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PREDICTING OCCUPANCY OF WINTERING MIGRATORY BIRDS: IS MICROHABITAT INFORMATION NECESSARY?

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Abstract. Information regarding microhabitat, here defined as small-scale vegetation structure, is often useful in predicting use of habitat by birds. Quantifying microhabitat, however, is expensive and labor intensive compared to assessment of habitat at a larger scale, possibly from remotely sensed imagery. To assess the importance of microhabitat information in constructing predictive models of habitat occupancy, we compared occupancy models built on the basis of macro- and microhabitat together and separately. We based our models on counts of wintering migratory bird species and vegetation surveys within Tuskegee National Forest, Alabama, completed during winter 2009. Models built from macrohabitat data only outperformed models built from microhabitat data only for five of the six species analyzed. However, the best model for every focal species included both macro- and microhabitat covariates. Pine forests—excluding plantation—were the only land-cover classification important to our focal species, and measures of density of vegetation were important in predicting occupancy. Our results suggest that migrants wintering at our study site select habitat at multiple scales—specializing in certain types of cover and then preferring specific structural aspects of vegetation within them. We conclude that microhabitat information is important for inference into use of habitat by wintering migratory birds.

Key words: *East Gulf Coastal Plain, habitat, microhabitat, migratory birds, occupancy analysis, winter ecology.*

Prediciendo la Ocupación de Aves Migratorias Invernales: ¿Es Necesaria la Información del Micro Hábitat?

Resumen. La información relacionada al micro hábitat, definida aquí como la estructura de la vegetación a pequeña escala, es usualmente útil para predecir el uso de hábitat por parte de las aves. La cuantificación del micro hábitat es, sin embargo, costosa y demanda mucho esfuerzo, comparado con la evaluación del hábitat a gran escala, posiblemente a partir de imágenes remotas. Para evaluar la importancia de la información de micro hábitat en la construcción de modelos predictivos de ocupación de hábitat, comparamos modelos de ocupación construidos sobre la base de macro y micro hábitat juntos y por separado. Basamos nuestros modelos en conteos de especies de aves migratorias invernales y muestreos de vegetación dentro del Bosque Nacional Tuskegee, Alabama, completados durante el invierno de 2009. Los modelos construidos sólo con datos de macro hábitat fueron mejores que los modelos construidos sólo con datos de micro hábitat para cinco de las seis especies analizadas. Sin embargo, el mejor modelo para cada especie focal incluyó covariables tanto de macro como de micro hábitat. Los bosques de pino—excluyendo las plantaciones—fueron la única clasificación de cobertura del suelo importante para nuestras especies focales y las medidas de densidad de la vegetación fueron importantes para predecir ocupación. Nuestros resultados sugieren que los migrantes invernales en nuestro sitio de estudio seleccionan el hábitat a múltiples escalas—especializándose en ciertos tipos de cobertura y luego prefiriendo aspectos estructurales específicos de la vegetación dentro de ellos. Concluimos que la información de micro hábitat es importante para inferir el uso del hábitat por parte de aves migratorias invernales.

INTRODUCTION

A major challenge to conservation biologists is prioritizing wildlife habitat for preservation because habitat preservation is a fundamental component of most efforts to maintain animal populations and biodiversity (e.g., Stattersfield

et al. 1998, Woodrey et al. 1998, Faaborg et al. 2010a). When only a fraction of existing natural areas can be preserved, it becomes critical to understand how animals use habitats so that areas of greatest value to the conservation of wildlife can be prioritized. Toward this end, Partners in Flight—an organization concentrating on conservation of bird populations

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in the Western Hemisphere—has listed identification of high-quality habitats as a research priority for conservation of bird species in North America (Donovan et al. 2002).

The identification of the most valuable habitat for birds becomes more challenging when the species being managed migrate between distinct breeding and nonbreeding ranges. Migratory bird species use different geographical areas for breeding, during the nonbreeding season, and for moving between the two areas (Martin and Finch 1995, Faaborg et al. 2010b), and often the habitat needs of a given species of bird are different in each of these areas of seasonal use. Most research on the habitat associations of migratory birds in North America has been conducted during the breeding season, but it has been suggested that populations of migratory land birds are limited by mortality during winter (e.g., Lack 1968, Sherry and Holmes 1996, Rappole et al. 2003). Moreover, nonbreeding habitat can affect the physical condition of individuals and produce effects that carry over into the breeding season (Norris et al. 2004, Studds and Marra 2005). Therefore, understanding habitat associations and needs in the winter is a conservation priority (Sherry and Holmes 1995, 1996). Despite a growing acknowledgement of its importance, knowledge of use of habitat by wintering birds remains limited (e.g., Peterjohn 2003, Faaborg et al. 2010a).

