MICROHABITAT ASSOCIATIONS OF WINTERING BIRDS IN A

SOUTHEASTERN BOTTOMLAND FOREST WITHIN THE

EASTERN GULF COASTAL PLAIN OF FLORIDA

Except where reference is made to the work of others, the work described in this thesis is my own or was done in collaboration with my advisory committee. This thesis does not include proprietary or classified information.

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Brian William Rolek

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MICROHABITAT ASSOCIATIONS OF WINTERING BIRDS IN A

SOUTHEASTERN BOTTOMLAND FOREST WITHIN THE

EASTERN GULF COASTAL PLAIN OF FLORIDA

Brian William Rolek

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VITA

Brian William Rolek, son of William Rolek and Donna Wroblewski, was born 5 November 1980 in Media, Pennsylvania. He graduated from Malvern Preparatory School in 1998 where he played ice hockey. He attended the University of Massachusetts in Amherst, Massachusetts, where he volunteered for research on Chestnut-sided Warblers which sparked his interest in conservation and birds. He graduated with a Bachelor of Science degree in biology in May, 2003. After working as a technician researching Eastern Bluebirds for Auburn University Biological Sciences Department, he entered Graduate School, Auburn University, in August, 2006.

THESIS ABSTRACT

MICROHABITAT ASSOCIATIONS OF WINTERING BIRDS IN A

SOUTHEASTERN BOTTOMLAND FOREST WITHIN THE

EASTERN GULF COASTAL PLAIN OF FLORIDA

Brian William Rolek

Master of Science, August 10, 2009
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I examined microhabitat characteristics affecting the occupancy of wintering birds
in a southeastern bottomland forest with repeated point counts at 186 sites. Models were
derived *a priori* based on published literature and personal observations. I assessed 34
species and their microhabitat preferences within the Choctawhatchee River Basin. I
then created microhabitat groups based on all habitat associations that allowed for a
simplified interpretation of results. Microhabitat characteristics were important for 25 of
34 species of birds and were important predictors their occupancies 34 times. The

occupancy of species was influenced similarly by physiognomic and floristic characteristics; the former influenced occupancy of 12 species and the latter occupancy of 19 species. The basal area of Tupelo (*Nyssa*) was the most important floristic predictor, and for five of six species it negatively affected the presence of birds. Number of woody stems (< 10 cm dbh) was the most important physiognomic predictor of species occupancy. Woody stems affected occupancies of four species. Presence of standing water and oak-hickory (*Quercus + Carya aquatica*) community affected occupancies of three species. Oak-gum-cypress (*Quercus + Nyssa + Taxodium distichum*) community affected occupancies of two species. The probability of detecting birds was most frequently affected by date and observer differences. Also affecting the probability of detection were wind, temperature, and time after sunrise. Microhabitat is an important component of habitat selection by birds and should be incorporated into models of occupancy that are used for conservation purposes. My study provides empirically tested associations between occupancy and microhabitat characteristics, and can provide a starting point for future habitat modeling efforts.

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INTRODUCTION 1.1

Predicting whether a habitat is suitable for a species has frequently emerged as an

important topic in conservation biology and wildlife management (e.g., Kellner et al.

1992, Sergio and Newton 2003, Carrascal and Seoane 2009, Tittensor et al. 2009).

Knowledge of habitat quality and habitat selection creates the foundation for protection

and management of wildlife. Here, I investigate southeastern bottomland forests using an

occupancy modeling approach to identify microhabitats of wintering birds. I subscribe to

the definition of microhabitat as specific, recognizable features of the environment that

act as proximal cues to elicit a settling response from an individual bird (Block and

Brennan 1993). I restricted this definition further to the scale at which I quantified

vegetation (0.08 ha).

Many studies of wintering birds have focused on migrants wintering in the

tropics, but the southeastern United States also provides important winter habitat for

many migratory birds. The winter habitats occupied by migratory birds effect individual

condition which can carry over to succeeding stages of the annual cycle (Studds and

Marra 2005). Migratory birds can spend over five months on their winter grounds and

factors limiting populations of some migratory birds may be occurring on winter grounds rather than on breeding grounds (Rappole et al. 2003).

For most birds in North America, breeding habitat is much better known than winter habitat. Even for species that are resident within a region, seasonal shifts in diet (e.g., Yarbrough and Johnston 1965, Wheelwright 1986, Mills 2007) and foraging patterns (e.g., Conner 1981) may cause species to alter niches and occupancy of habitats (e.g., Shackleford and Conner 1997) between seasons. Limited information is available for management and habitat requirements of wintering resident and migratory birds. Many studies have explored habitat relationships of breeding birds in southeastern bottomland forests (e.g., Wakeley and Roberts 1996, Sallabanks et al. 2000, Graves 2001, Moorman et al. 2002, Harrison and Kilgo 2004, Heltzel and Leberg 2006), but few studies have quantitatively assessed habitat relationships of wintering birds.

Approximately 78% of pre-settlement bottomland hardwood forests in the Southeastern United States have been lost as a result of changing land-use practices (Harris 1984). Wide-scale destruction of southeastern forests began with the invention of the cotton gin in 1793 (Wear and Greis 2002). The cotton gin enabled large-scale farming operations to thrive and resulted in clear-cutting of land and draining of wetlands for agriculture (Wear and Greis 2002). Much of the loss of bottomland forests can be attributed to damming of rivers and draining of wetlands which altered water regimes (Wear and Greis 2002) upon which bottomland forests are highly dependent (Hodges 1997). Cheap transportation of lumber increased profitability of logging after 1835 as railroads were built in the South (Wear and Greis 2002). After a lull in lumber demand resulting from an industrial shift to steel (Wear and Greis 2002), the World Wars

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increased demand for lumber once more, and German prisoners of war offered a cheap source of labor for timber harvest (Jackson 2004).

Centuries of exploitation resulted in most pristine bottomland forest being degraded. Within Florida, more than 98% of pre-European old-growth forests have been altered or destroyed (Wear and Greis 2002). Up to 80% of the Mississippi Alluvial Valley, the largest continuous patch of southeastern bottomlands, was destroyed from a combination of aforementioned factors (MacDonald et al. 1979).

I conducted a study of the winter habitat associations of birds in the bottomland hardwood forests along the Choctawhatchee River in Florida. Because my study site within the Choctawhatchee River Basin of Florida was only partially and selectively logged, has mostly regenerated, and has never been dammed, population studies at this site may provide insight into the natural state of southeastern bottomland forests and avian communities within them.

