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SEASONAL USE OF HABITAT BY SHRUB-BREEDING BIRDS IN A SOUTHEASTERN NATIONAL FOREST

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ABSTRACT.—Populations of shrub-breeding birds are declining in eastern North America, and loss of habitat has been implicated in these declines. Seasonal use of habitat by shrub-breeding birds in the southeastern US remains understudied despite the fact that it is well documented that species resident within a region can shift habitat use dramatically between seasons. To better understand year-round habitat occupancy by shrub-breeding birds, we conducted bird counts and vegetation surveys during summer and winter 2008–2009 within Tuskegee National Forest, Alabama. We used multi-season occupancy models to examine use of habitat and to contrast seasonal occupancy patterns of four species of resident shrub-breeding birds—Brown Thrashers (*Toxostoma rufum*), Eastern Towhees (*Pipilo erythrophthalmus*), Northern Cardinals (*Cardinalis cardinalis*) and Carolina Wrens (*Thryothorus ludovicianus*). Brown Thrashers and Eastern Towhees are partially migratory—meaning some populations have separate breeding and wintering areas—whereas Carolina Wrens and Northern Cardinals are non-migratory. All four species showed seasonal changes in use of habitat between summer and winter, and all species were associated with both vegetation structure and certain types of cover. Further, partially migratory shrub-breeding species had greater site-turnover and increases in occupancy between summer and winter than non-migratory species. Our results suggest that: (1) management actions based on breeding habitat requirements will likely not create suitable winter habitat, and (2) management of resident shrub-breeding birds will require not only the creation and maintenance of certain types of cover, but also certain structural aspects of vegetation within habitats. *Received 1 March 2013. Accepted 23 August 2013.*

Key words: early successional habitats, Gulf Coastal Plain, multi-season occupancy analysis, shrub-breeding birds, shrubland, wildlife opening.

Use of habitat by birds is likely to change between breeding and non-breeding periods because of seasonal changes in resource availability and vegetation structure as well as constraints on birds to find suitable nest sites during summer (e.g., Bilcke 1984, Morrison et al. 1986, Keller and Yahner 2007). For instance, many migratory species will switch from using scrub during the breeding season to forested habitat in the winter, and vice-versa (Robbins et al. 1989). Therefore, a complete understanding of the habitat requirements of a given species can be achieved only through a multi-season perspective.

As a group, shrub-breeding birds are in decline because of habitat loss resulting from changes in agricultural practices, maturation of forests, and urbanization (e.g., Askins 1993, Dettmers 2003, Murphy and Moore 2003). Despite calls for the creation and preservation of habitat for shrub-breeding birds in the eastern US (e.g., Woodrey et al. 1998, Askins 2001, Dettmers 2003), the specific habitat requirements of most shrub-breeding birds remain poorly understood. Most studies of habitat use by shrub-breeding species focus on the breeding season (e.g., Chandler et al. 2009, King et al. 2009a, Schlossberg et al. 2010), and the use of habitat by shrub-breeding birds during winter remains poorly known (Schlossberg and King 2007).

A seasonal approach to studies of habitat use by shrub-breeding birds is especially needed in the southeastern US. Populations of shrub-breeding birds in the northeastern US and southeastern Canada have experienced the most drastic declines (e.g., Askins 1993, Hagan 1993, Sauer et al. 2008), and many of these species, such as the Brown Thrasher (*Toxostoma rufum*) and Eastern Towhee (*Pipilo erythrophthalmus*), winter in the southeast (Hagan 1993, Schlossberg and King 2007). Therefore, knowledge of seasonal habitat use by shrub-breeding birds within the southeast can inform the management of populations that breed elsewhere.

Site selection by birds is considered a hierarchical process with birds first selecting the type of cover in which to settle and then choosing specific sites with preferred structural aspects of vegetation (e.g., Johnson 1980, Hutto 1985, Hagan and Meehan 2002). Therefore, investigations into use of both cover-type and vegetation structure are

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needed to accurately describe the habitat needs of birds (Wiens 1989, Knick and Rotenberry 1995). A previous study of migratory birds wintering within the same study site surveyed here for scrub birds found that models including information regarding both cover-type and vegetation structure out-performed models which included either scale alone (McClure et al. 2012). A multi-scale approach to studies of habitat use by shrub-breeding birds may be especially important because shrub-nesting birds have clear preferences for certain types of cover (e.g., Bulluck and Buehler 2006, Fink et al. 2006, King et al. 2009b), and their life-history makes them inherently dependent on certain structural aspects of vegetation for nesting, cover, and foraging (e.g., Hagan and Meehan 2002, MacFaden and Capen 2002, Schlossberg et al. 2010).

