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RESEARCH ARTICLE

Environmental predictors of nestling condition, postfledging movement, and postfledging survival in a migratory songbird, the Wood Thrush (*Hylocichla mustelina*)

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ABSTRACT

Given that population dynamics of birds are known to be sensitive to high fledgling mortality, a comprehensive understanding of the environmental factors that drive variation in fledgling survival is essential to avian conservation. We quantified multiple aspects of the Wood Thrush postfledging period using breeding and radio-telemetry data collected over the course of 4 breeding seasons in southern Indiana, USA. First, we examined how drought, forest cover, and brood parasitism affected nestling body condition and brood size. Second, after controlling for the age-specific increase in survival, we used multimodel inference to examine how brood parasitism, drought, forest cover, nestling body condition, and nest vegetation structure influenced postfledging survival. Finally, we measured the relationship between these covariates and fledgling movements. Drought decreased cumulative survival probabilities, with the youngest age group ($<$4 days postfledging) being most affected; however, this relationship was dependent on the amount of mature forest cover. During non-drought years, fledgling survival was lower in study plots with a high proportion of mature forest cover. By contrast, postfledging survival during a drought year was higher in study plots with a high proportion of forest cover. This drought year was also associated with lower nestling body condition and brood size, and with delayed postfledging dispersal from natal territories. Our results suggest that while Wood Thrush postfledging survival is relatively insensitive to both nest vegetation structure and brood parasitism, forest cover and breeding-season precipitation interact to affect multiple aspects of the species' postfledging period.

Keywords: brood parasitism, dispersal, drought, *Hylocichla*, postfledging survival, Wood Thrush

Predictores ambientales de la condición del polluelo, del movimiento post emplumamiento y de la supervivencia post emplumamiento en *Hylocichla mustelina*, un ave canora migratoria

RESUMEN

Dado que las dinámicas poblacionales de las aves son conocidas por ser sensibles a la alta mortalidad de los volantones, es esencial lograr un entendimiento exhaustivo de los factores ambientales que determinan la supervivencia de los volantones para la conservación de las aves. En este estudio, cuantificamos múltiples aspectos del período post emplumamiento de *Hylocichla mustelina* usando datos de cría y de radio telemetría colectados a lo largo de 4 estaciones reproductivas en el sur de Indiana. Primero, examinamos como la sequía, la cobertura del bosque y el parasitismo de nidada afectan la condición corporal de los polluelos y el tamaño de la nidada. Segundo, luego de controlar por el incremento específico de la supervivencia en relación a la edad, usamos inferencia de modelos múltiples para examinar como el parasitismo de nidada, la sequía, la cobertura del bosque, la condición corporal de los polluelos y la estructura de la vegetación del nido influencian la supervivencia post emplumamiento. Finalmente, medimos la relación entre estas covariables y los movimientos de los volantones. La sequía disminuyó las probabilidades acumuladas de supervivencia, siendo el más afectado el grupo de edad más joven ($<$4 días post emplumamiento); sin embargo, esta relación dependió de la cantidad de cobertura de bosque maduro. Durante los años sin sequía, la supervivencia de los volantones fue más baja en las parcelas de estudio con una alta proporción de cobertura de bosque maduro. En contraste, la supervivencia post emplumamiento durante un año de sequía fue más alta en las parcelas de estudio con una alta proporción de cobertura del bosque. Este año de sequía estuvo también asociado con una menor condición corporal del polluelo y del tamaño de la nidada, y con una dispersión atrasada post emplumamiento desde los territorios de nacimiento. Nuestros resultados sugieren que mientras la supervivencia post emplumamiento de *H. mustelina* es relativamente insensible a la estructura de la vegetación y al parasitismo de nidada, la cobertura del bosque y la precipitación de la estación reproductiva interactúan para afectar múltiples aspectos del período post emplumamiento de la especie.

Palabras clave: dispersión, *Hylocichla mustelina*, parasitismo de nidada, sequía, supervivencia post emplumamiento

INTRODUCTION

The postfledging period in passerines is characterized by high mortality and affects natal dispersal, immigration, and, ultimately, recruitment into the breeding population (Naef-Daenzer et al. 2001, Yackel Adams et al. 2006, Schaub and Abadi 2011, Robinson et al. 2014, Naef-Daenzer and Grüebler 2016). Investigations of this phase of the annual cycle have demonstrated that mortality is concentrated within the first week after fledging, decreases nonlinearly with fledgling age, can be negatively correlated with body condition prior to fledging, and tends to increase over the breeding season (reviewed by Newton 1998, Cox et al. 2014). We know considerably less about how environmental factors affect fledging condition as well as postfledging movement and survival.

