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Dynamic versus static occupancy: How stable are habitat associations through a breeding season?

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Abstract. Most studies of habitat use by animals assume that there is little movement by individuals once they have settled. This assumption of static occupancy is especially true in studies of birds, even though many bird species are known to abandon failed nest sites in search of better habitat or to move up a habitat gradient as the season proceeds. If birds move into different habitats as the season progresses, studies assuming static use of habitat may provide misleading or incomplete inference into habitat use. We tested the hypothesis that birds use different habitats as the breeding season progresses by analyzing point counts conducted early and late in the breeding season within Tuskegee National Forest, AL. For 15 species of conservation concern, we compared models that assumed static occupancy with models that estimated apparent movement between early and late-season surveys. Models that estimated movement outcompeted static models for every species. Furthermore, patterns of movement provided inference that would not have been gained through a static modeling approach, with species moving into habitats traditionally known to be of high quality, and moving out of those assumed to be of poor quality. Our results suggest that studies of habitat use would benefit from estimating movement within a season.

Key words: Alabama; bird; birds of concern; breeding biology; Gulf Coastal Plain; habitat use; occupancy modeling.

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INTRODUCTION

Migratory animals are characterized by movement, and ecologists generally recognize four "seasons" in the life cycles of such migrants: breeding season, season of movement away from the breeding area, non-breeding season, and season of movement toward the breeding area. Studies of habitat associations are typically made within one of these seasons, and a critical assumption of most such studies is that there is little movement by individuals once they settle in a habitat in either the breeding or non-breeding seasons (Betts et al. 2008, Johnson 2009). Accordingly, most studies pool surveys across a breeding or non-breeding season, making the implicit assumption that use of a habitat is static throughout a season (e.g., Reeder et al. 2005, Johnson et al. 2008, McClure et al. 2011*b*). Indeed, commonly used statistical models of habitat use, such as single-season occupancy models (MacKenzie et al. 2002, MacKenzie et al. 2006), make the explicit assumption that a species will neither colonize nor vacate a site during the survey period.

This assumption of constant habitat use is prevalent in studies of breeding birds. Surveys for birds during the breeding season in the north temperate regions are typically conducted in May and June when birds are most vocal and hence most detectable (Ralph et al. 1995). The breeding season for most migratory birds in the north temperate region, however, extends through July. Data collected during the early breeding season, therefore, may not be representative of the entire breeding season. If the assumption of static use of habitat is violated, estimates of habitat use may be biased (MacKenzie et al. 2002, MacKenzie et al. 2006) and important information may be lost.

There are many situations in which an assumption of static use of habitat across a breeding season is known to be violated, especially in the case of breeding birds. For instance, birds often switch sites between nesting attempts in search of better habitat (Krebs 1971, Hoover 2003, Betts et al. 2008). Even territorial species will move their territories after failed nesting attempts (Beletsky and Gordon 1991, Haas 1998, Hoover 2003). For instance, American Robins (*Turdus migratorius*) renest farther from previously unsuccessful nesting sites than successful sites within the same season (Haas 1998), and Black Kites (*Milvus migrans*) often abandon unsuccessful nest sites and attempt to renest in better habitat (Forero et al. 1999). Such emigration from a given patch or type of habitat by many individuals during the breeding season may lead to population-wide shifts in habitat occupancy within a season. Further, even if emigration occurs between sites within the same habitat-type, the assumption of a closed population may still be violated, biasing estimates of both occupancy and abundance (MacKenzie et al. 2002, Rota et al. 2009, Chandler et al. 2011).

If information regarding quality of habitat is not immediately available when animals first begin to settle (Stamps et al. 2005), many individuals may shift locations as they gain knowledge of available habitats through experience (Haas 1998, Hoover 2003) or social information (reviewed in Nocera and Betts 2010). Inexperienced individuals, in particular, may initially settle in sub-optimal habitats and then adjust as they learn a local area (Betts et al. 2008). For instance, Betts et al. (2008) showed that some Black-throated blue Warblers (*Dendroica caerulescens*) colonize previously vacant sites of higher quality as the breeding season progresses and quality of habitat becomes apparent. Studies conducted before inexperienced individuals are able to move up a habitat-gradient, or that fail to consider such within-season movement, may place undue emphasis on lower quality habitats settled by naïve individuals.

We tested the assumption that birds are static in their association with habitat within a breeding season by analyzing data from early- and late-season point counts taken in a study area centered on Tuskegee National Forest, AL. We focused on 15 bird species of conservation priority. We use dynamic occupancy models (MacKenzie et al. 2003), which control for imperfect detection while investigating occupancy as well as immigration to and emigration from sites (hereafter: colonization and vacancy, respectively, Betts et al. 2008). Because we analyzed data from point counts and not marked individuals we did not directly measure movement of individuals but instead estimated "apparent movement" (Betts et al. 2008). This method has the benefit of estimating movement without having to trap and mark individuals. We hypothesized that as the breeding season progressed birds would move into different habitat. Therefore, we predicted that our focal species would show changes in use of cover types in late-season compared to early-season surveys.

METHODS

Study site

Tuskegee National Forest is located within the East Gulf Coastal Plain physiographic region in Macon County, AL. Our study site was a 3-km-radius circle, centered on the southwest corner of Tuskegee National Forest. We established 372 bird survey locations, each separated by roughly 250 m. Survey locations were located mostly within the national forest, although some were also located on private lands to which we were allowed access.

Bird surveys

Birds were surveyed at each point count location by a single trained observer using 5-min counts (Ralph et al. 1995). Point counts were conducted under a removal protocol (Farnsworth et al. 2002). During each point count the observer recorded all birds seen or heard within a 100-m radius. The observer recorded the minute in which each individual was detected. There were two separate rounds of point counts in which each bird count location was surveyed. Points were surveyed from 15 May–15 June 2005 during the first round and from 15 June–15 July 2005 during the second round. Our survey dates were chosen with respect to "safe dates"—dates during which bird counters are unlikely to encounter migrating individuals—for birds within the state of Alabama (Haggerty 2009). The early safe date is the date when the last spring migrants are assumed to have moved through, and summer residents begin establishing territories. The late safe date corresponds to assumed territory abandonment at the end the summer. Working within safe dates insured that few migrants would be encountered during either round of our bird surveys. On average, the length of time between the first and second surveys at each site was 24 days. All point counts were conducted between 0530 and 1100 local time.

