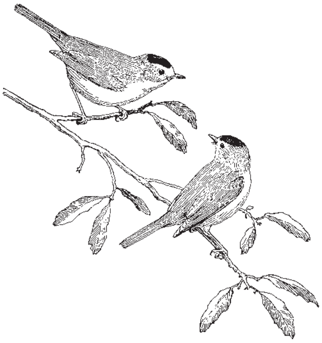

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 129, NO. 2 June 2017 PAGES 235–428

The Wilson Journal of Ornithology 129(2):235–246, 2017

VARIATION IN EARLY-SUCCESSIONAL HABITAT USE AMONG INDEPENDENT JUVENILE FOREST BREEDING BIRDS

ALICIA D. BURKE,[1,3,4] FRANK R. THOMPSON III,[2] AND JOHN FAABORG[1]

ABSTRACT.—Adults and juveniles of some forest breeding birds shift habitat use during the post breeding season from late to early successional forest. Juveniles of smaller passerine species are difficult to radio-track, and there is limited information on their habitat preferences, especially once they become older and independent. We determined if independent hatch-year birds captured in early-successional habitat remained there for extended periods, or if these habitats were only occupied infrequently during foraging activities. We determined habitat use for Ovenbirds (*Seiurus aurocapilla*), Worm-eating Warblers (*Helmitheros vermivorum*) and Red-eyed Vireos (*Vireo olivaceus*) during the independent post-fledging period in the Missouri Ozarks. We placed radio transmitters on 29 hatch-year birds captured in clearcuts and attempted to relocate them for 24 days in the summer of 2012. All three species had a greater relative probability of use of clearcut forest stands with small trees than older forests. Ovenbirds and Worm-eating Warblers remained in the early-successional habitat where initially captured, whereas Red-eyed Vireos used both late and early-successional habitat. Management efforts have primarily focused on breeding habitat for migratory songbirds, but the post-breeding period could be equally important given that hatch-year birds can spend an equal or greater amount of time in this stage. More information is needed to determine how widespread this habitat shift is for mature forest-breeding birds. *Received 3 April 2015. Accepted 2 July 2016.*

Key words: early-successional habitat, habitat use, juvenile, Ovenbird, radio-tracking, Red-eyed Vireo, Worm-eating Warbler.

Some Neotropical migrant songbirds have declined in abundance over the last several decades because of habitat loss and fragmentation on their breeding and wintering grounds (Robinson et al. 1995, Holmes 2007, Sauer et al. 2012). Most songbird studies focus on the breeding season with the primary emphasis on adults and nest success (Robinson et al. 1995, Campbell et al. 2007, Bakermans et al. 2012). Adult migrant songbirds typically spend 1–3 months nesting and 2–3 months postbreeding before migration, while juveniles spend a couple of weeks in the nest, 3–4 weeks as dependent fledglings, and 2–3 months as independent fledglings before migration. The timing and duration of nesting, fledging, and independence of young vary among species, geographically and are affected by nest predation. Birds in the southern U.S. arrive earlier and have a longer breeding season than birds in New England and Canada and may spend more time in the post-

[1] Division of Biological Sciences, University of Missouri, Columbia, MO, USA.

[2] USDA Forest Service Northern Research Station, University of Missouri, Columbia, MO, USA.

[3] Current address: 3602 Timber Run Drive, Columbia, MO 65203, USA.

[4] Corresponding author; e-mail: alicia.d.burke@gmail.com

breeding period than the breeding period. The post breeding period is an important and understudied period in a songbird's annual cycle (Cox et al. 2014).

Juvenile post-breeding habitat use is difficult to determine, because these birds rarely sing or maintain territories and may disperse from their breeding areas. Some dependent fledgling Wood Thrushes (*Hylocichla mustelina*), Ovenbirds (*Seiurus aurocapilla*), Worm-eating Warblers (*Helmitheros vermivorum*), and Swainson's Thrushes (*Catharus ustulatus*) shift to early-successional habitat while still dependent upon parental care (Anders et al. 1997, White et al. 2005, Vitz and Rodewald 2010). Most studies of fledglings have radio-tracked the birds for several weeks while the young are still primarily dependent on their parents. Wood Thrushes have been radio-tracked for longer periods, because they can carry a bigger, longer-lived transmitter on their larger body size. Post-breeding adult and juvenile Wood Thrushes travel long distances to find patches of early-successional habitat, where they remain for an extended period (Anders et al. 1997, Vega Rivera et al. 1998, Fink 2003). The shift from mature forest to early-successional habitat may occur because birds are selecting habitats with high insect and fruit abundance or cover from predators while preparing for migration (Vega Rivera et al. 1998, Vitz and Rodewald 2007, Stoleson 2013).

Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos (*Vireo olivaceus*) are Neotropical migrants that nest in mature forest but have been captured in early-successional habitat after breeding in Missouri, South Carolina, and New Hampshire (Pagen et al. 2000, Bowen et al. 2007, Chandler et al. 2012, Porneluzi et al. 2014). There is evidence from radio-telemetry studies in Ohio and Minnesota that Ovenbirds and Worm-eating Warblers shift habitats during the post-breeding period (Vitz and Rodewald 2010, Streby and Andersen 2012); however, these studies did not focus on habitat use by independent fledglings. We investigated movements and habitat use of independent fledgling Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos. We radio-tracked independent fledglings captured in early-successional habitat to determine if they preferred early successional habitat and remained in one patch, moved among patches, or made greater use of the surrounding mature forest. We used an information theoretical approach (Burnham and Anderson 2002) to evaluate our hypothesis that independent fledglings made greater use of forests recently clearcut than those treated by partial cuts or stands that received no treatment.