Given the need to identify and preserve habitat, conservationists must determine what aspects of an area signify its quality as habitat. Habitat can be defined as distinct environmental conditions and resources within an area that allow for reproduction and survival (or occupancy) of an organism (Hall et al. 1997). Many aspects of the environment, including availability of food, nest sites, cover, and competitors, interact with behavior and morphology to allow occupancy of a habitat (Cody 1981, Wiens 1989a, b, Block and Brennan 1993). Habitats of highest quality should contain the fittest individuals, i.e., individuals that contribute most to the overall population of the species (Van Horne 1983, Wiens 1989a, Franklin et al. 2000, Jones 2001). Thus quality of a habitat can be inferred by mean fitness of individuals per unit area of habitat (Van Horne 1983). This requires knowledge of survival, fecundity, and density (Van Horne 1983), which often is difficult to obtain (Johnson 2009).

Information regarding distributions of animals, such as occupancy and density, is relatively inexpensive to obtain compared to data needed to calculate mean fitness associated with a habitat, but estimates of occupancy and density can reveal which habitats are used most often (Johnson 2009). There are scenarios in which birds may not occupy highest-quality habitats (Van Horne 1983, Johnson 2009) but, in most cases, density (Bock and Jones 2004, Johnson et al. 2006) and occupancy are positively correlated with quality of habitat (Ferrer and Donazar 1996, Sergio and Newton 2003) and with each other (Gaston et al. 2000). Therefore, occupancy, or the presence of individuals within an area, has become an often-used measure of the quality of an area as habitat (MacKenzie 2005). Because occupancy is often used as a surrogate for

habitat quality, determining which aspects of an area influence occupancy of organisms is important for conservation.

Another challenge related to understanding the habitat requirements of birds is identifying the scale at which they select habitat (Donovan et al. 2002). Macrohabitat generally refers to larger-scale attributes of landscape such as vegetation type or seral stage (Johnson 1980, Block and Brennan 1993, Hall et al. 1997), whereas microhabitat relates to smaller-scale features of floristics and physiognomy (Block and Brennan 1993) such as number of snags, density of shrub layer, or basal area of oaks (*Quercus*). Johnson (1980) and Hutto (1985) described birds' selection of habitat as a spatially hierarchical process. An individual bird may be seen as making choices first at the macrohabitat scale, selecting a broad habitat type, then at the microhabitat level, identifying specific areas in which to forage and spend time (Johnson 1980, Hutto 1985).

Habitat selection at broader, geographic scales is likely genetically determined, whereas selection at finer scales is influenced by learning and availability of food (Wiens 1972, Hutto 1985). Because selection at different scales is sometimes the result of different processes, differing scales of investigation can lead to conflicting conclusions regarding birds' habitat needs (Wiens et al. 1987, Wiens 1989a). Any one scale of inference is unlikely to accurately predict use of habitat across a group of species, because birds perceive habitat on a scale that reflects their unique life-history strategies (Mitchell et al. 2001; Lee et al. 2002). Also, a complete habitat model for any species of bird may involve multiple scales of investigation (Wiens 1989c, Knick and Rotenberry 1995).

Because birds choose habitat at multiple scales, microhabitat information may improve the performance of models that predict a species' presence (Hagan and Meehan 2002). There is disparity between the scales, however, in the cost of information. Information regarding microhabitat typically requires costly labor-intensive surveys (Fearer et al. 2007), whereas, within Europe and North America, macrohabitat information can be obtained from publicly available satellite imagery. Use of habitat by wintering migrants could therefore be assessed more easily if researchers could demonstrate that microhabitat information does not improve the inference gained from occupancy models.