Although shrub-nesting birds are generally considered to prefer early successional types of cover such as clearcuts and beaver meadows (e.g., Greenberg et al. 1995, Bulluck and Buehler 2006, Chandler et al. 2009), many will use forested areas with appropriate vegetation structure (Engstrom et al. 1984, Hamel 1992, Schlossberg and King 2007). We conducted bird counts and surveys of vegetation during summer and winter across a forested matrix in the Southeast that contained several types of early successional habitat. We contrasted the occupancy patterns and habitat use of four resident—i.e., present year-round—shrub-nesting species that represent two different situations. Northern Cardinals (*Cardinalis cardinalis*) and Carolina Wrens (*Thryothorus ludovicianus*) are non-migratory (Dow and Scott 1971, Taylor et al. 1983) and their populations have increased significantly range-wide since the 1960s (Sauer et al. 2011), whereas Brown Thrashers and Eastern Towhees are partially migratory—having some populations that breed in the northeast US and winter in the southeast, and other populations that remain in the same region year-round (Hagan 1993, Schlossberg and King 2007)—and have significantly declining populations (Sauer et al. 2011). We predicted that partial migrants would show greater changes in occupancy and higher rates of site-turnover between summer and winter than the non-migrants, that patterns of habitat use would differ for all species between seasons, and that all species would be associated with aspects of habitat at multiple scales.

METHODS

Study Area.—Our study site was centered on the Tuskegee National Forest (TNF) in Macon County, Alabama (32° 25.899′ N, 85° 38.637′ W). This area contained a range of habitats including several early successional habitats such as clearcuts, old fields, wildlife openings and beaver meadows, as well as native hardwood and pine forests (Table 1). Management units within TNF are burned every 2–5 years. We conducted bird surveys at locations within the southwest portion of the national forest (Fig. 1) which were previously established to examine the effects of bird communities on virus transmission (Jacob et al. 2010, Estep et al. 2011, Estep et al. 2012). Survey locations were in a systematic grid, and were not biased toward any particular type of cover. All survey points were roughly 250 m from the next nearest point.

Surveys of Breeding Birds.—Four trained observers conducted surveys of breeding birds at 338 bird survey locations in 2008. We conducted point counts (Ralph et al. 1995) following the protocols of Hamel (1992) and recommendations of Mackenzie and Royle (2005). During a point count, we recorded all birds detected by sight or sound within a 100-m radius, excluding flyovers. Observers also recorded weather variables hypothesized to affect detection of birds such as cloud-cover, temperature and wind speed. Using this protocol, each point was surveyed on two different dates and at two different times of day. We conducted three consecutive 4-min counts during each round of surveys. We rotated observers between rounds to ensure two different observers surveyed each point and that each observer conducted approximately the same number of surveys in each cover-type. All surveys were conducted between 15 May and 31 June and between 0500–1100 CDT.

Surveys of Winter Birds.—Three trained observers conducted winter point counts at 205 of the summer bird survey sites within Tuskegee National Forest from 28 January through 28 February 2009 between 0600–1400 CST according to the recommendations of Rollfinke and Yahner (1990). Point counts lasted 20 mins and were divided into 4-min intervals during which we recorded all birds detected within 100 m, excluding flyovers. Survey locations were only visited once. However, we were careful to ensure that each observer conducted surveys within each

TABLE 1. Models tested regarding the use of habitat by resident shrub-breeding birds at both the cover-type and vegetation scales as well as the sources of the hypothesis for each model.

	Model	Source of hypothesis
Cover-type	Canopy cover	(MacArthur and MacArthur 1961, Shugart and James 1973)
	Development	(Beissinger and Osborne 1982, Oneal and Rotenberry 2009, Bried et al. 2011)
	Clearcuts	(Conner et al. 1979, Thompson et al. 1992, Greenberg et al. 1995)
	Hardwoods	(Dickson 1978, Sallabanks et al. 2000, Bowen et al. 2007)
	Floodplain	(Dickson 1978, Sallabanks et al. 2000, Bowen et al. 2007)
	Natural Pine	(Engstrom et al. 1984, Allen et al. 2006, Bried et al. 2011)
	Wildlife Openings + Agriculture	(Schlossberg and King 2007, King et al. 2009b, Johnson 2010)
	Development + Agriculture + Scrub	(Hamel 1992, Murphy and Moore 2003, Schlossberg and King 2007)
Vegetation	Basal Area	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Grass Layer Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Canopy Cover	(MacArthur and MacArthur 1961, Shugart and James 1973)
	Midstory Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Shrub Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Ground Cover + Leaf Litter	(Hamel 1992, Schlossberg and King 2007)
	Canopy Cover + Leaf Litter	(Hamel 1992, Schlossberg and King 2007)
	Ground Cover + Grass layer Density + Midstorey Density + Basal Area	(MacArthur and MacArthur 1961, Hamel 1992, Schlossberg and King 2007)

