Assessing Some Key Approaches Used to Monitor and Study Populations of Birds

by

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Abstract

Efforts to monitor birds and determine their distributions often make assumptions that allow for inference into parameters of interest but necessitate that potentially confounding factors be ignored. In any scientific endeavor it is fundamental to assess assumptions to confirm that more is gained in inference than is lost in simplification. In this dissertation, I use data collected in and around Tuskegee National Forest (TNF), Alabama to test assumptions of bird monitoring programs, sampling protocols, and models of distributions. Many monitoring programs assume the number of animals detected is strictly a function of the number of animals present. However, climate change may be causing birds to breed earlier, thus systematically changing bird vocalization and violating the assumption of constant detectability. I showed that if the breeding date of the bird community shifted earlier by one week, migratory birds will become less detectable during June. Further, the change in bird detection was not correlated with trends in abundance calculated using data from the Breeding Bird Survey. Next, I assessed assumptions related to assessment of habitat associations of birds. Many studies designed to predict or examine distributions of birds assume that birds choose habitat using broad scale information such as cover-type. This assumption is violated if birds choose sites using criteria other than land cover or within urban areas that are not adequately described by cover-type alone. I tested whether species ecology and urbanization affect Alabama Gap Analysis Program's (GAP) accuracy when predicting distributions of birds. GAP performed best when predicting distributions of insectivorous birds that do not nest in cavities and within TNF rather than Auburn (a close-by urbanized area). I also tested whether addition of fine-scale habitat information increased inference into habitat use of migratory birds wintering in TNF. I found that occupancy models were improved by addition of fine-scale habitat variables. Finally, I assessed the assumption that birds retain the same habitat associations throughout the breeding season. I found that models which incorporated movement between sites outperformed models that assumed constant occupancy throughout the breeding season. The results of my studies should guide future studies of bird populations and distributions.

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CHAPTER I: INTRODUCTION

A substantial portion of the money and effort devoted to bird conservation is focused on elucidating the population trends and habitat requirements of species. It is therefore imperative that surveys and habitat association studies are conducted in an effective manner—providing useful inference into population trends and habitat use, while minimizing expenditure of time and resources (Field et al. 2005; Nichols and Williams 2006). Many monitoring programs, sampling protocols, and models of distributions make assumptions about the biology of populations or species to make inferences without having to collect surplus data (e.g., MacKenzie et al. 2002; Silvano et al. 2007; Sauer et al. 2011). My purpose in this work is to test some of the assumptions that underlie efforts to monitor and preserve populations of birds. From these assessments, I will determine whether the assumptions are justified, or whether sampling protocols or modeling schemes should be adjusted to better reflect reality.

Populations of animals are often monitored to determine if, when, where, and why changes in populations are occurring. Most bird monitoring programs rest on an assumption that bird species are not becoming harder (or easier) to detect as years go by (e.g., National Audubon Society 2002; Sauer et al. 2011). One can imagine, for example, that if a species is growing progressively quieter each time a survey is conducted, fewer individuals will be detected with each survey. This trend in fewer individuals being detected could then be misinterpreted as a population decline (Simons et al. 2007). Such a systematic change in bird detectability – the probability of detecting a bird, given that it is present – seemed unlikely until recently. Studies have shown that many bird species are breeding and migrating earlier, presumably due to climate change (reviewed in Crick 2004). Because bird song rate is tied to breeding stage (Best 1981; Best and Petersen 1982; Wilson and Bart 1985), a progressively earlier breeding date could potentially shift the timing of peak song rate, thus causing birds to be progressively harder (or easier) to detect during survey dates each year. To address this assumption of unchanging detection in the face of climate change, we first had to determine whether bird detectability changes within a single breeding season. We used audio recordings within Tuskegee National Forest, AL to examine seasonal changes in the detectabilities of 31 species during the breeding season of 2008. Next, we calculated the effect of a one-week shift in breeding activity by shifting the timing of peak detectability one week later and determining the effect of that shift on the detectability of each species during the month of June and then tested whether changes in detectability were correlated with population trends reported using Breeding Bird Survey data within the state of Alabama.

Because many populations of birds are declining due to lack of suitable habitat (Wilcove et al. 1998), it is increasingly important to identify areas containing quality habitat for birds. Gap Analysis Program (GAP) uses vegetation maps and expert opinion to predict the distributions of animals and thus identify areas of high biodiversity which are not currently set aside for conservation (Scott and Jennings 1997; Jennings 2000). Gap Analysis Programs have the implicit assumption that distributions of species can be modeled accurately using information gathered from vegetation maps (Schlossberg and King 2009). This assumption allows for animal distributions to be mapped without having to collect costly fine-scale habitat data, but it may not be valid for some species which choose sites based on fine-scale aspects of habitat (such as vegetation structure, which is lacking from most vegetation maps), or within landscapes such as urban areas which are poorly quantified using maps of land-cover (Cadenasso et al. 2007). We used point counts to test the accuracy of Alabama Gap Analysis Program's (ALGAP) predictions of bird distributions within Auburn, AL and Tuskegee National Forest, AL. We examined whether ALGAP was more accurate when predicting the distributions of certain suites of species such as cavity nesters, migrants, and insectivores, and whether ALGAP performed better in a rural (Tuskegee National Forest) or urbanized (Auburn, AL) setting.

Populations of migratory birds have experienced recent declines (reviewed in Martin and Finch 1995) and identifying the scale at which their distributions are best examined is a research priority (Donovan et al. 2002). Further, use of habitat by wintering migratory birds is poorly understood (e.g, Schlossberg and King 2007; Rolek 2009; Faaborg et al. 2010). When examining habitat use by wintering migrants, data on fine-scale aspects of habitat such as vegetation structure may be important (White et al. 1996), but prohibitively expensive to collect (Fearer et al. 2007). The amount of resources needed to conduct a study of habitat use by wintering migrants would therefore be greatly reduced if fine-scale aspects of habitat could be ignored. We examined the use of habitat by migratory birds wintering in Tuskegee National Forest, AL. We collected data regarding broad-scale features of habitat such as type of cover and fine-scale aspects of habitat concerning vegetation structure and floristics to determine whether collecting fine-scale habitat information improved the inference gained from occupancy analysis.

Many studies of habitats used by birds assume that once breeding territories are established, use of habitat remains static (e.g., Mitchell et al. 2001; Stratford and Robinson 2005; McClure et al. in press). In fact, commonly used survey protocols (Hutto et al. 1986) recommend conducting surveys early in the breeding season when birds are most detectable, and statistical models of habitat use (e.g., MacKenzie et al. 2002) often make the explicit assumption that species do not move between sites during the sampling season. This assumption allows for surveys to be conducted only once during the breeding season, instead of investing time and manpower in conducting multiple rounds of surveys. However, birds often abandon unsuccessful nest sites in search of better habitat (Krebs 1971; Hoover 2003; Betts et al. 2008) or will learn which sites contain better habitat as the season progresses (Betts et al. 2008). We tested this assumption of constant use of habitat by examining data collected during the early and late breeding season. We tested models that assumed constant use of habitat across the breeding season (MacKenzie et al. 2002) against models that allowed for colonization and vacancy of sites within the breeding season (MacKenzie et al. 2003).

Considering the current conservation crisus, it is important that efforts to monitor populations, predict species distributions, or examine habitat use maximize useful inference while minimizing cost. This efficient use of resources can only be achieved if assumptions underlying conservation efforts are justified. In this work I have endeavored to rigorously test assumptions upon which efforts to monitor and conserve populations of birds depend. Hopefully, results from this work will both increase confidence in our current programs and techniques and, where needed, lead to changes that will further our understanding of bird ecology and help to conserve populations of birds and their habitats.

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CHAPTER II: ACTUAL OR PERCEIVED ABUNDANCE? INTERPRETING ANNUAL SURVEY DATA IN THE FACE OF CHANGING PHENOLOGIES

Abstract. Many annual monitoring programs assume that availability—the probability that an animal will be visible, make an audible sound, or leave other evidence of its presence—does not change systematically from year to year. Until recently, this assumption of unchanging availability seemed reasonable, but recent studies report changes in breeding phenology that are presumed to be linked to climate change. Because the rate of bird song is often correlated with stage of breeding, earlier breeding could shift timing of peak bird availability, changing the number of birds counted during annual surveys on set dates. Such changes could be erroneously interpreted as population trends. To better understand how changes in phenology might affect the probability of detecting birds, we modeled availabilities of 31 species in southern Alabama through the breeding season, documenting strong seasonal variation in availability. Then, using our availability estimates, we investigated whether changes in detection probabilities could underlie observed changes in the abundances of some species. We calculated the expected change in the number of times a species would be recorded during surveys conducted within fixed dates by assuming a 1-week shift in breeding activity. We found that summer residents were more likely to show changes in availability but that such changes in availability did not account for trends in Breeding Bird Survey (BBS) data for Alabama. Our results suggest that while summer residents' availability may be declining during BBS dates, population declines observed in BBS data for Alabama cannot be dismissed as due to shifting phenology.

INTRODUCTION

A major focus of conservation biologists is monitoring the abundances of species and taking actions to stop and reverse population declines. Breeding birds are particularly amenable to being counted because they are active and vocal during the day, and birds are perhaps the best-monitored taxonomic class of animals in North America (Davis 1982). Despite birds' suitability for being counted, the probability of detecting a given individual bird during a designated count period is likely to be less than one (Johnson 2008, Nichols et al. 2008, Simons et al. 2009). For a bird to be detected it must be visible or make an audible signal such as a song or call, and the observer must perceive and correctly identify the bird. These two components of detection are referred to as the availability and perceptibility of a bird, respectively (Marsh and Sinclair 1989, Johnson 2008, Nichols et al. 2008). Availability is a function of bird behavior, whereas perceptibility is often affected by differences among observers and the conditions under which surveys are conducted (Johnson 2008). The rate at which birds sing (vocalizations per unit of time) has a particularly strong effect on bird availability (Alldredge et al. 2007).

Primarily within the past decade, conservation and wildlife biologists have developed statistical tools to take into account imperfect detection of birds in models of species' abundance (reviewed in Johnson 2008, Nichols et al. 2008, Simons et al. 2009). The development of this detection theory has provided important new insight into the process of monitoring bird populations, and it has revealed key assumptions in estimates of species' abundance. One key assumption of surveys conducted on fixed dates that are used to track the population trends of species is that the availability of bird species does not change from year to year.

For essentially all bird species, availability changes within a breeding season. A primary reason for changing availability within a breeding season is that song rate of many species varies through the breeding season (Slagsvold 1977, Best 1981, Ralph 1981, Skirvin 1981). This variation in song rate is affected by environmental conditions (Slagsvold 1977, Gordo et al. 2008), whether the bird is paired (Sayre et al. 1980, Hayes et al. 1986, Gibbs and Wenny 1993), and nest stage (Best 1981, Best and Petersen 1982, Wilson and Bart 1985). For example, Lampe and Espmark (1987) showed that song activity of the Redwing (*Turdus iliacus*) peaks 2 weeks before egg laying, and Logan (1983) found an increase in singing during nest building in the Northern Mockingbird (*Mimus polyglottos*). Seasonal variation in song rate may impart variation in the number of individuals available to be detected through the breeding season, potentially biasing the results of studies that fail to correct for seasonal changes in availability (Diefenbach et al. 2007).

Many monitoring programs have attempted to overcome temporal changes in bird availability by standardizing protocols so that birds are surveyed at the same date and time of day each year (e.g., Holmes and Sherry 2001, Linder and Buehler 2005, Sauer et al. 2008). One such program, the North American Breeding Bird Survey (BBS), is the primary tool used to assess the population status of birds in North America (Sauer et al. 2005). The BBS is a database of approximately 3700 routes, each consisting of 50 point counts—fixed-position surveys in which an observer records all birds detected—along a standardized route. Most bird detections during point counts are auditory (Scott et al. 1981, DeJong and Emlen 1985, Sauer et al. 1994a), so song rate greatly influences detection probability during such surveys (Alldredge et al. 2007). The BBS can provide data useful for determining changes in relative abundance of a species between years, but this use of the count data relies on the critical assumption that bird availability does not change systematically over time. Because song rate is tied to state of breeding, an assumption that a species' availability is constant is an assumption that its breeding phenology remains constant across years. Until recently, such an assumption seemed entirely reasonable.

The past century has seen a rise in global temperatures (Houghton et al. 1995) with significant effects on birds (Crick 2004). Bird phenology seems to be particularly influenced by warming temperatures, with many species migrating earlier (e.g., Mason 1995, Jenkins and Watson 2000, Butler 2003, Huppop and Huppop 2003, Marra et al. 2005, Vegvari et al. 2010). Additionally, nesting dates for many species have become earlier in both Europe (Crick et al. 1997, Winkel and Hudde 1997, McCleery and Perrins 1998, Both et al. 2004) and North America (Bradley et al. 1999, Brown et al. 1999, Dunn and Winkler 1999). The recent, well-documented changes in the phenology of many birds raise questions about the reliability of reported changes in abundance that are based on monitoring programs dependent on an assumption of constant availability (Simons et al. 2007).

The seasonal timing and synchrony of breeding within a population determine the effects that changing phenology will have on perceived abundances. If a species normally breeds near the survey dates and sings at its maximal rate during this period, then annual surveys at this time of year will have maximal ability to detect the species. If, however, the species undergoes a phenological shift and breeds earlier than normal in a given year, such that the peak of singing occurs before the survey date, then fewer individuals will be counted during the survey, even if the same number of birds is present. Conversely, if a species that normally peaks in song activity after the survey date shifts toward earlier breeding, a greater proportion of individuals of that species will be counted as the date of breeding moves closer to the survey period. The synchrony of breeding may also affect trends perceived during surveys. Birds that breed more synchronously show more marked changes in song rate as the breeding season progresses (Slagsvold 1977). Migratory birds tend to breed more synchronously than do residents (Spottiswoode and Møller 2004), so changes in phenology may have a greater effect on the availability of migratory species than on resident species. Several studies have reported declines in Neotropical migrants (Holmes et al. 1979, Hall 1984, Leck et al. 1988, Robbins et al. 1989, Holmes and Sherry 2001, Holmes 2007) without considering the potential effect of changes in migratory bird phenology.

To obtain accurate estimates of a species' population trends, it is imperative to understand seasonal changes in availability and determine how changes in phenology may affect availability during surveys. Our study had three goals: (1) to document changes in the availability of various bird species across the breeding season within our study site in Tuskegee National Forest, Alabama, (2) to determine how a shift in phenology would affect bird availability during annual bird surveys, and (3) to determine whether our estimated changes in bird availability due to shifts in phenology are correlated with population trends as estimated by the BBS within the state of Alabama. We predicted that migratory species should show more seasonal variation in availability than residents, and that this should translate into larger changes in availability due to shifts in phenology during annual surveys. We also predicted that the changes in availability due to changes in phenology should correlate with population trends in BBS data.

METHODS

BIRD SURVEYS

To estimate bird availability we used audio recordings from 13 locations in Tuskegee National Forest (32° N, 85° W, Macon County, Alabama), on the northern edge of the East Gulf Coastal

Plain. Each of the 13 locations was along a 2400-m transect oriented northeast–southwest, and each location was separated from other locations by 200 m. The sample area spanned several habitat types including open marsh, hardwood bottomland, upland pine, and mixed pine-hardwood and deciduous forest. We did not record birds during rain or high wind events. We recorded bird vocalizations for 5 min at each station between 07:00 and 08:00 CDT weekly from late April through the end of July, 2008, by using a digital linear PCM recorder (model LS-10, Olympus America, Inc.) held at breast height. Two experts in bird-song identification examined each recording thoroughly, collaborating to determine the presence/absence of each species. Our methods control for weather, time of day, and observer bias in detection probability by using audio recordings made under favorable weather conditions, within the same hour each day, and by having the same two experts review the recordings together. In our analysis, by holding bird perceptibility constant, we were able to base our detection estimates on the availability of birds during the breeding season within our study site. Because point counts in forested habitats rely almost entirely on auditory detection (Faanes and Bystrak 1981, Scott et al. 1981, DeJong and Emlen 1985), our counts produce data like conventional point counts even though we eliminated visual observations and relied entirely on auditory detections.

STATISTICAL ANALYSES

We used generalized linear mixed models with a binomial distribution and a logit link to create availability curves (Cunningham and Rowell 2006). Each model containes a random effect for site. We fit models by using restricted maximum likelihood. For each species analyzed, we built three models representing hypothesized changes in species availability throughout the season: (1) a null model containing only the intercept, (2) a linear model containing a covariate for the week in which each observation was made, and (3) a quadratic model that contained covariates for the week in which each observation was made and that week squared. Models were ranked and compared by Akaike's information criterion corrected for small sample size (AIC$_c$; Hurvich and Tsai 1989). We considered a model competitive for inference if the covariates in the top model were not a subset of covariates in the competing model (Burnham and Anderson 2002, Devries et al. 2008, Arnold 2010). If any competitive model was within two AIC$_c$ units of the top model, we model-averaged across the entire model set (Burnham and Anderson 2002) to develop the final model. We used final models for inference only if the confidence intervals of at least one parameter excluded zero (Chandler et al. 2009). We analyzed species only detected on four or more counts during the study period. Using species detected for at least 4 weeks enabled us to avoid convergence problems inherent with small sample sizes yet still obtain a biologically relevant temporal sampling of bird availability. Because we are less than certain of the presence or absence of a species during our surveys (e.g., a species may have been present but undetected), our availability curves represent indices of availability rather than true availability. Nevertheless, our indices of availability should be useful in examining the availability of a species to a given observer.