Habitat data

We used the Alabama Gap Land Cover Map (Kleiner et al. 2007) within ArcGIS (ESRI 2008) to quantify the percentage of pixels of each land cover classification within 100 m buffers around each bird survey location. When it was biologically appropriate, we combined similar land cover classifications to form broader classifications in accordance with McClure et al. (2011*b*). For instance, pasture/hay and row crop were combined to form a broader, agricultural classification. Subclassifications of pine forests were combined to form pine and natural pine (which excludes plantations) classifications; successional scrub subclassifications were combined to form a broad, scrub classification; low-intensity, medium-intensity, high-intensity developed areas and developed open spaces were combined to form a broad habitat class that we termed "developed"; and, floodplain and mesic slope forests were combined to form a hardwood classification. We also quantified the percent canopy cover within 100-m buffers of each survey location using the National Landcover Database Tree Canopy Cover Map (Homer et al. 2004) which was developed using data collected in 2001. All of the maps that we used to derive habitat characteristics have a 30-m pixel resolution meaning that roughly 35 pixels fell within 100-m buffers surrounding each bird survey location.

Analysis

We first converted our point count data into presence-absence data. Occupancy models can analyze data in which not all sites were sampled over all occasions (MacKenzie et al. 2003, MacKenzie 2006). Therefore occupancy models can be used to analyze data collected under a removal protocol (see page 102 in MacKenzie et al. 2006). Each detection history recorded the minute in which the species was first detected at each point. We did not know whether the species was detected in subsequent occasions, therefore all occasions following the one in which the species was first detected were recorded as "–" which signifies a missing occasion. For example, if a species was detected during the third minute of a point count, the detection history would be "001– –".

We analyzed data using the multi-season occupancy function in program PRESENCE (Hines 2006) which uses dynamic occupancy models (MacKenzie et al. 2003). These models assume population closure between secondary sampling occasions (i.e., each minute of the 5-min point counts) but allows for movement between primary sampling occasions (i.e., each round of point counts). Dynamic occupancy models estimate initial occupancy (ψ), detection (p), colonization (γ), and vacancy (ε), where ψ is the probability that a species is present at a site, p is the probability that the species is detected when present, γ is the probability that a species immigrates into a site that was vacant in the previous period, and ε is the probability that a species will emigrate from a site that was occupied in the previous period (MacKenzie et al. 2003).

We examined use of habitat by species classified as "overall priority", "physiographic area priority", or "global priority" by Partners in Flight (Woodrey et al. 1998), and were detected during at least 10 surveys of one of the survey rounds. We used a hierarchical modeling approach in order to limit the amount of models built (Olson et al. 2005, Betts et al. 2008). We first modeled detection while holding other parameters constant across all sites. In general, the rate at which birds sing declines toward the end of the

Table 1. Variables hypothesized to affect occupancy patterns of Swainson's Warbler, Brown-headed Nuthatch, Prothonotary Warbler, Prairie Warbler, Kentucky Warbler, Orchard Oriole, Yellow-billed Cuckoo, Chimney Swift, Eastern-wood Pewee, and Purple Martin. Ones indicate that a covariate was considered for model building and hypothesized to affect initial occupancy, settlement, and vacancy. Blank spaces indicate that a variable was not considered for model building. Species abbreviations are presented in Table 3.

Variable	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA
Canopy cover	1	1	1	1	1	1	1	1	1	1
Canopy cover ^{2}				1		1				
Pine forest	1	1	1	1	1	1	1	1	1	1
Natural pine forest		1		1					1	
Hardwood forest	1	1	1	1	1	1	1	1	1	1
Floodplain forest	1		1		1		1			
Mesic slope forest							1			
Development	1	1	1	1	1	1	1	1	1	1
Developed open space						1		1		1
Mixed pine-hardwood forest		1			1	1	1		1	
Scrub	1	1	1	1	1	1	1	1	1	1
Agriculture	1	1	1	1	1	1	1	1	1	1
Clearcut				1						
Pasture						1		1		1
Row crop								1		1
Water			1					1		1

breeding season, making species less detectable during late-summer surveys (e.g., Slagsvold 1977, Best 1981, McClure et al. 2011*a*). This seasonal change in detection could bias results if not controlled for statistically. Therefore we tested detection models which estimated the two rounds both together and separately. We also built models which included the date and time of each observation. We ranked and compared models using Akaike's information criterion corrected for small sample size (AIC_c, Hurvich and Tsai 1989) and included the model with the lowest AIC_c value in all subsequent models.

Table 2. Variables hypothesized to affect occupancy patterns of Carolina Chickadee, Field Sparrow, Eastern Kingbird, Wood Thrush, and Louisiana Waterthrush. Ones indicate that a covariate was considered for model building and hypothesized to affect initial occupancy, settlement, and vacancy. Blank spaces indicate that a variable was not considered for model building. Species abbreviations are presented in Table 3.