cover type within our study site, thus reducing potential observer bias. Our protocol of counting birds within a 100-m radius is supported by previous research demonstrating that data collected using a count radius of 100-m produces well-performing models of habitat use by wintering birds within our study site (McClure et al. 2012). We also recorded weather variables hypothesized to influence detection.

Surveys of Vegetation.—We measured vegetation structure within 16-m radius plots centered on bird survey points (Anderson and Shugart 1974, La Sorte et al. 2009). We quantified canopy cover by taking densitometer readings at 4-m intervals along 16-m transects in all cardinal directions from the center (Robinson 1947). We quantified depth of leaf litter at the ends of the transects (Ortega and Capen 1999). We measured the density of vegetation using a modified, 12-m Robel pole placed in the center of the plot (Mills et al. 1991). The pole was painted with alternating 10-cm black-and-white stripes. We quantified density of vegetation at 0–0.6 m, 0.6–4.6 m, 4.6–7.6 m, and 7.6–12 m (MacArthur and MacArthur 1961) by calculating the percentage of stripes obscured by vegetation within each interval. Observers recorded pole measurements from the edge of the plot in all cardinal directions. We also measured diameter at breast height (dbh) of all trees >10-cm dbh within the plots during 2008–2009. Plots were only surveyed once for dbh measurements, because we assumed they would remain unchanged between seasons. Diameter at breast height measurements were taken during 2008–2009. All other vegetation measurements were conducted concurrent with bird surveys and separate vegetation measures were collected during breeding and wintering seasons. Because of logistical constraints we were only able to survey vegetation and birds at 89 sites during both summer and winter.

Land Cover.—We quantified percentage of each cover-type within 100-m radius buffers drawn with ArcGIS (ESRI 2008) using the Alabama Gap Analysis Program Land Cover Map (Kleiner et al. 2007). We combined similar landcover classes following McClure et al. (2011). For instance, pixels classified as pasture and row crop were combined to form a broader agricultural classification and, low-intensity, medium-intensity, high-intensity developed areas and developed open spaces were combined to form a broad habitat class that we termed ‘‘developed.’’ Successional scrub subclassifica-