METHODS

Study Area

We studied birds during the summer of 2012 in the Ozarks of southeast Missouri (Shannon and Carter counties) in the Current River Conservation Area (Fig. 1). This area is ~84% forested, and tree composition is predominately 50% oak (*Quercus* spp.), 13% hickory (*Carya* spp.), and 15% short-leaf pine (*Pinus echinata*; Shifley and Brookshire 2000). We selected four stands to capture birds for radio-tracking based on mist-netting data from 2010 and 2011. The four stands were 5.7–13.8 ha, had been clearcut in the last 3–6 years (Table 1), and were composed of oak-hickory and pine seedlings and saplings and dense fruit-bearing vegetation such as blackberries and raspberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), grapes (*Vitis* spp.), and winged sumacs (*Rhus copallina latifolia*; Shifley and Kabrick 2002).

Radio Telemetry

We captured birds at four sites using constant effort mist-netting from 1 June to 3 August 2012. We placed 12 nets (12 m $\times$ 2.6 m, 30-mm mesh) end-to-end within each clearcut, 1–2 times/week. We opened nets at sunrise for 5–6 hrs, and we checked nets for birds every 15–20 min. We attached 0.3-g radio transmitters with a 24-day life expectancy (model A2414; Advanced Telemetry Systems Inc., Isanti, MN, USA) to Ovenbirds (~19 g), Worm-eating Warblers (~13 g), and Red-eyed Vireos (~16 g), because the birds were reasonably abundant and large enough so that transmitters were 1.5–2% of their body weight. Focal species were determined to be HY or AHY by physical characteristics such as molt, plumage patterns, and gape; the AHY birds were banded and released (Pyle 1997). We evaluated independence for HY birds based on the same, as well as, observing the activity of nearby birds that would indicate parental interaction or dependence, such as excessive alarm and chipping. We aged the birds and determined their independence in order to

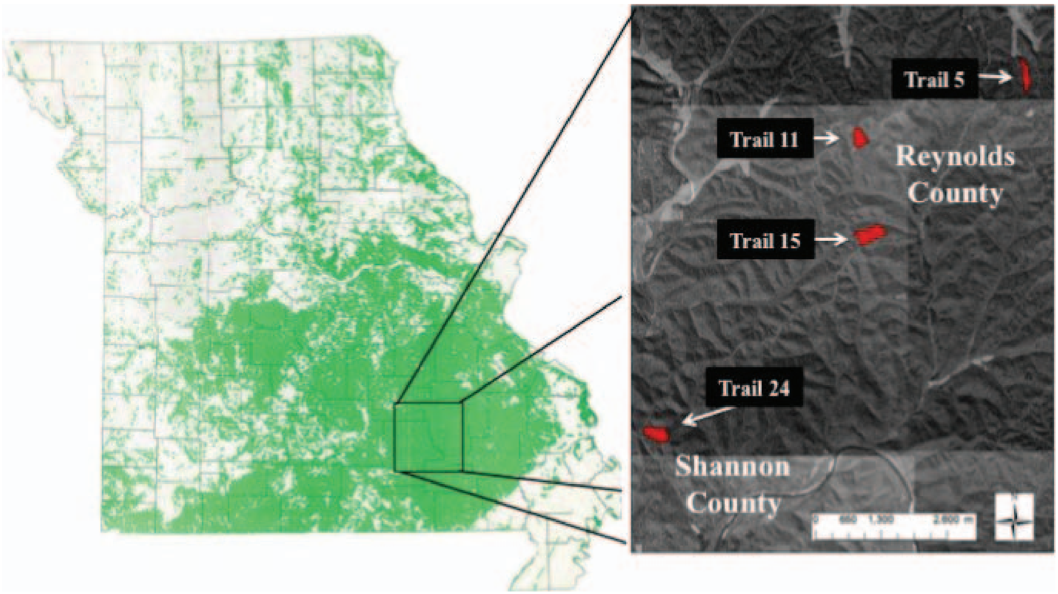

FIG. 1. Location of study sites in Missouri in which we captured and radio-tracked fledgling Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos in the Current River Conservation Area, 2012.

ensure that we were only placing transmitters on post fledging young of the year. We glued transmitters to the two central tail feathers (e.g., Stanton 2013), so birds would shed the transmitter when they molted within the next year.

We used triangulation and homing (White and Garrott 1990) to locate the birds with hand-held, three-element Yagi antennas and receivers (model R-1000; Communications Specialists Inc., Orange, CA, USA) from 20 June to 8 August 2012. We attempted to relocate each bird at least every 24 hrs. If we were unable to find a bird near its previous location, we would drive and search the surrounding area (Current River CA) for a min of 1 hr, covering as much of the 11,853-ha area as possible via established trails and logging roads. If we had multiple birds, we scanned for all individuals and ensured at least 1 hr was spent on each bird. Typically, there were two searches per day (05:00–11:00 and 15:00–20:00 hrs Central Daylight Time [CDT]) that lasted 5–6 hrs (depending on number of birds) and covered the entire Current River Conservation Area. We used a magnetically mounted Omni antenna (Laird, Earth City, MO, USA) placed on the roof of a truck. A bird was classified as missing if it moved away from the clearcut where it was initially banded and we were unable to locate it. We continued to search for all missing birds for the 24-day life of the transmitter's battery. When we located a bird in the forest, we were usually able to view the bird and would take a single geographic location (Universal Transverse Mercator coordinate system, UTM) with a GPSMAP 76 and eTrex Legend H (Garmin International Inc., Olathe, KS, USA; 3–5-m accuracy) global positioning system (GPS). Dense vegetation prevented our homing to the location of a bird in clearcuts; in this case we took 3–5 bearings from the perimeter. We triangulated locations from bearings using the program Location Of A Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary; www.