Environmental factors such as brood parasitism, drought, forest cover, habitat structure, and body condition can influence the postfledging period (Cox et al. 2014). While brood parasitism reduces nest success in many passerine species (Payne and Payne 1998), its effect on postfledging survival remains ambiguous, with both negative and neutral effects reported (Rasmussen and Sealy 2006, Vitz and Rodewald 2011, Peterson et al. 2012, Jenkins and Faaborg 2016). Drought, however, has been shown to lower postfledging survival directly via changes in resource availability and indirectly via changes in vegetation structure (Yackel Adams et al. 2006). Moreover, postfledging survival has been found to be higher in habitats with dense vegetation structure and greater food abundance (e.g., successional, riparian, or forest edge habitat; Fink 2003, White et al. 2005, King et al. 2006, Vitz and Rodewald 2011). These habitat relationships suggest that fledglings experience lower survival in areas with a high proportion of mature forest cover that lack favorable habitat, but formal tests of how forest cover influences postfledging survival are rare (but see Rush and Stutchbury 2008, Moore et al. 2010). Furthermore, the effects of body condition on survival remain unclear, with some studies reporting a positive relationship between nestling condition and survival (Cox et al. 2014) and others suggesting that the hazard type (e.g., predation or exposure) determines the importance of body condition for postfledging survival (Jones et al. 2017).

One of the most studied passerines during the postfledging period is the Wood Thrush (*Hylocichla mustelina*), a Neotropical migrant that has suffered loss and degradation of breeding habitat and experienced long-term population declines (Evans et al. 2011, Rushing et al. 2016). The species' reproductive ecology has been well documented, and its postfledging period lasts ~21 days (Anders et al. 1997, Evans et al. 2011). Fledgling movement is initially restricted to the natal territory and may be constrained by body condition at fledging, by parental behavior, and by environmental variation. Independent juveniles disperse to habitats with dense understories (e.g., early- to mid-successional or riparian forests) that provide both abundant food and protection from predators (Anders et al. 1998, Fink 2003). Previous studies have focused on postfledging survival patterns (Anders et al. 1997, Schmidt et al. 2008) but were not designed to test how environmental factors affect nestling body condition or how body condition and the environment affect survival.

Here, we investigate how environmental factors and body condition influence the survival probability of fledgling Wood Thrushes. We also examine how brood parasitism, forest cover, and drought affect nestling condition, brood size, and fledgling movement. We used radio telemetry to track fledglings at 12 heterogeneous forest sites across 4 yr in southern Indiana, USA. After accounting for a nonlinear increase in survival with fledgling age (Cox et al. 2014), we built known-fate survival models to test how brood parasitism, forest cover, drought, habitat structure, and nestling body condition affected postfledging survival. On the basis of previous research, we expected that postfledging survival would be (1) lower in nests parasitized by Brown-headed Cowbirds (*Molothrus ater*), (2) lower during drought conditions, (3) lower in areas with a high proportion of forest cover, (4) higher in areas with greater understory vegetation density, and (5) higher when nestlings were in better body condition. Our objective was to elucidate the relationship between environmental predictors and different aspects of the postfledging period (e.g., nest conditions, movement, and survival). With a better understanding of this critical life stage, conservation efforts can more effectively improve breeding productivity, particularly for declining species that are strongly limited by breeding-season events (Cox et al. 2014).

METHODS

Study Area

We tracked fledgling Wood Thrushes on twelve 40–60 ha plots in southern Indiana in 2011–2014. Plots were located on Crane naval base (Crane; 38.83°N, 86.79°W), in Big Oaks National Wildlife Refuge (BONWR; 38.95°N, 85.4°W), and within parks operated by the Indiana Department of Natural Resources in the greater Bloomington area (IDNR; 39.16°N, 86.53°W). Plots were chosen to represent a continuum of habitat quality, ranging from small fragments of secondary growth to continuous old-growth deciduous forest (see Appendix Table 4). Common tree species included white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), flowering dogwood (*Cornus florida*), boxelder (*Acer negundo*), American elm (*Ulmus americana*), hickory (*Carya* spp.), American hornbeam (*Carpinus caroliniana*), sugar maple (*A. saccharum*), oak (*Quercus* spp.), eastern redbud (*Cercis canadensis*), American sycamore (*Platanus occidentalis*), and tuliptree (*Liriodendron tulipifera*). The understory was dominated by spicebush (*Lindera benzoin*), serviceberry (*Amelanchier arborea*), elderberry (*Sambucus canadensis*), and multiflora rose (*Rosa multiflora*).

A severe regional drought affected our study sites during June and July 2012 (Mallya et al. 2013). Cumulative precipitation from April to August for 2011, 2013, and 2014 ranged from 24.67 to 27.54 inches (http://www.ncdc.noaa.gov/cdo-web/; retrieved July 2015). However, cumulative precipitation between April and August 2012 was substantially lower at 13.33 inches, with consistent deficits across these months.