We tested observations of each species for spatial autocorrelation with Mantel tests (Legendre and Legendre 1998). We calculated the Mantel test statistic (Mantel 1967) between a geographical distance matrix and a presence–absence matrix for each focal species. We calculated probability values by using 10 000 random permutations.

We used our availability models to assess the effect of a 1-week shift in phenology on the number of individuals perceived in the month of June. We chose a 1-week shift because Butler (2003) found that, in North America, migrants arrived approximately 8 days earlier between 1951 and 1993 than between 1903 and 1950. Also, in Wisconsin, spring events (e.g., trees blossoming, migrants' arrival, nest dates) shifted 7 days earlier over a 61-year period (Bradley et al. 1999). Because bird phenology is assumed to have shifted 1 week earlier, we can estimate previous (historical) bird availability by shifting our observed curve 1 week later. For each species we calculated the difference between the area under the detection curve as observed in 2008 and the area under the curve shifted 1 week later (Fig.1). The area under the detection curve represents the number of times a species was available for detection (hereafter "detections") per survey station during the study period, given that the species was present. Therefore, the difference between the areas under the 2008 curves and the curves shifted by 1 week represents the change in the number of detections if breeding phenology shifted by 1 week. We calculated detections during June because that is when the majority of BBS surveys are conducted (Sauer et al. 2008).

Because populations of many neotropical migrants began declining in approximately 1978 (Robbins et al. 1989), we calculated changes in observed abundance on the basis of all BBS routes (50 stops at 0.8-km intervals) within the state of Alabama (n = 102) for the entire BBS dataset 1966–2007, and from 1978 to 2007 separately (Sauer et al. 2008). We calculated trends in populations from data in Sauer et al. (2008) by using a linear route-regression approach based on estimating equations with the methods described by Geissler and Sauer (1990). This analysis method is commonly used to estimate trends in BBS data (e.g., Robbins et al. 1989, Martin and Finch 1995, Link and Sauer 1998). These estimating equations control for observer differences in detectability (Sauer et al. 1994b, Link and Sauer 1998) but do not incorporate yearly changes in the proportion of birds sampled due to shifts in availability. We considered populations showing nonsignificant trends ($P > 0.05$) in BBS data to be unchanged. We used general linear models to determine if the observed trends in BBS data could be a function of changing bird availability and migratory status. We built models representing four hypotheses to predict the trends in BBS data: (1) a null model containing only the intercept, (2) a model containing a binary factor indicating the migratory status of each species (1 = migrant, 0 = resident), (3) a model containing the calculated change in availability, and (4) a model containing both the binary factor indicating migratory status and the change in availability. Using AIC_c (Burnham and Anderson 2002), we ranked and compared models separately for BBS trends 1967–2007 and 1978–2007.

It is possible that the heights and slopes of availability curves during 2008 are not representative of a species' average availability from year to year. However, species of birds are often stereotyped with respect to the stage of nesting at which they peak in song rate (e.g., Slagsvold 1977, Logan 1983, Lampe and Espmark 1987). In fact, Slagsvold (1977) suggested that song rate could be used to analyze breeding status. Therefore, even if the heights and slopes of curves calculated from 2008 data are not completely accurate representations of a species' availability, the locations of peaks are likely to be representative. We therefore performed a binomial test to determine if the direction of the change in availability (increasing, decreasing, or stable) could correctly predict the direction of observed trends in BBS data. Thus species with trends in detection that matched the trends in BBS data received a "1," and species with trends in detection that differed from BBS trends received a "0." We analyzed BBS trends 1967–2007 and 1978–2007 separately. This binomial test should be robust to uncertainty in the heights and slopes of availability curves as well as to uncertainty in the magnitude of shifts in phenology because it simply analyzes whether the direction of BBS trends matches the direction of changes in availability, regardless of magnitude.

To test the assumption that population trends in the vicinity of Tuskegee National Forest are representative of changes in bird abundance across Alabama, we examined data from the BBS route that runs through Tuskegee National Forest (Warrior Stand). Using a Pearson's product-moment correlation test, we tested for correlations between trends on the Warrior Stand route relative to trends for birds across all BBS routes in Alabama from 1967 to 2007 and between our calculated changes in availability within Tuskegee National Forest and population trends along the Warrior Stand route. We used R version 2.9.2 (R Development Core Team 2009) for all statistical analyses.

RESULTS

Of 48 bird species detected during the study, 31 were detected on at least four counts, and we analyzed availabilities of those 31 species only. The Prothonotary Warbler, Common Yellowthroat, and Red-winged Blackbird (see Table 1 for scientific names) had competitive models within two AIC_c units of the top model (Table 1), so we model-averaged across their entire model sets to develop their final models. Eleven species showed correlations between availability and the week in which observations were made (Table 1, Fig. 2), indicating changes in availability within the study period. Mantel tests revealed significant ($P < 0.05$) spatial autocorrelation for the Red-eyed Vireo ($r = 0.08$) and Northern Parula ($r = 0.10$). We recognize that this may lead to an increased rate of type I error for these two species (Dormann et al. 2007) but believe that it does not affect the inference drawn from our study because visual inspection of the data shows obvious changes in availability throughout the study period (Fig. 2). It should also be noted that our data are far more likely to suffer from spatial autocorrelation than are BBS data because the distance between our survey stations is 200 m, while the distance between BBS stops is 800 m.

The availabilities of migrant species were more likely than those of residents to change through the sampling period: eight of 13 migrants but only three of 18 residents changed (Fisher's exact test, *P* = 0.02). The intercept-only model was the best predictor of BBS trends 1967–2007 and 1978–2007 (Table 2). The model containing the calculated change in availability showed a nonsignificant negative correlation between the BBS trends and change in availability (1967–2007: β= –4.027, SE = 4.141, *t* = –0.972, *P* = 0.339; 1978–2007: β= –4.943, SE = 4.337, *t* = –1.140, *P* = 0.264; Fig. 3). The direction of the change in detections matched the direction of BBS trends of 13 species for the entire BBS dataset (Table 3, binomial test: *P* = 0.10) and 12 species from 1978 to 2007 (Table 3, binomial test: *P* = 0.07). Therefore, we could not reject the hypothesis that the direction of the change in availability was random with respect to the direction of trends in the BBS. Population trends along the Warrior Stand route were significantly correlated with BBS trends across Alabama (*r* = 0.39, *t* = 2.27, df = 28, *P* = 0.03) and were not correlated with calculated changes in availability within Tuskegee National Forest (*r* = –0.22, *t* = –1.22, df = 28, *P* = 0.23).

DISCUSSION

A critical assumption of animal surveys that are conducted at the same time each year, like the BBS, is that the availability of target species does not change systematically over the years. To begin to assess this assumption we first have to understand how the availability of various bird species changes within a breeding season. By analyzing intervals of bird songs recorded through the breeding season in southern Alabama, we were able to show that the availability of many species varies seasonally. Furthermore, the availability of migrants changed more within a breeding season than did the availability of residents. These patterns likely reflect that the synchrony of breeding of migratory birds is greater than that of residents (Spottiswoode and

Møller 2004). Greater synchrony leads to the population-wide availability of migratory species during the breeding season being peaked than that of residents (Slagsvold 1977).

Many resident birds begin breeding before the period that we monitored in this study (Haggerty 2009), which may explain why we failed to observe a peak in detection for some species—for these species detection likely peaked before we began our observations. Resident birds may also defend territories year round, resulting in a more constant song rate and availability (Best 1981). Our results suggest that although some residents' availability varies seasonally, change in availability through the breeding season is more characteristic of migratory species.

Our observations of systematic changes in the availability of some species support the prediction that a shift in peak availability would cause a change in the availability of many species on the BBS. As a group, migrants showed a stronger effect of date on availability, and for most migrants the outcome of the change in availability was reduced detections. Such declines in the availability of species could resemble declines in abundances if counts taken on the same date each year were compared. Thus the pattern of decline in Neotropical migrants with respect to resident birds is consistent with the hypothesis that such changes are due to changes in a species' availability rather than to true population declines.

We tested this hypothesis by testing for a correlation between predicted changes in the number of detections and the population trends observed in the BBS dataset. We found that the shifts in availability were not correlated with observed trends in BBS data in Alabama. Interestingly though, since the 1970s, the mean date on which BBS routes are run within the state of Alabama has moved forward by roughly 7 days (Sauer et al. 2008). This 7-day change in count date may offset the 7-day change in bird phenology. The reason for the change in count date is unknown, but we can speculate that the birders who run the routes may be compensating for the phenologies of breeding birds shifting earlier. Whether there has been such a shift in count dates beyond Alabama remains to be assessed.

This study shows seasonal changes in the availability of several species of birds while controlling for weather, time of day, and observer effects. By using sound recordings we were able to examine each survey thoroughly, thus controlling for bias due to observer effects or misidentification. However, the use of audio recordings allowed for accurate detection (or nondetection) at the species level only because individuals could not be accurately counted or tracked. We believe that the use of presence/absence data to address the utility of programs used to estimate trends in abundance is valid because the availability of a species during surveys is a function of the availabilities of individuals of that species (Royle and Nichols 2003). This study was designed to assess broad changes in the availability of birds, regardless of habitat. Our estimates of availability are likely higher than those encountered during BBS surveys because of our longer count period (Dawson et al. 1995, Thompson and Schwalbach 1995, Dettmers et al. 1999). However, because availability is a function of song rate, and thus phenology, we expect the seasonal changes of availability during BBS surveys to mirror our estimates. We believe that our availability estimates approximate availability during BBS surveys within Alabama and that the relationship between seasonal bird availability and BBS trends should hold for the BBS in general.

The timing of breeding of other animals (such as amphibians and butterflies) is also shifting in accordance with climate change (reviewed in Parmesan 2007). Many of these species are monitored by large-scale, annual surveys that may also be affected by changes in availability due to climate change (Weir et al. 2005, Kéry and Plattner 2007), reinforcing calls for all monitoring programs to incorporate the probability of detection into population estimates (e.g., Anderson 2001, Weir et al. 2005, Kéry and Plattner 2007). Furthermore, other bird-monitoring programs that use survey methods other than point counts, such as the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992), are also susceptible to changes in bird phenology because the data are collected between fixed dates every year.

Because song rate is correlated with nesting stage (Best 1981, Best and Petersen 1982, Wilson and Bart 1985) and pairing status (Sayre et al. 1980, Hayes et al. 1986, Gibbs and Wenny 1993), we can make inferences about the breeding phenology of migratory species based on availability at our study site (Slagsvold 1977). For instance, in the Louisiana Waterthrush, song rate peaks prior to pair formation (Craig 1981), so the falling availability curve that we observed for the Louisiana Waterthrush (Fig. 2) suggests that most male waterthrushes on our study site had paired prior to the beginning of our surveys. Similarly, the Acadian Flycatcher's song rate decreases after the young hatch (Wiley 2005), and the falling availability curve that we observed for the Acadian Flycatcher (Fig. 2) indicates that most of the young had hatched by June. Inferences about nesting stage deduced from availability curves must be made cautiously but may be useful when logistical constraints prohibit intensive nest searching and monitoring.

Our results suggest that, if global warming is causing birds to breed earlier, the availability of migratory species will decline during June. A change in availability over time may produce trends within datasets recorded between fixed dates every year. However, our data indicate that a decrease in availability is not producing the current trends in bird abundance observed in BBS data within the state of Alabama. The effects of changing phenology may have been offset in Alabama by survey dates shifting earlier within June. The effect of shifting phenology on bird availability and hence on trends in bird abundance should be tested in other regions of North America and on other sets of long-term data recorded within fixed dates.

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TABLE 1. Coefficient values (β) and standard errors (SE) in final models of bird availability, as well as deviance, the difference in AIC_c between a given model and the top-ranked model (ΔAIC_c), and model weights (w_i) for generalized linear mixed models examining bird availability in Tuskegee National Forest from late April through July 2008. Models represent hypotheses of unchanging availability (intercept), linear association with the week in which an observation was made (week), and quadratic association with the week in which an observation was made (week^2).

Species	Model	β(SE)	Deviance	ΔAIC_c[a]	w_i
Great Blue Heron	Week^2	–0.19 (0.119)	25.6	0 (34.68)	0.78
(*Ardea herodias*)	Week	1.62 (1.088)	30.78	2.73	0.20
	Intercept	–3.62 (2.341)	37.14	6.77	0.03
Red-shouldered	Intercept	–2.08[b] (0.306)	75.35	0 (79.46)	0.56
Hawk (*Buteo*	Week		74.72	1.49	0.27
lineatus)	Week^2		73.45	2.37	0.17
Mourning Dove	Intercept	–2.39[b] (0.485)	34.06	0 (38.28)	0.52
(*Zenaida macroura*)	Week^2		30.6	1.08	0.31
	Week		34.06	2.22	0.17
Yellow-billed	Intercept	–1.57[b] (0.24)	112.06	0 (116.16)	0.65
Cuckoo (*Coccyzus*	Week		112.06	2.1	0.23
americanus)[c]	Week^2		111.24	3.43	0.12
Red-bellied	Intercept	–1.6[b] (0.34)	64.1	0 (68.28)	0.65
Woodpecker	Week		63.79	1.88	0.26

(*Melanerpes carolinus*)	Week^2		63.61	3.94	0.09
Downy Woodpecker	Intercept	–2.31[b] (0.316)	25.6	0 (34.68)	0.78
(*Picoides pubescens*)	Week		30.78	2.73	0.20
	Week^2		37.14	6.77	0.03
Pileated Woodpecker	Intercept	–2.247 (0.581)	85.76	0 (89.85)	0.44
(*Dryocopus pileatus*)	Week		83.9	0.23	0.39
	Week^2		83.53	1.99	0.16
Eastern Wood-	Intercept	–1.45[b] (0.393)	40.9	0 (45.21)	0.58
Pewee (*Contopus*	Week		39.73	1.16	0.32
virens)[c]	Week^2		39.7	3.57	0.10
Acadian Flycatcher	Week^2	–0.06[b] (0.021)	129.3	0 (137.60)	0.99
(*Empidonax*	Week	0.61[b] (0.276)	140.41	8.99	0.01
virescens)[c]	Intercept	–1.429 (0.897)	157.27	23.76	0.00
Great Crested	Week	–0.29[b] (0.064)	124.14	0 (130.34)	0.56
Flycatcher	Week^2		122.48	0.48	0.44
(*Myiarchus crinitus*)[c]	Intercept	1.07[b] (0.468)	149.57	23.33	0.00
White-eyed Vireo	Week^2	–0.04[b] (0.015)	159.14	0 (167.45)	0.70
(*Vireo griseus*)[c]	Intercept	–2.76[b] (0.86)	165.91	2.56	0.20
	Week	0.58[b] (0.238)	165.2	3.93	0.10
Yellow-throated	Intercept	–1.68[b] (0.328)	60.89	0 (65.07)	0.69

Vireo (*Vireo*	Week		60.84	2.14	0.23
flavifrons)[c]	$Week^2$		60.74	4.29	0.08
Red-eyed Vireo	Week	–0.14[b] (0.043)	219.36	0 (225.50)	0.73
(*Vireo olivaceus*)[c]	$Week^2$		219.34	2.08	0.26
	Intercept	1.13[b] (0.48)	229.88	8.45	0.01
Blue Jay (*Cyanocitta*	$Week^2$	–0.07[b] (0.02)	139.33	0 (147.61)_	0.99
cristata)	Intercept	–3.94[b] (0.206)	154.64	11.11	0.00
	Week	0.95[b] (0.303)	154.26	12.81	0.00
Fish Crow (*Corvus*	Intercept	–1.15[b] (0.359)	104.15	0 (108.28)	0.47
ossifragus)	Week		102.51	0.5	0.36
	$Week^2$		101.84	2.01	0.17
American Crow	Intercept	–1.4[b] (0.038)	150.08	0 (154.16)	0.55
(*Corvus*	Week		149.07	1.07	0.32
brachyrhynchos)	$Week^2$		148.84	2.95	0.13
Carolina Chickadee	Intercept	–1.91[b] (0.224)	137.02	0 (141.09)	0.59
(*Poecile*	Week		136.32	1.37	0.30
carolinensis)	$Week^2$		136.2	3.34	0.11
Tufted Titmouse	Week	–0.1[b] (0.04)	224.1	0 (230.27)	0.57
(*Baeolophus bicolor*)	$Week^2$		223.1	1.04	0.34
	Intercept	0.16 (0.4)	229.8	3.61	0.09
Carolina Wren	Intercept	–0.23 (0.182)	243.64	0 (247.71)	0.65
(*Thryothorus*	Week		243.46	1.88	0.26
ludovicianus)	$Week^2$		243.44	3.96	0.09