In this study, we used occupancy models to determine the use of habitats by migratory birds wintering in the Tuskegee National Forest, Alabama. We focused on species with breeding distributions lying entirely north of the study area, so we studied individual birds that had moved from a distant breeding area to the Tuskegee National Forest for the nonbreeding period. Birds wintering in the southeast United States are often referred to as "short-distance migrants" because they do not travel south of the United States border, but many of these species move a great distance to reach the Tuskegee National Forest. We had two primary goals in this study: (1) to develop habitat-occupancy models to predict where our focal species occur during the nonbreeding season

and (2) to assess performance of occupancy models with and without microhabitat data. We therefore assessed the importance of microhabitat data to understanding winter habitat use by birds.

METHODS

BIRD SURVEYS

We established a systematic grid of 92 bird-survey points within the southwest corner of Tuskegee National Forest in Macon County, Alabama (32° 26' N, 85° 39' W). This study site consisted mostly of pine and floodplain forests but also included agricultural, scrub, and developed areas (Table 1). Each point was separated by roughly 250 m. We surveyed each point for birds by using five consecutive 4-min point counts and following protocols of Hamel et al. (1996) and recommendations of Mackenzie and Royle (2005). Observers recorded every bird detected within a 100-m radius during each count as well as weather information such as wind speed and temperature. Although many studies count birds within a smaller radius, many others use 100-m counts (e.g., Rich et al. 1994, Hanowski and Niemi 1995, Bolger et al. 1997, Kreisel and Stein 1999). Furthermore, a 100-m radius has been empirically shown to be best for grassland birds (Savard and Hooper 1995) and some forest birds (Laurent et al. 2005). The surveys extended from 28 January to 28 February 2009 and 06:00 to 14:00 CST, according to the recommendations of Rollfinke and Yahner (1990).

MACROHABITAT

Using the Alabama Gap Analysis Program Land Cover Map (Kleiner et al. 2007) and the National Landcover Database Tree Canopy Cover Map (Homer et al. 2004), we calculated the percent cover of each land-cover class within a 100-m buffer surrounding each point with ArcGIS (ESRI 2008). Following McClure et al. (2011), we combined subclassifications of broad landscape classes. For instance, we combined low-intensity, medium-intensity, high-intensity developed areas and developed open spaces to form a broad habitat class that we termed “developed.” We combined subclassifications of successional scrub to form a broad scrub classification, those of pasture and row crops to form an agricultural classification, those of pine forests were to form pine and natural pine (which excludes plantations) classifications, and those of floodplain and mesic slope forests to form a hardwood classification (Table 2 in McClure et al. 2011).

MICROHABITAT

We quantified microhabitat within 16-m-radius plots (Anderson and Shugart 1974, La Sorte et al. 2009) centered on each bird survey location. We recorded the diameter at breast height (dbh) and species of all trees ≥ 10 cm dbh (Avery 1975). We measured the canopy and ground cover with a densitometer by sampling every 4 m along 16-m transects in all cardinal directions from

TABLE 1. Abbreviations, means, standard deviations (SD), and maximum values recorded for habitat variables quantified in the Tuskegee National Forest, Alabama, 28 January–28 February 2009. The minimum for each variable was zero.

Variable	Abbreviation	Mean	SD	Max
Ground layer thickness (%)	Ground	0.72	0.15	1.00
Shrub layer thickness (%)	Shrub	0.56	0.10	1.00
Upper shrub layer thickness (%)	Hi shrub	0.58	0.16	1.00
Midstory thickness (%)	Mid	0.53	0.21	1.00
Canopy cover, 16-m radius (%)	CC	0.14	0.10	0.70
Vegetative ground cover (%)	GC	0.11	0.10	1.00
Total basal area (m ²)	BATot	1.32	0.76	3.98
Basal area of pines (%)	BAPine	0.52	0.57	2.40
Basal area of oaks (%)	BAOak	0.28	0.36	1.63
Depth of leaf litter	LL	2.98	1.63	5.80
Developed area (%) ^a	Dev	0.01	0.05	0.59
Developed open space (%) ^a	DOS	0.01	0.04	0.50
Pine forest (%) ^a	Pine	0.52	0.17	1.00
Natural pine forest (%) ^a	NatPine	0.49	0.15	1.00
Hardwood forest (%) ^a	Hard	0.26	0.20	1.00
Mixed forest (%) ^a	Mix	0.02	0.03	0.37
Scrub area (%) ^a	Scrub	0.01	0.04	0.46
Agriculture (%) ^a	Ag	0.00	0.01	0.19
Floodplain forest (%) ^a	Flood	0.16	0.25	1.00
Canopy cover, 100-m radius (%) ^b	Can	0.77	0.01	0.88

^aFrom Kleiner et al. (2007).