Field Sampling

We located Wood Thrush nests using behavioral cues (e.g., nest building or provisioning) and systematic searching. For each nest, we documented stage (incubating, nestlings, etc.) and the presence of nestling cowbirds and recorded location to ~10 m accuracy with handheld GPS units. Nests were monitored every ~4 days until fledging or failure, following a protocol similar to that described in Martin and Geupel (1993). All nestling Wood Thrushes were banded during days 8–12 after hatching with a numbered federal band and colored leg bands. We measured tarsus length, body mass, and wing chord. One randomly selected individual per brood received a VHF radio transmitter (PipAg 392, 1 g, ~3% of nestling body mass; Lotek Wireless, Newmarket, Ontario, Canada) affixed with a leg-loop harness (Rappole and Tipton 1991). We assumed that this randomly selected individual was representative of the entire brood, given that Wood Thrushes are not known to divide broods postfledging (Vega Rivera et al. 2000). The radio-tagged individual always received a unique color-band combination to facilitate resighting during tracking sessions. Nest visits continued until fledging.

We searched for tagged fledglings once every 4 days using Biotracker programmable receivers and handheld, 3-element Yagi antennas (Lotek Wireless). Upon detecting a fledgling, we recorded its location with a handheld GPS unit and noted the presence of adults or other fledglings. Precaution was taken to never flush fledglings during tracking, and when a visual was not possible, we projected GPS waypoints to the estimated location. Fledglings were tracked until dispersal from study site (~21 days), predation, transmitter failure, or the end of the study (early to mid-August). A bird was considered depredated if remains (e.g., feather, tarsi, or color bands) or a damaged transmitter (e.g., bent antenna or broken harness) was found. When a signal could not be obtained for a bird that was too young to leave the natal territory (based on previous published estimates of age at independence), the area was searched for adults and/or fledglings. We assumed predation if we could not detect any signs of a family group (e.g., alarming calling by adults and/or fledglings begging) and resight the fledgling. Individuals that prematurely lost their tags (i.e. a tag was found with no obvious signs of remains, transmitter damage, and an intact harness) or had tag malfunctions were censored from the dataset at the estimated date of tag failure.

Vegetation Sampling and Forest Cover Calculation

We sampled vegetation composition within a circular plot (radius = 5 m) centered on each Wood Thrush nest. Vegetation metrics within each plot were (1) frequency of trees in different size classes and (2) vertical foliage density. The frequency of tree size classes was measured with a forester's prism, and each tree was classified into 4 size classes (2 to <5 cm, 5 to <20 cm, 20 to <30 cm, and ≥30 cm) using a tree DBH (diameter at breast height) tape. Vertical foliage measurements were taken at each cardinal direction on the plot edge, using a 5.5 m extendable pole. The extended pole was subdivided into 0.25 m increments from 0 to 3 m, and observers recorded whether or not any live woody vegetation (including stems, leaves, needles, branches, and tree trunks) contacted the pole in each increment.

To measure forest cover, we centered a circle (radius = 2 km, total area = 1,257 ha) on each study plot. This 2 km radius encompasses likely dispersal distances and home-range sizes for fledgling Wood Thrushes (Anders et al. 1998, Vega Riveria et al. 1998). Within each circle, we quantified the proportion of area classified as mature forest using the National Land Cover Database (NLCD; Fry et al. 2011).

Data on nestling condition, brood size, nest parasitism rates, vertical foliage density, and number of trees >30 cm DBH are summarized in Appendix Table 5.

Data Analysis

We used the RMark package (Laake 2013) in R (R Core Team 2015) to build known-fate models of postfledging survival. Known-fate models estimate daily survival probabilities given a detection probability of 1 and have the ability to examine the effect of covariates on survival (White and Burnham 1999). For our analysis, we used a 2-stage modeling approach in which the first model set accounted for the age-specific increase in postfledging survival and the second examined the relationship between 4 predictors and postfledging survival. For our second model set, we used the top model from our first model set as the base model to control for the temporal structure in fledgling survival. Candidate model sets were symmetrical with respect to all predictors (Doherty et al. 2012). We ranked models using Akaike's Information Criterion corrected for small sample size (AIC$_c$) and determined the relative likelihood of each model using model weights (w_i; Burnham and Anderson 2002). Parameters were considered informative based on the weight of evidence (i.e. Σw_i from relevant candidate models) and if the confidence interval of the estimate did not overlap the origin (Arnold 2010). Model results are given as standardized beta parameter estimates and 95% confidence intervals.

Our first model set included 7 different parameterizations of survival probability: (1) constant, (2) linearly increasing with fledgling age (Age), (3) nonlinearly increasing with fledgling age (Age^2), (4) fully time dependent (time), and (5–7) three models with different age-specific survival periods. For each of these parameterizations, a duplicate model was made that also incorporated seasonal changes (represented by fledge date) in fledgling survival. The number of survival periods and the number of days within each survival period in a given model were based on the survival estimates of other postfledging survival studies (e.g., Ausprey and Rodewald 2011) and on the developmental stages of fledgling Wood Thrushes (Anders et al. 1998, Evans et al. 2011). Survival periods included either 2 periods (days 1–7 and 8–30), 3 periods (days 1–7, 8–21, 22–30), or 4 periods (days 1–3, 4–7, 8–21, 22–30).