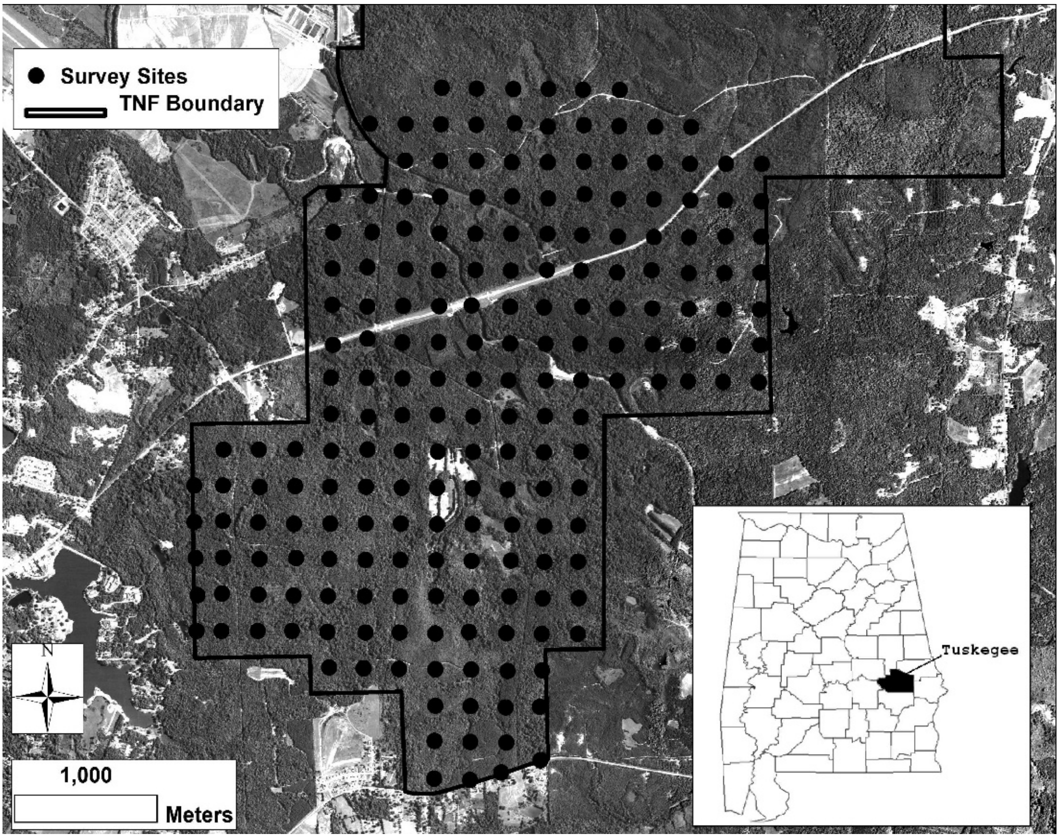

FIG. 1. Map of our study site within Tuskegee National Forest, Alabama. Only sites which were surveyed for birds in both summer and winter 2008–2009 are shown.

tions were combined to form a broad, scrub classification; floodplain and mesic slope forests were combined to form a hardwood classification; and, subclassifications of pine forests were combined to form pine and natural pine (which excludes plantations) classifications; (Table 2 in McClure et al. 2011). We also quantified the percentage of canopy cover within 100-m radius buffers using the National Landcover Database Tree Canopy Cover Map (Homer et al. 2004b). Both of the maps that we used to derive cover-type (Homer et al. 2004a, Kleiner et al. 2007) have a resolution of a 30-m pixel. Within our study site, successional habitats are found mostly within the land cover classifications of agriculture, successional scrub-other—which consists of wildlife openings—and, floodplain forest and water—which contain or surround beaver meadows. The only landcover classification indicating regeneration habitats is successional scrub-clearcut.

Analysis.—We restricted our analysis to species that were classified as successional or scrub breeders by Sauer et al. (2011) and that were detected during both summer and winter surveys. We used summer vegetation measurements for analysis of breeding habitat use, and winter vegetation measurements for analysis of habitat use during winter.

We used dynamic occupancy models to examine habitat use during both summer and winter (MacKenzie et al. 2003). Dynamic occupancy models allow calculation of initial occupancy (Ψ) and detection (p) as well as probability of colonization (γ) and vacancy (ε) between sampling occasions (MacKenzie et al. 2003).

We built occupancy models in a stepwise fashion—modeling one parameter at a time—in order to limit the number of models built (Olson et al. 2005). We first modeled summer detection, then winter detection. Next we modeled Ψ, γ, and

TABLE 2. Naïve breeding (ψ_b) and winter occupancy (ψ_w), estimated breeding ($\widehat{\Psi}b$) and derived winter ($\widehat{\Psi}w$) occupancy, and rate of turnover (τ) of resident shrub-breeding species within Tuskegee National Forest, 2008–2009. Breeding data were collected between 15 May and 30 June 2008; winter data were collected between 28 January and 28 February 2009. Standard errors are in parentheses.

Common name	Scientific name	Ψ_b	ψ_w	$\widehat{\Psi}b$	$\widehat{\Psi}b$	τ
Northern Cardinal	*Cardinalis cardinalis*	0.97	0.35	0.97 (0.02)	0.52 (0.10)	0.02 (0.03)
Carolina Wren	*Thryothorus ludovicianus*	0.73	0.53	0.78 (0.06)	0.67 (0.07)	0.14 (0.06)
Eastern Towhee	*Pipilo erythrophthalmus*	0.29	0.43	0.32 (0.06)	0.55 (0.08)	0.59 (0.08)
Brown Thrasher	*Toxostoma rufum*	0.03	0.06	0.03 (0.01)	0.12 (0.07)	1.0 (<0.01)

ε at the land cover scale, then the vegetation scale. At each step, we incorporated the most supported models from previous steps into subsequent models. Because we used consecutive sampling occasions, temporal autocorrelation between occasions was likely. To control for the possibility of temporal autocorrelation we also included a covariate indicating whether the species was detected in the previous occasion (t-1, Betts et al. 2008) in all models of detection. Because bird song rate is known to vary with stage of breeding (e.g., Wilson and Bart 1985), detection is likely to vary between seasons. We therefore also included a covariate indicating the season during which each observation was made in all models of detection. Although all of our observers were trained, professional ornithologists, it is possible that they differed in their ability to detect and identify birds. We therefore tested for observer effects by including dummy-coded covariates for observers. To simplify observer models and preserve degrees of freedom, if several observers had similar probabilities, they were lumped together and the model was re-run with the simpler structure. This protocol allowed us to test and control for effects of different detection abilities among observers. Models of detection were built using each covariate hypothesized to affect detection, separately. For each species, we ranked and compared all models of detection using Akaike's Information Criterion, (AIC, Burnham and Anderson 2002). We then incorporated the detection model with the lowest AIC into all models of Ψ.