^bFrom Homer et al. (2004).

the center (Robinson 1947). Depth of leaf litter was measured 16 m from the center in each cardinal direction (Ortega and Capen 1999). We quantified the density of the midstory, shrub layer, and understory with a striped 12-m modified Robel pole in the center of each plot (Mills et al. 1991). Observers recorded the number of stripes obscured by vegetation at heights of 0–0.6 m, 0.6–4.6 m, 4.6–7.6 m, and 7.6–12 m (MacArthur and MacArthur 1961) in each cardinal direction from the edge of the plot. We measured dbh in 2008 and 2009, all other measurements in the same year as the bird surveys.

We calculated total basal area of all tree species as well as basal area of pines and oaks within each plot. We calculated canopy and ground cover as the percentage of densitometer readings that encountered vegetation. At each plot, we calculated the thicknesses of the ground-cover, lower-shrub, upper-shrub, and midstory layers as the average percentage of Robel-pole readings in the intervals 0–0.6 m, 0.6–4.6 m, 4.6–7.6 m, and 7.6–12 m along the pole, respectively.

STATISTICAL ANALYSES

To model bird habitat, we used a two-step approach with the program Presence (Hines 2006). First we modeled detection—the probability that a species will be detected if it is present—while holding occupancy—the probability that a species is present—constant across all sites. We only used covariates hypothesized a priori to affect bird detection. Because we

TABLE 2. Covariates hypothesized a priori to affect patterns of occupancy of migrants wintering in the Tuskegee National Forest, Alabama. Ones indicate that a covariate was considered for model building for a given species. Abbreviations of habitat covariates are defined in Table 1.

Scale and covariate	Blue-headed Vireo	Golden-crowned Kinglet	Ruby-crowned Kinglet	Hermit Thrush	Yellow-rumped Warbler	White-throated Sparrow
Macro						
NPine	1	1	1	1	1	
Pine				1		1
Hard	1	1	1	1	1	1
Mix	1	1	1	1	1	1
Scrub	1	1	1	1	1	1
Ag	1	1	1	1	1	1
Flood				1	1	
Dev	1	1	1	1	1	1
DOS						1
Can	1	1	1	1	1	1
GC	1			1		1
Micro						
Ground	1			1		1
Shrub		1	1	1	1	1
Shrub ²		1	1		1	
Hi Shrub	1	1	1	1	1	1
Hi Shrub ²	1	1	1		1	
Mid	1	1	1	1	1	1
Mid ²	1	1	1		1	
CC	1	1	1	1	1	1
CC ²	1	1	1	1	1	
LL				1		1
LL ²				1		
BATot	1	1	1	1	1	1
BAOak					1	
BAPine	1	1	1		1	

sampled on five consecutive occasions, there is a chance of temporal autocorrelation; a bird being observed at time t may be conditional on its being observed at time $t - 1$. Therefore, we also considered a binary covariate that indicated if a species was detected at $t - 1$ (Betts et al. 2008). We had no a priori expectation of which combination of covariates best described detection. For instance, we hypothesized that time, date, wind, temperature, and observer may influence the probability of detecting the Blue-headed Vireo (for scientific names see Table 3). But we had no reason to hypothesize that date and time, together, would predict detection better than the rest of the covariates together, or any other combination of covariates. Therefore, we used a manual forward-stepwise procedure for model building (King et al. 2009) in which we built models containing each covariate separately, then sequentially added covariates that lowered Akaike's information criterion, corrected for small sample size (AIC_c ; Burnham and Anderson 2002). We then incorporated this final detection model into all subsequent models. Next we examined use of

TABLE 3. Species, number of detections (n), and naïve occupancy rate (Ψ) of migrants wintering in the Tuskegee National Forest, Alabama, 28 January–28 February 2009.