TABLE 1. Characteristics of clearcut stands in which we captured and radio-tracked fledgling Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos in the Current River Conservation Area, 2012.

Site	Harvest date	Regeneration cut age (yr)	Size (ha)
Trail 24	April 2007	3–5 yr	9.3
Trail 15	November 2007	2–4 yr	13.75
Trail 11	December 2007	3–4 yr	5.66
Trail 5	August 2006	4–5 yr	7.28

ecostats.com/web/LOAS) and excluded locations where the error ellipse was greater than the size of the clearcut (5.66–13.75 ha). We were always able to determine if the bird was inside or outside of a clearcut based on bearings in the field.

Data Analysis

We used discrete choice models (Millspaugh and Marzluff 2001) to evaluate the effects of stand treatment and tree size on habitat by comparing used points to available points for Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos. We constrained available habitat to a mean daily distance traveled for each species. We assumed 3rd-order selection as defined by Johnson (1980), where our actual distribution of each species across the different stand treatments and tree sizes is the end result of the habitat selection process. We acknowledge that there had been many decisions made for these individuals by their parents in terms of habitat selection (Johnson 1980). Based on plumage characteristics and behavior, we determined that the birds selected for our study were independent of parental care.

We used timber sale records, stand inventory data (H. Burm, pers. comm.), and aerial photographs (Missouri Spatial Data Information Service, Columbia, MO, USA; U.S. Forest Service, Columbia, MO, USA) in a Geographic Information System (GIS) to create stand specific habitat classifications. Forest stands are contiguous groups of trees delineated by the Missouri Department of Conservation based upon similarity in age, size class, and location that are sufficiently distinguishable from surrounding stands. We classified each stand based on inventories and according to forestry treatment as clearcut, partial cut, or no treatment. We classified forest stand treatments as clearcuts if the overstory had been removed within the last 6 years. Stands were classified as partial cut if the inventory indicated intermediate harvest, timber stand improvement, select cut, or uneven age management. Stands were classified as no treatment if the inventory indicated mature forest or old growth and there was no recent record of a treatment. Additionally, we classified each stand by tree size-class based upon the forest inventory; small tree (<12.7 cm), or pole timber (12.7–27.9 cm) or sawtimber (>27.9 cm; H. Burm, pers. comm.)

We estimated daily movements from GPS coordinates of located individual birds using Excel. We calculated linear distance moved, distance moved per hr, and mean daily distance for each species. We used the mean daily distance for each species to create a buffer around each location, within which we located five random points as available habitat to compare in our discrete choice analysis. We used Hawth's tools (Beyer 2004) to generate the random points and intersected both point groups with our habitat classifications to assign values for treatment and tree size class.

We used an informational theoretic approach to evaluate what variables best explained habitat use by Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos based on Akaike's Information Criterion for small sample size (AIC_c; Burnham and Anderson 2002). We fit discrete choice models for each species to determine habitat use, because they allowed us to define habitat availability for each individual. We assumed that the individual, when given a set of resources defined by the randomly selected points around each location, made its selection based on maximum utility (Millspaugh and Marzluff 2001). We fit models for each species and used the robust sandwich variance estimate in the PHREG procedure in SAS to account for repeated choices by individuals (Lin and Wei 1989). For each species, we plotted predicted relative probabilities of use across the range of observed values for supported variables of supported models to demonstrate habitat relationships.

We used treatment (clearcut-CC, partial cut-PC, and no treatment-NT) and tree size (small tree-ST, pole timber-P, and saw timber-S) as categorical variables. We considered NT and S as our reference categories and excluded them from our models to avoid linear dependent covariates (Fig. 2).

RESULTS

We placed a total of 29 radio transmitters on independent hatch year Red-eyed Vireos ($n = 15$), Worm-eating Warblers ($n = 7$), and Ovenbirds ($n = 7$) that we captured in the summer of 2012. Our number of captures was limited because of a severe drought in the Midwestern United States