Variable	CACH	FISP	EAKI	WOTH	LOWA
Canopy cover	1	1	1	1	1
Canopy cover ^{2}		1			
Pine forest	1	1	1	1	1
Natural pine forest	1				
Hardwood forest	1	1	1	1	1
Floodplain forest				1	1
Mesic slope forest				1	1
Development	1	1	1	1	1
Developed open space		1	1		
Mixed pine-hardwood forest	1			1	
Scrub	1	1	1	1	1
Agriculture	1	1	1	1	1
Clearcut		1			
Pasture		1	1		
Row crop		1	1		
Water					1

Next, we modeled occupancy within the first survey period (i.e., initial occupancy) using covariates that we considered a priori (Tables 1 and 2) to be biologically relevant to each species. Because did not know a priori which combination of covariates would best describe use of habitat, we used a manual, forward stepwise selection method in which we built models containing each covariate separately, and then sequentially added covariates to the model with the lowest AIC_c value until addition of covariates no longer resulted in a reduction of AIC_c (King et al. 2009*a*). We then incorporated the final model of initial occupancy into all subsequent models. We modeled settlement and vacancy using the same procedure described above for initial occupancy, and incorporated the final settlement model into all subsequent models of vacancy. Finally, we tested the hypothesis that birds showed movement between habitats within the breeding season by building a single season model that represents the hypothesis of static use of habitat throughout the sampling period (Betts et al. 2008). This single season model contained

Table 3. Common name, Latin name, code, naïve early (15 May–15 June, ψ_e) and late (16 June–15 July, ψ_l) breeding season occupancy, and estimated early (Ψ_e) and late (Ψ_l) breeding season occupancy (±SE) for bird species of conservation concern within Tuskegee National Forest, AL 2005.

Common name	Latin name	Code	ψ_e	ψ_l	$\hat{\Psi}_e$	$\hat{\Psi}_l$
Brown-headed Nuthatch	*Sitta pusilla*	BHNU	0.03	0.02	0.04 (0.02)	0.03 (0.02)
Carolina Chickadee	*Poecile carolinensis*	CACH	0.23	0.16	0.24 (0.04)	0.17 (0.03)
Chimney Swift	*Chaetura pelagica*	CHSW	0.07	0.05	0.13 (0.06)	0.09 (0.04)
Eastern Kingbird	*Tyrannus tyrannus*	EAKI	0.04	0.03	0.05 (0.01)	0.04 (0.02)
Eastern Wood-Pewee	*Contopus virens*	EAWP	0.15	0.12	0.15 (0.03)	0.13 (0.03)
Field Sparrow	*Spizella pusilla*	FISP	0.05	0.02	0.05 (0.01)	0.09 (0.02)
Kentucky Warbler	*Oporornis formosus*	KEWA	0.16	0.17	0.16 (0.02)	0.19 (0.03)
Louisiana Waterthrush	*Seiurus motacilla*	LOWA	0.06	0.05	0.15 (0.03)	0.14 (0.04)
Orchard Oriole	*Icterus spurius*	OROR	0.08	0.03	0.08 (0.02)	0.03 (0.01)
Prairie Warbler	*Dendroica discolor*	PRAW	0.13	0.08	0.13 (0.03)	0.12 (0.03)
Prothonotary Warbler	*Protonotaria citrea*	PROW	0.03	0.02	0.03 (0.01)	0.05 (0.02)
Purple Martin	*Progne subis*	PUMA	0.05	0.08	0.08 (0.02)	0.08 (0.02)
Swainson's Warbler	*Limnothlypis swainsonii*	SWWA	0.08	0.09	0.09 (0.02)	0.11 (0.03)
Wood Thrush	*Hylocichla mustelina*	WOTH	0.11	0.09	0.15 (0.03)	0.13 (0.04)
Yellow-billed Cuckoo	*Coccyzus americanus*	YBCU	0.30	0.22	0.44 (0.07)	0.32 (0.06)

the same covariates for initial occupancy and detection that were present in the final multi-season model, but did not contain parameters for vacancy or colonization. Model selection based on AIC_c favors the retention of covariates with 85% confidence intervals that exclude zero (Burnham and Anderson 2002, Arnold 2010), making 85% confidence intervals more appropriate than 95% under an AIC_c framework (Arnold 2010). We therefore considered covariates with 85% confidence intervals as useful for inference. We present results as the coefficient value ± SE, see Table 3 for scientific names of focal species.

RESULTS

We detected 15 species of conservation priority on enough sites for analysis (Table 3). Several species showed differing rates of detection between the early and late breeding season. Detection of Brown-headed Nuthatch was negatively associated with date (−8.55 ± 3.61). Prothonotary Warbler was more detectable in the early breeding season (1.09 ± 0.59) than the late breeding season (−0.26 ± 0.63), as was Prairie Warbler (early = 0.21 ± 0.24, late = −3.41 ± 0.58) although detection of Prairie Warbler was positively associated with date during the late breeding season (18.61 ± 3.16). Orchard Oriole was more detectable in the late breeding (1.17± 0.58) season than the early breeding season (−1.79 ± 0.76) and detection was correlated with date during the late breeding season (10.53 ± 4.11). Detection of Eastern Kingbird (9.62 ± 4.80) and Eastern Wood-pewee (5.28 ± 1.66) increased with date. Time-of-day affected the detection of Field Sparrow (6.34 ± 3.08), Carolina Chickadee (−3.10 ± 1.30), Kentucky Warbler (−4.61 ± 1.32), Louisiana Waterthrush (−7.66 ± 1.55), and Wood Thrush (−7.21 ± 1.47). Because we were able to estimate and account for detectability in each sampling period, changes in the detectability of various species between sampling periods could not have accounted for the changes in species occupancy reported in this study.