The second model set used the 4-age-class parameterization from the first set in all candidate models and considered 6 additional variables that we predicted would affect survival probability: (1) presence or absence of brood parasites (binary), (2) vertical foliage density surrounding the nest, (3) number of trees $>$30 cm in DBH, (4) amount of mature forest cover within a circle (radius = 2 km) around each study plot, (5) a dummy variable representing a drought year, and (6) nestling body condition prior to fledging. We considered models with 1 or 2 predictors in addition to age-dependent effects on survival. Candidate models included both additive and factorial combinations of predictors. A nest was considered to be parasitized if a nestling cowbird was detected during any nest check. We included vertical foliage density around the nest because shrub density has previously been shown to be an important predictor of postfledging survival (Fink 2003, Cox et al. 2014). We also included the number of trees $>$30 cm in DBH because this habitat feature also predicts Wood Thrush fecundity (Rushing et al. 2017). Furthermore, we used a dummy variable (rather than monthly or weekly values) to represent the drought year because of the consistent monthly deficits across the 2012 breeding season (Mallya et al. 2013). We calculated Peig and Green's (2009) scaled mass index using mass and tarsus length measured shortly before fledging. Nestlings were weighed at different stages of development, but allometric growth patterns showed that tarsus length, an index of structural size, was positively correlated with age ($r_{1368} = 0.69$, $P < 0.001$). This mass index controlled for age-based size variation.

To further understand the effects of brood parasitism, drought, and forest cover on the postfledging period, we also tested the effects of these covariates on nestling brood size, nestling condition, and postfledging movement. We compared nestling condition (among all nestlings banded) and brood size between parasitized and nonparasitized nests and across drought and non-drought years using Student's t-test. We also tested the effect of forest cover on nestling condition and brood size using linear regression. For our movement analysis, we calculated the Euclidean distance between each fledgling detection and its nest. We did not quantify daily movements because our tracking schedule confounds estimates of an individual's daily movements (i.e. birds were tracked once every 3–4 days). We used AIC$_c$ to compare linear mixed models with additive effects of each variable (condition, drought, forest cover, and brood parasitism) and age class (as defined in our first model set), an interactive effect of each variable and age class, a model with just age class, and a null model. All covariates were modeled as fixed effects, and individual was included as a random effect. We log-transformed the response, average distance from nest, to meet model assumptions. These statistical analyses were performed using R and the "lme4" package (Bates et al. 2015).

RESULTS

Of the 210 fledgling Wood Thrushes tracked from 2011 to 2014 (2011, $n = 47$; 2012, $n = 53$; 2013, $n = 66$; 2014, $n = 44$), 110 individuals survived for 21 days, the average age of independence. Radio-tagged individuals were tracked from 1 to 48 days (mean = 14.39 ± 10.1). Among the 61 individuals with known mortalities, 27 were due to predation, 5 were due to exposure, and 29 died of unknown causes. Of the 39 censored individuals, 8 individuals were due to tag failure, 28 had unknown fates, and 3 were tracked until the end of the field season.

Our first model set revealed strong statistical support for 4 age-specific survival periods (0–3, 4–7, 8–20, and $\geq$21 days since fledging; $\sum w_i = 0.84$; Table 1). Fledgling survival probability tended to decline with ordinal day, but this relationship had weak statistical support compared to constant survival over the breeding season (Table 1). Therefore, we used 4 age classes and constant survival over the breeding season as the base model parameterization in the second candidate set.

The top model of our second model set included an interaction between drought and the amount of forest at the landscape scale ($\beta_{\text{droughtxforest}} = 0.003$, 95% CI: 2.39e-4 to 6.97e-3), with drought effects receiving more support ($\sum w_i = 0.63$) than forest cover ($\sum w_i = 0.4$). Cumulative survival (i.e. the probability of surviving to 30 days after

TABLE 1. Akaike's Information Criterion (AIC) rankings of our 10 best-fitting known-fate models examining the temporal structure of fledgling Wood Thrush survival on our study sites in southern Indiana, USA. Daily survivorship rates change between 2 (~AgeClass2), 3 (~AgeClass3), and 4 (~Ageclass4) survival periods, remain constant (~1), vary daily (~time), are a linear (Age) or quadratic function (Age + Age^2), and depend on fledge date (FD).