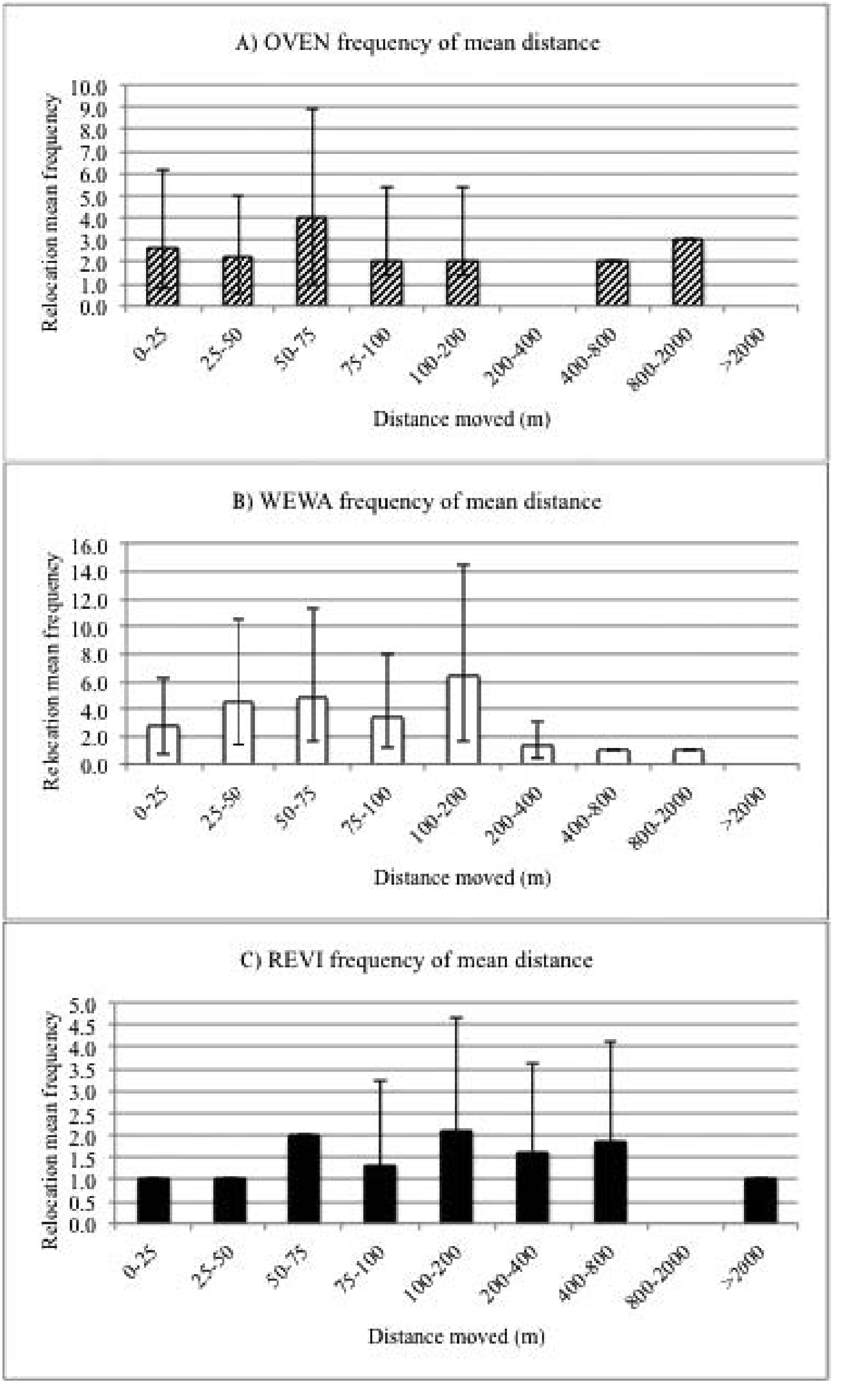

FIG. 2. Frequency of mean distances moved between relocations (m) with standard error bars, among individual juvenile (A) Ovenbirds (OVEN), (B) Worm-eating Warblers (WEWA), and (C) Red-eyed Vireos (REVI) in the Missouri Ozarks, 2012. Sample sizes for each movement category were 0–25 m, $n = 8$, 14, 2; 25–50 m, $n = 9$, 18, 2; 50–75 m, $n = 16$, 24, 2; 75–100 m, $n = 6$, 17, 8; 100–200 m, $n = 6$, 32, 17; 200–400 m, $n = 0$, 5, 13; 400–800 m, $n = 2$, 1, 11; 800–2,000 m, $n = 3$, 0, 0; >2,000 m, $n = 0$, 0, 3; for Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos, respectively.

TABLE 2. Support for discrete choice models predicting relative probability of use as a function of tree size class and stand treatment for fledgling Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos in the Current River Conservation Area, 2012

Species and model	K	Log-likelihood	AIC_c	ΔAIC_c	ω_i
Ovenbird					
Tree size	3	−66.462	139.353	0.000	0.979
Stand treatment	3	−70.290	147.008	7.655	0.021
Null model	2	−104.101	212.413	73.060	0.000
Worm-eating Warbler					
Tree size	3	−141.318	288.843	0.000	0.548
Stand treatment	3	−141.512	289.231	0.388	0.452
Null model	2	−214.241	432.585	143.741	0.000
Red-eyed Vireo					
Tree size	3	−123.198	252.744	0.000	0.699
Stand treatment	3	124.132	254.612	1.868	0.274
Null model	2	−127.572	259.315	6.571	0.026

TABLE 3. Comparison of movements of individual Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos in the Current River Conservation Area, standardized to m/hr. Numbers under individuals for each species represent radio frequency, and n is the number of relocations for that individual. We were only able to locate individuals with asterisks (*) once; this resulted in a single distance moved, so mean and variance were not meaningful.