The dynamic occupancy model outperformed the single season model for every focal species (Table 4). Canopy cover described the initial occupancy of seven species analyzed (Fig. 1) with Brown-headed Nuthatch (−5.41 ± 2.19), Eastern Wood-pewee (−2.55 ± 1.55), Prairie Warbler (−2.59 ± 1.49), Orchard Oriole (Canopy = 8.46 ± 4.25, $\text{Canopy}^2 = -11.18 \pm 3.37$), and Eastern Kingbird (−7.7 ± 1.52) negatively associated with canopy cover (Fig. 1). Carolina Chickadee (1.51 ± 0.71) and Kentucky Warbler (5.21 ± 1.37) were positively associated with canopy cover (Fig. 1). Swainson's Warbler (1.01 ± 0.34), Prothonotary Warbler (2.94 ± 0.69), and Yellow-billed Cuckoo (0.97 ± 0.33) were associated with floodplain forest (Fig. 1). Initial occupancies of Prairie Warbler (−5.77 ± 1.72), Eastern Wood-pewee (−6.54 ± 2.33), and Brown-headed Nuthatch (−4.72 ± 2.15) were negatively and Chimney Swift (2.16 ± 1.26) positively associated with

Table 4. Akaike's Information Criterion value corrected for small sample size (AIC_c), the difference in AIC_c between the model with the lowest AIC_c and a given model (ΔAIC_c), and the Akaike weights (w_i) for models either assuming static occupancy during the breeding season (Static) and models that estimate settlement and vacancy of sites during the breeding season (Dynamic). Models were tested for 15 species of conservation priority within Tuskegee National Forest, AL 15 May–15 July 2005. Species codes are presented in Table 3.

Species	Model	AIC_c	ΔAIC_c	w_i
BHNU	Dynamic	101.12	0	1
	Static	214.43	13.33	0
CACH	Dynamic	1070.54	0	1
	Static	1165.69	95.15	0
CHSW	Dynamic	429.85	0	1
	Static	440.27	10.42	0
EAKI	Dynamic	210.46	0	1
	Static	219.19	8.73	0
EAWP	Dynamic	727.8	0	1
	Static	760.65	32.85	0
FISP	Dynamic	216.62	0	0.82
	Static	219.65	3.03	0.18
KEWA	Dynamic	805.38	0	1
	Static	853.88	48.5	0
LOWA	Dynamic	644.86	0	1
	Static	663.91	19.05	0
OROR	Dynamic	267.73	0	1
	Static	301.94	34.21	0
PRAW	Dynamic	500.69	0	1
	Static	525.94	25.25	0
PROW	Dynamic	160.25	0	0.93
	Static	165.54	5.29	0.07
PUMA	Dynamic	485.32	0	1
	Static	500.01	14.69	0
SWWA	Dynamic	546.18	0	1
	Static	560.94	14.76	0
WOTH	Dynamic	647.85	0	1
	Static	666.57	18.72	0
YBCU	Dynamic	1447.75	0	1
	Static	1461.79	14.04	0

agriculture (Fig. 1). Initial occupancies of Prairie Warbler (2.47 ± 0.7) and Field Sparrow (2.87 ± 0.8) were positively associated with clear cuts and Eastern Wood-pewee (1.88 ± 0.48) was associated with pine forests (Fig. 1). Prairie Warbler was negatively associated with hardwood forests (–2.33 ± 0.65) and Chimney Swifts (3.8 ± 0.83) were positively associated with developed areas (Fig. 1). Carolina Chickadee (–1.92 ± 0.74) and Louisiana Waterthrush (–1.35 ± 0.86) were negatively associated with mixed pine-hardwood forests and scrub areas, respectively (Fig. 1).

Several species showed patterns of colonization over the breeding season. Kentucky Warbler (4.61 ± 2.4), Louisiana Waterthrush (5.89 ± 3.45), and Yellow-billed Cuckoo (2.00 ± 1.33) were more likely to colonize areas with high canopy cover, while Carolina Chickadee (–3.12 ± 1.36) and Orchard Oriole (–7.73 ± 2.05) were less likely to colonize sites with high canopy cover (Fig. 2). Kentucky Warbler (0.73 ± 0.48) and Purple Martin (–1.17 ± 0.58) were likely to colonize sites surrounded by high and low amounts of hardwood forest, respectively (Fig. 2). Eastern Wood-pewee (–3.44 ± 2.33) and Carolina Chickadee (–4.4 ± 1.69) were less likely to colonize sites surrounded by agriculture. Colonization of Brown-headed Nuthatch (3.98 ± 2.02), Field Sparrow (5.54 ± 2.62), and Eastern Kingbird (5.15 ± 1.98) was positively associated with natural pine forests, clearcuts, and developed areas, respectively (Fig. 2). And, colonization of Louisiana Waterthrush was positively associated with water (6.82 ± 2.79; Fig. 2).

Focal species also showed patterns in abandonment of sites. Brown-headed Nuthatch (–8.74 ± 5.51) and Orchard Oriole (–18.81 ± 8.08) were less likely to leave sites that were associated with scrub areas, whereas Prothonotary Warbler was more likely to abandon sites associated with scrub (10.37 ± 6.69; Fig. 3). Vacancy of Swainson's Warbler was positively associated with developed areas (5.57 ± 2.6) and vacancy of Orchard Oriole was negatively associated with developed areas (–10.73 ± 5.16; Fig. 3). Yellow-billed Cuckoo (–0.93 ± 0.48) and Wood Thrush (–1.25 ± 0.81) were less likely to abandon sites within floodplain forest (Fig. 3). Orchard Oriole was less likely to abandon sites associated with hardwood forests (–7.94 ± 3.96), but more likely to abandon sites associated mixed pine-hardwood forests (8.48 ± 5.66; Fig. 3). Field Sparrow was less likely to leave clearcut areas (–4.63 ± 2.55; Fig. 2).