Blue-gray Gnatcatcher (*Polioptila caerulea*)	Intercept	–1.54[b] (1.053)	153.03	0 (157.10)	0.66
	Week		153.03	2.08	0.23
	Week^2		152.53	3.68	0.11
Northern Parula (*Parula americana*)[c]	Week^2	–0.07[b] (0.026)	102.01	0 (110.35)	0.96
	Week	0.66[b] (0.333)	110.32	6.17	0.04
	Intercept	–2.26[b] (1.003)	120.05	13.8	0.00
Prothonotary Warbler (*Protonotaria citrea*)[c]	Week^2	–0.05 (0.048)	56.35	0 (65.01)	0.66
	Week	0.12 (0.551)	59.91	1.28	0.34
	Intercept	0.75 (1.39)	82.49	21.67	0.00
Pine Warbler (*Dendroica pinus*)	Week	–0.5[b] (0.168)	40.4	0 (46.77)	0.58
	Week^2		38.78	0.62	0.42
	Intercept	0.77 (0.761)	57.42	14.83	0.00
Louisiana Waterthrush (*Parkesia motacilla*)[c]	Week	–0.27[b] (0.129)	41.62	0 (47.93)	0.64
	Week^2		41.2	1.8	0.26
	Intercept	–0.71 (0.718)	47.47	3.7	0.10
Common Yellowthroat (*Geothlypis trichas*)	Week^2	–0.01 (0.0188)	82.77	0 (91.42)	0.39
	Week	0.27 (0.32)	85.52	0.49	0.31
	Intercept	–1.34 (1.26)	87.78	0.54	0.30
Hooded Warbler (*Wilsonia citrina*)[c]	Intercept	–1.53[b] (0.285)	78.83	0 (82.98)	0.42
	Week^2		75.16	0.69	0.30
	Week		77.46	0.78	0.28

Eastern Towhee (*Pipilo erythrophthalmus*)	Intercept	–1.5[b] (0.464)	40.75	0 (45.06)	0.66
	Week		40.74	2.31	0.21
	Week^2		39.18	3.21	0.13
Summer Tanager (*Piranga rubra*)[c]	Week^2	–0.11[b] (0.042)	71.12	0 (79.49)	0.99
	Intercept	–7.3[b] (2.335)	84.87	9.49	0.01
	Week	1.68[b] (0.637)	84.87	11.6	0.00
Northern Cardinal (*Cardinalis cardinalis*)	Intercept	–0.16 (0.213)	242.54	0 (246.61)	0.64
	Week		242.54	2.07	0.23
	Week^2		241.44	3.06	0.14
Indigo Bunting (*Passerina cyanea*)[c]	Week	0.11[b] (0.05)	160.01	0 (166.19)	0.61
	Week^2		159.97	2.08	0.21
	Intercept	–1.74[b] (0.508)	164.54	2.44	0.18
Red-winged Blackbird (*Agelaius phoeniceus*)	Week^2	–0.03 (0.037)	41.05	0 (49.84)	0.45
	Week	0.18 (0.474)	43.75	0.38	0.37
	Intercept	–1.79 (1.64)	47.48	1.88	0.18

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[a] Minimum AIC$_c$ value in parentheses.

[b] Confidence interval does not include zero.

[c] Migrant.

TABLE 2. Deviance, the difference in AIC_c between a given model and the top-ranked model ($\Delta\mathrm{AIC}_c$), and model weight (w_i) for general linear models describing the relationship between population trends according to the Breeding Bird Survey (BBS) and change in availability (Δ availability), migratory status, and both change in availability and migratory status (Δavailability + migratory status). Models were built from BBS data from 1967–2007 and 1978–2007 separately.

Interval	Model	Deviance	$\Delta\mathrm{AIC}_c$[a]	w_i
1967–2007	Intercept only	100.31	0.00	0.52
	ΔAvailability	97.14	1.47	0.25
	Migratory status	99.99	2.36	0.16
	ΔAvailability + migratory status	97.14	4.12	0.07
1978–2007	Intercept only	111.30	0.00	0.49
	ΔAvailability	106.53	1.10	0.28
	Migratory status	111.14	2.41	0.15
	ΔAvailability + migratory status	106.46	3.73	0.08

[a] Minimum AIC_c values are 128.80 for 1967–2007 and 132.03 for 1978–2007.

TABLE 3. Trends in the Breeding Bird Survey and associated variances 1967–2007 and 1978–2007 for the state of Alabama, as well as the change in the number of detections (Δdetections) per survey calculated as the difference between area under curves of observed availability and curves shifted 1 week later to estimate past availability[a].

Species	1967–2007	Variance	1978–2007	Variance	Δ Detections
Great Blue Heron	5.52***	1.25	5.37***	1.59	0
Red-shouldered Hawk	1.07	1.94	0.28	0.58	0
Mourning Dove	–1.38**	0.14	–2.41***	0.15	0
Yellow-billed Cuckoo[b]	–2.31***	0.04	–3.00***	0.08	0
Red-bellied Woodpecker	–0.04	0.14	–0.46	0.16	0
Downy Woodpecker	–1.83**	0.25	–2.09**	0.42	0
Pileated Woodpecker	1.35*	0.39	1.16	0.47	–0.08
Eastern Wood Pewee[b]	–2.35***	0.16	–2.26**	0.39	0
Acadian Flycatcher[b]	0.63	0.27	1.13*	0.21	–0.29
Great Crested Flycatcher[b]	1.58***	0.13	1.4**	0.17	–0.22
White-eyed Vireo[b]	0.76*	0.10	0.5	0.13	0.05
Yellow-throated Vireo[b]	0.58	0.77	1.56	0.71	0
Red-eyed Vireo[b]	1.23*	0.24	0.8	0.17	–0.14
Blue Jay	–2.38***	0.14	–1.78**	0.22	–0.04
Fish Crow	–1.10	1.53	–1.19	2.05	0

American Crow	0.29	0.95	1.04**	0.07	0
Carolina Chickadee	–1.95***	0.16	–3.01***	0.48	0
Tufted Titmouse	0.41	0.20	0.72	0.15	–0.09
Carolina Wren	0.33	0.09	0.65	0.11	0
Blue-gray Gnatcatcher	0.48	0.40	–0.34	0.64	0
Northern Parula[b]	1.15	1.06	0.44	0.79	–0.02
Prothonotary Warbler[b]	–3.79***	0.19	–3.63**	0.84	–0.34
Pine Warbler	0.37	0.19	–0.72	0.35	–0.10
Louisiana Waterthrush[b]	–0.29	2.48	–1.52	2.45	–0.06
Common Yellowthroat	0.03	0.68	0.58	0.54	0
Hooded Warbler[b]	2.28***	0.29	1.35*	0.27	0
Eastern Towhee	–0.86**	0.07	–0.51	0.13	0
Summer Tanager[b]	0.01	0.19	–0.5	0.13	–0.01
Northern Cardinal	–0.63**	0.04	–0.28	0.06	0
Indigo Bunting[b]	–0.67	0.13	–0.23	0.08	0.08
Red-winged Blackbird	–4.46***	0.26	–5.71***	0.22	–0.09

[a] Probabilities: *$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$

[b] Migrant.

FIGURE 1. Method for calculating changes in the number of detections per survey of the Acadian Flycatcher (a) and Great Crested Flycatcher (b). The change in the number of detections was calculated as the difference between the areas under the observed curve (solid) and the curve shifted a week later during the month of June.

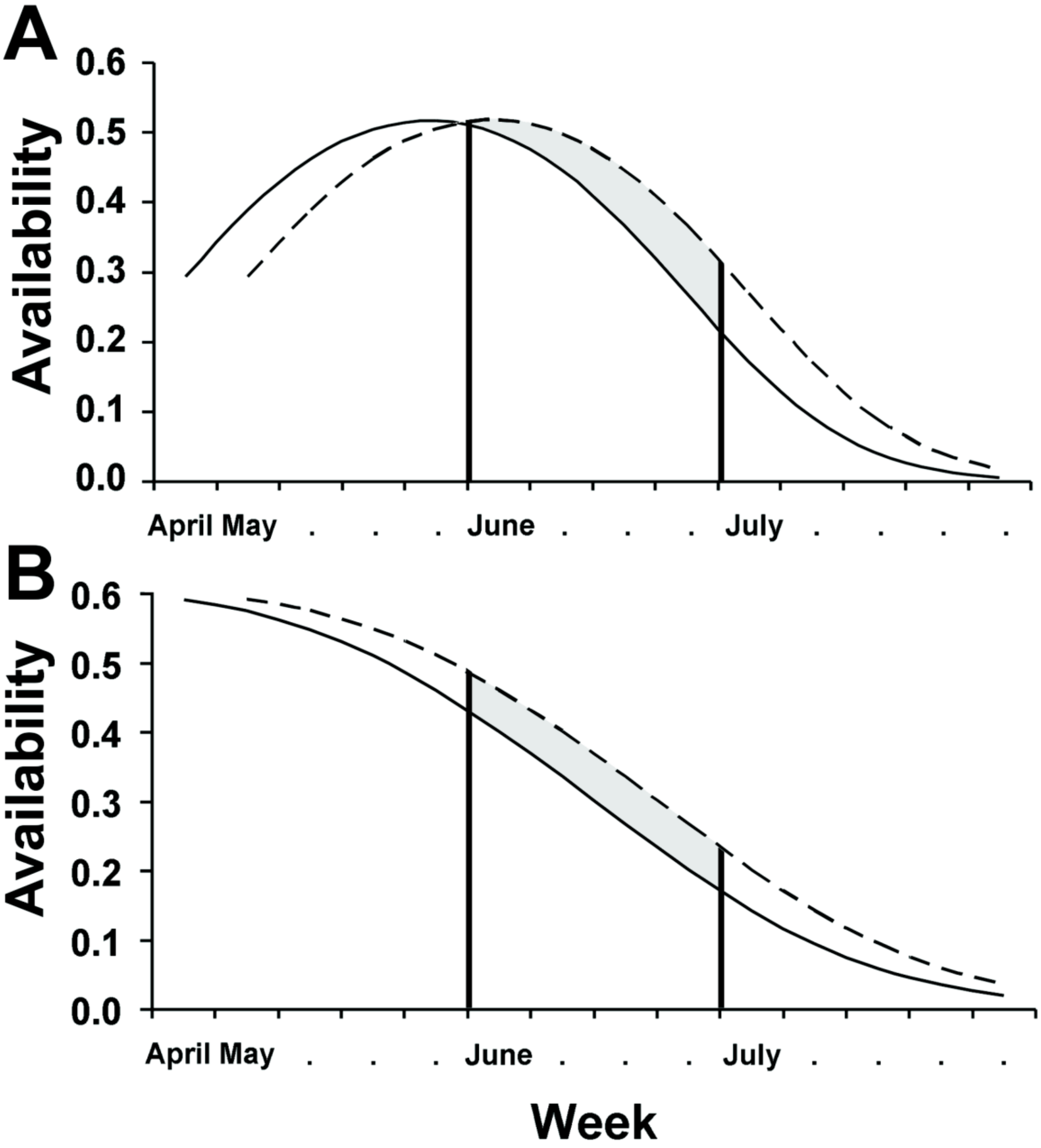


FIGURE 2. Results of generalized linear mixed models for birds showing changes in availability from late April through July 2008 in Tuskegee National Forest Alabama. Points represent the weekly average availability of a given species.

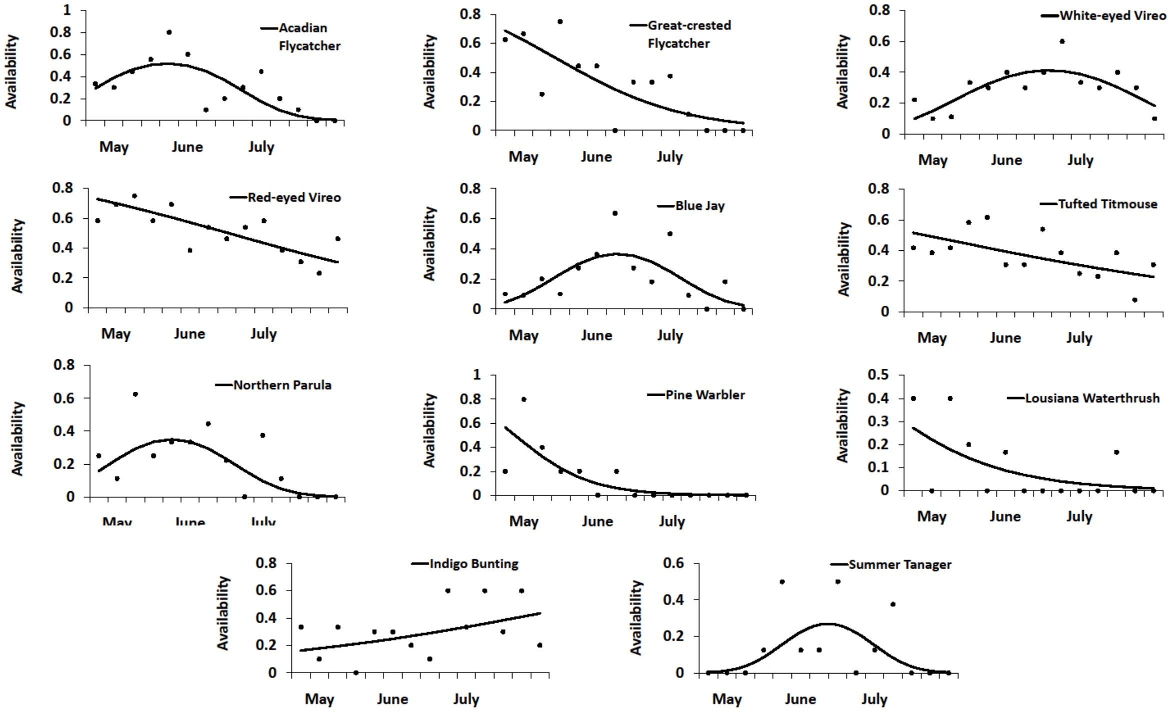
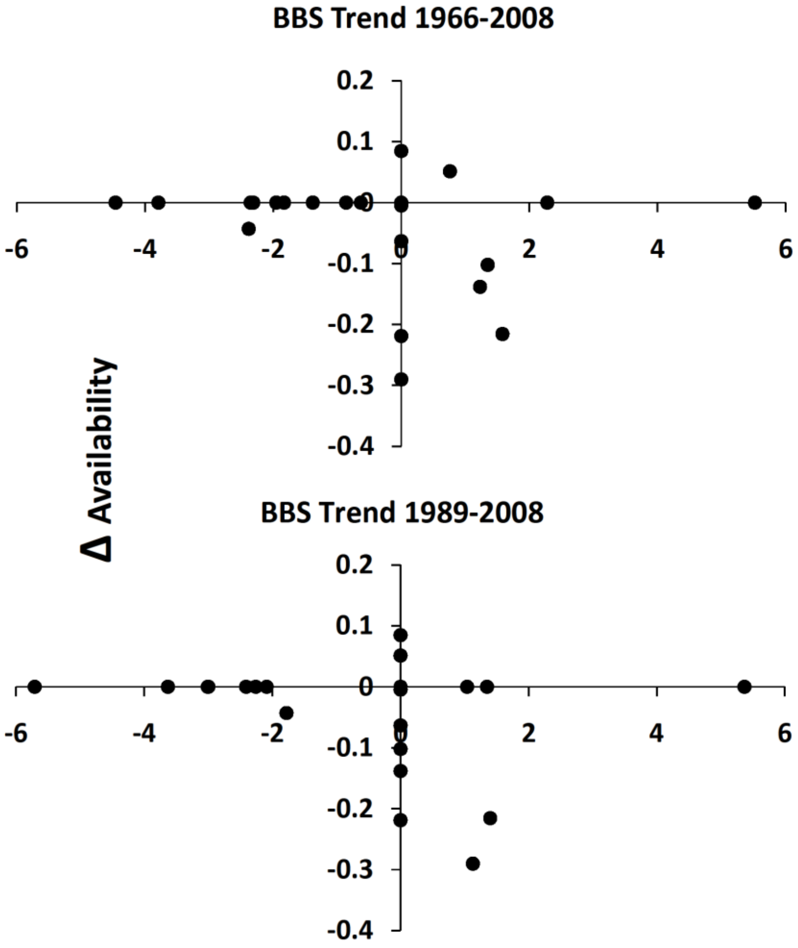


FIGURE 3. Scatterplot of population trends according to the Breeding Bird Survey (BBS) and the assumed changes in availability for each species analyzed.