Species and Individual	n	Mean	Variance	95% Confidence interval (low–high)
Ovenbird				
4.972	14	2.81	5.15	1.62–4
5.473	15	2.93	3.81	1.94–3.91
5.513	11	4.64	10.37	2.73–6.54
5.552	10	11.58	132.79	4.44–18.72
Worm-eating Warbler				
5.332	33	5.14	10.37	4.04–6.24
5.409	31	6.5	29.39	4.59–8.41
5.543	32	7.34	69.88	4.45–10.24
5.571	5	7.17	28.09	2.52–11.82
5.642	8	2.15	2.47	1.06–3.24
5.652	2	3.09	0.32	2.13–3.87
Red-eyed Vireo				
4.922	10	5.43	32.51	1.89–8.96
4.959	8	10.88	114.13	3.48–18. 29
5.003*	1	–	–	–
5.011	2	7.9	35.48	0–16.15
5.364	7	12.15	242.33	0.62–23.68
5.438	2	2.47	3.08	0.04–4.90
5.451	5	13.66	403.66	0–31.27
5.462*	1	–	–	–
5.532*	1	–	–	–
5.582	10	8.43	99.01	2.27–14.60
5.634	4	23.36	658.15	0–48.5
5.664	7	16.9	287.57	4.34–29.46

during the summer of 2012; capture numbers for 2012 decreased overall when compared to 2010 and 2011 capture data. The number of relocations for individuals radio-tagged was also limited because of predation and transmitter attachment failure (5 out of 29); three total predation events – 1 Worm-eating Warbler and 2 Red-eyed Vireos, two dropped radios –1 Red-eyed Vireo and 1 Ovenbird (Ovenbird recaptured 3 weeks later in same CC). Other limitations for relocation included individuals disappearing from our search area, and the number of days available for tracking provided by the transmitter (~24 days). We fit two discrete choice models that described habitat selection for each of the three species.

Ovenbird

We captured and radio-tagged seven Ovenbirds but were only able to radio-track four for a total of 50 relocations during the summer of 2012 (Table 3). We found birds on average every 28.2 hrs (8.1–120.1 hrs). The mean distance moved between locations was 133.5 m (6.1–1,145.3 m, Fig. 2). Locations corresponded predominately with clear-cut study sites, and 75% of the Ovenbirds remained in the same clearcut where captured. Location points were clustered within the clear-cuts, but significant movement occurred from day to day and even while taking GPS points for triangulation (Fig. 3).

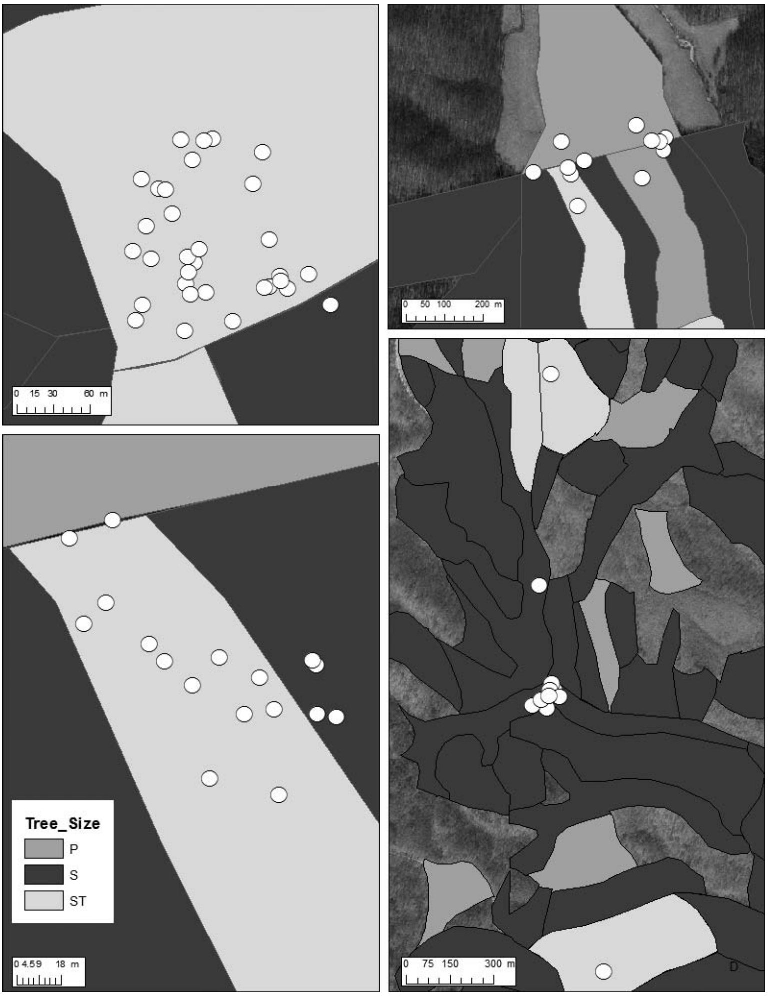

FIG. 3. Examples of radio telemetry locations to visually depict distribution across habitats for individual Worm-eating Warblers, Red-eyed Vireos, and Ovenbirds (left to right) in the Ozarks of SE Missouri, Current River Conservation Area. Missouri, 2012. Maps are at varying scales to accommodate each individual bird's movement. Light gray, medium gray, and dark gray areas represent stands dominated by small trees, poles, and saw timber–sized trees, respectively. The clustered locations for the Ovenbirds in the lower right map are in a stand classified as saw timber but in a canopy gap in second-growth vegetation.