DISCUSSION

We found evidence of apparent re-settlement between the early and late breeding season by all 15 bird species of concern within our study site. Further, all species except the Prairie Warbler showed changes in habitat use as the season progressed. Thus, we were able to reject the assumption that use of habitat is static within the bird community across the breeding season. We

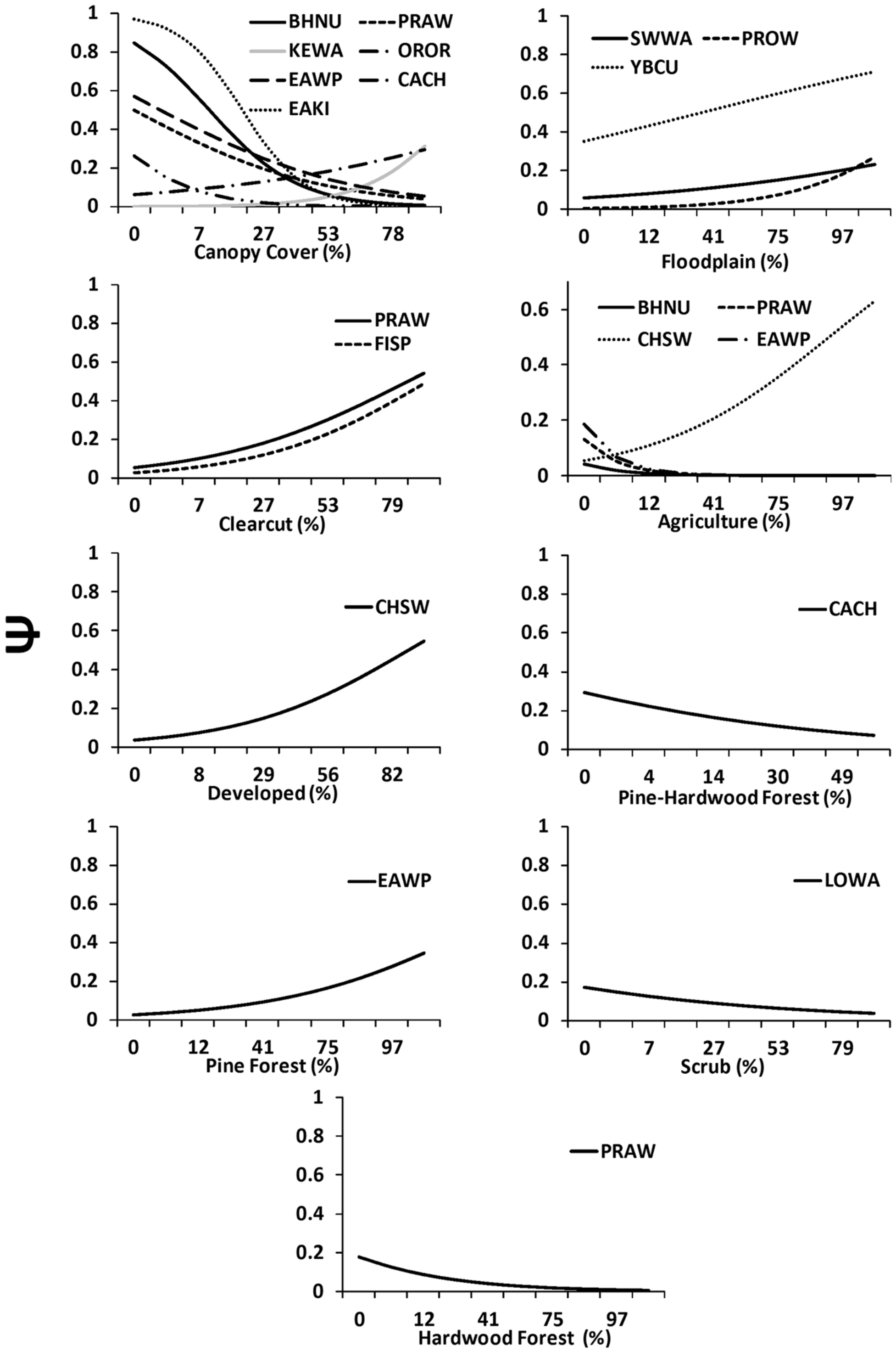

Fig. 1. Relationship between initial occupancy (Ψ) of species of conservation concern and habitat variables within Tuskegee National Forest, AL. from 15 May–15 June 2005. Species codes are presented in Table 3.