Rank	Model	K [a]	ΔAIC_c [b]	w_i [c]	Deviance
1	~AgeClass4	4	0	0.59	89.99
2	~AgeClass4 + FD	5	1.89	0.23	557.64
3	~Age + Age^2	3	4.12	0.08	96.12
4	~(Age+Age^2) + FD	4	6.03	0.03	563.79
5	~Age	2	6.54	0.02	100.54
6	~AgeClass4*FD	8	7.85	0.01	557.57
7	~Age + FD	3	8.45	0.01	568.21
8	~(Age + Age^2)*FD	6	8.88	0.01	562.62
9	~Age*FD	4	10.43	0	568.19
10	~AgeClass2	2	11.09	0	105.09

[a] Number of parameters in each model.
[b] Difference in AIC score (corrected for small sample size, AIC_c) between each model and the best-fitting model ($\text{AIC}_c = 565.77$ for the top-ranked model).
[c] Model weight.

fledging) was lower in 2012, the drought year (0.53, 95% CI: 0.35–0.6; $\beta_{\text{drought}} = -4.24$, 95% CI: –7.69 to –0.8), compared to the cumulative survival probability for 2011, 2013, and 2014 (0.69, 95% CI: 0.58–0.78; Figure 1). The relationship between forest cover and fledgling survival was weak ($\beta_{\text{forest}} = -0.002$, 95% CI: –9.5e-05 to –0.004), with birds in less forested landscapes having higher survival. Decreases in survival during the drought year were most pronounced among fledglings 0–3 days old; and, during drought years, birds from study plots with lower forest cover showed the steepest decline in survival. By contrast, fledglings 0–3 days old in more forested landscapes had roughly equivalent survival during drought and non-drought years (Figure 1). Furthermore, brood parasitism and nestling condition were not strongly related to the survival of fledgling Wood Thrushes on our study sites (Table 2). Although the second-ranked model suggests support for an effect of vertical foliage density, the beta confidence intervals include zero (–0.08, 95% CI: –0.16 to 0.00). Similarly, we found no evidence that the number of trees >30 cm DBH near nest sites affected postfledging survival.

Nestling condition and brood size were both influenced by drought and brood parasitism, but not by forest cover. Specifically, nestlings were in significantly poorer body condition during the drought year compared to the 3 non-drought years ($\mu_{\text{drought}} = 26.52 \pm 0.34$ g [$n = 263$ nestlings, $n = 112$ nests], $\mu_{\text{non-drought}} = 28.88 \pm 0.11$ g [$n = 1{,}116$ nestlings, $n = 431$ nests], $t_{315} = -8.81$, $P < 0.001$; Figure 2), and nestlings from parasitized nests had higher body-condition indices ($\mu_{\text{parasitized}} = 29.15 \pm 0.24$ g, $\mu_{\text{nonparasitized}}$

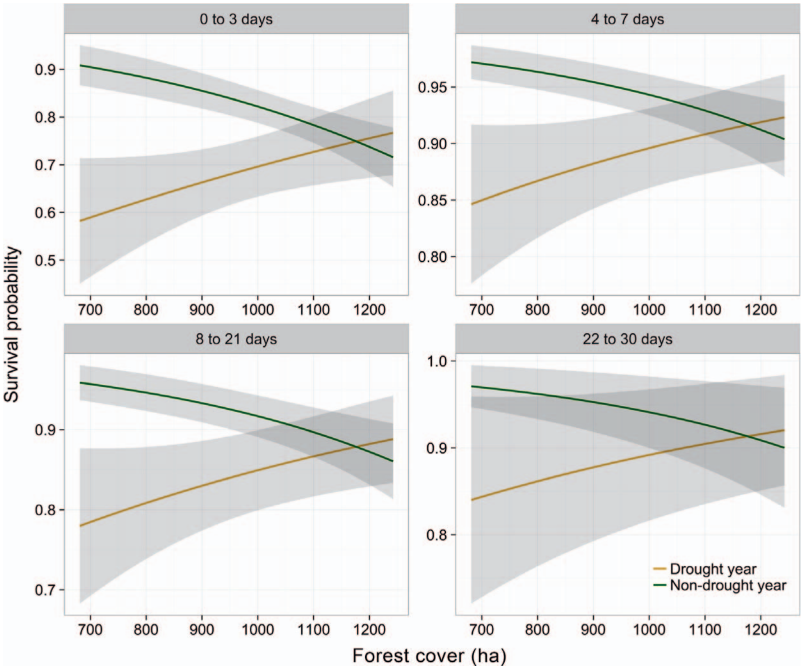

FIGURE 1. Wood Thrush postfledging survival on our study sites in southern Indiana, USA, as a function of the interaction between drought and the amount of mature forest cover within a circle centered on each study plot (radius = 2 km, maximum forest cover = 1,257 ha). Lines represent estimates of survival probability (± SE) from our top-ranked known-fate survival model. The highest mortality occurred in the first 3 days postfledging in areas with low forest cover during a drought year. Note that *y*-axis scales vary by age class.

TABLE 2. Akaike's Information Criterion (AIC) rankings of our 10 best-fitting known-fate models examining the effects of drought; forest cover within 2 km of study plot (Forest); 2 measurements of local vegetation structure, vertical foliage density (VFD) and count of trees with DBH >30 cm (DBH); Brown-headed Cowbird nest parasitism (BHCO); and nestling body condition (BCI) on Wood Thrush postfledging survival on our study sites in southern Indiana, USA.