In this study, my goals were to (1) determine whether wintering birds in bottomland forests select sites based on microhabitat characteristics and (2) determine which microhabitats are important for wintering birds within southeastern bottomland forests. Previously published studies have assessed habitat preferences of wintering birds in the Southeastern United States (e.g., Zeller and Collazo 1995, Shackelford and Conner 1997, Kwit et al. 2004, Leonard and Stout 2006), but few studies have incorporated the probability of detection into occupancy estimates. In my study, I use methods designed to estimate detectability and incorporate these into occupancy estimates of individual species to facilitate testing relationships between occupancy and microhabitats. Occupancy methods allow me to compensate for inherent sampling error.

Bird surveys are traditionally conducted with many brief counts at pre-assigned points. This method has the advantage of being rapid, allowing for many replicates to be conducted, but it necessarily under samples birds that are present (MacKenzie et al. 2006). Occupancy modeling enables estimation of the probability that a species occupies a site (occupancy) and the probability of detecting a species (detectability) (MacKenzie et al. 2002). Without adjusting for detectability of a species, occupancy tends to be underestimated; however, by repeatedly sampling a site, we can estimate the probability that a species is detected during a sampling effort (MacKenzie et al. 2002). Detectability can then be incorporated into estimates of occupancy, adjusting occupancy estimates for missed detections. By including a detectability parameter, we can adjust estimates of occupancy or abundance correcting for variables that influence detectability of a species (e.g., poor weather, time of day, observer bias) (MacKenzie et al. 2006). An additional advantage of using occupancy modeling for assessing habitat preferences is that habitat quality is frequently correlated with site occupancy for specific species, making occupancy a potential indicator of habitat quality (Sergio and Newton 2003).

Sampling error results from false negatives and false positives when surveying for a species. Within a sample location, a species is either present or absent. However, when a site is surveyed four outcomes are possible: (1) a species of interest may be detected but not present (false positive), (2) a species may be detected and present (true positive), (3) a species may not be detected and absent (true negative), or (4) a species may not be detected and present (false negative). We can control for false positives (1) by using competent observers. For accurate results, we prefer only true positives and true negatives (2 and 3) during all surveys, but this assumes that detectability of a species is

equal to one. Rarely is any animal detected during 100% of surveys when the animal is present at a site, making this assumption unreasonable for most instances (MacKenzie et al. 2002). We can correct for false negatives (4) by incorporating detectability into occupancy estimates (MacKenzie et al. 2002).

The scale of measurement and analysis is of frequent concern in biological studies. Scale of an investigation is central to understanding concepts of territory quality and habitat selection. All habitats are heterogeneous at some spatial scale (Forman 1995). An observer might detect an animal at a site, but the reason an animal selects a site could be attributed to features at many scales (Mitchell et al. 2001). According to Allen and Hoekstra (1992), it is necessary to consider three scales at once: the one in question, the one below, which provides mechanisms, and the one above, which provides context (summarized by Saab 1999). Block and Brennan (1993) assert that while assessing habitats, researchers should consider multiple scales. Mitchell et al. (2001) and MacFaden and Capen (2002) demonstrate that the pertinent scale of habitat measurements varies between species or groups of species.

In my study, I examine variable microhabitats within a single macrohabitat. Within the Eastern Gulf Coastal Plain region, meandering of rivers across broad floodplains has resulted in the formation of a diverse topography composed of natural levees, ridges, backwater swamps, and sloughs (Hodges 1997). Within bottomland forests, vegetation communities vary according to differences in hydroperiod (Mitsch and Gosselink 1993, Hodges 1997, Hupp 2000). Thus, on a coarse scale, this study site was all one forest type. However, on a fine scale, my field site contained diverse topography and vegetation types (Hodges 1997, Hupp 2000). Because water regimes create diverse

topography and vegetation types, I hypothesized that in southeastern bottomland forests within the Gulf Coastal Plain Region (i.e. the Choctawhatchee River), bird occupancy will be influenced by available microhabitats.

Habitat selection by birds based on variable microhabitats is suggested by foliage height diversity literature, where bird species diversity increases as foliage height diversity increases (MacArthur 1961). MacArthur (1961) hypothesized that increased foliage height diversity provides species with more niches. Thus, occurrence of many species of birds may respond to small-scale habitat variations in addition to large-scale landscape variations. Most landscape-scale habitat assessments have not incorporated microhabitat characteristics in their predictive models.

METHODS 1.2

Study Site

I surveyed a 60 km^2 area within the Choctawhatchee River Basin in Holmes, Washington, and Walton counties in Florida. This study site was limited to land owned by the Northwest Florida Water Management District within the Choctawhatchee River Basin. The northern boundary of the study site was near Interstate 10 at UTM 16 R 3403000N and its southern boundary was located at UTM 16 R 3384500N (WGS84) (Fig. 1). The site includes tributaries and distributaries Old Creek, Cypress Slough, Gum Creek, Yates Mill Creek, Carlisle Lakes, and Bruce Creek, from north to south. Eastern and western boundaries of the study site were defined by Northwest Florida Wildlife Management District property.

This study site was located entirely within the Eastern Gulf Coastal Plain geographic region. The study area primarily consisted of deciduous bottomland forest and was classified by the Cowardin wetland classification system and the National Wetlands Inventory as palustrine forested wetland (Cowardin et al. 1979, USFWS 2007). Subclasses varied but included broad-leaved deciduous and needle-leaved deciduous forests. Forest age varied due to natural fluctuations in water regimes, weather related events, and selective logging during the 20th century. Most tracts of bottomland forest abutted planted stands of Slash (*Pinus elliottii*) or Loblolly Pine, (*P. taeda*) which were logged frequently.

Sampling Design and Surveys

To conform to the floodplain of the Choctawhatchee River, the study area was divided into 0.25-km^2 grids. Eight of these grids were joined to create irregularly shaped 2-km^2 search grids. Within these 2-km^2 search grids, east-west point transects spaced $\geq$ 250 m were randomly selected until six points per grid were selected (Fig. 1). Selecting 2-km^2 grids increased interspersion, while placement of point transects increased randomization as opposed to a systematic design.

I repeatedly surveyed 186 sites using randomly placed point transects from 6 January 2008 through 25 February 2008. Each point was surveyed using three consecutive 4-min point counts on two different days, totaling six counts. Points were counted before 1100 CST. Distance to each bird from the center of the point was recorded with a rangefinder. Because this study focused on microhabitat, for most species, birds beyond 100 m were truncated from analyses, but I relaxed this restriction for species where insufficient sample sizes were obtained within 100 m (Appendix I).