Species	n	Ψ
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	139	0.38
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	92	0.40
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	32	0.16
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	92	0.32
Hermit Thrush (<i>Catharus guttatus</i>)	41	0.24
Blue-headed Vireo (<i>Vireo solitarius</i>)	30	0.15
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	25	0.05
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	11	0.08
Fox Sparrow (<i>Passerella iliaca</i>)	13	0.04
Winter Wren (<i>Troglodytes hiemalis</i>)	3	0.01
Song Sparrow (<i>Melospiza melodia</i>)	2	0.02
Dark-eyed Junco (<i>Junco hyemalis</i>)	4	0.02
Swamp Sparrow (<i>Melospiza georgiana</i>)	3	0.02

macrohabitat with covariates hypothesized a priori to affect habitat use at the macro-scale (Table 2). We used the global model, which included all hypothesized covariates (Table 2), to calculate the overdispersion-correction factor ($\hat{c}$) and used $\hat{c}$ to correct AIC_c for overdispersion if $\hat{c} > 1$ ($QAIC_c$, Burnham and Anderson 2002). We then used the same stepwise procedure described for modeling detection to develop a model minimizing $QAIC_c$ and the same stepwise procedure described above to model occupancy, using only microhabitat covariates that we hypothesized a priori (Table 2) to affect habitat use.

Next, we incorporated hypothesized microhabitat covariates into the macrohabitat models by the same stepwise procedure as above. If addition of microhabitat information created more parsimonious models, we would expect that models including both macro- and microhabitat covariates would receive a lower AIC_c (or $QAIC_c$) value than would the final macrohabitat model. We analyzed each focal species separately and considered covariates to be useful for inference if they were in the final model and if their 85% confidence intervals did not include zero. We used 85% confidence intervals because they are more consistent with an AIC approach than are 95% confidence intervals (Arnold 2010). All percentage variables were arcsine-square root transformed to assure normality. We scaled all variables to between 10 and -10 to aid in model convergence. We analyzed only species that were detected at >10 survey sites to avoid difficulties with model convergence inherent with small sample sizes. Although the choice to model species detected at >10 survey sites was arbitrary, we believe that it should not bias the results of our study.

MODEL PERFORMANCE

To determine the performance of our final models we calculated the area under the receiver operator characteristics curve

(AUC; Zweig and Campbell 1993, Fielding and Bell 1997, Pearce and Ferrier 2000). An AUC value represents the probability that if we randomly chose a site within the dataset at which a species was present, then randomly drew one at which the species was absent, a model will assign a higher probability of occupancy to the site at which the species was detected (Bonn and Schroder 2001). Models with AUC values >0.7 are considered useful, models with values >0.8 are considered good, and models with AUC values >0.9 are considered excellent (Pearce and Ferrier 2000). Because we calculated AUC values from the same dataset we used to build the models, AUC values should be interpreted as a measure of model fit, not of predictive ability (Seavy and Alexander 2011). We calculated AUC values with the ROC package (Sing et al. 2005) in the R statistical programming environment (R Development Core Team 2008).

RESULTS

During our surveys, we detected 16 species of wintering migrants. Six species were detected on enough sites (>10) to be analyzed (Table 3). We first assessed factors that affected the detectability of species and present results as the coefficient $\pm$ SE. Rates of detection of the Blue-headed Vireo (-3.93 ± 2.55), Hermit Thrush (3.88 ± 1.54), and Ruby-crowned Kinglet were affected by time of day (-2.64 ± 1.10). Yellow-rumped Warblers (1.23 ± 0.35) were more likely to be detected if they were detected on the previous survey. Date (55.01 ± 3.21) and wind speed (-3.37 ± 1.65) affected the rate of detection of the Yellow-rumped Warbler only. Ability to detect the Ruby-crowned Kinglet (observer 1 = -1.46 ± 0.66 , observer 2 = 0.15 ± 0.39) and Yellow-rumped Warbler (observer 1 = -0.54 ± 0.7 , observer 2 = 0.66 ± 0.42) differed by observer.

We then constructed models to predict occupancy with microhabitat data only, macrohabitat data only, or both and assessed how these three sets of models performed. For all species except the White-throated Sparrow, models built with only microhabitat covariates performed poorly compared to models containing only macrohabitat covariates (Table 4). However, addition of microhabitat covariates to the macrohabitat models reduced AIC_c (or $QAIC_c$) for each focal species, resulting in more parsimonious models. Addition of microhabitat covariates for the Golden-crowned Kinglet, Yellow-rumped Warbler, and White-throated Sparrow resulted in models $>2\Delta AIC_c$ from the model built with only macrohabitat covariates, suggesting that models including both micro- and macrohabitat information are substantially more supported for these species than are models ignoring microhabitat (Table 4, Burnham and Anderson 2002). Thus we failed to support the hypothesis that macrohabitat alone is sufficient to model habitat occupancy by birds wintering in the Tuskegee National Forest.

