging.

The Red-bellied Woodpecker is an opportunistic generalist adapted to a variety of habitats and changes in seasonal food availability (Shackelford et al. 2000), which may lead to juveniles' survival rates being higher than those observed in specialists. Juvenile Northern Goshawks experience a decline in survival following dispersal from the natal territory, which is most likely because of their inability to capture prey effectively in unfamiliar habitats (Wiens et al. 2006). The opportunistic foraging style of the Red-bellied Woodpecker may be easier for young birds to master. In addition, generalists are less susceptible to declines in abundance of particular food items (Dall and Cuthill 1997).

Another explanation for the relatively high survival rate we identified might be associated with the benefits of cavity nesting. Previous investigations of post-fledging survival (summarized above) focused on cup nesters, and development of nestlings of cavity-nesting birds tends to be longer than that of open-cup nesters (Martin and Li 1992). 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 high survival rates we noted may be explained by spatial or temporal variance. However, although our study only spanned 2 years, we found no effects of year on survival. In addition, we believe we sampled woodpeckers across a region large enough (juveniles' locations spanned 8505 ha) to encompass many territories of predators and across a gradient of forest cover large enough (range in proportion of natal area forested 17.9–99.7%) to encompass a wide diversity of predators. Although we were unable to determine predator-specific sources of mortality, reports of predators of adult Red-bellied Woodpeckers include rat snakes, Cooper's Hawks (*Accipiter cooperii*), and Sharp-shinned Hawks (*A. striatus*; Stickel 1963, Saul 1983), and these species were common on our sites as well. Therefore, we do not believe that the risk of mortality from typical woodpecker predators at our study sites was abnormally low.

In models of population persistence, the juvenile life stage is the most elastic and most variable for short-lived animals (Wisdom et al. 2000). For birds, however, our knowledge of first-year survival is poor. Age-dependent vulnerability to predation has been shown in a wide range of species (Carey and Moore 1986, Iverson 1991, Lingle et al. 2008), and transitions between a vulnerable and less vulnerable state are integral to maintaining population balance, especially in seasonal environments (Abrams and Walters 1996). Thus a precise understanding of changes in survival rates throughout the juvenile stage is integral to modeling population change accurately. In our study, for example, we found that Red-bellied Woodpeckers suffered greater mortality in the first few weeks after fledging. However, survival quickly increased to a less vulnerable state, even during the potentially risky behaviors of prospecting and dispersal. First-year survival would have been drastically underestimated if the lower rate of survival soon after fledging had been extrapolated to the entire juvenile period. Juvenile Red-bellied Woodpeckers may also experience a decrease in survival during the winter months. Additional future research focused on patterns of survival in juvenile birds will expand our understanding of a neglected life-history stage and improve the accuracy of population models necessary for the conservation and management of birds.

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