Observer bias, temporal data (i.e., minutes after sunrise and date), and weather conditions (i.e., wind speed and temperature) were hypothesized to affect the probability of detection (Wintle et al. 2005) of birds and were recorded at each point count. Wind speed was estimated using the Beaufort scale. Temperature was measured at each point using a digital thermometer.

Habitat characteristics that were hypothesized to influence the occupancy of birds were measured at each point using 0.08-ha circular plots 16 m from the center of the point. Diameter at breast height (dbh) was measured for all trees $\geq$ 10 cm dbh within the plot and identified to species (Avery 1975). If epiphytes were present, their abundance was estimated based on percentage of trees within the plot with epiphytes present. Height and canopy depth of the three most dominant trees were measured using a clinometer and a rangefinder (Avery 1975). Canopy density was measured using a densitometer to estimate percentage of cover by sampling in the four cardinal directions from the center of the plot (Robinson 1947). Ground cover was measured by inverting the densitometer and sampling in the four cardinal directions. Leaf litter was quantified by measuring the leaf depth with a ruler in the center and in four cardinal directions on the outer edge of the plot (Meyers and Wright 2003). Common understory plants were identified to species. Volume of downed woody debris was quantified by measuring length and diameter of all wood having one end $\geq$ 10 cm diameter within the plot (Sallabanks et al. 2006). I measured all snags $\geq$ 10 cm dbh. Hydrology of the Choctawhatchee River Basin included rapidly fluctuating water levels; therefore, water within a plot was noted at the time of point counts as running, standing, or not present. Two habitat communities, oak-hickory and oak-gum-cypress, were calculated by

summing the basal area of the genera, *Quercus + Carya*, and *Quercus + Nyssa + Taxodium*, respectively, where all genera were represented at the site. After deriving habitat covariates, I segregated these into structural (physiognomic) and floristic covariates (Table 1)

Statistical Analysis

Hypotheses Construction

Following guidelines from Anderson and Burnham (2002), I developed *a priori* predictions for each species based on hypothesized relationships with the environment that were represented by distinct models. Variables affecting detectability were hypothesized from published research (Wintle et al. 2005), personal observations, and personal correspondence.

To objectively synthesize hypotheses, I created five tables of microhabitat associations based on foraging guilds, diet (BNA), habitat associations (BNA), Hamel (1992), and personal observations. Each category received a score of "1" if that microhabitat was noted as having a positive or negative association with an individual species in each account or "0" if it was not mentioned. Because Hamel (1992) is frequently cited in BNA, habitat associations that cited Hamel as a source in accounts published in BNA were counted only once. Values from each of the five categories were added to create one importance value for each microhabitat characteristic (foraging guild + diet + BNA habitat + Hamel + personal observation) for each species, so that the microhabitat characteristics with higher importance values were more likely to be included in tested models. These methods resulted in a high number of predicted model

parameters; therefore, to decrease the probability of a Type I error, I eliminated habitat variables with the lowest total scores first.

Occupancy Analyses

I used a Pearson's correlation coefficient to test within floristic, physiognomic, and detectability covariates for relationships using SPSS (SPSS Inc., Chicago IL, USA). Significantly correlated covariates ($p \leq 0.05$) were not analyzed within the same model. I analyzed microhabitat relationships using the program PRESENCE (Patuxent Wildlife Research Center, Laurel, MD, USA) single-season models and statistical methods outlined by MacKenzie et al. (2003). Maximum-likelihood estimators were used to quantify detectability and occupancy for each species (MacKenzie et al. 2003). A parametric bootstrap was used to test the goodness-of-fit (1,000 replicates) and the most parsimonious models were selected using Quasi-Akaike's Information Criteria (QAIC) (Burnham and Anderson 2002, MacKenzie et al. 2006). For species that small sample sizes were obtained, I corrected QAIC values using QAIC corrected (QAICc). I selected the "best" models with the lowest ΔQAIC values (ΔQAIC = 0). While this is a simplification of proper model selection (Burnham and Anderson 2002), the large amount of data analyzed needed to be summarized and simplified systematically.

I incorporated detectability covariates first by hierarchically analyzing occupancy data. I then analyzed physiognomic and floristic covariates separately, incorporating detectability covariates into these models. Lastly, the models with low ΔQAIC (mostly ΔQAIC < 2) values and the highest QAIC weights from physiognomic covariates and floristic models were combined and directly compared using QAIC (Fig. 2).

Microhabitat Grouping

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Lastly, I created groups of species according to their microhabitat associations for additional insight into how birds might respond when habitat variables are altered or managed. To create a group, all species that were affected by a particular microhabitat variable were grouped. Groups were derived directly from statistical associations between occupancy and habitat from the best (ΔQAIC $= 0$) habitat models. For ease of interpretation, both negative and positive associations were included in the same habitat groups, so that managers can identify microhabitat that they plan to alter and reference the effects on each species that might be influenced by such alterations. Groups cannot be interpreted as a positive or negative association specifically, but can be interpreted simply as an association (either positive or negative) with that specific microhabitat variable. To test whether floristic or physiognomic covariates were more important to birds, I used a Yates continuity correction χ^2 test.

RESULTS 1.3

My research assistants and I counted 8,209 birds during 1,116 points counts and detected 53 species at least once. I obtained suitable samples ($n \geq 10$) for 23 species truncating birds detected beyond a distance of 100 m. I was able to include 11 additional species by including detections > 100 m, totaling 34 species (Appendix I).

Variables Affecting Detectability

Variables most frequently affecting detectability of species were date and observer. Date and differences among observers affected detectability of 10 species. Temperature, wind, and time after sunrise were less important, but were frequently influential. All covariates hypothesized to affect the probability of detection were important for models of several species (Table 1, Appendix II).

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Occupancy Overview

In the most parsimonious models, 34 microhabitat covariates were important. Six of seventeen tested physiognomic characteristics were important for 13 species (Table 1 and Table 2). Ten of twenty floristic covariates were influential for 18 species (Table 1 and Table 2). There was no statistically significant difference between the number of physiognomic and floristic covariates that were important for species (Yates' continuity corrected $\chi^2 = 0.00$, p = 0.93, df = 1, Fig. 3). Hypothesized microhabitat covariates were not important for nine species.