Relationships between the occupancy of focal species and informative habitat variables are presented in Figure 1. The

TABLE 4. AIC_c , ΔAIC_c , model weights (w_i), and area under curves of receiver operating characteristics (AUC) for models describing occupancy of migrants wintering in Tuskegee National Forest, Alabama, 28 January–28 February 2009. Models were built with macrohabitat covariates (macro), microhabitat covariates (micro), or both (macro + micro).

Species and scale	Covariates ^a	ΔAIC_c ^b	w_i	AUC
Blue-headed Vireo				
macro + micro	NPine + Ground	0	0.7	0.841
macro	NPine	1.74	0.29	
micro	Null	12.22	0	
Golden-crowned Kinglet				
macro + micro	NPine + CC + Shrub ² + BATot	0	0.99	0.884
macro	NPine	9.35	0.01	
micro	CC + Shrub ² + BATot	12.99	0	
Ruby-crowned Kinglet				
macro + micro	NPine + Can + BAPine	0 ^c	0.56	0.737
macro	NPine + Can	0.53 ^c	0.43	
micro	Null	6.82 ^c	0.02	
Hermit Thrush				
macro + micro	NPine + Scrub + LL ² + Mid	0	0.48	0.757
macro	NPine + Scrub	1.08	0.28	
micro	LL ² + Mid	1.39	0.24	
Yellow-rumped Warbler				
macro + micro	NPine + BAOak	0 ^c	0.81	0.817
macro	NPine	3.37 ^c	0.15	
micro	CC ²	5.89 ^c	0.04	
White-throated Sparrow				
macro + micro	DOS + Can + Mid	0 ^c	0.49	0.852
micro	BATot + Mid	0.54 ^c	0.37	
macro	DOS + Can	2.53 ^c	0.14	

^aFor abbreviations see Table 1.

^bMinimum values of AIC_c : 157.69 for the Blue-headed Vireo, 156.33 for the Golden-crowned Kinglet, 330.19 for the Ruby-crowned Kinglet, 231.23 for the Hermit Thrush, 264.61 for the Yellow-rumped Warbler, and 138.37 for the White-throated Sparrow.

^c $\Delta QAIC_c$.

Blue-headed Vireo (4.66 ± 1.54), Golden-crowned (11.11 ± 3.36) and Ruby-crowned (2.20 ± 0.90) Kinglets, Hermit Thrush (1.02 ± 0.76), and Yellow-rumped Warbler (7.04 ± 2.62) were all associated with natural pine forests. The Golden-crowned Kinglet was also positively associated with canopy cover (4.28 ± 2.10) within the vegetation plots, negatively associated with total basal area (-5.0 ± 1.56), and showed a quadratic association with thickness of shrub layer (shrub = -21.07 ± 5.35 , shrub² = 14.78 ± 3.53). The Hermit Thrush showed a quadratic relationship with depth of leaf litter (leaf litter = 19.15 ± 8.52 , leaf litter² = -31.29 ± 15.04), a positive relationship with midstory thickness (19.15 ± 8.52), and a negative association with scrub areas (-3.67 ± 2.43). The Ruby-crowned Kinglet