The tree size class model had the greatest support (Table 2); conditional on this model, the relative probability of use was much greater for stands in the small-tree class than pole or sawtimber class (Fig. 4). There was also some support for the stand treatment model (Table 2); conditional on this model, the relative probability of use was much greater for stands treated by clearcuts than partial cuts or no treatment (Fig. 5). There was no support for our null model (Table 2).

We tracked a single Ovenbird (frequency 165.552) 981 m from Trail 15, where it was captured, to a canopy gap where it remained for 2 days (Fig. 3). It then made a series of northern movements over 2 days of 1.14 km to one of our other study sites (Trail 11, Fig. 1). Later the same day, we located it 1.14 km south in the same canopy gap where it remained for 10 more days, but after that we were unable to locate it. This bird was still using early-successional habitat for all of

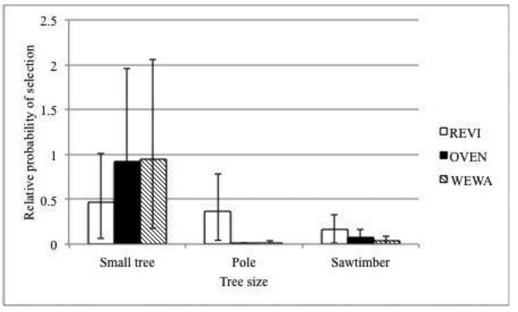

FIG. 4. Predicted relative probability of use as a function of tree size class for juvenile Red-eyed Vireos, Ovenbirds, and Worm-eating Warblers in the Current River Conservation Area, Missouri, 2012.

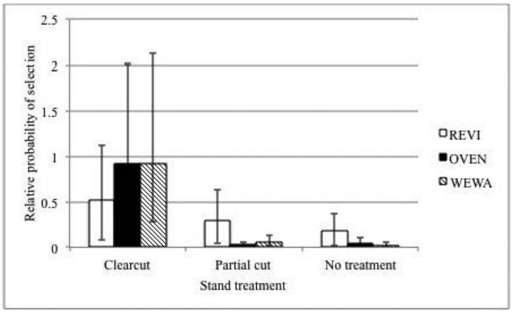

FIG. 5. Predicted relative probability of use as a function of stand treatment for juvenile Red-eyed Vireos, Ovenbirds, and Worm-eating Warblers in the Current River Conservation Area, Missouri, 2012.

the points where it was located, though it used a smaller patch (tree fall). This stand was classified as sawtimber and had received no treatment. The mean distance/hr by this Ovenbird (11.6 m/hr) was substantially greater than for other Ovenbirds (2.8–4.6 m/hr; Table 3).

Worm-Eating Warbler

We captured and radio-tagged seven Worm-eating Warblers and were able to locate six for a total of 112 locations during the summer of 2012 (Table 3). Birds were located on average every 21 hrs (6.4–215.4 hrs). The mean distance moved between locations was 89m (6.1–448.8 m, Fig. 2). Locations were predominately in stands treated by clearcuts, and all Worm-eating Warblers remained in or near the same location where captured (Fig. 3). Location points were clustered within the clearcuts, but significant movement occurred from day to day and even while taking GPS points for triangulation. Mean distance moved/hr ranged from 2.2–7.5 m, and confidence intervals overlapped for most individuals (Table 3).

The tree size class model had the greatest support (Table 2), and conditional on this model, the relative probability of use was much greater for stands in the small-tree class than pole or sawtimber class (Fig. 4). There was also significant support for the stand treatment model, and conditional on this model, the relative probability of use was much greater for stands treated by clearcuts than partial cuts or no treatment (Table 2 and Fig. 5). There was no support for our null model (Table 2).

Red-Eyed Vireo

We captured and radio-tagged 15 Red-eyed Vireos and were able to locate 12 for a total of 58 locations (Table 3). Birds were located on average every 40 hrs (8.51–136.28 hrs). The mean distance moved between relocations was 434 m (15.5–4032.6 vm, Fig. 2). Red-eyed Vireos were captured initially in clearcuts, but the birds also selected forested areas (Fig. 3).

The tree size class model had the greatest support (Table 2). Conditional on this model, the relative probability of use was greater for small tree (52%) than pole (32%) or sawtimber (16%) stands (Fig. 4). There was also some support for the stand treatment model, and conditional on this model, relative probability of use was greater for clearcut (53%) than partial cut (30%) or no treatment (17%) stands (Table 2 and Fig. 5). There was no significant support for our null model (Table 3).

We observed a large movement by one Red-eyed Vireo (165.582). It was captured 20 July 2012 in a clearcut (Trail 11, Fig. 3), and its subsequent locations were in surrounding pole sized partial cuts and sawtimber stands that had received no treatment. Locations over the next 15 days were split equally between the two treatment types and tree sizes, with the bird appearing to alternate locations for consecutive locations. The bird then was missing until 8 August 2012 when we located it over 4 km southwest of all previous locations in a partial-cut stand classified as sawtimber. The mean distance moved/hr ranged 2.5–23.4 m, and its movements were more variable than for the other species; confidence intervals overlapped among individuals (Table 3).

DISCUSSION

We found juveniles of mature forest-breeding birds made greater use of early-successional habitat than mature forest during the post-breeding period, which reinforces the results from studies in Missouri, Ohio, Pennsylvania, Minnesota, and Quebec (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Streby et al. 2011, Major and Desrochers 2012, Stoleson 2013). The majority of these studies reported limited movement and habitat use information after day 24, the approximate date of independence. Our study expanded on this information and captured habitat use for juvenile Ovenbirds, Worm-eating Warblers, and Red-eyed Vireos post-independence.