Rank	Model	K [a]	ΔAIC_c [b]	w_i [c]	Deviance
1	∼AgeClass4 + Drought*Forest	7	0.00	0.17	513.05
2	∼AgeClass4 + VFD*Drought	7	0.27	0.15	513.32
3	∼AgeClass4 + BCI*Forest	7	1.14	0.10	514.19
4	∼AgeClass4 + Drought	5	1.63	0.08	81.14
5	∼AgeClass4 + Forest + Drought	6	2.48	0.05	517.54
6	∼AgeClass4 + DBH + Drought	6	3.10	0.04	518.16
7	∼AgeClass4	4	3.16	0.04	84.68
8	∼AgeClass4 + VFD + Drought	6	3.19	0.03	518.25
9	∼AgeClass4 + Drought + BCI	6	3.30	0.03	518.36
10	∼AgeClass4 + Drought + BHCO	6	3.40	0.03	80.90

[a] Number of parameters in each model.

[b] Difference in AIC score (corrected for small sample size, AIC_c) between each model and the best-fitting model ($AIC_c = 527.09$ for the top-ranked model).

[c] Model weight.

$= 28.15 \pm 0.14$ g, $t_{221} = -3.60$, $P < 0.001$). Brood size was significantly lower in parasitized nests ($\mu_{\text{parasitized}} = 2.35 \pm 0.08$, $\mu_{\text{nonparasitized}} = 2.61 \pm 0.05$, $t_{221} = 2.66$, $P < 0.01$) and during a drought year ($\mu_{\text{drought}} = 2.35 \pm 0.09$, $\mu_{\text{non-drought}} = 2.60 \pm 0.05$, $t_{168} = -2.4$, $P < 0.02$). Drought also influenced fledgling movements, with the best-supported model of fledgling movement including an interaction between age class and drought ($w_i = 0.74$; Table 3). Fledglings stayed closer to the nest and remained within the natal territory longer during the drought year (Figure 3). By contrast, we found no evidence for a relationship between brood parasitism, forest cover, or nestling body condition and movement.

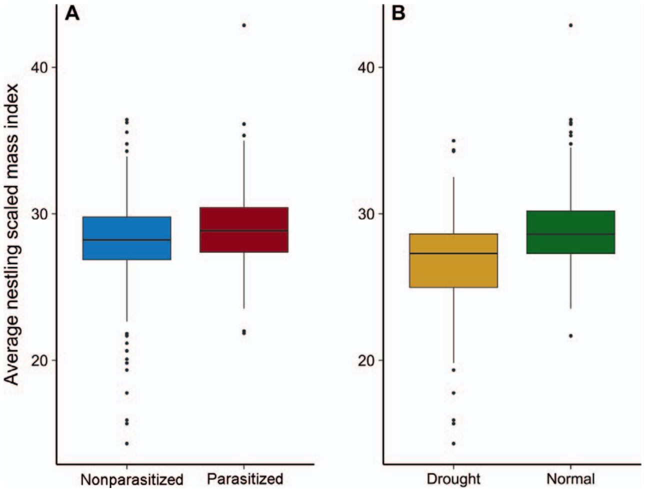

FIGURE 2. Scaled mass indices from nestling Wood Thrushes measured shortly before fledging on our study sites in southern Indiana, USA. (**A**) Nestlings from parasitized nests were in significantly better body condition. (**B**) During a drought year, nestlings were in significantly poorer body condition.

DISCUSSION

Postfledging survival is a key component of recruitment and predictor of avian population growth (Sæther and Bakke 2000, Robinson et al. 2014), but we lack a comprehensive understanding of how environmental heterogeneity affects postfledging movement, dispersal dynamics, and survival probability. Here, we used 4 yr of postfledging data to examine how brood parasitism, drought, nestling condition, forest cover, and local habitat structure influence postfledging survival. Consistent with findings from other studies (Naef-Daenzer and Grüebler 2016), our results show strong age-specific patterns of survival, with the majority of mortality occurring during the first 4 days postfledging. Furthermore, of the 5 predictors considered, drought received the most support and had a negative effect on cumulative survival probability.

Cumulative fledgling survival estimates (i.e. probability of surviving to ≥21 days) for Wood Thrushes in southern Indiana were similar to those documented from other parts of the breeding range ($\phi = 0.42$ to 0.79; Anders et al. 1997, Schmidt et al. 2008) and to estimates for similar-sized species ($\phi = 0.62$ to 0.87; Cohen and Lindell 2004, Moore et al. 2010, Tarof et al. 2011). However, we did not find an association with fledge date, in contrast to several studies of postfledging survival, but consistent with other investigations of Wood Thrushes (reviewed in Cox et al. 2014). Unlike other songbirds, fledgling Wood Thrushes may not be affected by within-breeding-season trends in predator behavior or resource availability (Tarof et al. 2011).