Physiognomic Effects on Occupancy

Results of physiognomic analyses are listed below in order of frequency of importance by habitat group in descending order. Number of stems influenced occupancy by four species. These species included Downy Woodpeckers (*Picoides pubescens*) ($\beta = -0.48 \pm 0.20$), Hermit Thrushes (*Catharus guttatus*) ($\beta = 0.53 \pm 0.53$), Rusty Blackbirds (*Euphagus carolinus*) ($\beta = -1.05 \pm 0.71$) and Winter Wrens (*Troglodytes troglodytes*) ($\beta = -0.45 \pm 0.26$). Presence or absence of water was important for three species including Eastern Phoebes (*Sayornis phoebe*) ($\beta = 0.89 \pm 0.45$), Hermit Thrushes ($\beta = -1.19 \pm 0.80$), and Wood Ducks (*Aix sponosa*) ($\beta = 0.70 \pm 0.41$). Ground cover was negatively associated with both American Goldfinches (*Carduelis tristis*) ($\beta = -0.86 \pm 0.61$) and American Robins (*Turdus migratorius*) ($\beta = -0.93 \pm 0.37$). Leaf litter depth was associated positively with the occupancy by Common Grackles (*Quiscalus quiscula*) ($\beta = 0.34 \pm 0.21$) and Pine Warblers (*Dendroica pinus*) ($\beta = 0.34 \pm 0.16$). Total basal area was negatively associated with occupancy by Blue-headed Vireos (*Vireo*

solitarius) (β = -0.38 ± 0.16). Canopy cover was important for Cedar Waxwings (*Bombycilla cedrorum*) (β = 0.54 ± 0.27) (Fig. 4).

Floristic Effects on Occupancy

Results of floristic analyses are listed below in order of importance by habitat group in descending order. Basal area of tupelo (*Nyssa*) was an important characteristic for six species. Species affected included American Goldfinches (β = -1.54 ± 1.05), Barred Owls (*Strix varia*) (β = -0.96 ± 0.58), Black Vultures (*Coragyps atratus*) (β = 0.78 ± 0.28), Common Grackles (*Quiscalus quiscula*) (β = -1.04 ± 0.68), Ruby-crowned Kinglets (*Regulus calendula*) (β = -0.52 ± 0.18) and Winter Wrens, (β = -0.63 ± 0.38). All occupancy relationships with tupelo forests were negative except Black Vultures. American holly (*Ilex opaca*) was important for Northern Cardinals (*Cardinalis cardinalis*) (β = 15.58 ± 9.32) and Red-bellied Woodpeckers (*Melanerpes carolinus*) (β = 37.76 ± 15.07). Pine (*Pinus*) was an important predictor for Golden-crowned Kinglets (*Regulus satrapa*) (β = 4.08 ± 3.22) and Yellow-rumped Warblers (*Dendroica coronata*) (β = -3.45 ± 1.88). Hickory (*Carya aquatica*) was associated positively with Wood Ducks (*Aix sponosa*) (β = 3.10 ± 1.46) and Yellow-bellied Sapsuckers (*Sphyrapicus varius*) (β = 3.88 ± 1.23). Elm (*Planera aquatica* and *Ulmus*) was negatively associated with Red-shouldered Hawks (*Buteo lineatus*) (β = -95.98 ± 85.22). Sweetgum (*Liquidambar styraciflua*) was associated positively with American Goldfinches (β = 0.77 ± 0.53). Maple (*Acer*) was important for Hairy Woodpeckers (*Picoides villosus*) (β = 2.03 ± 0.95). Saw palmetto (*Serenoa repens*) was an important characteristic for Hermit Thrushes (β = 1.00 ± 0.65). Floristic-community covariates were important for five species. Oak-gum-cypress community positively influenced occupancy by Pileated

Woodpeckers (*Dryocopus pileatus*) ($\beta = 2.23 \pm 1.28$) and Red-shouldered Hawks ($\beta = 0.44 \pm 0.26$). Oak-hickory community was an important predictor for American Crows (*Corvus brachyrhynchos*) ($\beta = -0.48 \pm 0.18$), Cedar Waxwings ($\beta = 0.54 \pm 0.33$), and Eastern Towhees ($\beta = -1.42 \pm 0.75$) (Fig. 5, Tables 1 and 2).

Hypothesized habitat covariates were not important for nine species. Birds that occupied heterogeneous habitats represented by the null model and had the lowest QAIC value (ΔQAIC = 0) included Blue Jays (*Cyanocitta cristata*), Brown Creepers (*Certhia americana*), Carolina Chickadees (*Thryothorus ludovicianus*), Carolina Wrens (*Thryothorus ludovicianus*), Eastern Bluebirds (*Sialia sialis*), Tufted Titmice (*Baeolophus bicolor*), Fish Crows (*Corvus ossifragus*), Turkey Vultures (*Cathartes aura*), and Northern Flickers (*Colaptes auratus*).

DISCUSSION 1.4

Results of this research support my hypothesis that microhabitat is important for many species of birds during winter and should be included in predictive models. Microhabitat was important for 25 of 34 species (74%). Nine species did not have an association with microhabitat. The number of covariates considered important are conservative because I only selected the most parsimonious models (ΔQAIC = 0) from the set of hypothesized models. Burnham and Anderson (2002) recommended including models with higher ΔQAIC (ΔQAIC > 0) values and lower QAIC weights by model averaging. If I had averaged models, more microhabitat covariates would have been included in our final models.

If applied to the forests surveyed in this study, land-use and land-cover maps would have had limited predictive capabilities compared to microhabitat characteristics that I used because land-use and land-cover maps are mostly homogeneous across my field site. Presumably, landscape scale analyses such as GAP could be refined by incorporating microhabitat characteristics. Similar to my results, in a comparative study, MacFaden and Capen (2002) demonstrated that during the breeding season, southeastern birds tended to be modeled best by microhabitat variables rather than by landscape variables. In addition, selection of microhabitats would be expected to increase during the breeding season compared to the non-breeding season, because birds need appropriate foraging and roost sites but also must find appropriate nesting sites.

Overall, floristic and physiognomic microhabitat covariates were statistically similar in predicting occupancy by wintering birds. Floristic covariates that occurred in models with lowest QAIC values outnumbered physiognomic covariates (21 to 14), although this difference was not statistically significant when accounting for differences in the frequency that each category was tested in models (206 and 162, respectively). Floristic and physiognomic characteristics appear to be equally important across species (Fig. 3).