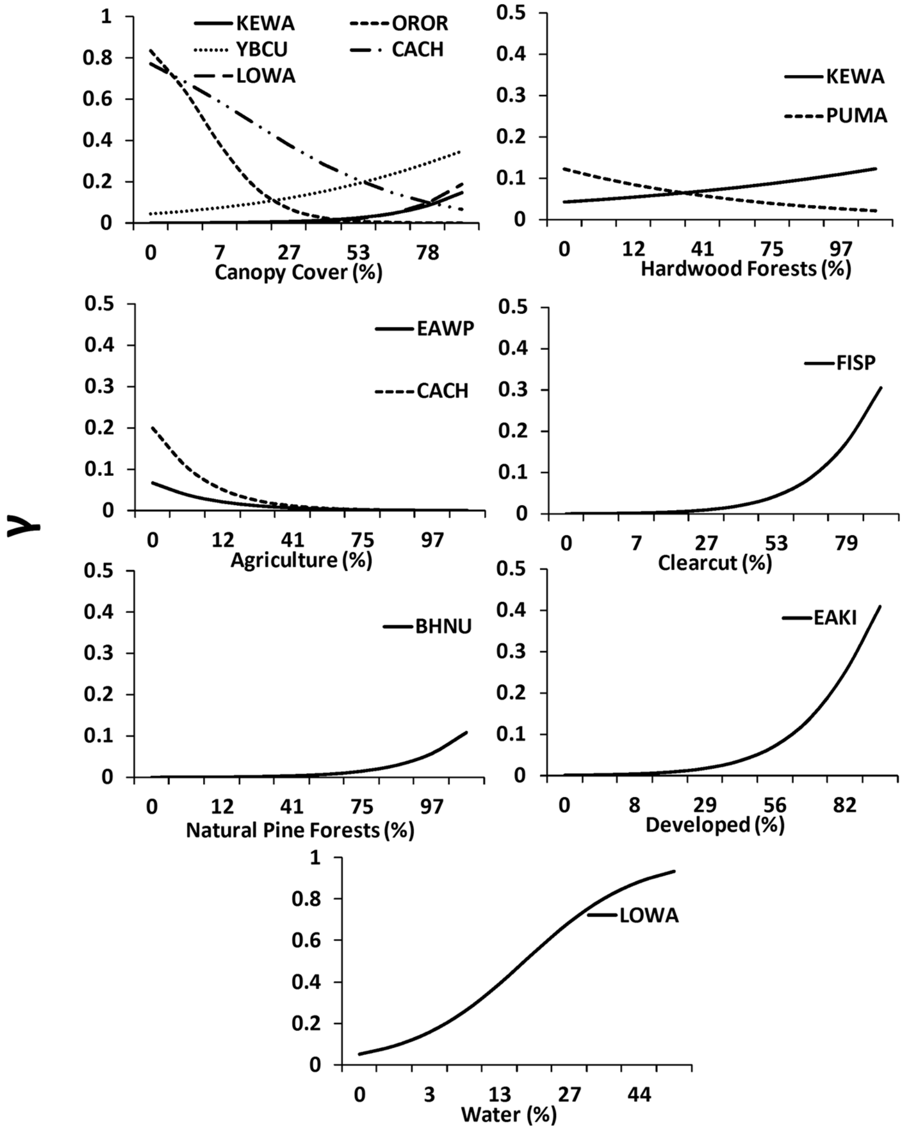

Fig. 2. Relationship between settlement (γ) of species of conservation concern and habitat variables within Tuskegee National Forest, AL. from 15 May–15 June and 16 June–15 July 2005. Species codes are presented in Table 3.

interpret the changes in habitat associations to represent resettlement into or out of survey locations, not necessarily shifts within individual territories. In support of the conclusions that birds resettled rather than just shifting use within established territories, the changes in habitat associations of focal species were in all cases toward what is regarded in the literature as the optimal habitat for that species. Moreover, the magnitude of the model weights of the dynamic models was striking when compared to the single-season models. We are therefore confident that our results reveal resettlement of focal species into new habitats within the breeding season.

By and large, our estimates of initial occupancy support past studies of use of habitat by our focal species. For instance, Field Sparrow and Prairie Warbler breed in early successional habitats (Schlossberg and King 2007, King et al. 2009*b*),

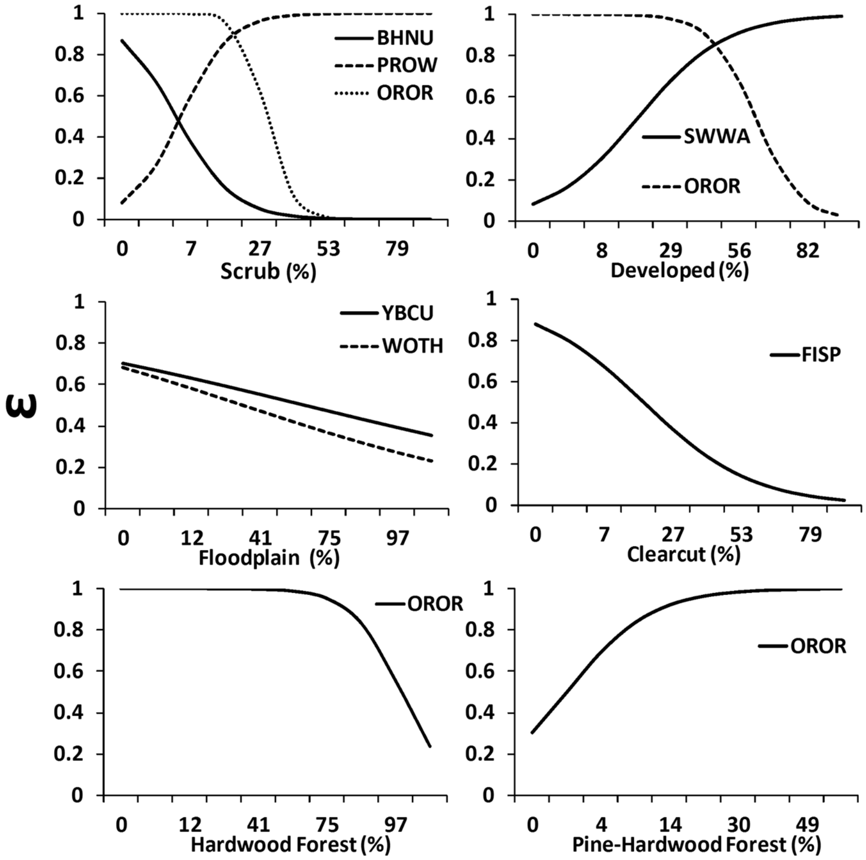

Fig. 3. Relationship between abandonment (ε) of species of conservation concern and habitat variables within Tuskegee National Forest, AL. from 15 May–15 June and 16 June–15 July 2005. Species codes are presented in Table 3.

so it is unsurprising that they are associated with clearcuts during our study. Our observation that Chimney Swift is associated with development and agriculture supports the conventional wisdom that they are birds of residential and other open areas (Hamel 1992). Swainson's Warbler, Prothonotary Warbler, and Yellow-billed Cuckoo are known to breed in wet, deciduous forests (Hamel 1992, Hoover 2003, Bednarz et al. 2005), which are represented by floodplain forests within our study site. Our results also support past studies showing that Eastern Wood-pewee prefers pine forests within the southern portion of the breeding range (Johnston and Odum 1956, Hamel 1992).

Although information regarding occupancy during the early breeding season is informative, further inference is gained by examining patterns of vacancy and settlement. For instance, initial occupancy of Wood Thrushes showed no association with measured habitat variables, but the species was less likely to abandon floodplain forests, suggesting floodplain forests as important breeding habitat for Wood Thrush. Louisiana Waterthrush, a species known to prefer riparian areas (Hamel 1992) was only negatively associated with scrub areas during the first round of point counts. However, Louisiana Waterthrush was more likely to shift into sites containing water as the season progressed, revealing the species' preference for riparian sites. A similar pattern is evident for Brown-headed Nuthatches for which initial occupancy is mostly determined by canopy cover, but for which settlement patterns reveal the species' traditionally recognized preference: natural pine forests (Hamel 1992). Furthermore, although Kentucky Warbler is generally considered a bird of hardwood forests (Hamel 1992, McShea et al. 1995), a previous study using data collected during the early breeding season within our study site found that abundance of Kentucky Warbler was correlated with canopy cover, not with hardwood forests in particular (McClure et al. 2011*b*). Initial occupancy of Kentucky Warbler was also correlated with increased canopy cover in the current study. However, as the breeding season progressed, Kentucky Warbler was likely to colonize areas of hardwood forests—inference that would not be gained if only early-breeding season data were collected or if data from throughout the breeding season were pooled.