A drought-associated reduction in passerine postfledging survival has been documented by only one other study

TABLE 3. Akaike's Information Criterion (AIC) rankings of our 10 best-fitting models examining the effects of drought, brood parasitism (BHCO), forest cover within 2 km of study plot (Forest), nestling condition (BCI), and age (Age; i.e. the 4 age groups used in Table 2) on Wood Thrush postfledging movement on our study sites in southern Indiana, USA.

Rank	Model	K [a]	ΔAIC_c [b]	w_i [c]	Deviance
1	~Age*Drought	10	0.00	0.74	1,601.17
2	~Age + Drought + BCI	8	2.27	0.24	1,450.65
3	~Age + Drought	7	8.96	0.01	1,592.28
4	~Age + BCI	7	10.73	0.00	1,597.92
5	~Age + Drought + BHCO	8	10.80	0.00	1,601.12
6	~Age + Drought + Forest	8	11.00	0.00	1,601.16
7	~Age + BCI + BHCO	8	12.38	0.00	1,450.50
8	~Age + BCI + Forest	8	12.77	0.00	1,446.19
9	~Age*BCI	10	13.09	0.00	1,444.42
10	~Age	6	13.15	0.00	1,450.65

[a] Number of parameters in each model.

[b] Difference in AIC score (corrected for small sample size, AIC_c) between each model and the best-fitting model ($AIC_c = 1{,}449.63$ for the top-ranked model).

[c] Model weight.

(Yackel Adams et al. 2006). Our study design did not allow us to determine the mechanism, but the effects of drought were likely mediated by resource limitation; both nestling condition and brood size were significantly lower during the drought. This hypothesis is supported by previous work showing that Wood Thrush prey abundance is positively correlated with soil moisture, and that individuals in poorer condition are more susceptible to predation or starvation early in the postfledging period (Cox et al. 2014, Jirinec et al. 2016). We did not find support for a relationship between nestling body condition and postfledging survival. However, our measure of nestling condition may not be a useful predictor of fledgling body condition and, hence, survival probability (e.g., Streby et al. 2014). The effect of drought on fledgling survival may also be mediated by landscape-scale habitat features.

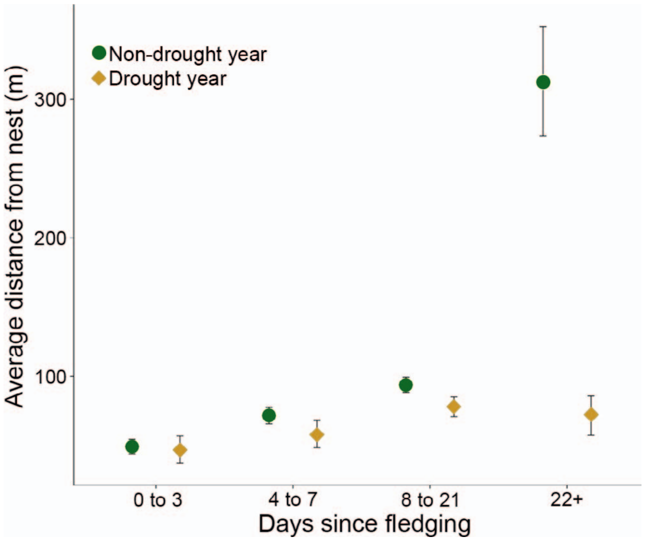

FIGURE 3. Average distance (± SE) from the nest moved by fledgling Wood Thrushes, as a function of age (days since fledging) and environmental conditions (drought) on our study sites in southern Indiana, USA. During drought years, fledglings stayed, on average, closer to the nest from which they fledged and appeared to delay dispersal.

Although we did not find strong associations between nest vegetation structure and postfledging survival of Wood Thrushes in southern Indiana, our analyses revealed that the amount of mature forest cover and drought interacted to affect survival probability. Daily survival probability in non-drought years declined as the amount of forest cover increased, particularly for the youngest fledglings (Figure 1). By contrast, less forested landscapes exhibited declines in fledgling survival in the drought year, whereas forested landscapes appeared to be buffered. Areas of high mature forest cover have understory microclimates that are more resilient to climatic perturbations because canopy cover mediates understory soil moisture, a predictor of Wood Thrush prey availability (Chen et al. 1993, von Arx et al. 2012, Jirinec et al. 2016). The negative relationship between forest cover and fledgling survival during non-drought years is likely due to differences in nestling development and habitat availability. Nestling Wood Thrush growth rates are greater closer to forest edges (Kaiser and Lindell 2007), and more developed nestlings have higher postfledging survival (Jones et al. 2017). The negative relationship between forest cover and vertical foliage density ($r_{1966} = -0.19$, $P < 0.001$) also suggests that favorable fledgling habitat may be limited in areas with extensive, mature forest.