Accounting for differences in detectability from date and observer are necessary for most studies of bird habitats. Date and observer were found to have recurrent and large effects on detectability. Wind had a consistently negative affect on detectability. Time and temperature also frequently affected detectability. These results demonstrate that not accounting for detectability can bias results leading to less accurate and less precise conclusions in population studies. Effects of wind, time, and date reveal that not

accounting for detectability would bias my results daily and seasonally, depending upon exactly when surveys were employed. From my models, researchers can optimize their survey times and dates by surveying when target species are most available for detection.

The basal area of tupelo trees was the most common predictor of species' occupancy (Table 2, Fig. 5). All but one of these associations were negative, indicating that while tupelo forest is a common component of this ecosystem (present on 27.4% of sites), it is not necessarily important for wintering birds. This finding is surprising given that many hollow tupelo trees are present throughout my field site that had cavities excavated by woodpeckers and that woodpeckers have potential as indicators of species richness at larger scales (Drever et al. 2008). Tupelo areas are most frequently flooded during the winter season. The avoidance of tupelo may represent a response to high water levels present at tupelo sites. While not important for most wintering species, tupelo-cypress communities support species of breeding birds that have low abundances elsewhere (Wakeley and Roberts 1996).

Number of woody stems < 10 cm dbh was the second most common predictor of occupancy (Table 2, Fig. 4). The number of woody stems could have several physiognomic interpretations. In the case of Hermit Thrushes, stems likely represent midstory and woody thickets that Hermit Thrushes select (Aldrich 1968). For Rusty Blackbirds, which seemingly select foraging on open ground (Dickinson and Noble 1978, personal observations), stems could be an obstruction blocking access to the ground.

Presence or absence of water was important for three species (Table 2, Fig. 4). The amount of water flowing down the Choctawhatcheee River can fluctuate greatly even within a 24-hr period and dictates the extent of standing water in the study area. I

hypothesized that water would affect occupancy of ground foragers negatively by reducing access to foraging habitat during flooding events. Indeed, the changing water levels negatively affected the occupancy of ground feeding Hermit Thrushes. This suggests that water may disrupt foraging activities; however, other ground foraging species such as American Robins, Eastern Towhees, Rusty Blackbirds, and Winter Wrens were not directly affected by the presence or absence of water. Eastern Phoebes were frequently observed hawking insects over water on the river and over standing water within forested swamps (personal observation); therefore, I predicted a positive association of Eastern Phoebe occupancy with water. This relationship between occupancy of Eastern Phoebes and water was statistically important and positive.

Hickory basal area was associated positively with two species, Wood Ducks and Yellow-bellied Sapsuckers (Table 2, Fig. 5). This relationship has been documented previously in Yellow-bellied Sapsuckers (Wilkins 2001) and my results reaffirm this relationship. Hickory trees were present on 69.4 % of sites. Water Hickories made up 100% of hickory trees measured within the field site.

Oak-hickory community was important for predicting occupancy by American Crows, Cedar Waxwings, and Eastern Towhees (Table 2, Fig. 5). American Crows and Eastern Towhees avoided oak-hickory forest, but Cedar Waxwings were more common in oak-hickory. Oak-hickory community occupied 67.2 % of sites. Occupancy may be influenced annually by abundant or scarce mast for some species of tree. Because this is a one-year study, the possibility remains that birds shift occupancy based on availability of these food supplies.

Oak-gum-cypress community was associated positively with occupancy of Pileated Woodpeckers and Red-shouldered Hawks (Table 2, Fig. 5). For Pileated Woodpeckers, this association was expected because clustered large cavities in tupelo and cypress trees were frequently observed throughout the forest. I observed several Red-shouldered Hawks nesting toward the end of my field season; therefore, my data may represent microhabitat preferences for Red-shouldered Hawks during the breeding season.

Nine species selected heterogeneous microhabitats throughout my field site. These species might not select habitat based on microhabitat; they might select for larger features of the landscape; they may be generalists that occupy heterogeneous habitats; or they may respond to some combination of microhabitats. A few species included here selected habitats at larger scales. In a study by Howell et al. (2006), Carolina Wrens were best predicted by landscape features within 144-ha grids. Some birds in my study also might require microhabitats that were not measured or tested in this study. Several species were expected to occupy heterogeneous habitat types and did occupy heterogeneous habitats, such as Carolina Chickadees and Tufted Titmice.

For species with inadequate sample sizes (Appendix I), I recommend more targeted survey methods, more sample sites, longer point count intervals, or a combination of these to obtain suitable sample sizes. Specifically, the migrant warblers, Yellow-throated Warblers (*Dendroica dominica*), Black-and-white Warblers (*Mniotilta varia*), and Orange-crowned Warblers (*Vermivora celata*) were difficult to detect and rarely occurred at points. Orange-crowned Warblers appeared to prefer dense understory near the edges of creeks (personal observations). Yellow-throated Warblers and Black-

and-white Warblers frequently traveled with flocks of other species (personal observations). American Woodcocks (*Scolopax minor*) were rarely detected except when birds were fleeing from walking surveyors (personal observations). Linear transects would have likely been a more appropriate survey method for the aforementioned species. Also, active searches of large gridded areas would have likely increased detections of Orange-crowned Warblers, Yellow-throated Warblers, Black-and-white Warblers, and American Woodcocks. Some bird species were rare because southeastern bottomland forests are not optimal habitat for that particular species (e.g., Eastern Bluebird).

Some of the microhabitats that had no significant effects on bird occupancy were surprising since they are mentioned often in published literature as predictors. Specifically, oaks were probably the most frequently mentioned floristic habitat and acorns were frequently mentioned as food for wintering birds. This led to oak being the most frequently tested microhabitat covariate; however, by itself oak did not predict the occupancy of any bird species (Table 1). This lack of association could result from a low mast year during the year of this study. Alternatively, oaks may have been too uniformly abundant across the study area (present at 89% of sites) for occupancy related to oaks to be detected.

Some general patterns were not observed that have been observed in other studies. Shackleford and Conner (1997) reported that dead wood predicted the presence of woodpeckers at sites in Texas. I did not detect a relationship between woodpeckers and dead wood. The scale of my study was limited to bottomland forest, which is known for its high densities of woodpeckers and large amounts of dead wood (Tanner 1942),

whereas Shackleford and Conner (1997) observed abundance of woodpeckers across a variety of upland and bottomland habitats. Therefore, dead wood may have been saturated at my field site to the point where woodpeckers do not appear limited by dead wood. My results indicating no relationship with woodpeckers and snags are consistent with Leonard and Stout (2006). Their study was also limited to bottomland forests and found no relationship between woodpeckers and snags. Other potential explanations include incorporation of the probability of detection, geographic variation, or there is no true relationship between woodpeckers and dead wood during winter in southeastern bottomland forests. I believe that the lack of this association is most likely an artifact of the scale of my study and the large number of woodpeckers present throughout bottomland forest.