CHAPTER III: EFFECTS OF SPECIES ECOLOGY AND URBANIZATION ON ACCURACY OF A COVER-TYPE MODEL: A TEST USING GAP ANALYSIS

Abstract

Models of vertebrate distributions based on dominant vegetation cover or land-use classification are commonly used for conservation planning, but these models may be inappropriate for species that choose sites using criteria other than land cover or within urban areas that are not adequately described by cover-type alone. We compared the accuracy of predicted occupancy of birds for a set of cover-type models—Alabama Gap Analysis Program's (ALGAP) vertebrate distribution maps—between urban and rural landscapes in east-central Alabama. We performed analysis at two scales of investigation—0.03-km^2 plots or 28.26-km^2 landscapes—using point counts conducted during summers 2004-2006. We tested ALGAP's ability to predict the occupancy of habitat by birds grouped by three life-history parameters: migrant, resident, insectivore, carnivore, and omnivore, forest dweller, and cavity nester. ALGAP performed well at the scale of entire landscapes, but poorly at the scale of individual point counts. At the point-count scale, ALGAP was least accurate for cavity nesting species that do not feed on insects. ALGAP also performed better in rural compared to urban sites at the landscape scale, and it had higher commission errors in the urban landscape. Variation in the ability of ALGAP to predict species occupancy was likely due to: 1) poor models when certain species chose sites using criteria other than cover type, and 2) the inadequacy of ALGAP to describe a heterogeneous urbanized landscape. Our results highlight pitfalls of using land cover information to model species distributions in situations where it may be inappropriate.

Keywords: birds, Alabama, insectivore, cavity-nester, land-cover, GAP analysis, land cover

1. Introduction

Models relating habitat to the occurrence of wildlife are commonly used to predict locations of animals based on land-cover information collected either remotely or by directly assessing a site (Morrison et al., 1998). Cover-type models are often built using expert opinion and assume that occupancy of an area by a species depends heavily on the response of that species to the dominant vegetation (Schlossberg and King, 2009). These models are commonly used to identify biodiversity "hotspots," prioritize areas to conserve, and predict the responses of wildlife to management (Scott et al., 1993). Because a great emphasis is often placed on such models, it is essential to have some means to validate their accuracy, and one means by which to test such models is to compare what the models predict to what is observed via direct observation. Testing models of animal distributions using independent datasets enables researchers to estimate overall accuracy and error rates (Fielding and Bell, 1997). It would be expected that cover-type models will perform with different success in different contexts, such as rural or urban environments, and for different categories of birds, such as insectivores or omnivores. Thus, it is important to test models for accuracy across different groups of birds in multiple contexts. In this way researchers can assess the contexts in which models are most appropriately used, when models are prone to errors, or even when inferences from the models are likely to be misleading (McPherson and Jetz, 2007).

Predictive weaknesses of models built to predict vertebrate distributions can often be anticipated based on the ecology of a given species (e.g., Kilgo et al., 2002; McPherson and Jetz, 2007; Mitchell et al., 2001) especially when the models are built using broad-scale information. Distributions of species associated with fine-scale aspects of habitat that are not readily captured by satellite imagery or land cover classifications may be poorly predicted (Fielding and Haworth, 1995). For instance, models describing distributions of habitat generalists often perform poorly compared to models applied to specialists (e.g., Hepinstall et al., 2002; Mitchell et al., 2001; Segurado and Araújo, 2004), possibly because generalists respond more to finer-scale, structural aspects of habitat (Pearson, 1993) which are not well-captured by land cover classifications or satellite imagery. Migratory status also affects performance of models of vertebrate distributions based on land cover classifications, with migrants often better predicted than resident species in North America (Flather and Sauer, 1996; Mitchell et al., 2001), and resident species better predicted than migrants in southern Africa (McPherson and Jetz, 2007). The difference in ability to predict the distribution of migrants versus residents may arise because migrants are adapted to certain cover-types or seral stages that experience seasonal fluctuations in food availability and therefore have relatively specialized habitat preferences (Sherry and Holmes, 1995). Further, distributions of species that occupy higher trophic levels may be influenced by unmodeled biotic interactions making their distributions difficult to predict using habitat characteristics alone (McPherson and Jetz, 2007).

Models built using satellite imagery or maps of land cover may also be poor at predicting distributions within some types of landscapes. For example, the National Land-Cover Database (Homer et al., 2004) classifies developed areas on a scale of low, medium, and high-intensity according to amount of impervious surface. Broad classification schemes such as those used by the National Land-Cover Database often fail to adequately capture heterogeneity (Cadenasso et al., 2007) or vegetative cover within urbanized or residential landscapes (Pennington and Blair, 2011). Thus, models built using only information from existing land cover maps may be missing information key to predicting the distribution of some species (Cadenasso et al., 2007; Pennington and Blair, 2011).

Gap Analysis Programs (GAP) use cover-type models to identify areas of high species diversity that are not currently protected by existing conservation lands (Jennings, 2000; Scott and Jennings, 1997). GAP creates models using literature review and expert opinion, then applies these models to vegetation maps such as the National Land-Cover Database (Homer et al., 2004) to predict distributions of species (Csuti and Crist, 1998; Scott and Jennings, 1997). GAP's standards call for the correct assignment of the presence or absence of a species within a sample area in 80% of judgments (Crist and Jennings, 2000; Csuti and Crist, 1998). However, a meta-analysis of cover-type models (mostly GAP) by Schlossberg and King (2009) showed that the presence of a species was correctly assigned in only 71% of judgments, on average. GAP models also often perform modestly in predicting species occupancy when compared to empirical models (e.g., Howell et al., 2008; Peterson, 2005) and, because GAP operates at a coarse spatial scale (1:100,000; Scott et al., 1993), tends to perform best at larger scales (Edwards et al., 1996; Schlossberg and King, 2009), potentially limiting their usefulness in smaller-scale applications.

Although the accuracy of predictions of species distributions by GAP do not meet GAP's standards, on average they may be more accurate for certain suites of species or within landscapes that are well characterized by maps of vegetative cover. Knowledge of the situations in which GAP analysis is best applied would help wildlife biologists and managers to use GAP to its maximum effectiveness. Our goal in this study was to assess and contrast the accuracy of Alabama GAP (ALGAP; Silvano et al., 2007) in predicting the distribution of bird species based on aspects of species ecology, such as migratory status, nesting guild, habitat specificity, and trophic level, as well as to compare ALGAP's predictive abilities in an urban and rural landscape.

We tested ALGAP's predictions at the scale of the individual survey location and at the scale of entire 28.26 km^2 study-sites. We predicted that ALGAP would have higher accuracy rates and lower commission errors in a rural versus an urban landscape. We further predicted that GAP would perform most poorly when predicting distributions of species such as generalists, residents, cavity nesters, and species occupying high trophic levels which we hypothesize choose sites based on characteristics other than cover-type, alone. We also predicted that ALGAP would perform better at the scale of the entire study sites than at the scale of the individual point counts.

2. Materials and Methods

2.1. Alabama GAP species distribution maps

The species distribution models from ALGAP are based on literature review and expert opinion. ALGAP incorporates patch size and forest edge/interior characteristics as well as cover-type into the modeling procedure (Silvano et al., 2007). ALGAP habitat models were applied to land-cover maps (Kleiner et al., 2007) to create species distribution maps for bird species within Alabama. The resulting maps are 30 m resolution binary matrices of suitable and unsuitable habitat (Silvano et al., 2007).

2.2. Study Sites

Our rural landscape was centered on Tuskegee National Forest (TNF), located on the northern edge of the East Gulf Coastal Plain. Our study sites were within a 3-km-radius circle centered in the southwest portion of the national forest (32° 25.899' N, 85° 38.637' W). These sites were selected for a mosquito and virus study with bird surveys added later (Estep et al., 2011). There is no reason our site selection should bias the results of the current study. TNF contains a variety of natural habitats including bottomland hardwood forest and upland longleaf pine forest. This study site contains < 0.1% urbanized area (defined as > 50% impervious surface) and 8% developed area (Kleiner et al., 2007). Within this study site, 373 bird survey points were established using a systematic grid with each point separated from the next closest point by roughly 250 m. Most survey points were within the national forest boundary, although several points fell within surrounding neighborhoods and farmland.

The urban landscape was the city of Auburn, AL, located within the East Gulf Coastal Plain roughly 20 km northeast of our rural site. Our study site was a 3-km-radius circle centered on the campus of Auburn University (32°35.517 N, 85°29.417' W). The study site contains an urban center as well as surrounding neighborhoods, parks, farmland and some forested land. This site contains approximately 18% urbanized area and 63% developed area (Kleiner et al., 2007). We established a grid of 439 bird survey points each separated by roughly 250 m.

2.3. Bird Surveys

Birds were surveyed by trained observers using point counts (Ralph et al., 1995) in which all birds encountered within a 100-m radius were recorded. Each point was surveyed for a total of 16 min. In the rural site all points were surveyed twice using 5-min counts in 2004 and twice using 3-min counts in 2005. In the urban site points were surveyed twice using 5-min counts in 2005 and twice using 3-min counts in 2006. We used 5-min counts during one year because Farnsworth et al. (2002) recommended 5-min counts when using their method to calculate detection probabilities. We used 3-min counts the next year due to logistical constraints. During 3-min point counts, the total number of individuals of each species observed was recorded. During 5-min point counts, the number of new individuals observed during each 1-min interval of the total 5-min session was recorded so that detection probabilities could be calculated following the approach of Farnsworth et al. (2002). All counts were conducted between 0500-1100 CST and between 26 May and 11 August each year and care was taken so that locations were not surveyed twice at the same time or date.

3. Statistical Analysis

3.1. Point Scale

We assumed that a species was predicted as present by ALGAP if ≥ 1 pixels within a 100-m buffer of each point were predicted as suitable habitat by ALGAP's vertebrate species distribution maps (Silvano et al., 2007). We also considered a species as present at a survey location if it was detected at that location during at least one survey, and absent if it was never detected. We then calculated accuracy as the percentage of bird survey locations where ALGAP's predictions matched presence or absence as determined by our bird surveys, commission error as the percentage of points where a species was predicted as present by ALGAP, but never detected, and omission error as the percentage of points where the species was predicted as absent, but was detected.

To test the hypotheses that ALGAP's accuracy, commission error, and omission error at the scale of individual surveys are affected by urbanization or ecological factors, we built general linear models containing binary factors indicating landscape (1 = urban, 0 = rural), migratory status (1 = migrant, 0 = resident), whether the species is associated with forest interior conditions, whether it nests in cavities, and whether it is an insectivore, carnivore, or omnivore as well as a covariate for the number of habitats used by the species. All ecological data were gathered from Hamel (1992). We built models representing all possible combinations of factors then ranked and compared models separately for accuracy, commission, and omission using Akaike's Information Criterion corrected for small sample size (AIC_c, Burnham and Anderson, 2002). We considered models as competitive for inference if they were within $\Delta AIC_c \leq 2$ of the best model and did not contain uninformative parameters (Arnold, 2010; Burnham and Anderson, 2002). If > 1 model was competitive, we model averaged across all competitive models to produce final models used for inference (Burnham and Anderson, 2002). We further considered ecological factors as useful for inference if their 95 % confidence intervals did not include zero (Chandler et al., 2009). We used an arcsine-square root transformation of all percentage variables to ensure normality.

3.2. Landscape Scale

We considered a species to be predicted as present by ALGAP if any pixel within the 3-km buffer was classified as present. We then used our point-count dataset to determine the overall accuracy as well as the commission and omission error rates within each landscape assuming that a species was observed as present if it was detected during any survey. The predictive measures for the two landscapes were then compared using Fisher's exact test. We also modeled accuracy and commission errors using logistic regression and the same factors and model building procedures described for the point-scale models. To control for uncertainty in commission error we included only species that were encountered at either site during the study period. For instance, American Woodcock (*Scolopax minor*) was predicted as present in both study sites but was never encountered, so it was excluded from analysis. All point- and landscape-scale statistical operations described above were performed using R version 2.13.1 (R Development Core Team, 2011).

3.3. Estimating Detection Probability

Our analyses of differences in accuracy and error rates between landscapes and ecological traits were potentially subject to bias if there were differences in the probability of detection of species between sites. For instance, a species may simply be more detectable in one landscape over another, biasing measures of accuracy and error rates. To address this possibility, we estimated detection probabilities for species at each site using the approach of Farnsworth et al. (2002). This approach uses a removal model, whereby the estimates of detection probability of a species during each interval of an observation session are obtained through maximization of a multinomial likelihood function conditioned on the total number of individuals of that species observed during the session (Farnsworth et al., 2002). We implemented this approach to estimation using program SURVIV. We fit the simplest model to the data for each species at each site; this model assumes no heterogeneity among individuals of the same species in detection. Species-sites combinations for which error messages resulted from attempts to fit with this simplest model were excluded from further analysis.

To determine if inference from this study could be affected by differences in species detection rates, we compared species' detectabilities within the urban and rural landscapes and across ecological traits. We used Spearman rank correlations to determine if the difference in detectability between sites is correlated with the difference in accuracy, commission, and omission error rates. Further, using Spearman rank correlations, we tested whether a species' average detectability across landscapes (urban and rural) was correlated with overall accuracy, commission and omission error rates, as well as ecological traits. We also used a binomial test to determine whether differences in detection caused species to be observed in one landscape over another by determining how many species were, in fact, observed in the landscape in which they were more detectable, but not in the other.

4. Results

Overall, 92 bird species were detected including 77 in the urban landscape and 88 in the rural landscape. European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) were not modeled by ALGAP and were not included in the analysis. There were 59 and 48 species detected at > 9 survey points within the rural and urban landscapes, respectively. Overall accuracy at the scale of the point counts was 0.47 (SE = 0.02), commission error was 0.45 (SE = 0.02) and omission error was 0.03 (SE = 0.01). There were two competitive models for accuracy at the point count scale. We therefore used model averaging to create the final model of accuracy at the scale of the individual point counts. This model included a negative association with cavity nesters and number of habitats with which a species is associated and positive associations with forest species and insectivores (Table 1, Fig. 1), although the confidence intervals for cavity nesters and insectivores were the only ones that excluded zero. There were two competitive models describing commission errors at the scale of the point counts. Model averaging of parameter estimates resulted in a final model for commission error at the point count scale, which included positive associations with number of habitats and cavity nesters, and negative associations with forest birds, carnivores and the urbanized landscape, although the confidence intervals for number of habitats and carnivores included zero (Table 1). The only competitive model for omission error at the scale of the point counts included positive associations with omnivores and insectivores, and a negative association with cavity nesters, with all confidence intervals excluding zero (Table 1)

GAP performed much better at the scale of the landscape than at the point count scale. The urban landscape had an overall accuracy of 0.82 and the rural landscape had an overall accuracy of 0.95 (Table 2). Fisher’s exact test showed a significant difference in ALGAP’s accuracy between the two sites (p = 0.007). Commission error rates were significantly higher in the urban site (0.13) than in the rural site (0.03, $p = 0.024$, Table 2). The only competitive model for accuracy at the level of the landscape included a positive association with number of habitats and negative association with the urbanized landscape: confidence intervals for both parameters excluded zero (Table 1). The only competitive model for commission error included a positive association with the urbanized landscape with confidence intervals excluding zero (Table 1).

One-minute detection probabilities were calculated for 75 species. Extending 1-minute detection probability estimates (p_1) to 16-minutes, the total length of time of observations at each point over the course of the study, the total detection probability—or probability of detecting an individual of a given species during our 16-mins of surveying, given that it is present—for a species-site combination equals $1- (1-p_1)^{16}$ (MacKenzie et al., 2002). Estimates of this total 16-minute detection probability averaged 0.99 (SE = 0.01, n = 66) for species in the rural landscape and 0.97 (SE = 0.02, n = 53) for species in the urban landscape. Differences in detection between landscapes were not correlated ($p > 0.05$) with differences in accuracy ($r < -0.01$), commission ($r = 0.12$), or omission ($r = -0.15$) error rates. Average detectability of species across landscapes was not correlated with cavity nesters ($r = -0.12$), forest birds ($r = 0.06$), migrants ($r = 0.15$), number of habitats ($r = 0.15$), insectivores ($r = -0.10$), omnivores ($r = 0.21$), carnivores ($r = 0.02$), or scavengers ($r = -0.16$). At the landscape scale, only 10 of 45 species were detected in the landscape in which they were most detectable, and not in the other landscape, significantly lower than would be expected by chance (binomial test: $p < 0.001$). We were therefore able to reject the hypothesis that observed differences in ALGAP's predictive abilities were due to heterogeneity in probability of detection.

5. Discussion and Conclusions

The distributions of species predicted by cover-type models such as GAP are commonly used in conservation plans and actions (Rondinini et al., 2005; Scott et al., 1993). Although many GAP models have been tested broadly (Schlossberg and King, 2009), no study has determined whether the accuracy of these models is dependent on the ecology of target species or the type of landscape to which the models are applied. In this study we sought to determine the accuracy of GAP models when they are applied to species or landscapes that vary in how well they are characterized by land-cover maps.