When modeling Ψ, γ, and ε, we tested models containing combinations of covariates which we hypothesized *a priori* based on previously published studies would explain bird occupancy at both the vegetation and cover-type levels (Table 1). Models within ΔAIC < 2 are considered to be the best models (Burnham and Anderson 2002) Therefore, for Ψ, γ, and ε at both the vegetation and cover-type levels, we based inference on models ΔAIC < 2. Model selection using AIC favors the retention of covariates with 85% confidence intervals that exclude zero (Burnham and Anderson 2002, Arnold 2010), making 85% confidence intervals more consistent than 95% confidence intervals with model selection based on AIC (Arnold 2010). We therefore considered covariates with 85% confidence intervals that excluded zero and within models ΔAIC < 2 which were ranked higher than the null as useful for inference. All data were analyzed using the package unmarked (Fiske and Chandler 2011) in R (R Development Core Team 2011). To avoid convergence problems inherent with small sample sizes and still obtain a biologically relevant sample, we only modeled parameters for which we had at least 10 observations. For instance, we only modeled colonization if at least 10 sites which were observed as occupied during winter were also observed as unoccupied during summer. Unmodeled parameters were held constant at the intercept.

We also assessed differences in occupancy between summer and winter by using the final model for each species to estimate summer occupancy and derive winter occupancy (MacKenzie et al. 2003, MacKenzie et al. 2006). We further derived estimates of turnover for each species. Regarding this study, turnover is defined as the probability that a site occupied during winter was not occupied the previous summer and is derived using the equation: $\tau = \gamma(1 - \Psi_w)/\Psi_s$ (adapted from Royle and Kéry 2007) where τ is turnover between summer and winter, Ψ_s is summer occupancy, and Ψ_w is winter occupancy. Turnover rates of 1 indicate that no sites occupied during winter were occupied during summer and rates of zero indicate that all sites occupied during winter were occupied during summer (Nichols et al. 1998). Turnover is therefore a measure of the

TABLE 3. The AIC-best model of detection for resident shrub-nesting birds. Values (β [SE]) for each covariate are shown as well as the model weight (w_i) for each model.

	Intercept	t-1	Winter	Date	Winter × Date	Observer	w_i
Northern Cardinal	4.53 (1.02)	1.07 (0.19)	−6.49 (1.27)	−0.03 (0.01)	0.05 (0.02)		0.82
Eastern Towhee	6.23 (2.04)	1.13 (0.28)	−10.63 (2.22)	−0.04 (0.01)	0.13 (0.03)		1
Brown Thrasher	−0.22 (0.44)	1.13 (0.63)	−2.01 (0.67)				1
Carolina Wren	−0.3 (0.16)	1.49 (0.21)	−0.77 (0.23)			−1.05 (0.26)	0.91

difference in the spatial pattern of occupancy between summer and winter (Nichols et al. 1998). We estimated standard errors of summer and winter occupancy as well as turnover using a parametric bootstrap with 1,000 iterations. Results are presented as coefficient values ± SE.

RESULTS

We detected Eastern Towhees and Carolina Wrens at enough sites to analyze use of both vegetation structure and cover-type during both summer and winter (Table 2). During summer, we detected Northern Cardinals at nearly every site (Table 2). Therefore, there was not enough variation in the data on Northern Cardinals for us to model summer occupancy or colonization. Brown Thrashers were not detected on enough sites at which vegetation surveys were conducted for us to analyze associations of habitat use with measurements of vegetation. We therefore analyzed use of habitat by Brown Thrashers using cover-type measurements at all sites that were surveyed for birds in both summer and winter. The only parameter for which we had enough data for Brown Thrashers was colonization (11 sites). Occupancy of Northern Cardinals and Carolina Wrens decreased between summer and winter, and occupancy of Brown Thrashers and Eastern Towhees increased (Table 2). Rates of turnover mirrored occupancy estimates with Northern Cardinals and Carolina Wrens having lower rates of turnover than Brown Thrashers and Eastern Towhees (Table 2).