Microhabitat could affect occupancy in several ways. Species might select similar microhabitat characteristics across a diversity of landscapes. In this case, microhabitat could be a driving factor in the selection of habitat across a variety of landscapes and microhabitat would be a better predictor of occupancy by species over large areas compared to coarse-scale measurements, similar to the results of MacFaden and Capen (2002). Alternatively, birds might select different microhabitats within different landscapes. In this case, I would expect that hierarchical analyses including landscape variables first, then the inclusion of progressively finer-scaled variables would be the most accurate predictors of occupancy. Additionally, particular landscapes may be more likely to include microhabitats, and therefore, may be useful as surrogates, but a loss of precision and accuracy of occupancy estimates would be expected.

I do not negate the importance of landscape characteristics, but I stress the importance of the inclusion of microhabitat characteristics in predictive models. Some birds select habitat based on landscapes (e.g., MacFaden and Capen 2002, Mitchell et al. 2001). Models using landscape-scale characteristics have likely provided substantial improvements for predicting the occurrence of species. Each species observes the environment on a unique suite of scales of space and time, and different species select habitats from their own unique perspective (Levin 1992). The importance of fine-scale versus coarse-scale habitats will also depend highly upon the scale of conservation objectives. Ultimately, no single scale is correct for describing all populations (Levin 1992, Mitchell et al. 2001).

Selection of a particular habitat does not necessarily translate into optimal survival or reproductive output; therefore, researchers have advocated that habitat selection and habitat quality should be considered separately because ecological traps (reviewed by Battin 2004, e.g., Arlt and Part 2007) and non-ideal habitat selection (e.g., Weldon and Haddad 2005) can confound results. Nevertheless, in a review Sergio and Newton (2003) demonstrated that occupancy was correlated with various measures of territory quality in 17 of 22 studies. In addition, ecological traps appear to be uncommon and caused by anthropogenic influences on landscapes (Battin 2004). Anthropogenic influences on my field site were minimal because of low human population densities. Furthermore, ecological traps are believed to be caused by a conflicting optimization of fecundity and survival (Kristan 2007). However, during the non-breeding season, no such conflict between life history traits should arise. Thus, wintering species should be less likely to select habitats that are ecological traps during winter studies.

21

Recent advances in remote-sensing techniques and resolution are allowing researchers to derive increasingly detailed habitat characteristics from remote-sensing techniques. Examples of recent advances in habitat measurements include the use of multitemporal and multispectral satellite imagery (Townsend and Walsh 2001), LiDAR, and high-resolution imagery. With such technological advances, characteristics of microhabitats should be easier and less costly to obtain, allowing large-scale habitat assessments to include finer-scaled habitat variables.

Microhabitat is important for predicting occupancy by birds, and habitat studies should include microhabitat in analyses. Researchers often rely on expert opinion for hypotheses of habitat relationships. My models provide a foundation for future analyses with empirically-tested microhabitats for southeastern bottomland birds. These models along with software such as GENPRES (Patuxent Wildlife Research Center, Laurel, MD, USA) can inform future studies of expected detection probabilities, samples size needed, survey effort needed, and appropriate microhabitats to target. Furthermore, these microhabitat models can inform habitat prioritization and management decisions within southeastern bottomland forests. Information provided from this study can be applied directly towards the research, conservation, and management of individual species.

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Table 1. Covariates affecting detectability and microhabitat characteristics that were tested in an assessment of habitat selection with their designated category, name, explanation, number of species tested, and number of times covariates were found important.

Category	Covariate name	Explanation	Number of species tested	Number of models with QAIC = 0
Detectability	Date	Scaled Julian date	34	18
	Time	Minutes after sunrise	34	5
	Temp	Temperature (Celsius)	34	6
	Wind	Wind speed Beaufort scale	34	10
	Observer	Observer	34	10
Physiognomic	Basal area	Total basal area	22	1
	Deciduous	Basal area of deciduous trees	1	0
	Evergreen	Basal area of evergreen trees	3	0
	Snags	Basal area of snags	9	0
	Woody debris	Volume of downed woody debris	5	0
	Canopy	Upward densitometer readings in 4-cardinal directions	27	1
	Ground	Downward densitometer readings in 4-cardinal directions	22	2
	Woody stems	Number of woody stems < 10-cm dbh	21	4
	Height	Height of 3 tallest trees	6	0
	Length	Canopy length of 3 tallest trees	2	0
	Leaf litter	Average depth of leaf litter measured in 4 cardinal directions at the edge and center of the plot	14	2
	Mixed	Index of mixed pine and non-pine forest	4	0
	Number of trees	Number of trees	5	0
	Bark	Exposed bark calculated as the surface area of a cone from the 3 most dominant trees	5	0
	Number of trees > 30 cm	Number of large trees > 30-cm dbh	1	0
	Woody debris > 30 cm	Volume of large woody debris > 30 cm at one end	1	0
	Water	Presence or absence of water	14	3
Floristic	Oak	*Quercus nigra ,Q. michauxii, Q. lyrata*	30	0
	Holly	*Ilex opaca*	10	2
	Tupelo	Mostly *Nyssa aquatica*, also *N. sylvatica*	19	6
	Elm	*Planera aquatica, Ulmus americana*	7	1
	Cypress	*Taxodium distichum*	18	0
	Pine	*Pinus taeda, P. glabra*	18	2
	Cottonwood	*Populus*	7	0
	Sweetgum	*Liquidambar styraciflua*	4	1
	Maple	Mostly *Acer rubrum*	3	1
	Ash	Mostly *Fraxinus pennsylvanica*	11	0

Table 1. continued.