In our assessment of ALGAP we found that the model performed poorly at the scale of a point count (0.03 km^2) having an average accuracy of 0.47, slightly worse than random. Therefore, ALGAP is likely of limited use at this scale. In contrast, ALGAP performed well at the scale of the entire study site (28.26 km^2) having accuracy rates higher than GAP's standard of 0.80 (Crist and Jennings, 2000; Csuti and Crist, 1998) within both the rural and urban landscapes. In fact, within the rural landscape, ALGAP had a higher accuracy (0.95) than any model reported by Schlossberg and King (2009). These observations support past research showing similar models performing best at larger scales (Edwards et al., 1996; Schlossberg and King, 2009). Although these results are perhaps not surprising, it is important to clearly show the problems inherent in using GAP at fine scales. Overall, our assessment suggests that ALGAP is best used at larger scales, in efforts such as identifying areas for preserves or when predicting large-scale responses to changes in land use or climate.

Although, on average, ALGAP performed poorly at the point count level, some species were still predicted relatively well. Important inference into the usefulness of the methodology used by GAP can be made if errors are associated with certain suites of species whose ecology may not be adequately explained by GAP's models. Accuracy of ALGAP at the level of individual point counts was highest for insectivores that do not nest within cavities, and lowest for cavity nesters that are not insectivores. Increased accuracy for insectivores may be because they are associated with particular vegetation-types that are apparent on maps of land cover and that experience seasonal fluctuations of insect abundance (MacArthur, 1959). Although ALGAP did relatively well predicting the distribution of insectivores, the significantly higher rate of omission error for insectivores suggests that ALGAP is still under-predicting distributions of species in this guild.

The relative ability of ALGAP to predict occurrence of insectivores stands in contrast to its poor performance in predicting birds that nest in cavities. Cavity nesting birds necessarily choose nesting sites based, at least in part, on the presence of nesting cavities or substrates in which to create them (Brawn and Balda, 1988; Raphael and White, 1984). The poor performance by ALGAP in predicting presence of cavity nesters may be because the presence of snags and cavities cannot be determined by the 30-m pixels used by ALGAP. Also, distributions of secondary cavity nesters—species that do not create their own cavities—are partly dependent on the distribution of the primary cavity nesters that create cavities (e.g., Blanc and Walters, 2008; Martin et al., 2004; Martin and Eadie, 1999). Such biotic interactions may be important in determining the presence of cavity nesting birds but are not considered in GAP analysis. Further, errors of commission and omission by ALGAP were significantly higher for species that nest in cavities, but the effect was far greater for errors of commission, corroborating the assertion by Lawler and Edwards (2002) that when models do not include fine-scale aspects of habitat they will likely over-predict occupancy of cavity nesting species.

Other patterns of errors by ALGAP committed at the scale of individual bird surveys provide further inference. Omnivores were significantly under-predicted by ALGAP when compared to species with more specific food preferences. Omnivores are generalists in their food requirements, which may cause them to be more wide-ranging and unpredictable in their occurrence at a fine scale. Also, commission errors were significantly higher for forest birds when compared to birds that do not require forests, suggesting that ALGAP over-predicts occupancy by species that require extensive forest. Over-prediction of forest bird occupancy may be because forest birds often choose sites base on small scale attributes such as vegetation structure (MacArthur and MacArthur, 1961) which is not incorporated into GAP's models.

Migratory status was not correlated with accuracy or error rates at either scale of investigation. Past studies have found that models built using broad-scale information are more accurate when predicting Neotropical migrant distributions when compared to residents (Flather and Sauer, 1996; Mitchell et al., 2001). Most Neotropical migrants are insectivores (Rotenberry et al., 1995), so other studies may have had success in predicting migrant species due their insectivorous nature. Further, our study may not have detected an effect of migratory status because we account for insectivory.

At the scale of the landscape, accuracy was significantly higher in the rural area and commission errors were higher in the urban area, supporting the hypothesis that maps of land cover used by GAP do not describe urban areas as well as rural areas (Cadenasso et al., 2007). At the scale of individual bird surveys, however, commission errors were higher within the rural landscape suggesting that more patches of habitat go unfilled in a relatively homogeneous landscape. Another unexpected result was that the accuracy of the model at the landscape level was positively correlated with the number of habitats that a species can occupy. Contrary to other models (e.g, McPherson and Jetz, 2007; Mitchell et al., 2001; Segurado and Araújo, 2004) ALGAP was more likely to predict the presence or absence of species, within a landscape, that were generalists in their habitat preferences. Our results may differ from some other studies because of the nature of the models tested. Empirical models may have difficulty predicting distributions of habitat generalists because there is little variation in their occupancy across a study site, making it difficult to statistically discern habitat preferences (Brotons et al., 2004). However, Kilgo et al. (2002) and Dettmers et al. (2002) both tested a cover-type model built using expert opinion (Hamel, 1992) and found that it performed better when predicting habitat specialists over generalists. The differences between the Kilgo et al.(2002) and Dettmers et al. (2002) studies and our study are again likely attributable to scale. Kilgo et al.(2002) and Dettmers et al. (2002) were testing predictions at the individual stand level, whereas we tested predictions at a larger scale of 28.26 km^2 study sites. Generalists may move around a landscape to the extent that their occupancy of any given patch is hard to predict. In contrast, it may be much more reliable to predict that they will occur somewhere within a large patch of habitat, and that is essentially what we found in this study.

It is essential to test models against independent data to assess their predictive abilities (Fielding and Bell, 1997), but independent survey data are not without their own errors. For instance, we used point-count data collected 2004-2007 to test maps built from habitat data collected in 2001. Because maps of land cover are updated roughly once every ten years, GAP analysis will rarely be completely up-to-date. Therefore, use of point counts conducted concurrent with collection of land-cover data would not present a test of GAP’s usefulness in real-world applications. Further, heterogeneity in the probability of detection across species and sites can confound model performance (Boone and Krohn, 1999; Schaefer and Krohn, 2002; Schlossberg and King, 2009). Species with lower probabilities of detection are less likely to be recorded and thus may have artificially inflated commission errors (Boone and Krohn, 1999;

Schaefer and Krohn, 2002). Our analysis of bird detection rates shows that, among the species analyzed, average detection rates were extremely high at both sites (rural = 0.99, urban = 0.97). Our results also show that detection rates were not correlated with ecological traits or landscape context. Therefore, we believe that it is unlikely that any of our results are artifacts of imperfect detection and that our point-count data provide a valid test of ALGAP's predictive abilities.

When testing a model it is important to remember that utility is not determined by how well it describes the "truth," but by its usefulness in answering a specific question (Starfield, 1997). Our results highlight the pitfalls of using cover-type models to predict distributions of birds in certain situations. Collecting habitat information that is not captured in the land cover maps used by GAP would likely improve accuracy in some situations. However, GAP vertebrate distribution maps are built to identify areas that contain high biodiversity, at a large scale, thus helping to prioritize areas to set aside for conservation (Jennings, 2000; Scott and Jennings, 1997). At a large scale, ALGAP performed well, exceeding GAP's standard of 80% accuracy in both a rural and an urban landscape. With scarce conservation funding available, cover-type models will likely become more attractive compared to empirical models, or models that incorporate fine-scale attributes of habitat. Therefore it is important, moving forward, to understand where cover-type models are most useful, and not apply them in contexts for which they are inappropriate.

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Table 1. Coefficient estimates (β) and Akaike weights (w_i) for variables in models describing the relationship between the accuracy, commission error rates and omission error rate of Alabama Gap Analysis Programs maps of breeding bird distributions at the scale of individual point counts and the landscape. Models shown were built by building models containing all possible combinations of predictor variables and then model averaging across all models with ΔAICc ≤ 2 which did not contain uninformative parameters. Values in parentheses are standard errors.

Point count scale

Accuracy	β_0	Cavity	Forest	Habitats	Insectivore	Omnivore	Carnivore	Site
β	0.8 (0.07)	-0.2 (0.07)	0.07 (0.05)	-0.01 (0.01)	0.13 (0.06)			
w_i	1.00	0.95	0.69	0.99	0.86			
Commission								
β	0.73 (0.08)	0.24 (0.07)	-0.21 (0.06)	0.01 (0.01)			-0.08 (0.06)	-0.12 (0.05)
w_i	1.00	0.99	0.99	0.99			0.65	0.80
Omission								
β	0.06 (0.02)	-0.07 (0.03)			0.07 (0.03)	0.09 (0.03)		
w_i	1.00	0.93			0.76	0.74		

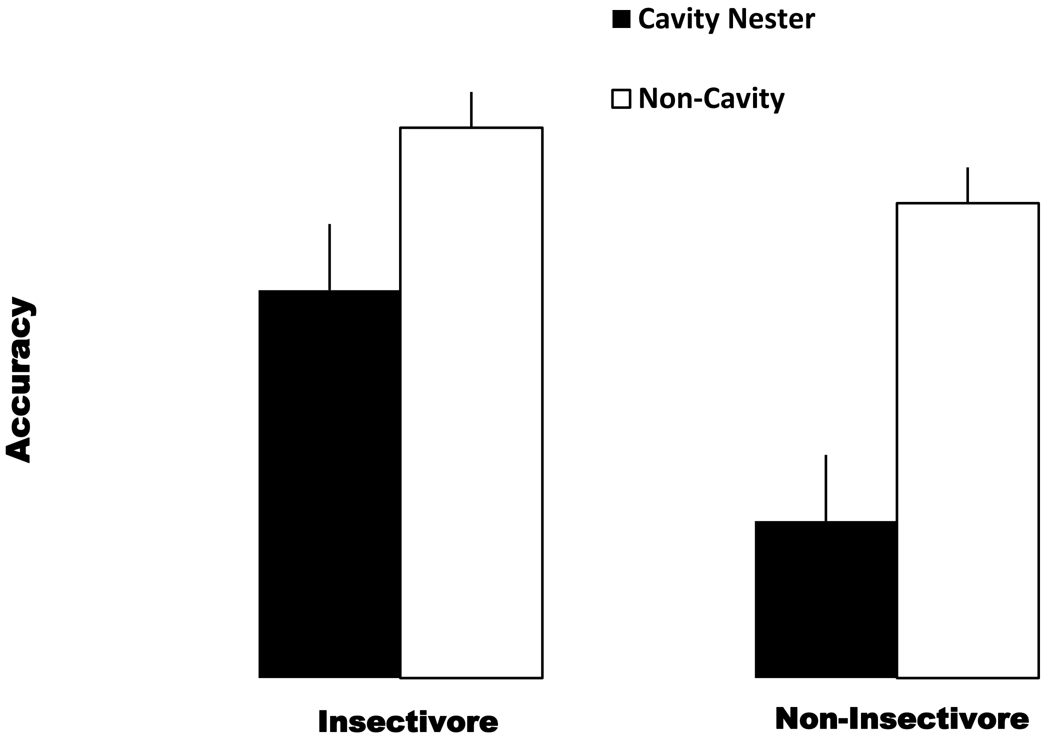
Landscape Scale

Accuracy	β_0	Cavity	Forest	Habitats	Insectivore	Omnivore	Carnivore	Site
β	2.03 (0.65)			0.11 (0.05)				-1.66 (0.59)
w_i	1.00			0.99				0.98
Commission								
β	-3.39 (0.59)							1.5 (0.66)
w_i	1.00							0.89

Table 2. Contingency table for the overall accuracy, commission, and omission errors of Alabama Gap Analysis Program's maps of breeding bird distributions within an urban site in Auburn, AL and a rural site in Tuskegee National Forest, AL.

	Site	Correct	Incorrect	Fisher's Exact Test
Accuracy	**Urban**	75	17	*p* = 0.007
	Rural	87	5	
Commission	**Urban**	71	11	*p* = 0.024
	Rural	86	3	
Omission	**Urban**	4	6	not calculated
	Rural	1	2	

Fig. 1. Average (SE) accuracy values for Alabama Gap Analysis Program's maps of breeding bird distributions (Silvano et al., 2007) for insectivorous and cavity-nesting bird species at Auburn, AL and Tuskegee National Forest, AL 2004-2006.



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

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 larger scale habitat, which can be determined from remotly-sensed imagery. To assess the importance of microhabitat information in constructing predictive models of habitat occupancy, we compared occupancy models built using 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 conducted during winter 2009. We observed that models built using only macrohabitat data outperformed models built using only microhabitat data for 5 of the 6 species analyzed. However, the best model for every focal species included both macro- and microhabitat covariates. Pine forests—excluding plantation—were the only landcover classification important to our focal species and measures of density of vegetation were important in predicting occupancy. Our results suggest that wintering migrants within 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 collection of 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

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. 2010). 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 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 non-breeding areas. Migratory bird species use different geographical areas for breeding, during the non-breeding season, and for moving between the two areas (Martin and Finch 1995), 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, non-breeding 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; Sherry and Holmes 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. 2010).

Given the need to identify and preserve habitat, it is important to determine what aspects of an area signify its quality as habitat. Habitat can be defined as the 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 environment, including availability of food, nest sites, cover, and competitors, interact with behavior and morphology of an individual 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 are difficult to obtain (Johnson 2009).

Information regarding distributions of animals, such as occupancy and density, is relatively inexpensive to obtain compared to parameters 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, it is important to determine what aspects of an area influence occupancy of organisms.

Another challenge related to understanding the habitat requirements of birds is identifying the scale at which habitat selection occurs (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 selection of habitat as a spatially hierarchical process for birds. Individuals first select at the macrohabitat scale within the geographic range of the species (Johnson 1980; Hutto 1985) and then, within broad vegetation types, individuals select specific patches of habitat for home range establishment (Johnson 1980; Hutto 1985). Within its home range, an individual must then choose in which microhabitat to forage and spend time (Johnson 1980; Hutto 1985).

Hutto (1985) suggested that 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 the habitat needs of birds (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 presence of bird species (Hagan and Meehan 2002). There is disparity, however, in the cost of information regarding microhabitat versus macrohabitat. 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 it could be shown that microhabitat information did not improve the inference gained from occupancy models.

In this study, we used occupancy models to determine the use of habitats by migratory bird species during winter within Tuskegee National Forest (TNF), 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 TNF for the non-breeding period. Birds wintering in the southeastern 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 TNF. We had two primary goals in this study: 1) to develop habitat occupancy models to predict where our focal species will occur during the non-breeding 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, AL (32° 25.899' N, 85° 38.637' 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 using five consecutive four-min point counts 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. Bird surveys were conducted 28 January – 28 February 2009 and between 0600 and 1400 CST according to the recommendations of Rollfinke and Yahner (1990).

MACROHABITAT

Percent cover of each landcover class within a 100-m buffer was calculated with ArcGIS (ESRI 2008) 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). Subclassifications of broad landscape classes were combined following McClure et al. (*in press*). For instance, 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 subclassifications were combined to form a broad, scrub classification; pasture and row-crop subclassifications were combined to form an agricultural classification; subclassifications of pine forests were combined to form pine and natural pine (which excludes plantations) classifications; and, floodplain and mesic slope forests were combined to form a hardwood classification (Table 2 in McClure et al. *in press*).

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 diameter at breast height (dbh) and species of all trees ≥10 cm dbh (Avery 1975). Canopy and ground cover were measured using a densitometer by sampling every 4 m along 16-m transects in all cardinal directions from 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 density of midstory, shrub, and understory using a striped, 12-m modified Robel-pole in the center of each plot (Mills et al. 1991). Observers recorded number of stripes obscured by vegetation at 0-0.6-m, 0.6-4.6-m, 4.6-7.6-m, and 7.6-12-m height intervals (MacArthur and MacArthur 1961) in each cardinal direction from the edge of the plot. Diameter at breast height measurements were made in 2008 and 2009. All other measurements were made during the same time-frame as 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. We calculated the ground layer, lower-shrub, upper-shrub, and mid-story thickness as the average percentage of Robel-pole readings from 0-0.6, 0.6-4.6, 4.6-7.6, and 7.6-12-m intervals along the pole (respectively) at each plot.

STATISTICAL ANALYSES

We used a two-step approach to model bird habitat using 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 used five consecutive sampling occasions, there is a chance of temporal autocorrelation; a bird being observed in time *t* may be conditional on it being heard in time *t*-1. Therefore, we also considered a binary covariate that indicated if a species was detected in *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 Blue-headed Vireos (Latin names are provided in 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). This final detection model was then incorporated into all subsequent models. Next we examined use of macrohabitat using 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 $QAIC_c$. We then used the same stepwise procedure described above to model occupancy using only microhabitat covariates that were hypothesized a priori (Table 2) to affect habitat use.

Next, we incorporated hypothesized microhabitat covariates into the macrohabitat models using 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 the final macrohabitat model. Analysis was performed for each focal species separately. We 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 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 only analyzed 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, and 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 using the same dataset we used to build the models, AUC values should be interpreted as a measure of model fit, not predictive ability (Seavy and Alexander 2011). We calculated AUC values using the ROCR package (Sing et al. 2005) in the R statistical programming environment (R Development Core Team 2008).

RESULTS

We detected 16 species of wintering migrants during our bird surveys. Six species were detected on enough sites (>10) to be analyzed (Table 3). We first assessed factors that affected the detectability of species. Detection of Blue-headed Vireo, Hermit Thrush, and Ruby-crowned Kinglet was affected by time of day (Table 2). Yellow-rumped Warbler and Ruby-crowned Kinglet were more likely to be detected if they were detected in the previous occasion. Date and wind speed only affected detection of Yellow-rumped Warbler. And detection of Ruby-crowned Kinglet and Yellow-rumped Warbler differed among observers.