The best model of detection for each species received most of the model weight (Table 3) of useful models. Detection of all species was affected significantly by season. Brown Thrashers and Carolina Wrens were both less detectable during winter, and one observer was less likely to detect Carolina Wrens. The interaction between the factor indicating winter surveys and date was useful for inference for both Northern Cardinals and Eastern Towhees indicating that detection of both species decreased over the summer and increased during the winter.

Every species was associated with certain types of cover. Covariates considered to be useful for inference indicated that Northern Cardinals were less likely to abandon sites surrounded by development (Fig. 1, Table 4, −7.41 ± 3.91). Habitat use of Eastern Towhees was characterized by an avoidance of hardwoods with summer occupancy negatively correlated with both floodplain (Fig. 1, Table 4, −1.44 ± 0.59) and hardwood forest (Fig. 1, Table 4, −1.59 ± 0.64). Colonization by Eastern Towhees was also negatively correlated with both floodplain (Fig. 1, Table 4, −1.47 ± 0.75) and hardwood forest (Fig. 1, Table 4, −2.06 ± 0.92). Carolina Wrens were more likely to occupy sites within floodplain forest during summer (Fig. 1, Table 4, 3.04 ± 2.09). Brown Thrashers were likely to colonize areas characterized as successional scrub-other—which consist mostly of wildlife openings in our study site—in the winter (Fig. 1, Table 4, 6.59 ± 3.16).

Associations with vegetational structure during both seasons reveal further habitat selection once birds settle within a cover-type. Carolina Wrens were more likely to abandon sites with dense vegetation >7.6 m tall during winter (Fig. 2, Table 4, 5.56 ± 2.58), and less likely to abandon sites with dense ground cover (Fig. 2, Table 4, 5.69 ± 2.99) and high basal area (Fig. 2, Table 4, 1.35 ± 0.83). Ground cover was important for site use of Eastern Towhees during both summer and winter with summer occupancy being negatively associated with ground cover (Fig. 2, Table 4, −2.81 ± 1.84) and dense vegetation >7.6 m tall (Fig. 2, Table 4, −2.81 ± 1.84). Eastern Towhees were more likely to colonize sites with dense ground cover (Fig. 2, Table 4, 23.91 ± 12.08) and less likely to colonize sites with deep leaf litter (Fig. 2, Table 4, −17.75 ± 11.06). Northern Cardinals were less likely to abandon sites with dense winter shrub density (Fig. 2, Table 4, −2.3

TABLE 4. Number of parameters (k) Akaike's Information Criterion value (AIC), difference in AIC from the top ranked model (ΔAIC) and model weight (w_i) for models of summer occupancy (Ψ), and colonization (γ) and local extinction (ε) of resident shrub-nesting birds in Tuskegee National Forest, Alabama. Only models within <2ΔAIC are shown.

Northern Cardinal				
Cover-type	k	AIC	ΔAIC	w_i
Development	9	950.46	0.00	0.42
Development + Agriculture + Scrub	11	952.06	1.60	0.19
Vegetation				
Grass Layer Density	10	947.36	0.00	0.36
Shrub Density	10	947.40	0.03	0.36
Eastern Towhee				
Ψ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	9	648.92	0.00	0.41
Hardwoods	9	648.93	0.01	0.41
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	13	647.09	0.00	0.29
Basal Area	10	648.86	1.77	0.12
Null	9	648.92	1.83	0.12
γ				
Cover-type	k	AIC	ΔAIC	w_i
Hardwoods	14	643.20	0.00	0.49
Floodplain	14	644.95	1.75	0.21
Vegetation				
Ground Cover + Leaf Litter Depth	16	637.60	0.00	0.82
Cover-type				
Null	16	637.60	0.00	0.33
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	20	629.04	0.00	0.88
Brown Thrasher				
γ				
Cover-type	k	AIC	ΔAIC	w_i
Successional Scrub (Other) + Agriculture	8	250.38	0.00	0.56
Carolina Wren				
Ψ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	8	1011.44	0.00	0.60
Vegetation				
Null	8	1011.44	0.00	0.25
γ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	9	1010.96	0.00	0.22
Natural Pine	9	1011.19	0.23	0.19

TABLE 4. Continued.

Null	8	1011.44	0.48	0.17
Vegetation				
Canopy Cover + Leaf Litter	11	1003.03	0.00	0.54
Canopy Cover	10	1004.05	1.02	0.32
Cover-type				
Null	11	1003.03	0.00	0.26
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	15	990.79	0.00	0.97

± 1.16) and winter ground cover (Fig. 2, Table 4, −1.93 ± 0.94).