Category	Covariate name	Explanation	Number of species tested	Number of models with QAIC = 0
Floristic	Hickory	*Carya aquatica*	20	2
	Magnolia	Mostly *Magnolia grandiflora*, also M. *virginiana*	1	0
	Willow	Mostly *Salix nigra*	1	0
	Sycamore	*Platanus occidentalis*	10	0
	Wateroak	*Quercus nigra*	1	0
	Oak-gum-cypress	*Quercus + Nyssa + Taxodium* community where all three are present	20	2
	Oak-hickory	*Quercus + Carya* community where both are present	20	3
	Mistletoe	*Phoradendron*	2	0
	Cane	Cover of giant cane; *Arundinaria gigantea*	1	0
	Palmetto	Cover of saw palmetto; *Serenoa repens*	3	1

Table 2. Species grouped by covariates with their β values for each species where an association was determined by the best models (QAIC = 0). Table 1 explains each microhabitat characteristic group.

| Category	Covariate Group	Species	β (SE)
Physiognomic	Woody stems	Winter Wren	-0.45 (0.26)
		Downy Woodpecker	-0.48 (0.20)
		Rusty Blackbird	-1.05 (0.71)
		Hermit Thrush	0.53 (0.53)
	Water	Hermit Thrush	-1.19 (0.80)
		Wood Duck	0.70 (0.41)
		Eastern Phoebe	0.89 (0.45)
	Ground	American Goldfinch	-0.86 (0.61)
		American Robin	-0.93 (0.37)
	Leaf litter	Pine Warbler	0.34 (0.16)
		Common Grackle	0.34 (0.21)
	Basal area	Blue-headed Vireo	-0.38 (0.16)
	Canopy	Cedar Waxwing	0.54 (0.27)
Floristic	Tupelo	Ruby-crowned Kinglet	-0.52 (0.18)
		Winter Wren	-0.63 (0.38)
		Barred Owl	-0.96 (0.58)
		Common Grackle	-1.04 (0.68)
		American Goldfinch	-1.54 (1.05)
		Black Vulture	0.78 (0.28)
	Holly	Northern Cardinal	15.58 (9.32)
		Red-bellied Woodpecker	37.76 (15.07)
	Pine	Yellow-rumped Warbler	-3.45 (1.88)
		Golden-crowned Kinglet	4.08 (3.22)
	Hickory	Wood Duck	3.10 (1.46)
		Yellow-bellied Sapsucker	3.88 (1.23)
	Elm	Red-shouldered Hawk	-95.98 (85.22)
	Sweetgum	American Goldfinch	0.77 (0.53)
	Maple	Hairy Woodpecker	2.03 (0.95)
	Palmetto	Hermit Thrush	1.00 (0.65)
	Oak-gum-cypress	Red-shouldered Hawk	0.44 (0.26)
		Pileated Woodpecker	2.23 (1.28)
	Oak-hickory	American Crow	-0.48 (0.18)
		Eastern Towhee	-1.42 (0.75)
		Cedar Waxwing	0.54 (0.33)
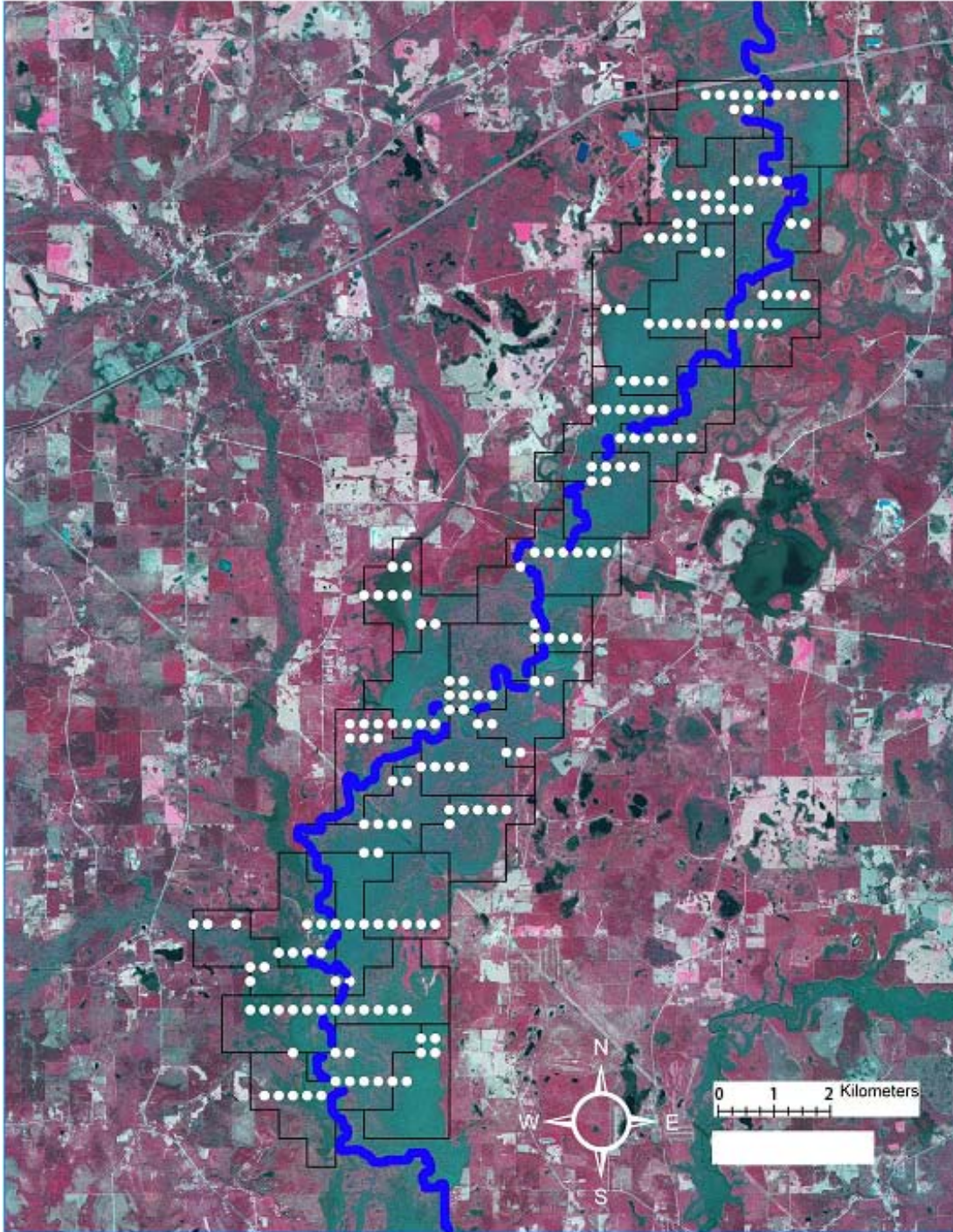
Figure 1. Sites sampled in the Choctawhatchee River Basin, FL for assessing habitat selection by wintering birds. Irregular 2-km^2 grids conformed to the river basin and point transects were randomly selected from within each grid. Variations in vegetation are more distinct in infrared photographs than in aerial photographs.
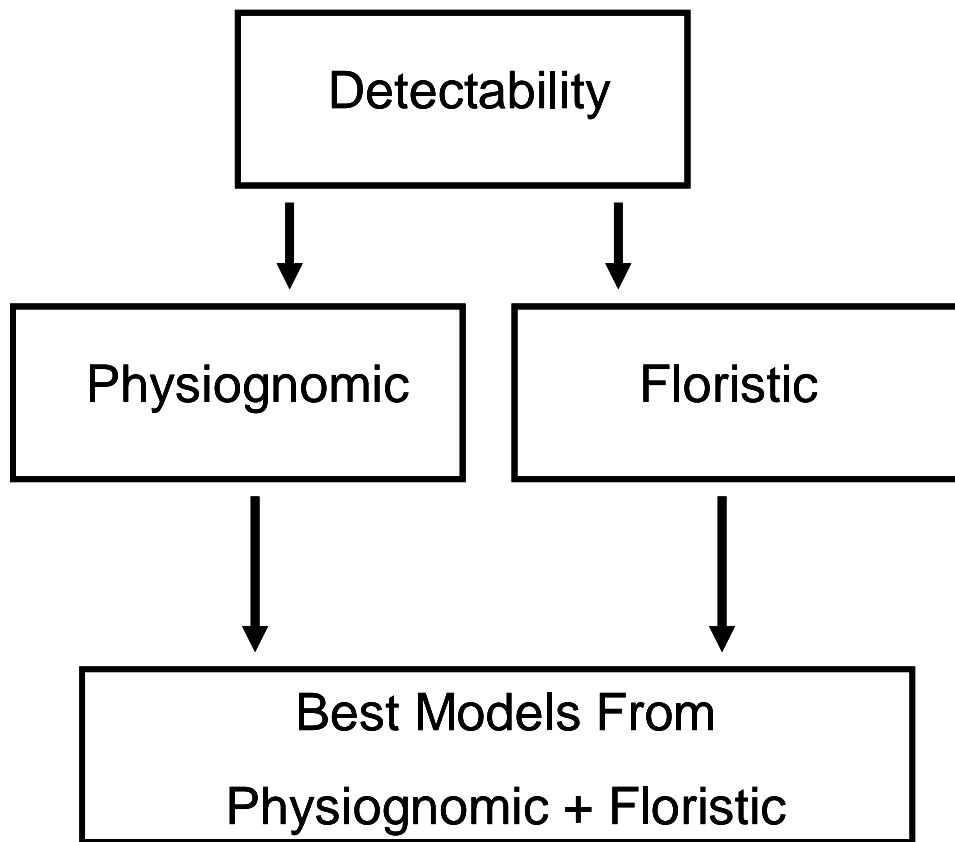
Figure 2. The hierarchical structure of occupancy analyses used in an assessment of habitat selection by wintering birds in the Choctawhatchee River Basin, Florida. Detectability covariates were tested first and incorporated within all subsequent analyses. Physiognomic and floristic covariates were tested. Lastly, physiognomic and floristic models were combined and compared. I only incorporated models with ΔQAIC values $\leq$ 2.0 and models with high weights from physiognomic and floristic result into the final analysis.