Fledglings also made shorter movements from the nest and delayed dispersal from their natal territory during the 2012 drought. This relationship was strongest in the 2 oldest age groups, after the majority of mortality occurred, which suggests that the observed changes in movement behavior did not affect fledgling survival. We did not find an effect of condition on postfledging movement, but our condition measurement was taken prior to fledging. Nestling condition appears to be predictive of passerine fledgling movements only during the first few days after leaving the nest (Cox et al. 2014). A reduction in food availability during the drought year could have extended the postfledging period by slowing fledgling development. Such condition-dependent natal dispersal (Ims and Hjermann 2001) affects fitness because these individuals disperse into poorer-quality habitat and have lower lifetime reproductive success (Lens and Dhondt 1994, Verhulst et al. 1997, Visser and Verboven 1999, Barbraud et al. 2003). Alternatively, the distribution of dispersal distances during 2012 may have been bimodal, with some birds dispersing short distances and others dispersing long distances (i.e. outside of the study area and thus undetectable). However, mean postfledging dispersal in Wood Thrushes is <2 km (Anders et al. 1998, Vega Rivera et al. 1998). All individuals ($n = 9$) that survived to 21 days postfledging in 2012, presumed independent, exhibited delayed dispersal. Therefore, bimodal dispersal in 2012 seems unlikely.

Brood parasitism is another environmental factor that has been hypothesized to reduce postfledging survival (Cox et al. 2014). Counter to our expectation, but consistent with the results of other studies (e.g., Fink 2003, Jenkins and Faaborg 2016), brood parasitism did not influence postfledging survival or movement of Wood Thrushes in our study area. The negative effects of brood parasitism found in other passerine species have been attributed to asynchronous hatching (i.e. the parasite hatching before the host) or to a size advantage of the parasite nestling (Hauber 2003). Wood Thrushes are unlikely to be affected by these factors because their incubation period and nestling size are similar to those of Brown-headed Cowbirds. Nestlings from parasitized nests in southern Indiana were in significantly better condition, but the effect size was relatively small ($\mu_{\text{parasitized}} = 29.15 \pm 0.24$ g, $\mu_{\text{nonparasitized}} = 28.15 \pm 0.14$ g). Higher nestling condition in parasitized nests could be explained by a combination of brood-size reduction, increased provisioning by adults (e.g., Ursino et al. 2011), and increased parasite begging (Bolopo et al. 2015). Although nestlings from parasitized nests were in better condition, an increase in survival or fledgling movements was not expected, because we found no evidence that body condition was important for these parameters.

In conclusion, this research advances our understanding of how body condition, habitat structure, drought, and brood parasitism affect the postfledging period of migratory passerines. We found that drought, in particular, can influence nestling condition, brood size, and postfledging movement and survival, but its effect on survival depends on the amount of mature forest cover. Additional research is needed to discover how drought effects are mediated by resource availability, the predator community, and parental behavior. Our results also suggest that brood parasitism has a negligible effect on the postfledging period in Wood Thrushes. Investigations of how hosts select habitat and invest in fledgling Brown-headed Cowbirds may reveal effects of brood parasitism not captured by our study. Ultimately, determining the sensitivity of migratory birds' population dynamics to the postfledging period is essential for conservation planning and for mitigating the effects of future environmental change.

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APPENDIX TABLE 4. Size of study plots in southern Indiana, USA, and number of transmitters (*n*) deployed on each plot.

Plot	Region [a]	Size (ha)	*n*
AR07	BONWR	54	21
AR27	BONWR	54	38
AR41	BONWR	53	15
AR58	BONWR	48	15
EABO	Crane	57	20
FIRS	Crane	36	3
MART	IDNR	52	14
MCCR	IDNR	48	22
OWEN	IDNR	47	15
SEED	Crane	84	10
SPMI	IDNR	43	18
SULP	Crane	40	19

[a] BONWR = Big Oaks National Wildlife Refuge, Crane = Crane naval base, and IDNR = Indiana Department of Natural Resources.

APPENDIX TABLE 5. Annual mean (± SE) values for nestling Wood Thrush condition, brood size, vertical foliage density, and number of trees >30 cm DBH, and proportion of nests parasitized, on our study sites in southern Indiana, USA, for the 4 yr of the study.

	2011	2012	2013	2014
Mean nestling condition	29.55 ± 0.29	26.52 ± 0.34	28.7 ± 0.17	28.7 ± 0.15
Mean brood size	2.56 ± 0.1	2.35 ± 0.09	2.58 ± 0.08	2.64 ± 0.07
Proportion of nests parasitized	0.34	0.28	0.18	0.18
Mean vertical foliage density	3.1 ± 0.09	2.86 ± 0.07	3.02 ± 0.07	2.55 ± 0.05
Mean number of trees >30 cm DBH	15.02 ± 0.43	13.74 ± 0.37	11.6 ± 0.24	19.07 ± 0.34