DISCUSSION

Our results demonstrate that in habitats in the southeastern US, partially migratory shrub-nesting birds increased occupancy in winter and had higher rates of site turnover between summer and winter than non-migratory shrub-nesting birds. Further, all species showed patterns of differing habitat use between summer and winter and selected habitat at multiple scales. Occupancy of non-migratory Northern Cardinals and Carolina Wrens decreased or remained static between summer and winter, whereas occupancy of partially migratory Brown Thrashers and Eastern Towhees increased. The decreased occupancy of non-migratory species between summer and winter is likely because of high levels of emigration from areas with certain types of cover or vegetation structure within the national forest. For example, Northern Cardinals were less likely to abandon developed sites, and therefore may immigrate into surrounding developed areas after breeding. Although we did not track marked individuals, the observed increase in occupancy of Eastern Towhees and Brown Thrashers between summer and winter is likely because of an influx of migrants, highlighting the importance for managing habitat for wintering shrub-nesting birds.

Rates of turnover further highlight the contrasting site use by birds having different migratory strategies. Site turnover was much greater for partially migratory species. Therefore, within our study site, partially migratory species are more likely to use sites during winter that were not occupied during summer. The observed rates of turnover of partially migratory species are likely because of differences in habitat needs between the breeding and non-breeding periods, or perhaps seasonal changes in resource availability within our study site (e.g., Bilcke 1984, Morrison et al. 1986, Keller and Yahner 2007). A high rate of turnover indicates that sites managed for breeding habitat, or preserved because they contain breeding individuals, are not likely to be used by wintering Brown Thrashers or Eastern Towhees.

Although partially migratory species had higher rates of turnover, all species showed differing patterns of habitat use between summer and winter. For instance, Northern Cardinals and Brown Thrashers were too ubiquitous and too sparse, respectively, to be associated with any particular type of cover during the breeding season. Occupancy of Brown Thrashers was greater during winter and colonization was more likely within wildlife openings. Use of wildlife openings by Brown Thrashers is likely underappreciated because Brown Thrashers do not use these open spaces for breeding. For example, Johnson (2010) did not detect enough Brown Thrashers for analysis during breeding season surveys of wildlife openings within Alabama, and Schlossberg and King (2007) do not list wildlife openings as used by Brown Thrashers in the eastern US. Therefore, the propensity of Brown Thrashers within our study site to colonize wildlife openings during winter highlights the need for a multi-season approach to studies of wildlife-habitat relationships.

Certain aspects of vegetation structure were also associated with changes in habitat use between summer and winter, particularly mea-