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

White-throated Sparrow was the only focal species not positively associated with natural pine forests (Fig. 1, Table 2). Golden-crowned Kinglet was also positively associated with canopy cover within the vegetation plots, negatively associated with total basal area, and showed a quadratic association with thickness of shrub layer. Hermit Thrush showed a quadratic relationship with depth of leaf litter, a positive relationship with midstory thickness, and a negative association with scrub areas. Ruby-crowned Kinglet was positively associated with canopy cover within 100 m, and negatively associated with basal area of pine. White- throated Sparrow was negatively associated with canopy cover within 100 m and midstory thickness, and positively associated with developed open space. Yellow-rumped Warbler and Blue-headed Vireo 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 Hermit Thrush and Ruby-crowned Kinglet were considered useful (AUC > 0.7) and final models for Blue-headed Vireo, Golden-crowned Kinglet, Yellow-rumped Warbler, and White-throated Sparrow were considered 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 this 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. Further, AUC values revealed that our models fit the data well (AUC > 0.7). Thus, it appears that once wintering migrants settle in a certain land cover classification, they further select habitat based on structural or floristic aspects of an area (Hutto 1985), making it important to include both macro- and microhabitat data when assessing the occupancy of wintering migrants.

Wintering migratory birds within our study site used pine forests more than any other classification of land cover. Five of the six species analyzed—Blue-headed Vireos, Ruby- and Golden-crowned Kinglets, Yellow-rumped Warblers, and Hermit Thrushes—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 Ruby- and Golden-crowned Kinglets were positively associated with canopy cover. Further, 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 were most abundant in 10 year old pine stands with abundance declining as stands matured. In Georgia, wintering Golden-crowned Kinglets were less abundant in mature pine stands than they were in younger stands that have less basal area, although Ruby-crowned Kinglets showed no preference (White et al. 1996). 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 US prefer mid-stage pine forests, and suggest that Ruby-crowned Kinglet also prefers younger pine forests.

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

Yellow-rumped Warblers and Hermit Thrushes wintering in our study site also preferred pine forests with certain structural aspects. Hermit Thrushes preferred intermediate leaf-litter, likely because they often forage on the ground (Hamel 1992), and Yellow-rumped Warblers chose sites with increasing basal area of oaks. The association of Yellow-rumped Warblers with oaks may reflect a preference for moist, low-elevation areas (Hamel 1992) within pine forests.

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

Realistic inference into patterns of habitat use by a given species often requires multiple scales of investigation (Wiens 1989c; Knick and Rotenberry 1995). 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 when designing studies. 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, is important in the assessment of occupancy of migrants wintering in the southeastern US.

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TABLE 1. Abbreviations, averages, standard deviations (SD), and maximum values recorded for habitat variables collected 28 January – 28 February 2009.

Variable	Abbreviation	Average	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

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[a] collected from (Kleiner et al. 2007)

[b] collected from (Homer et al. 2004)

Table 2. Coefficient values (SE) for the intercept (β_0) and habitat covariates within final models of occupancy (Ψ) and detection (*p*) of wintering migrants within Tuskegee National Forest, Alabama 28 January – 28 February 2009. Zeros indicate that a covariate was considered for model building but was not included in the final model. Abbreviations of habitat covariates are presented in Table 2.

Ψ	Blue-Headed Vireo	Golden-crowned Kinglet	Ruby-crowned Kinglet	Hermit Thrush	Yellow-rumped Warbler	White-throated Sparrow
β_0	-6.68 (1.92)	-1.62 (3.13)	-7.89 (2.96)	-2.78 (1.29)	-6.1 (2.33)	13.06 (6.48)
Npine	4.66 (1.54)	11.11 (3.36)	2.2 (0.9)	1.02 (0.76)	7.04 (2.62)	
Pine				0		0
Hard	0	0	0	0	0	0
Mix	0	0	0	0	0	0
Scrub	0	0	0	-3.67 (2.43)	0	0
Ag	0	0	0	0	0	0
Flood				0	0	
Dev	0	0	0	0	0	0
DOS						6.58 (3.56)
Can	0	0	6.17 (2.77)	0	0	-11.89 (5.45)
*GC	2.28 (1.13)			0		0

*Ground	0			0		0
*Ground^2						
*Shrub		-21.07 (5.35)	0	0	0	0
*Shrub^2		14.78 (3.53)	0		0	
*Hi Shrub	0	0	0	0	0	0
*Hi Shrub^2	0	0	0		0	
*Mid	0	0	0	-1.27 (0.67)	0	-2.77 (1.51)
*Mid^2	0	0	0		0	
*CC	0	4.28 (2.1)	0	0	0	0
*CC^2	0	0	0	0	0	
*LL				19.15 (8.52)		0
*LL^2				-31.29 (15.04)		
*BATot	0	-5 (1.56)	0	0	0	0
*BAOak					7.09 (3.33)	
*BAPine	0	0	-1.06 (0.61)		0	

P	Blue-Headed Vireo	Golden-crowned Kinglet	Ruby-crowned Kinglet	Hermit Thrush	Yellow-rumped Warbler	White-throated Sparrow
β_0	0.67 (0.97)	-1.35 (0.28)	0.6 (0.66)	-2.29 (0.6)	-24.09 (1.3)	-1.79 (0.32)

t-1	0	0	0.47 (0.35)	0	1.23 (0.35)	0
time	-3.93 (2.55)	0	-2.64 (1.1)	3.88 (1.54)	0	0
date	0	0	0	0	55.01 (3.21)	0
wind	0	0	0	0	-3.37 (1.65)	0
Observer 1	0	0	-1.46 (0.66)	0	-0.54 (0.7)	0
Observer 2	0	0	0.15 (0.39)	0	0.66 (0.42)	0

*microhabitat variable

Table 3. Common name (*latin name*), number of detections (*n*), and naïve occupancy rate (Ψ) of wintering migrants detected within Tuskegee National Forest, Alabama from 28 January – 28 February 2009.

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

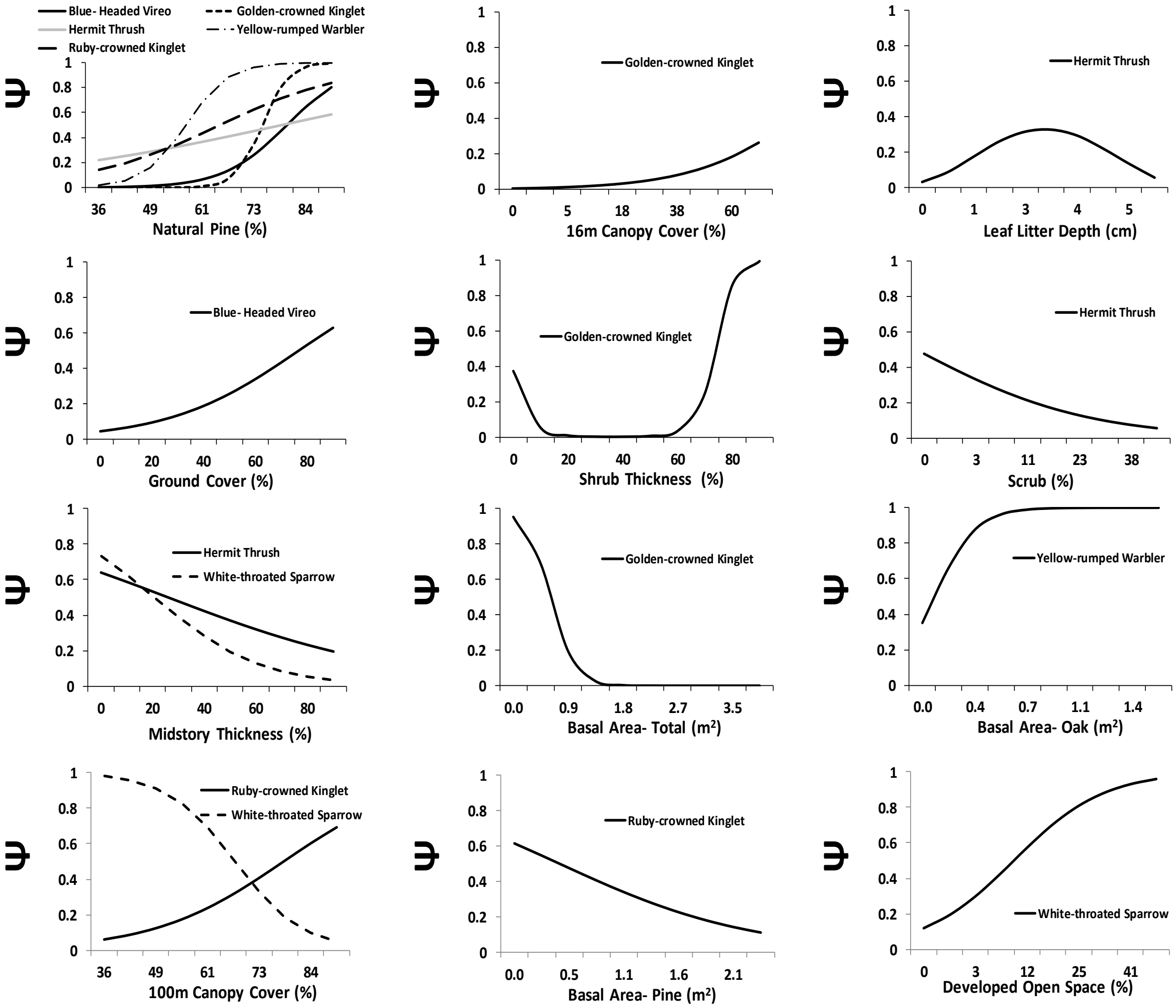
Table 4. AIC$_c$, ΔAIC$_c$, model weights (w$_i$), and area under receiver operating characteristics curves (AUC) for models describing occupancy of wintering migrants within Tuskegee National Forest, Alabama 28 January – 28 February 2009. Models were either built using macrohabitat covariates (macro), microhabitat covariates (micro) or both macro- and microhabitat covariates (macro+micro).

bird	model	ΔAIC$_c$^{a}	w$_i$	AUC
Blue- Headed Vireo	macro+micro	0	0.7	0.841
	macro	1.74	0.29	
	micro	12.22	0	
Golden-crowned Kinglet	macro+micro	0	0.99	0.884
	macro	9.35	0.01	
	micro	12.99	0	
Ruby-crowned Kinglet	macro+micro	0*	0.56	0.737
	macro	0.53*	0.43	
	micro	6.82*	0.02	
Hermit Thrush	macro+micro	0	0.48	0.757
	macro	1.08	0.28	
	micro	1.39	0.24	
Yellow-rumped Warbler	macro+micro	0*	0.81	0.817
	macro	3.37*	0.15	
	micro	5.89*	0.04	

White-throated Sparrow	macro+micro	0*	0.49	0.852
	micro	0.54*	0.37	
	macro	2.53*	0.14	

*ΔQAIC$_c$, [a] Minimum AIC$_c$ values were 157.69 for Blue-headed Vireo, 156.33 for Golden-crowned Kinglet, 330.19 for Ruby-crowned Kinglet, 231.23 for Hermit Thrush, 264.61 for Yellow-rumped Warbler, and 138.37 for White-throated Sparrow.

FIGURE 1. Relationship between probability of occupancy (Ψ) and habitat covariates within final models of occupancy of wintering migrants within Tuskegee National Forest, Alabama 28 January – 28 February 2009. Only estimates with 85% confidence intervals that exclude zero are shown.



V. DYNAMIC VERSUS STATIC OCCUPANCY: HOW STABLE ARE BIRD-HABITAT ASSOCIATIONS THROUGH A BREEDING SEASON?

Abstract

Most studies of bird habitat use assume that there is little movement by individuals once territories are established. Many species, however, are known to abandon failed nest sites in search of better habitat, or to move into better habitat 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 early and late breeding season point count data collected 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 which estimated movement outcompeted static models for every species. Further, patterns of movement provided inference that would not have been gained through a static modeling approach, with species moving into habitats traditionally assumed 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: *bird, habitat use, occupancy modeling, breeding biology, Gulf Coastal Plain, birds of concern, Alabama*

Introduction

Migratory birds are characterized by movement, and ornithologists recognize four "seasons" in the life cycles of such migrants: breeding season, season of movement away from the breeding region, non-breeding season, and season of movement toward the breeding region. Studies of bird 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 individual birds once they settle into 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., Mitchell et al. 2001, Stratford and Robinson 2005, McClure et al. in press). 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. Furthermore, surveys during the breeding season in the north temperate regions are typically conducted in May and June when birds are most detectable (Ralph et al. 1995). The breeding season for most migrants, 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. 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. 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*) re-nest 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 re-nest 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.

Use of habitat may not be static if information regarding quality of habitat is not immediately available when birds first begin to settle (Stamps et al. 2005), necessitating evaluation of habitat quality through prior experience at a given site (Haas 1998, Hoover 2003) or social information (reviewed in Nocera and Betts 2010). Because of imperfect information regarding habitat quality, birds may shift into more suitable sites after gaining information regarding habitat quality (Betts et al. 2008). Inexperienced birds, in particular, may initially settle in sub-optimal habitats and then adjust as they learn a local area. 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 birds are able to move up a gradient of habitat quality, 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 of static use of 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 used 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 hypothesize that as the breeding season progresses birds move into different habitat. Therefore, we predicted that our focal species would show changes in use of cover types as the season progresses.

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. Our site consists mostly of pine and floodplain forests, but also contains some agricultural lands and surrounding neighborhoods (Table 1). 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. 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 biologically appropriate we combined similar land cover classifications to form broader classifications in accordance with McClure et al. (*in press*). For instance, pasture/hay and row crop were combined to form a broader, agricultural 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).

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). We were therefore able to analyze our data using occupancy analysis even though they were collected under a removal protocol (Farnsworth et al. 2002). 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 3rd 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 number of models built (Olson et al. 2005, Betts et al. 2008). We first modeled detection while holding other parameters constant across all sites. We built detection models that estimated the two rounds separately. We built separate models that 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.

Next, we modeled occupancy within the first survey period (i.e., initial occupancy) using covariates that we considered *a priori* 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. 2009a). 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 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.

Results

We detected 15 species of conservation priority on enough sites for analysis (Table 2). The dynamic occupancy model outperformed the single season model for every focal species (Table 3). Canopy cover described the initial occupancy of seven species analyzed (Fig 1) with Brown-headed Nuthatch (see Table 2 for scientific names of focal species), Eastern Wood-pewee, Prairie Warbler, Orchard Oriole, and Eastern Kingbird negatively associated with canopy cover. Carolina Chickadee and Kentucky Warbler were positively associated with canopy cover. Swainson's Warbler, Prothonotary Warble, and Yellow-Billed Cuckoo were associated with floodplain forest. Initial occupancies of Prairie Warbler, Eastern Wood-pewee,and Brown-headed Nuthatch were negatively, and Chimney Swift positively, associated with agriculture. Initial occupancies of Prairie Warbler and Field Sparrow were positively associated with clear cuts and Eastern Wood-pewee was associated with pine forests. Prairie Warbler was negatively associated with hardwood forests and Chimney Swift positively associated with developed areas. Carolina Chickadee and Lousiana Waterthrush were negatively associated with mixed pine-hardwood forests and scrub areas, respectively.

Several species showed patterns of colonization over the breeding season. Kentucky Warbler, Louisiana Waterthrush, and Yellow-billed Cuckoo were more likely to colonize areas with high canopy cover, while Carolina Chickadee and Orchard Oriole were less likely to colonize sites with high canopy cover (Fig 2, Table 4). Kentucky Warbler and Purple Martin were likely to colonize sites surrounded by high and low amounts of hardwood forest, respectively. Eastern Wood-pewee and Carolina Chickadee were less likely to colonize sites surrounded by agriculture. Colonization of Brown- headed Nuthatch, Field Sparrow, and Eastern Kingbird was positively associated with natural pine forests, clearcuts, and developed areas, respectively, and colonization of Louisiana Waterthrush was positively associated with water.

Focal species also showed patterns in abandonment of sites. Brown-headed Nuthatch and Orchard Oriole were less likely to leave sites that were associated with scrub areas, whereas Prothonotary Warbler was more likely to abandon sites associated with scrub (Fig 3, Table 4). Vacancy by Swainson's Warbler and Orchard Oriole was positively and negatively associated with developed areas, respectively. Yellow-billed Cuckoo and Wood Thrush were less likely to abandon sites within floodplain forest. Orchard Oriole was less likely to abandon sites associated with hardwood forest, but more likely to abandon sites associated with mixed pine-hardwood forest. Field Sparrow was less likely to leave clearcut areas.

Discussion

We found evidence that all 15 of our focal bird species change habitat occupancy during the breeding season. Thus, we were able to reject the assumption that use of habitat is static across the breeding season. These conclusions are based on movement to or from survey locations, not necessarily movement between individual territories. Unless the territory size of a species matches the survey area of our point counts (3.14 ha), estimates of movement may be influenced by movements of birds into and out of survey areas, but still remaining in their territories (Betts et al. 2008). However, the apparent movement of our focal species was in biologically expected directions putting species into what seemed to be more appropriate habitat.