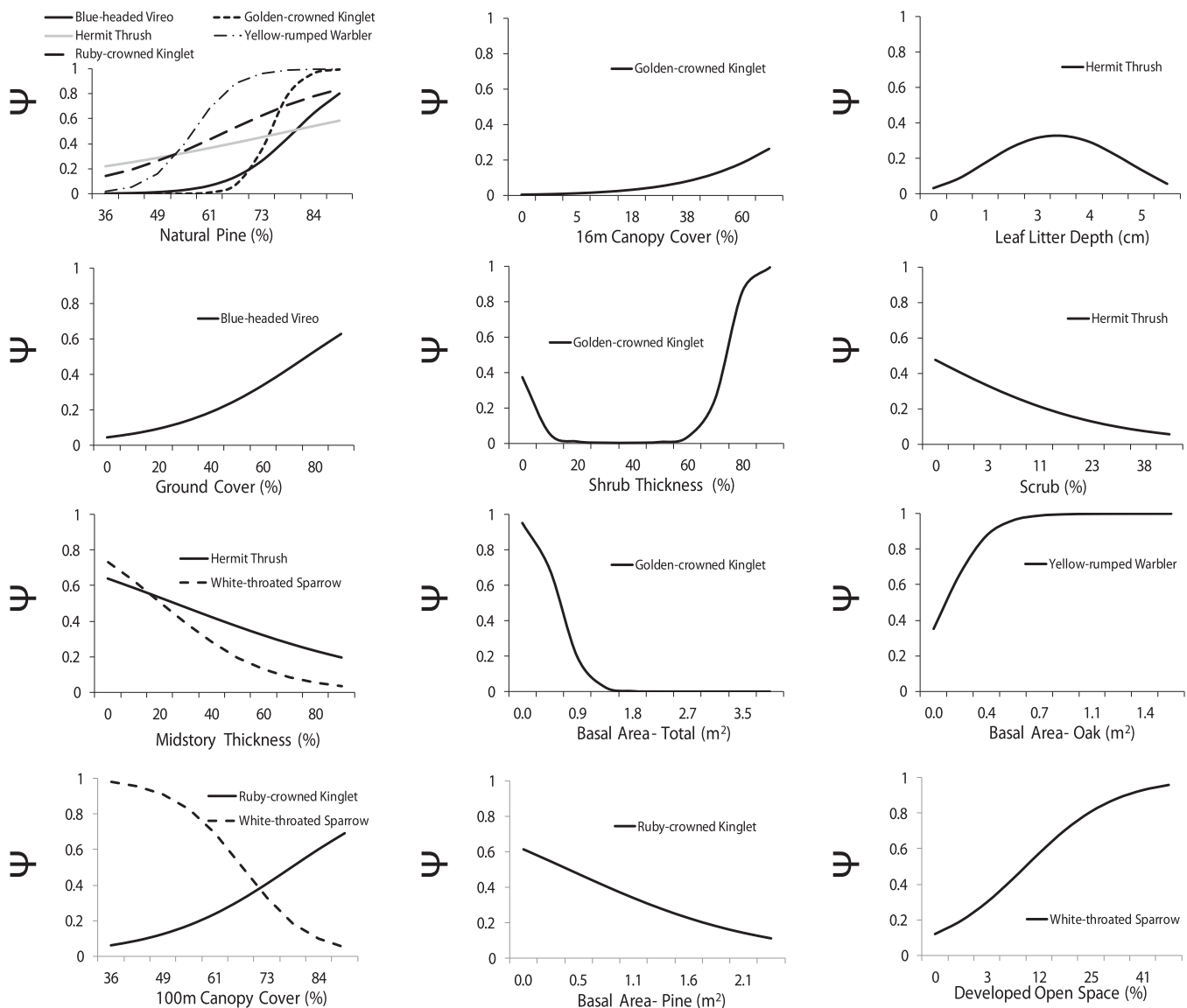


FIGURE 1. Relationship between probability of occupancy (Ψ) and habitat covariates within final models of occupancy of migrants wintering in Tuskegee National Forest, Alabama, 28 January–28 February 2009.

was positively associated with canopy cover within 100 m (6.17 ± 2.77) and negatively associated with basal area of pine (-1.06 ± 0.61). The White-throated Sparrow was negatively associated with canopy cover within 100 m (-11.89 ± 5.45) and midstory thickness (-2.77 ± 1.51) and positively associated with developed open space (6.58 ± 3.56). The Yellow-rumped Warbler (7.09 ± 3.33) and Blue-headed Vireo (2.28 ± 1.13) were positively associated with basal area of oak and ground cover, respectively.

Overall models of use of habitat that included both micro- and macro-habitat characterizations performed well in predicting occupancy by wintering migrants. Final models for the Hermit Thrush and Ruby-crowned Kinglet met the criterion for useful ($AUC > 0.7$, Table 4), and those for the Blue-headed

Vireo, Golden-crowned Kinglet, Yellow-rumped Warbler, and White-throated Sparrow met the criterion for good ($AUC > 0.8$, Table 4).