Patterns of site abandonment may also reveal potential areas with increased nest failure and abandonment. For example, Swainson's and Prothonotary Warblers are common victims of nest predation and cowbird (*Molothrus ater*) parasitism (Friedmann et al. 1977, Petit 1989, Benson et al. 2010). They frequently abandon nest sites after such failures (Petit 1991, Anich et al. 2010). Because nest predation and parasitism rates are higher in developed and early successional types of cover (e.g., Wilcove 1985, Martin 1993, Tewksbury et al. 2006) abandonment of sites surrounded by scrub and development by Prothonotary and Swainson's Warblers, respectively, may be a response to higher rates of nest failure in or near those cover types. Although estimates of initial occupancy revealed that these species prefer floodplain forests, only after examining movement patterns were we able to discern scrub and developed areas as potentially low quality habitats for these species.

An assumption of static use may also be violated if environmental conditions within an area change over the course of a season. For example, colonies of wintering Monarch Butterflies (*Danaus plexippus*) move down-slope as the season progresses both to avoid high winds and storms, and to be closer to water sources (Calvert and Brower 1986). And, Alpine Newts (*Mesotriton alpestris*) move from temporary to permanent sources of water over the course of the breeding season (Kopecký et al. 2010). Movement toward permanent sources of water may also explain some patterns we observed in our study. Water levels within our study site are lower during late summer (C. J. W. McClure, *personal observation*). Therefore, Prothonotary Warbler may be abandoning sites that are becoming dryer as the season progresses, and Louisiana Waterthrush may be settling in sites near more perennial sources of water that are evident on our habitat maps. A dynamic occupancy approach is valuable if species are responding to changing conditions at a site, because if researchers know which aspects of an area are changing, inference into conditions that enhance quality of habitat can be made. Further, an area that is abandoned early in the breeding season due to changing conditions is likely of less conservation value than one that is productive throughout the season.

If the goal of a habitat use study is to identify breeding habitat, then including late-season data may confound results if the surveys include a large proportion of recently dispersed juveniles. Juveniles of bird species that breed in mature forest often use early successional habitats after fledging (e.g., Anders et al. 1998, Pagen et al. 2000, Vitz et al. 2007) likely because dense vegetation within these habitats provides cover from predators and because of higher fruit abundance in early seral habitats (Anders et al. 1998, Vitz et al. 2007). Adult birds may also move into early successional habitats while undergoing prebasic molt because they are more vulnerable to predation during this period, and because the increased fruit abundance in early successional habitats may provide energy necessary during the demanding molt process (Vega Rivera et al. 1998, Vitz et al. 2007) and energy to add fat needed to fuel migration (Parrish 2000). If individuals are sampled post-breeding, early successional habitats may be incorrectly identified as quality breeding habitat for mature forest breeding species. We believe that our methods largely avoid this problem because point counts sample primarily singing adult males (Blondel et al. 1981), which are likely to be on breeding territories. Our results also show little evidence of mature forest species shifting into early successional habitats during our second sampling period, whereas several species moved into or remained in forests. We therefore believe it is unlikely that the patterns we observed are due to sampling of post-breeding individuals or juveniles.

Without supplementary data, causes of apparent resettlement must remain speculative. Past studies revealing patterns of nest abandonment and resettlement (e.g., Beletsky and Gordon 1991, Haas 1998, Hoover 2003) suggest that apparent moment at a population level may be driven by particular individuals that switch ("switchers") to different cover-types as the breeding season progresses. However, within a population of breeding Song Sparrows (*Melospiza melodia*) in Pennsylvania, 25% of the population was first-year males that began nesting late in the breeding season, whereas only 3.4% of the entire population nested in two separate territories within the same breeding season (Hughes and Hyman 2011). Patterns of apparent movement could therefore be produced by a large portion of the population that begins nesting late in the breeding season at sites that were previously unoccupied ("late breeders"), not switchers. Our results may therefore be a function of the behavior of switchers, late breeders or, most likely, a combination of the two. Future studies may be able to further examine mechanisms behind patterns of apparent settlement and abandonment by examining demography and changes in resource levels throughout the breeding season. Inference may also be strengthened by validating models of settlement and abandonment on independent data.

By conducting surveys during the early and late breeding periods, and using dynamic occupancy models to analyze movement of species we have shown that birds frequently shift habitat use as the breeding season progresses. Inference from studies conducted during the early breeding season may not therefore be applicable later in the season. Further, important inference into use of habitat may be lost if counts are pooled across a season without estimating apparent movement. We advocate use of both temporal and spatial patterns of use of habitat in order to maximize inference into quality of habitat.

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LITERATURE CITED

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.

Anich, N. M., T. J. Benson, J. D. Brown, C. Roa, J. C. Bednarz, R. E. Brown, and J. G. Dickson. 2010. Swainson's Warbler (*Limnothlypis swainsonii*). *In* A. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bednarz, J. C., P. Stiller-Krehel, and B. Cannon. 2005. Distribution and habitat use of Swainson's Warblers in eastern and northern Arkansas. PSW-GTR-191. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Beletsky, L. D. and H. O. Gordon. 1991. Effects of breeding experience and familiarity on site fidelity in female Red-Winged Blackbirds. Ecology 72:787–796.

Benson, T. J., N. M. Anich, J. D. Brown, and J. C. Bednarz. 2010. Habitat and landscape effects on brood parasitism, nest survival, and fledgling production in Swainson's Warblers. Journal of Wildlife Management 74:81–93.