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 movement of focal species 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. 2009b), 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). Sawinson’s Warbler, Prothonotory 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, although Kentucky Warbler is generally considered a bird of hardwood forests (Hamel 1992, McShea et al. 1995), initial occupancy of Kentucky Warbler is correlated with increased canopy cover within our study site, not with hardwood forests in particular. However, as the breeding season progresses, Kentucky Warbler is 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. Furthermore, 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 Nuthatch in which initial occupancy is mostly determined by canopy cover, but settlement patterns reveal the species' traditionally recognized preference: natural pine forests (Hamel 1992).

Patterns of site abandonment may also reveal potential edge effects, or area sensitivity that would not be apparent under a single-season approach. 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 near edges (Robinson et al. 1995, Rodewald and Yahner 2001, Benson et al. 2010), 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 near those habitat 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 of habitat may also be violated if habitat conditions change over the course of a season. For example, birds associated with water may move in response to changing hydrologic conditions. Water levels within our study site are lower during late summer (CJWM pers. obs.). 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 a habitat are changing, inference into conditions that enhance quality of habitat can be made. Further, a habitat 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 fledged juvenile birds. Juveniles of 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). Adults 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.

By conducting counts of birds during the early and late breeding periods, and using dynamic occupancy models to analyze apparent movement of individuals, 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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Table 1. Mean, standard deviation, and abbreviation of the percentage of habitat variables within 100 m of bird survey sites within Tuskegee National forest Alabama habitat. Data were collected from Kleiner et al. (2007).

Variable	Abbreviation	Mean	SD
Canopy Cover	Canopy	0.71	0.04
Pine	Pine	0.41	0.15
Natural Pine	NPine	0.40	0.15
East Gulf Coastal Plain Upland Longleaf Forest-Loblolly Modifier	Lob	0.32	0.12
Hardwood	Hard	0.19	0.19
East Gulf Coastal Plain Small Stream Floodplain Forest	Floodplain	0.13	0.22
Developed	Dev	0.04	0.07
East Gulf Coastal Plain Upland Longleaf Forest- Open Understory Modifier		0.03	0.04
Developed Open Space	DOS	0.03	0.06
East Gulf Coastal Plain Upland Longleaf Forest- Hardwood Modifier	Mix	0.03	0.04
Scrub	Scrub	0.03	0.05
Agriculture	Ag	0.01	0.05
Successional Scrub- Clearcut	Clearcut	0.01	0.04
East Gulf Coastal Plain Mesic Slope Forest	Mesic	0.01	0.03
Pasture/Hay	Pasture	0.01	0.04

Successional Scrub- Other		0.00	0.02
Row Crop	Row Crop	0.00	0.02
Low Intensity Developed		0.00	0.01
Evergreen Plantation		0.00	0.01
Water	Water	0.00	0.01
Mid Intensity Developed		0.00	0.00

Table 2. 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	Ψ_e	Ψ_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)

Table 3. 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 1.

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

Table 4. Coefficient values (SE) for initial occupancy (Ψ), colonization (γ), and local extinction (**ε**) of 15 birds of conservation concern within Tuskegee National Forest, AL from 15 May-15 July 2005. Zeros indicate that a covariate was considered for model building, but was not included in the final model. Abbreviations for habitat variables are presented in Table 1.

Ψ	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
β0	-2.79 (0.28)	2.88 (2.13)	-5.61 (0.82)	1.5 (1.59)	-7.15 (1.5)	-1.03 (1.28)	-0.62 (0.25)	-3.64 (0.5)	-0.24 (1.59)	-2.83 (0.24)	-2.39 (0.74)	-3.56 (0.34)	3.5 (1.16)	-1.55 (0.23)	-1.56 (0.23)
CC	0	-5.41 (2.19)	0	-2.59 (1.49)	5.21 (1.37)	8.46 (4.25)	0	0	-2.55 (1.55)	0	1.51 (0.71)	0	-7.7 (1.52)	0	0
CC^2				0		-11.18 (3.37)						0			
Pine	0	0	0	0	0	0	0	0	1.88 (0.48)	0	0	0	0	0	0
NPine		0		0					0		0				
Hard	0	-1.32 (1.17)	0	-2.33 (0.65)	0	0	0	0	0	0	0	0	0	0	0
Flood	1.01 (0.34)		2.94 (0.69)		0		0.97 (0.33)							0	0
Mesic							0							0	0
Dev	0	0	0	0	0	0	0	3.8 (0.83)	0	0	0	0	0	0	0
DOS						0		0		0		0	0		

(cont)	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
Mix		0			0	0	0		0		-1.92 (0.74)			0	

Scrub	0	0	0	0	0	0	0	0	0	0	0	0	0	-1.28 (0.89)	-1.35 (0.86)
Ag	0	-4.72 (2.15)	0	-5.77 (1.72)	0	0	0	2.16 (1.26)	-6.54 (2.33)	0	0	0	0	0	0
Clear				2.47 (0.7)								2.87 (0.8)			
Past						0		0		0		0	0		
Crop								0		0		0	0		
H_2O			0					3.78 (2.88)		0					0

γ	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
β_0	-3.08 (0.32)	-8.36 (2.53)	-5.83 (1.01)	-3.78 (0.47)	-7.72 (2.55)	1.62 (1.27)	-3.06 (1.38)	-3.16 (0.49)	-2.63 (0.3)	-1.97 (0.27)	1.73 (1.46)	-7.62 (2.08)	-6.93 (1.59)	-2.16 (0.35)	-8.8 (3.85)
CC	0	0	0	0	4.61 (2.4)	-7.73 (2.05)	2 (1.33)	0	0	0	-3.12 (1.36)	0	0	0	5.89 (3.45)
CC^2				0		0						0			
Pine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NPine		3.98 (2.02)		0					0		0				
Hard	0	0	0	0	0.73 (0.48)	0	0	0	0	-1.17 (0.58)	0	0	0	0	0
Flood	0		0		0		0							0	0

γ (cont)	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
Mesic							0							0	0
Dev	0	0	0	0	0	0	0	0	0	0	0	0	5.15 (1.98)	0	0
DOS								0		0		0	0		

Mix		0			0	0	0		0		0			0	
Scrub	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ag	0	0	0	0	0	0	0	0	-3.44 (2.33)	0	-4.4 (1.69)	0	0	-3.41 (3.44)	0
Clear				0								5.54 (2.62)			
Past						0		0		0		0	0		
Crop								0		0		0	0		
H_2O			0					3.78 (2.88)		0					6.82 (2.79)

ε	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
β0	-2.41 (1.08)	1.88 (1.18)	-2.43 (1.85)	-2.13 (3.19)	-1.21 (0.39)	15.11 (6.52)	0.86 (0.39)	0.84 (1.09)	1.02 (0.88)	2.8 (1.03)	1.08 (0.26)	1.98 (1.09)	0.61 (1.01)	0.77 (0.57)	-0.24 (0.56)
CC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CC^2				0		0						0			
Pine	0	0	0	-8.63 (7.18)	0	0	0	0	0	0	0	0	0	0	0
NPine		3.98 (2.02)		0					-1.26 (0.89)		0				

ε (cont)	SWWA	BHNU	PROW	PRAW	KEWA	OROR	YBCU	CHSW	EAWP	PUMA	CACH	FISP	EAKI	WOTH	LOWA
Hard	0	0	0	14.03 (11.33)	0	-7.94 (3.96)	0	0	0	0	0	0	0	0	0
Flood	0		0		0		-0.93 (0.48)							-1.25 (0.81)	3.67 (2.69)
Mesic							0							0	0
Dev	5.57 (2.6)	0	0	0	0	-10.73 (5.16)	0	0	0	0	0	0	0	0	0
DOS								0		0		0	0		

Mix		0			0	8.48 (5.66)	0		0		0			0	
Scrub	0	-8.74 (5.51)	10.37 (6.69)	0	0	-18.81 (8.08)	0	-5.18 (3.79)	0	0	0	0	-3.02 (2.78)	0	0
Ag	0	0	0	18.8 (13.93)	0	0	0	0	0	0	0	0	0	0	0
Clear				0								-4.63 (2.55)			
Past						0		7.14 (5.58)		0		0	0		
Crop								0		0		0	0		
H_2O			0					0		0					0

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 1. Only relationships with 85% confidence itervals which excluded zero are shown.

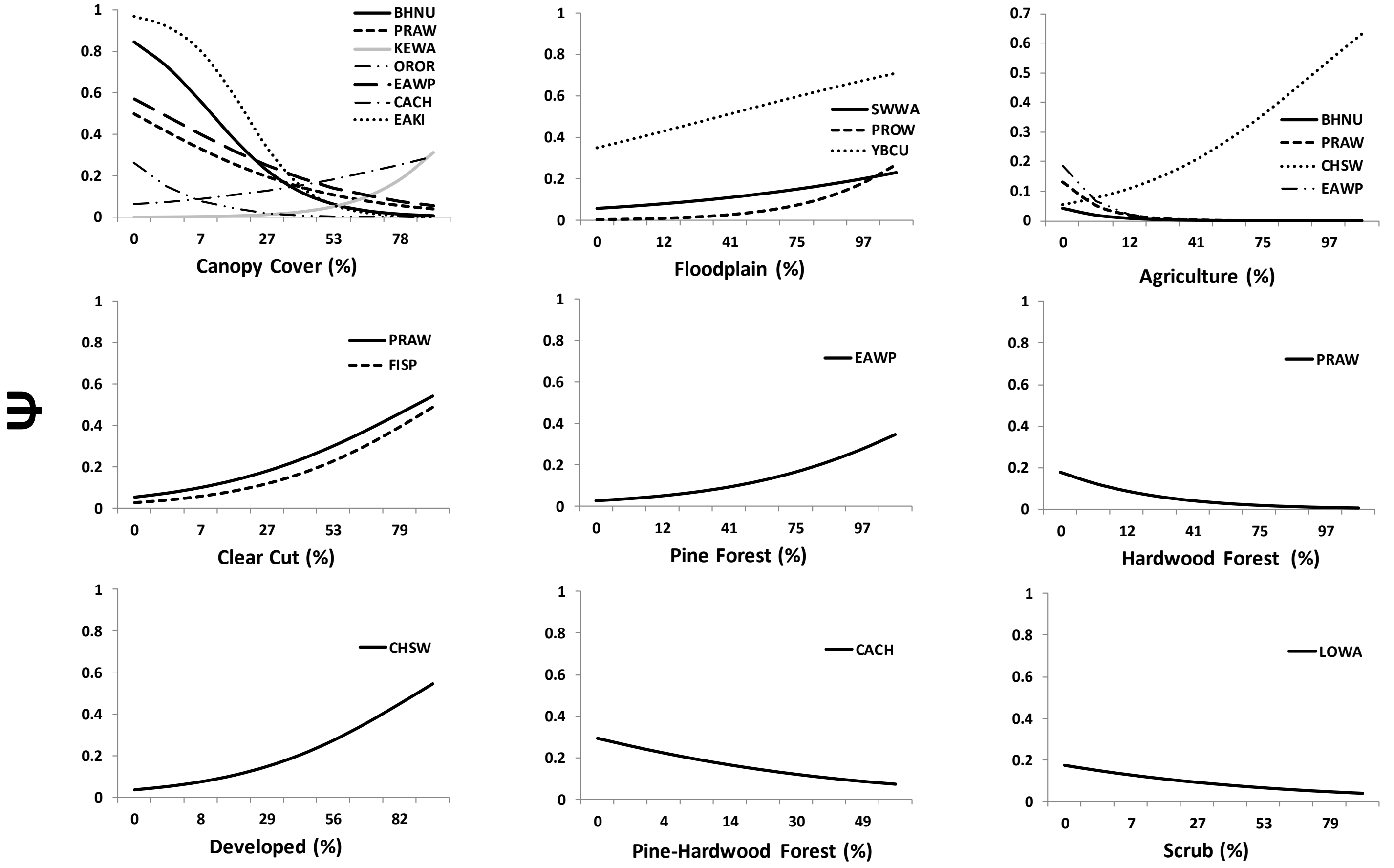


Fig. 2. Relationship between settlement (γ) of species of conservation concern and habitat variables within Tuskegee National Forest, AL. from 15 May-15 June and 16 June-15 July 2005. Species codes are presented in Table 1.

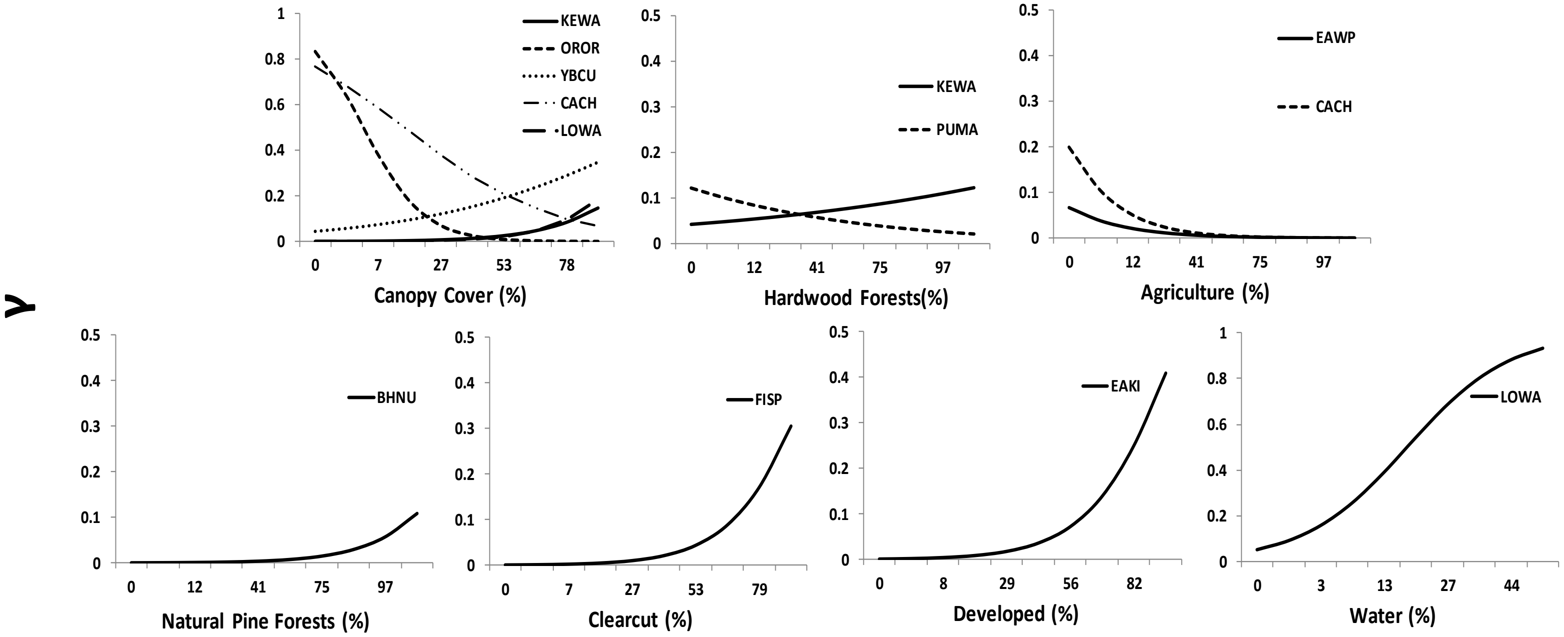
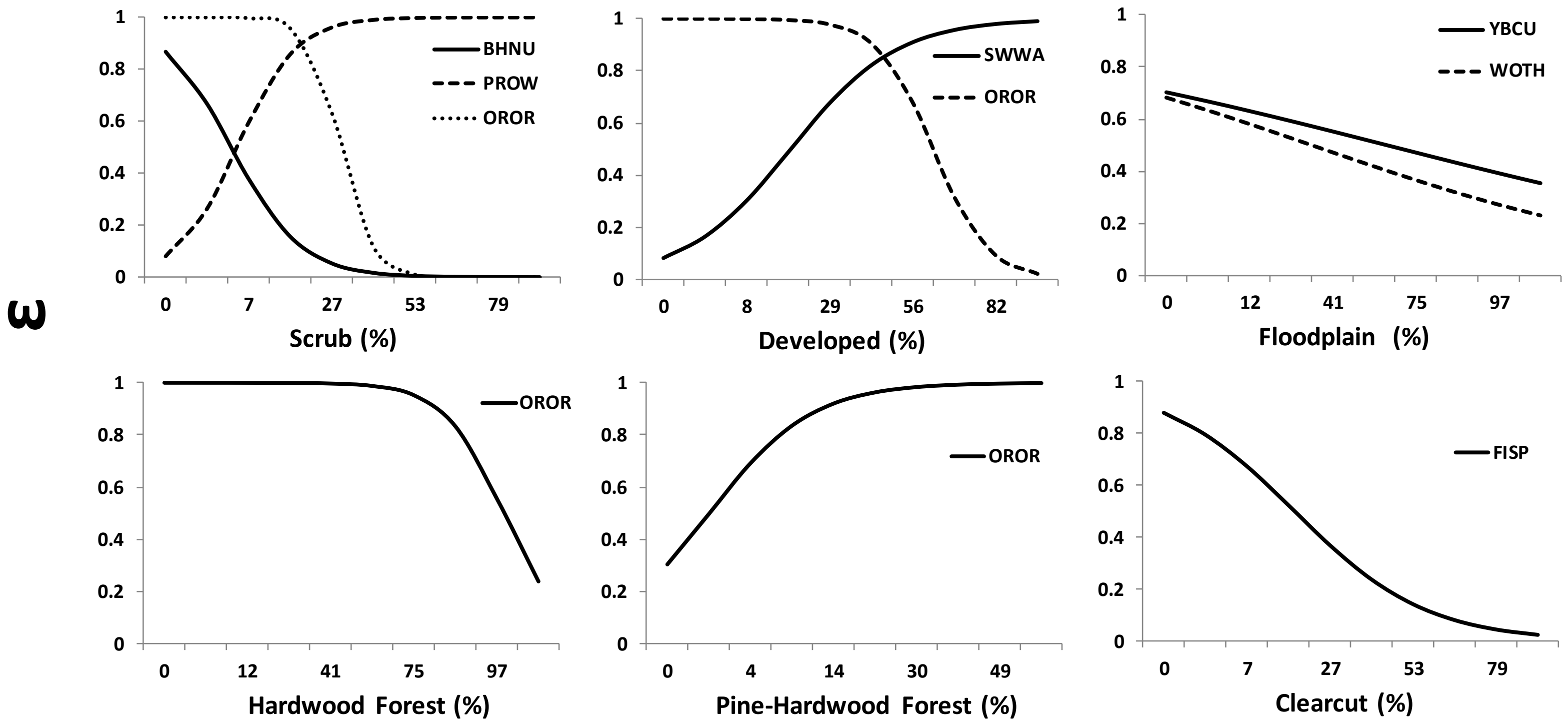


Fig. 3. Relationship between abandonment (ε) of species of conservation concern and habitat variables within Tuskegee National Forest, AL. from 15 May-15 June and 16 June-15 July 2005. Species codes are presented in Table 1.