DISCUSSION

Because collection of microhabitat data is labor intensive, it would be useful if researchers could rely strictly on macrohabitat data from publicly available remote imagery in constructing occupancy models. Justification for ignoring microhabitat data would be strongest if it could be shown that microhabitat lends little inference to models of animal occupancy beyond that provided by assessment of macrohabitat data. In our study of wintering birds, however, the effect of

adding microhabitat information is clear—occupancy models for each focal species improved with the addition of microhabitat information, and models for half of our focal species improved substantially. Furthermore, AUC values revealed that our models fit the data well ($AUC > 0.7$). Thus, it appears that when wintering migrants settle in a certain land-cover classification, they further select habitat on the basis of an area's structure or floristics (Hutto 1985), highlighting the importance of including both macro- and microhabitat data in assessments of the occupancy of wintering migrants.

At our study site, wintering migratory birds used pine forests more than any other classification of land cover. Five of the six species analyzed—the Blue-headed Vireo, Ruby- and Golden-crowned Kinglets, Yellow-rumped Warbler, and Hermit Thrush—were associated with natural pine forests, supporting past studies showing that these species prefer to winter in pine forests (Quay 1947, Hamel 1992). Coniferous forests provide wintering migrants with much needed shelter (Petit 1989) and contain an abundance of fruiting plants, such as waxmyrtle (*Morella cerifera*), that are important to wintering species such as Yellow-rumped Warbler and Hermit Thrush (Kwit et al. 2004). Our results support calls for the preservation of pine forests as habitat for wintering migrants (e.g., Woodrey et al. 1998).

Within pine forests, wintering migrants used sites with different structural characteristics. For instance, use of habitat by wintering Ruby- and Golden-crowned Kinglet was influenced by canopy cover. Our results support observations of Vaughan (2009) showing that wintering forest birds, including the two kinglets, are positively associated with canopy cover. Furthermore, the Ruby- and Golden-crowned Kinglets were negatively associated with basal area of pine and total basal area respectively. Conner et al. (1979) found that wintering Golden-crowned Kinglets to be most abundant in 10-year-old pine stands, declining in abundance as stands matured beyond that age. In Georgia, White et al. (1996) found wintering Golden-crowned Kinglets less abundant in mature pine stands than in younger stands with less basal area, although Ruby-crowned Kinglets showed no preference. Because stand age is correlated with basal area (e.g., Hedman et al. 2000), our results support past studies showing that Golden-crowned Kinglets wintering in the southeast U.S. prefer mid-stage pine forests and suggest that the Ruby-crowned Kinglet also prefers younger pine forests.

Within the pine forests we studied, Blue-headed Vireos were associated with areas of increased ground cover. In a study of the winter ecology of the Golden-cheeked Warbler (*Setophaga chrysoparia*) in Central America, Rappole et al. (1999) commonly observed Blue-headed Vireos with Golden-cheeked Warblers, which preferred areas of high ground cover. Our results suggest that at our study site wintering Blue-headed Vireos also prefer areas with high vegetative ground cover within pine forests.

Yellow-rumped Warblers and Hermit Thrushes wintering at our study site also preferred pine forests with certain

structural aspects. Hermit Thrushes preferred an intermediate level of leaf litter, likely because they often forage on the ground (Hamel 1992), and Yellow-rumped Warblers chose sites with a larger basal area of oaks. The Yellow-rumped Warbler's association with oaks may reflect a preference for moist low-lying areas (Hamel 1992) within pine forests.

The White-throated Sparrow was the only focal species not associated with pine forests. It was associated with developed open spaces, which at our study site consist mostly of unpaved roads. The White-throated Sparrow was also negatively associated with canopy cover within 100 m and density of the midstory, likely reflecting an affinity for edges. Our results therefore support past studies suggesting that White-throated Sparrows prefer woody margins and an open canopy (Hamel 1992, Vaughan 2009) and suggest that both macro- and microhabitat information contribute to inference of this species' habitat use.

Realistic inference into patterns of habitat use by a given species often requires multiple scales of investigation (Wiens 1989c, Knick and Rotenberry 1995). When designing studies, ecologists must consider the ecological neighborhood in which processes operate (Wiens 1989a, Pearson 1993) as well as the costs involved with the collection of data (Fearer et al. 2007) at multiple scales. Our results are consistent with the proposal that wintering migrants select habitat at multiple scales. Therefore, collection of microhabitat data, although costly and time-consuming, remains important and necessary in the assessment of occupancy of migrants wintering in the southeast U.S.

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