Best, L. B. 1981. Seasonal changes in detection of individual bird species. Studies in Avian Biology 6:252–261.

Betts, M. G., N. L. Rodenhouse, T. S. Sillett, P. J. Doran, and R. T. Holmes. 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. Ecography 31:592–600.

Blondel, J., C. Ferrya, and N. D. B. Fronchot. 1981. Point counts with unlimited distance. Studies in Avian Biology 6:414–420.

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

Calvert, W. H. and L. P. Brower. 1986. The location of monarch butterfly (*Danaus plexippus* L.) overwintering colonies in Mexico in relation to topography and climate. Journal of the Lepidopterists' Society 40:164–187.

Chandler, R. B., J. A. Royle, and D. I. King. 2011. Inference about density and temporary emigration in unmarked populations. Ecology 92:1429–1435.

ESRI. 2008. Arc GIS. Version 9.x. Environmental Systems Research Institute, Redlands, California, USA.

Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probabilities from point-count surveys. Auk 119:414–425.

Forero, M. G., J. A. Donázar, J. Blas, and F. Hiraldo. 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. Ecology 80:1298–1310.

Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contribution to Zoology 235:1–75.

Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115:929–936.

Haggerty, T. M. 2009. Alabama breeding bird atlas 2000-2006 Homepage. Alabama Ornithological Society.

Hamel, P. B. 1992. Land manager's guide to birds of the South. The Nature Conservancy, Southeastern Region, Chapel Hill, North Carolina, USA.

Hines, J. E. 2006. PRESENCE 2.0: Software to estimate patch occupancy and related parameters. USGS - PWRC, Laurel, Maryland, USA.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Development of a 2001 national landcover database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84:416–430.

Hughes, M. and J. Hyman. 2011. Should I stay or should I go now: late establishment and low site fidelity as alternative territorial behaviors. Ethology 117:979–991.

Hurvich, C. M. and C. L. Tsai. 1989. Regression and time-series model selection in small sample sizes. Biometrika 76:297–307.

Johnson, J., J. Gates, and W. Ford. 2008. Distribution and activity of bats at local and landscape scales within a rural–urban gradient. Urban Ecosystems 11:227–242.

Johnson, M. D. 2009. Measuring habitat quality: a review. Condor 109:489–504.

Johnston, D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the piedmont of Georgia. Ecology 37:50–62.

King, D. I., R. B. Chandler, J. M. Collins, W. R. Petersen, and T. E. Lautzenheiser. 2009*a*. Effects of width, edge and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. Biological Conservation 142:2672–2680.

King, D. I., R. B. Chandler, S. Schlossberg, and C. C. Chandler. 2009*b*. Habitat use and nest success of scrub-shrub birds in wildlife and silvicultural openings in western Massachusetts, USA. Forest Ecology and Management 257:421–426.

Kleiner, K. J., et al. 2007. GAP land cover map of ecological systems for the State of Alabama (Provisional). Alabama Gap Analysis Project. Auburn, Alabama, USA. http://www.gap.auburn.edu

Kopecký, O., J. Vojar, and M. Denoël. 2010. Movements of Alpine newts (*Mesotriton alpestris*) between small aquatic habitats (ruts) during the breeding season. Amphibia-Reptilia 31:109–116.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:2–22.

MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. Journal of Wildlife Management 70:367–374.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Burlington, Massachusetts, USA.

Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

McClure, C. J. W., N. D. Burkett-Cadena, R. A. Ligon, and G. E. Hill. 2011*a*. Actual or perceived abundance? Interpreting annual survey data in the face of changing phenologies. Condor 113:490–500.

McClure, C. J. W., L. K. Estep, and G. E. Hill. 2011*b*. Using public land cover data to determine habitat associations of breeding birds in Tuskegee National Forest, Alabama. Southern Journal of Applied Forestry 29:199–209.

McShea, W. J., M. V. McDonald, E. S. Morton, R. Meier, and J. H. Rappole. 1995. Long-term trends in habitat selection by Kentucky Warblers. Auk 112:375–381.

Nocera, J. J. and M. G. Betts. 2010. The role of social information in avian habitat selection. Condor 112:222–224.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management 69:918–932.

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.

Parrish, J. D. 2000. Behavioral, energetic, and conservation implications of foraging plasticity during migration. Pages 53–70. *in* F. R. Moore, editor. Stopover ecology of Nearctic-Neotropical landbird migrants: habitat relations and conservation implications. Studies in Avian Biology 20.

Petit, L. J. 1989. Breeding biology of prothonotary warblers in riverine habitat in Tennessee. Wilson Bulletin 101:51–61.

Petit, L. J. 1991. Adaptive tolerance of cowbird parasitism by prothonotary warblers: A consequence of nest-site limitation? Animal Behaviour 41:425–432.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. PSW-GTR-149. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Reeder, K. F., D. M. Debinski, and B. J. Danielson. 2005. Factors affecting butterfly use of filter strips in Midwestern USA. Agriculture, Ecosystems & Environment 109:40–47.

Rota, C. T., R. J. Fletcher, Jr, R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46:1173–1181.

Schlossberg, S. and D. I. King. 2007. Ecology and management of scrubshrub birds in New England: a comprehensive review. Natural Resources Conservation Service, Beltsville, Maryland, USA.

Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. Ornis Scandinavica 8:197–222.

Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology 86:510–518.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759–768.

Vega Rivera, J. H. W. J. McShea, J. H. Rappole, and C. A. Haas. 1998. Pattern and chronology of prebasic molt for the Wood Thrush and its relation to reproduction and migration departure. Wilson Bulletin 110:384–392.

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

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Woodrey, M. S., R. P. Ford, W. C. Hunter, and J. Taulman. 1998. East Gulf Coastal Plain Partners in Flight bird conservation plan (physiographic area #04). Mississippi Museum of Natural Science, Jackson, Mississippi, USA.