APPENDICES

Appendix A. Bird species predicted by Alabama Gap Analysis Program to be within the urban (Auburn, AL) and rural (Tuskegee National Forest, AL) landscapes. Accuracy is presented for species detected during surveys of breeding birds conducted 2004-2006.

			Accuracy		# Survey Locations	
Common Name	Scientific Name	code	Urban	Rural	Urban	Rural
Acadian Flycatcher[a]	*Empidonax virescens*	ACFL	0.90	0.74	2	133
American Crow	*Corvus brachyrhynchos*	AMCR	0.42	0.32	129	190
American Goldfinch	*Carduelis tristis*	AMGO	0.06	0.22	11	16
American Kestrel[ab]	*Falco sparverius*	AMKE	0.10	0.24	1	0
American Redstart[a]	*Setophaga ruticilla*	AMRE	0.99	0.74	2	12
American Robin[a]	*Turdus migratorius*	AMRO	0.37	0.21	228	9
American Woodcock[a]	*Scolopax minor*	AMWO	NA	NA	0	0
Bachmans Sparrow[a]	*Aimophila aestivalis*	BASP	0.99	0.89	0	5
Bald Eagle	*Haliaeetus leucocephalus*	BAEA	NA	NA	0	0
Baltimore Oriole[a]	*Icterus galbula*	BAOR	1.00	1.00	0	1
Barn Owl[b]	*Tyto alba*	BANO	NA	NA	0	0
Barn Swallow[a]	*Hirundo rustica*	BARS	0.15	0.44	56	58
Barred Owl[b]	*Strix varia*	BDOW	0.64	0.06	2	7
Belted Kingfisher[a]	*Ceryle alcyon*	BEKI	0.71	0.40	8	7
Black Vulture[b]	*Coragyps atratus*	BLVU	0.06	0.02	1	11
Black-and-white warbler[a]	*Mniotilta varia*	BAWW	0.93	0.71	1	8
Blue Grosbeak	*Passerina caerulea*	BLGR	0.16	0.38	50	83
Blue Jay	*Cyanocitta cristata*	BLJA	0.75	0.46	326	169
Blue-gray Gnatcatcher[a]	*Polioptila caerulea*	BGGN	0.50	0.64	194	238
Broad-winged Hawk	*Buteo platypterus*	BWHA	0.49	0.14	4	9
Brown Thrasher[a]	*Toxostoma rufum*	BRTH	0.44	0.28	234	31
Brown-headed Cowbird	*Molothrus ater*	BHCO	0.33	0.27	87	89
Brown-headed Nuthatch[ab]	*Sitta pusilla*	BHNU	0.50	0.17	92	29
Canada Goose	*Branta canadensis*	CAGO	0.05	0.41	4	1
Carolina Chickadee[ab]	*Poecile carolinensis*	CACH	0.51	0.43	218	157
Carolina Wren[ab]	*Thryothorus ludovicianus*	CARW	0.94	0.71	305	348
Cattle Egret[a]	*Bubulcus ibis*	CAEG	0.04	0.45	0	2
Chimney Swift[ab]	*Streptoprocne rutila*	CHSW	NA	NA	NA	NA
Chipping Sparrow	*Spizella passerina*	CHSP	0.06	0.21	20	2
Chuck-will's-widow	*Caprimulgus carolinensis*	CWWI	NA	NA	0	0
Cliff Swallow[a]	*Petrochelidon pyrrhonota*	CLSW	NA	NA	0	0
Common Grackle[a]	*Quiscalus quiscula*	COGR	0.47	0.22	278	50

Common Ground Dove	*Columbina passerina*	COGD	0.21	0.05	0	2
Common Nighthawk[a]	*Chordeiles minor*	CONI	NA	NA	0	0
Common Yellowthroat[a]	*Geothlypis trichas*	COYE	0.93	0.58	2	35
Cooper's Hawk	*Accipiter cooperii*	COHA	NA	NA	0	0
Dickcissel	*Spiza americana*	DICK	NA	NA	0	0
Downy Woodpecker[ab]	*Picoides pubescens*	DOWO	0.20	0.24	81	86
Eastern Bluebird[b]	*Sialia sialis*	EABL	0.25	0.21	100	21
Eastern Kingbird[a]	*Tyrannus tyrannus*	EAKI	0.39	0.18	41	32
Eastern Meadowlark[a]	*Sturnella magna*	EAME	0.84	0.94	24	5
Eastern Phoebe[a]	*Sayornis phoebe*	EAPH	0.51	0.31	38	9
Eastern Screech Owl[b]	*Otus asio*	EASO	0.00	0.01	0	3
Eastern Towhee	*Pipilo erythrophthalmus*	EATO	0.52	0.63	241	223
Eastern Wood-Pewee[a]	*Contopus virens*	EAWP	0.05	0.28	9	101
Eurasian Collared-Dove	*Streptopelia decaocto*	EUCD	0.03	0.13	30	16
Field Sparrow	*Spizella pusilla*	FISP	0.64	0.42	0	30
Fish Crow	*Corvus ossifragus*	FICR	0.01	0.07	12	49
Gray Catbird[a]	*Dumetella carolinensis*	GRCA	0.42	0.29	89	14
Great Crested Flycatcher[a]	*Myiarchus crinitus*	GCFL	0.38	0.39	79	140
Great Egret	*Ardea alba*	GREG	0.89	0.53	1	0
Great-blue Heron	*Ardea herodius*	GBHE	0.89	0.56	8	14
Great-horned Owl	*Bubo virginianus*	GHOW	0.21	0.97	0	2
Green Heron	*Butorides virescens*	GRHE	0.54	0.50	16	14
Hairy Woodpecker[ab]	*Picoides villosus*	HAWO	0.68	0.36	74	26
Hooded Warbler[a]	*Wilsonia citrina*	HOWA	0.87	0.54	6	172
House Finch	*Carpodacus mexicanus*	HOFI	0.42	0.41	240	6
Indigo Bunting	*Passerina cyanea*	INBU	0.55	0.65	71	202
Kentucky Warbler[a]	*Oporornis formosus*	KEWA	0.87	0.61	0	89
Killdeer[a]	*Charadrius vociferus*	KILL	0.15	0.45	32	3
Little-blue heron[a]	*Egretta caerulea*	LBHE	1.00	0.54	0	5
Loggerhead shrike[a]	*Lanius ludovicianus*	LOSH	0.84	0.92	3	0
Louisiana Waterthrush[a]	*Seiurus motacilla*	LOWA	0.98	0.73	9	30
Mallard	*Anas platyrhynchos*	MALL	1.00	1.00	1	0
Mississippi Kite[a]	*Ictinia mississippiensis*	MIKI	0.03	0.32	1	5
Mourning Dove	*Zenaida macroura*	MODO	0.59	0.81	306	70
Northern Bobwhite	*Colinus virginianus*	NOBO	0.75	0.23	0	37
Northern Cardinal	*Cardinalis cardinalis*	NOCA	0.59	0.81	402	365
Northern Flicker[ab]	*Colaptes auratus*	YSFL	0.07	0.08	29	29
Northern Mockingbird[a]	*Mimus polyglottos*	NOMO	0.38	0.28	370	47

Northern Parula[a]	*Parula americana*	NOPA	0.94	0.77	25	82
Northern Rough-winged Swallow[a]	*Stelgidoptryx serripennis*	NRWS	0.07	0.35	20	7
Orchard Oriole[a]	*Icterus spurius*	OROR	0.05	0.36	12	37
Pileated Woodpecker[ab]	*Dryocopus pileatus*	PIWO	0.37	0.17	25	63
Pine Warbler[ba]	*Dendroica pinus*	PIWA	0.90	0.54	36	108
Prairie Warbler[ab]	*Dendroica discolor*	PRAW	0.53	0.37	1	61
Prothonotary Warbler[ab]	*Protonotaria citrea*	PROW	1.00	0.74	1	13
Purple Martin[ab]	*Progne subis*	PUMA	0.09	0.41	35	65
Red-bellied Woodpecker[ab]	*Melanerpes carolinus*	RBWO	0.40	0.47	168	173
Red-cockaded Woodpecker[ab]	*Picoides borealis*	RCWO	NA	NA	0	0
Red-eyed Vireo[a]	*Vireo olivaceus*	REVI	0.15	0.58	7	244
Red-headed Woodpecker[ab]	*Melanerpes erythrocephalus*	RHWO	0.11	0.02	27	6
Red-shouldered Hawk	*Buteo Lineatus*	RSHA	0.24	0.35	24	64
Red-tailed Hawk	*Buteo jamaicensis*	RTHA	0.00	0.01	1	4
Red-winged Blackbird[a]	*Agelaius phoeniceus*	RWBL	0.26	0.71	36	17
Rock Pidgeon	*Columba livia*	RODO	0.21	0.60	70	1
Ruby-throated Hummingbird[a]	*Archilochus colubris*	RTHU	0.06	0.14	6	18
Scarlet Tanager[a]	*Piranga olivacea*	SCTA	1.00	0.99	0	1
Sharp-shinned Hawk	*Accipiter striatus*	SSHA	NA	NA	0	0
Summer Tanager[a]	*Piranga rubra*	SUTA	0.18	0.53	18	183
Swainsons Warbler[a]	*Limnothlypis swainsonii*	SWWA	1.00	0.72	1	50
Tufted Titmouse[ab]	*Baeolophus bicolor*	TUTI	0.42	0.77	181	287
Turkey Vulture[b]	*Cathartes aura*	TUVU	0.01	0.04	10	24
White Ibis	*Eudocimus albus*	WHIB	1.00	0.93	0	1
White-breasted Nuthatch[ab]	*Sitta carolinensis*	WBNU	NA	NA	0	0
White-eyed Vireo[a]	*Vireo griseus*	WEVI	0.59	0.63	22	290
Wild Turkey	*Meleagris gallopavo*	WITU	0.84	0.27	0	9
Wood Duck[b]	*Aix sponsa*	WODU	0.57	0.12	1	5
Wood Thrush[a]	*Hylocichla mustelina*	WOTH	0.76	0.47	50	117
Worm-eating Warbler[a]	*Helmitheros vermivorus*	WEWA	0.93	0.68	0	1
Yellow-billed Cuckoo[a]	*Coccyzus americanus*	YBCU	0.88	0.64	6	156
Yellow-breasted Chat[a]	*Icteria virens*	YBCH	0.46	0.53	2	146
Yellow-crowned Night-Heron	*Nyctanassa violacea*	YCNH	NA	NA	0	0
Yellow-throated Vireo[a]	*Vireo flavifrons*	YTVI	0.23	0.25	0	77
Yellow-throated Warbler[a]	*Dendroica dominica*	YTWA	0.84	0.55	0	22

[a]Insectivore, [b]Cavity Nester

Appendix B. Five-minute detection probabilities calculated from removal models (Farnsworth et al., 2002) for breeding bird species observed during point counts within an urban (Auburn, AL) and rural (Tuskegee National Forest, AL).

Species	5-min Detection Probability	
	Urban	Rural
ACFL	0.72 (0.72)	0.99 (0.01)
AMGO	0.68 (0.39)	0.97 (0.06)
AMRE		0.99 (0.01)
AMRO	0.84 (0.04)	0.76 (0.29)
BACS		0.99 (0.04)
BARS	0.98 (0.01)	0.86 (0.05)
BAWW		0.94 (0.10)
BDOW		1.00 (0.00)
BEKI	0.99 (0.02)	
BGGN	0.72 (0.36)	0.99 (0.00)
BHCO	0.69 (0.14)	0.30 (0.30)
BHNU	0.53 (0.21)	0.80 (0.16)
BLGR	0.98 (0.01)	0.98 (0.01)
BLJA	0.92 (0.02)	0.96 (0.02)
BLVU		0.98 (0.05)
BRTH	0.75 (0.07)	0.91 (0.07)
BWHA		0.39 (0.96)
CACH	0.97 (0.01)	0.99 (0.00)
CAGO	1.00 (0.00)	
CARW	0.97 (0.01)	0.98 (0.01)
CHSP	0.72 (0.29)	
COGR	0.86 (0.02)	0.89 (0.05)
COYE		0.99 (0.02)
DOWO	0.52 (0.25)	0.90 (0.06)
EABL	0.97 (0.01)	0.96 (0.06)
EAKI	0.95 (0.04)	1.00 (0.00)
EAME	0.99 (0.01)	
EAPH	0.98 (0.02)	0.98 (0.04)
EASO		0.72 (0.72)
EATO	0.99 (0.00)	0.99 (0.00)
EAWP		0.96 (0.02)
ETTI	0.97 (0.02)	0.99 (0.00)

EUCD	0.97 (0.02)	0.79 (0.18)
FISP		1.00 (0.00)
GBHE	1.00 (0.00)	1.00 (0.02)
GCFL	0.98 (0.02)	0.94 (0.03)

Species	5-min Detection Probability	
	Urban	Rural
GRCA	0.04 (0.43)	0.98 (0.04)
GRHE	0.97 (0.04)	0.91 (0.13)
HAWO	0.45 (0.43)	0.98 (0.03)
HOFI	0.93 (0.02)	
HOWA	0.86 (0.26)	0.97 (0.01)
INBU	0.99 (0.01)	0.98 (0.01)
KEWA		0.96 (0.02)
KILL	0.96 (0.03)	
LOSH	0.72 (0.72)	
LOWA	1.00 (0.00)	0.72 (0.27)
MALL	1.00 (0.00)	
MODO	0.93 (0.01)	0.91 (0.10)
NOBO		0.51 (0.66)
NOCA	0.99 (0.00)	0.99 (0.00)
NOFL	0.77 (0.30)	0.88 (0.16)
NOMO	0.97 (0.01)	0.98 (0.01)
NOPA		0.99 (0.00)
NRWS		0.88 (0.21)
OROR	0.39 (0.68)	0.99 (0.01)
PIWA	1.00 (0.00)	0.95 (0.02)
PIWO	0.90 (0.11)	0.96 (0.04)
PRAW		0.99 (0.01)
PROW		0.99 (0.01)
PUMA	0.98 (0.01)	0.92 (0.06)
RBWO	0.84 (0.06)	0.90 (0.04)
REVI	0.94 (0.13)	1.00 (0.00)
RODO	0.96 (0.01)	
RSHA	0.51 (0.66)	0.85 (0.14)
RTHU		0.74 (0.19)
RWBL	0.99 (0.01)	0.99 (0.01)
SUTA	1.00 (0.01)	0.95 (0.02)
TUVU	0.72 (0.72)	0.89 (0.13)
WEVI	0.90 (0.15)	0.99 (0.00)
WITU		0.91 (0.13)

WOTH	1.00 (0.00)	0.98 (0.02)
YBCH		0.97 (0.01)
YBCU		0.61 (0.15)
YTVI		1.00 (0.00)
YTWA		0.90 (0.10)