Habitat managers and ecologists now have habitat use information that encompasses the breeding and post-breeding season for Wood Thrushes (Anders et al. 1997, Vega Rivera et al. 1998, Fink 2003), Ovenbirds (Vitz and Rodewald 2010, Burke 2013, Streby and Andersen 2013), and Worm-eating Warblers (Vitz and Rodewald 2010, Burke 2013). Our results for Ovenbirds showed that they either stayed in a single clearcut, or moved from one clearcut to another via forest stands with patches of early-successional habitat (Fig. 3). Worm-eating Warblers appeared to be strongly clustered in the original clearcut as well, and preferred dense small tree vegetation when compared to available alternative habitat locations. Our results for Ovenbirds and Worm-eating Warblers reinforce the results from previous studies (Table 2, Fig. 3; Vitz and Rodewald 2010). Wood Thrush, because of its larger size, is one of the only species for which there is more continuous breeding season habitat use information (Anders et al. 1997, Vega Rivera et al. 1998, Fink 2003). Wood Thrushes have been shown to travel large distances to locate early-successional habitat, and similar to our results for Ovenbirds and Worm-eating Warblers, it appears they stay for long periods, indicating the importance of these habitats during the post-breeding season (Anders et al. 1997). Selection of early-successional habitat may also be considered important for independent juvenile Worm-eating Warblers and Ovenbirds, based on our observation of their exclusive use in the post-breeding season.

Not all species of mature forest-breeding birds exclusively use early-successional habitat during the post-breeding season. Adult Scarlet Tanagers in Virginia (*Piranga olivacea*) use mature forest as well as early-successional habitat during the breeding and post-breeding season (Vega Rivera et al. 2003). Post-breeding habitats selected by Red-eyed Vireos appear to most closely resemble those used by adult Scarlet Tanagers: selection of stands that receive no treatment, as well as clearcut habitat (Vega Rivera et al. 2003). Our observations for independent juvenile Red-eyed Vireos in Missouri are the only known habitat selection study for this age class for this species. Results for independent juvenile Red-eyed Vireos indicate that they may be doing something different from juvenile Wood Thrushes, Ovenbirds, and Worm-eating Warblers, with habitat use distributed between different habitat types (Table 2). Our models indicated selection for clearcuts, though these birds were also positively associated with partial cuts and stands with no treatment, though less often (Table 2, Fig. 2). There was a higher predicted probability of use for small trees and clearcuts, though they did use other habitats as well during the post-breeding season (Figs. 4–5). It is not clear if independent juvenile Red-eyed Vireos' selection of early-successional habitat can be considered an important part of their annual cycle or merely facultative. These data make evident the importance of obtaining whole annual cycle habitat use information for all species, even those classified within the same guild.

Early successional habitat may provide resources such as fruit and insects, as well as increased cover from predators, and may result in greater survival (Vitz and Rodewald 2006, Major and Desrochers 2012, Stoleson 2013). Current forestry practices create areas of early-successional habitat, though natural disturbances such as fire, wind, and tree falls also continue to provide these areas as well. We found that early-successional habitats are being selected and may be an important annual habitat for Ovenbirds, Worm-eating Warblers, and possibly Red-eyed Vireos. While we demonstrated selection of early successional habitats during the post-breeding season, we did not measure survival, growth, or other factors affecting fitness. Based on our results and others (Vitz and Rodewald 2006, Major and Desrochers 2012, Stoleson 2013), however, we suggest that selection of early successional habitats is conveying fitness benefits to these species.

Research and management often focuses on breeding habitat for migratory songbirds, but the post-breeding period could be equally important for their survival because individuals spend an equal or greater amount of time in the post-breeding stage. Conservation agencies and land managers need guidance for habitat management that extends beyond the breeding season. Species, such as Wood Thrush, Ovenbird, and Worm-eating Warbler make use of mature forest for nesting (Thompson et al. 1992, Annand and Thompson 1997, Wallendorf et al. 2007) and early successional habitat during the post-breeding period. This information can be used to guide management for these species.

Future Research

Our interest in post-fledging habitat shifts originated from netting forest birds in clearcuts later in the summer. In this study, we captured 30 different mature forest-breeding bird species in clearcuts of the Ozarks (Burke 2013), but this does not mean that these species are making a habitat shift. Post-breeding season habitat use has only been investigated for six of these species, and those species utilized early-successional habitat. Knowledge of the extent that mature forest birds require early-successional habitat may be critical to managing their populations. Habitat movement data suggest that for Wood Thrushes, Ovenbirds, and Worm-eating Warblers, there is a major habitat shift, but for species like the Red-eyed Vireo, Scarlet Tanager, and Acadian Flycatcher, there is a shift but to a lesser extent (Anders et al. 1998, Vega Rivera et al. 2003, White and Faaborg 2008, Vitz and Rodewald 2010, Streby et al. 2011, Jenkins 2016). We suggest further research to define post-breeding habitat use for mature forest-breeding birds, which could help optimize management and conservation efforts to increase declining populations of Neotropical migrant songbirds. Less information exists on post-fledging ecology after 25 days post-fledgling (Cox et al. 2014).