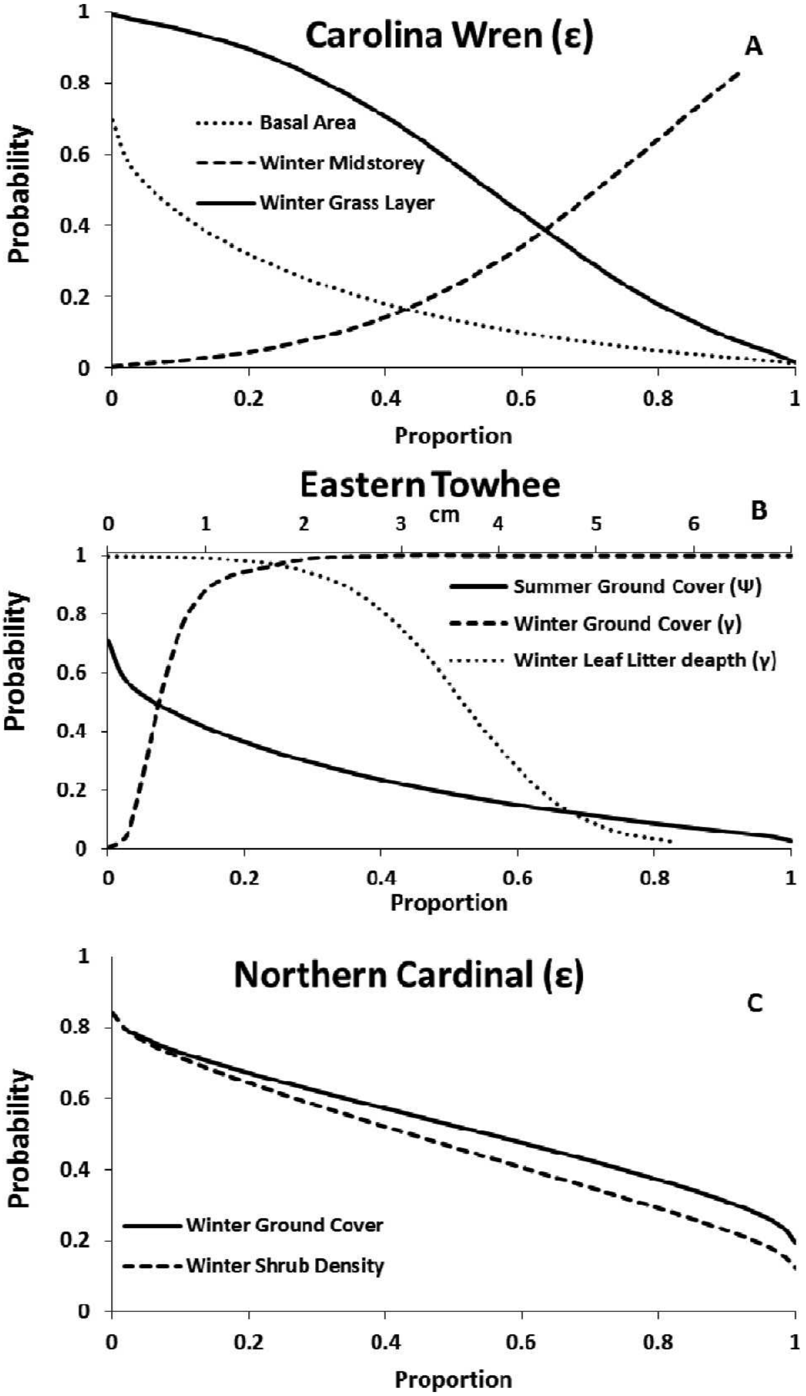

FIG. 2. A) Relationship between probability of local extinction (ε) between summer and winter of Carolina Wrens and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama. B) Relationships of breeding occupancy (Ψ) and winter colonization (γ) and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama. C) Relationship between probability of local extinction (ε) between summer and winter of Carolina Wrens and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama.

sures of vegetation near the ground. Use of the ground layer by a bird community also changed seasonally in Pennsylvania with birds less likely to forage near the ground in the winter (Yahner 1987). Carolina Wrens and Northern Cardinals were less likely to leave sites with dense winter grass layer and ground cover, respectively. The pattern of differing habitat use between seasons is most striking for Eastern Towhees, which are less likely to occupy sites with dense ground cover during summer but more likely to colonize sites with dense ground cover during winter. Also, Eastern Towhees were less likely to colonize sites with a deep layer of leaf litter. The contrasting association of Eastern Towhees and ground cover during summer and winter may be a result of an increasing importance of plant material as food during winter or the need for leaf litter for nesting and foraging during summer (Greenlaw 1996), but more study is needed. Regardless of the mechanism, differing patterns of use of vegetation between seasons further highlight the pitfalls of basing management decisions on a single season.

Our results support not only the importance of multi-season approaches to the studies of shrub-nesting birds but also the importance of the multi-scale approaches suggested by numerous authors (e.g., Wiens et al. 1987, Wiens 1989, McClure et al. 2012). All four species were associated with certain cover-types. For example, use of habitat by Eastern Towhee seems characterized by avoidance of hardwood forests within our study site. Summer occupancy and probability of colonization by Eastern Towhee were negatively associated with floodplain forests and hardwood forests, respectively. Past studies showed that Eastern Towhees avoid hardwood forests (Rolek 2009) and prefer dry areas (Schlossberg and King 2007) and pine forests with scattered shrubby understory (Engstrom et al. 1984, Allen et al. 2006). Avoidance of hardwoods by Eastern Towhees within our site may be because of a preference for drier habitat, because hardwoods within our study site consist of floodplain and mesic slope forest. Therefore, Eastern Towhees first select sites that are not within hardwood forests, then selects sites with certain aspects of ground-level vegetation, depending on the season.

Our study underscores the importance of season and spatial scale when attempting to draw inference about the habitat associations of birds. All species analyzed in this study showed different habitat associations across seasons. For the management of such resident species, different types of cover or structures of vegetation may need to be maintained within a region. Information regarding vegetation structure and cover-type were important for all of our focal species suggesting that not only should certain types of cover be created and maintained but so too should certain structural aspects of vegetation within each cover-type. Species may also differ in use of habitat across their range (Collins 1983, Shy 1984, Graves 2002); this may hamper effective management actions if conservation strategies are based on research from other regions. Therefore, analysis of use of habitat at other sites across seasons and multiple scales should be a research priority.

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