ACKNOWLEDGMENTS

Funding was provided by USFWS Southeast and the Midwest Migratory Bird Program; we specifically thank Dean Demarest and Steve Lewis. The U.S. Forest Service Northern Research Station provided additional support. We are indebted to K. Bird, M. Roach, S. Anderson, H. Finch, and the numerous volunteers who assisted with fieldwork over the course of this study. We would also like to thank T. Bonnot and W. Dijak for their assistance with discrete choice models and ArcGIS, R. Semlitsch for comments on previous drafts, D. Kesler for use of his equipment, and members of the MU Avian Ecology Lab. We are grateful to the Missouri Department of Conservation, specifically H. Burm, R. Jensen, A. Lanham, and S. Burm for logistical support and resources throughout our study.

LITERATURE CITED

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III. 1997. Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698–707.

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349–358.

Annand, E. M. and F. R. Thompson III. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management 61:159–171.

Bakermans, M. H., A. D. Rodewald, and A. C. Vitz. 2012. Influence of forest structure on density and nest success of mature forest birds in managed landscapes. Journal of Wildlife Management 76:1225–1234.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. Hawthorne Beyer. www.spatialecology.com/htools

Bowen, L. T., C. E. Moorman, and J. C. Kilgo. 2007. Seasonal bird use of canopy gaps in a bottomland forest. Wilson Journal of Ornithology 119:77–88.

Burke, A. D. 2013. Mature forest-breeding bird use of early-successional habitat. Thesis. University of Missouri-Columbia, Columbia, USA.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Campbell, S. P., J. W. Witham, and M. L. Hunter Jr. 2007. Long-term effects of group-selection timber harvesting on abundance of forest birds. Conservation Biology 21:1218–1229.

Chandler, C. C., D. I. King, and R. B. Chandler. 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? Forest Ecology and Management 264:1–9.

Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg. 2014. Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183–193.

Fink, M. L. 2003. Post-fledging ecology of juvenile Wood Thrush in fragmented and contiguous landscapes. Dissertation. University of Missouri-Columbia, Columbia, USA.

Holmes, R. T. 2007. Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. Ibis 149(Suppl. 2):2–13.

Jenkins, J. M. A. 2016. Nesting and postfledging ecology of Neotropical migrant songbirds in Missouri forest fragments. Dissertation. University of Missouri-Columbia, Columbia, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Lin, D. Y. and L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. Journal of the American Statistical Association 84:1074–1078.

Major, M. and A. Desrochers. 2012. Avian use of early-successional boreal forests in the postbreeding period. Auk 129:419–426.

Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. Forest Ecology and Management 183:127–135.

Millspaugh, J. J. and J. M. Marzluff (Editors). 2001. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor 102:738–747.

Porneluzi, P. A., R. Brito-Aguilar, R. L. Clawson, and J. Faaborg. 2014. Long-term dynamics of bird use of clearcuts in post-fledging period. Wilson Journal of Ornithology 126:623–634.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. State Creek Press, Point Reyes Station, Bolinas, California, USA.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2012. The North American Breeding Bird Survey, results and analysis 1966–2011. Version 12.13.2011. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Shifley, S. R. and B. L. Brookshire (Editors). 2000. Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. USDA, Forest Service, General Technical Report NC-208. North Central Research Station, St. Paul, Minnesota, USA.

Shifley, S. R. and J. M. Kabrick (Editors). 2002. Proceedings of the second Missouri Ozark Forest Ecosystem Project symposium: post-treatment results of the landscape experiment. USDA, Forest Service, General Technical Report NC-227. North Central Research Station, St. Paul, Minnesota, USA.

Stanton Jr., R. A. 2013. Habitat selection of Brown-headed Nuthatches at multiple spatial scales. Thesis. University of Missouri-Columbia, Columbia, USA.

Stoleson, S. H. 2013. Condition varies with habitat choice in postbreeding forest birds. Auk 130:417–428.

Streby, H. M. and D. E. Andersen. 2012. Movement and cover-type selection by fledgling Ovenbirds (*Seiurus aurocapilla*) after independence from adult care. Wilson Journal of Ornithology 124:620–625.

Streby, H. M. and D. E. Andersen. 2013. Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous–deciduous forests. Forest Ecology and Management 287:9–16.

Streby, H. M., S. M. Peterson, T. L. McAllister, and D. E. Andersen. 2011. Use of early-successional managed northern forest by mature-forest species during the post-fledging period. Condor 113:817–824.

Thompson III, F. R., W. D. Dijak, T. G. Kulowiec, and D. A. Hamilton. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. Journal of Wildlife Management 56:23–30.

Vega Rivera, J. H., W. J. McShea, and J. H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120:632–644.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69–78.

Vitz, A. C. and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. Biological Conservation 127:477–486.

Vitz, A. C. and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. Auk 124:494–507.

Vitz, A. C. and A. D. Rodewald. 2010. Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. Auk 127:364–371.

Wallendorf, M. J., P. A. Porneluzi, W. K. Gram, R. L. Clawson, and J. Faaborg. 2007. Bird response to clear cutting in Missouri Ozark forests. Journal of Wildlife Management 71:1899–1905.

WHITE, J. D. AND J. FAABORG. 2008. Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes. Wilson Journal of Ornithology 120:62–73.

WHITE, G. C. AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press Inc., San Diego, California, USA.

WHITE, J. D., T. GARDALI, F. R. THOMPSON III, AND J. FAABORG. 2005. Resource selection by juvenile Swainson's Thrushes during the postfledging period. Condor 107:388–401.