Figure 3. Physiognomic and floristic characteristics were included in the best models for a statistically similar number of bird species. There was no significant difference (Yates' continuity corrected χ^2=0.00, p=0.93, df = 1, Fig. 3) between observed and expected frequencies of microhabitat characteristics.

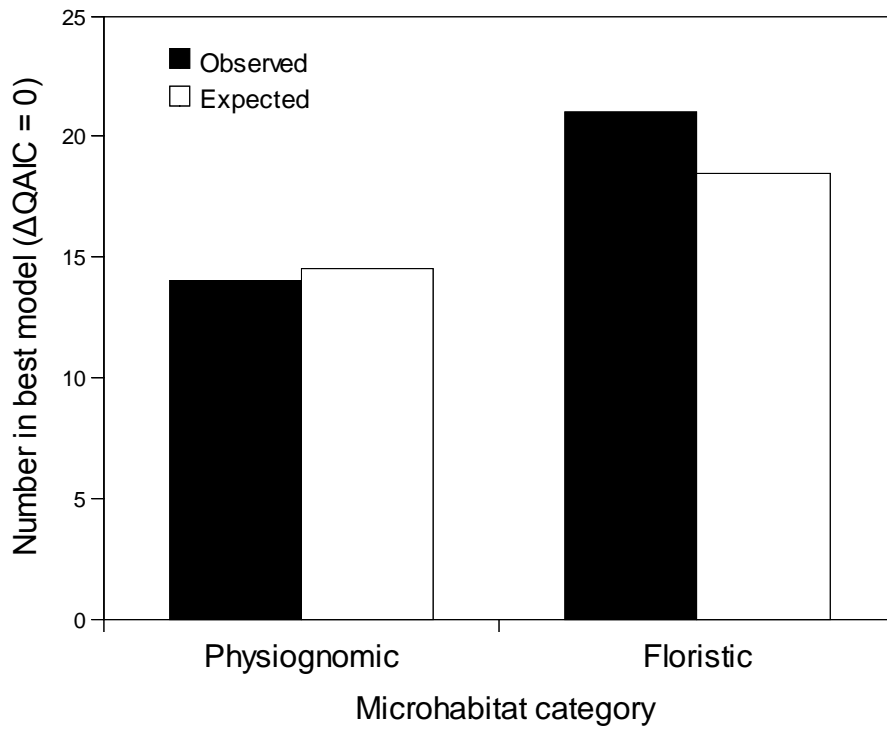Figure 4. Effects of physiognomic characteristics on occupancy of birds in an assessment of habitat selection by wintering birds in the Choctawhatchee River Basin, Florida. Modeled effects are (A) cover of palmetto on Hermit Thrushes (HETH), (B) depth of leaf litter on Common Grackles (COGR) and Pine Warblers (PIWA), (C) the presence or absence of water on Eastern Phoebes (EAPH), Hermit Thrushes, and Wood Ducks (WODU), (D) canopy cover on Cedar Waxwings (CEDW), (E) total basal area on Blue-headed Vireos (BHVI), (F) number of woody stems < 10-cm dbh on Downy Woodpeckers (DOWO), Hermit Thrushes, Rusty Blackbirds (RUBL), and Winter Wrens (WIWR), and (G) ground cover on American Goldfinches (AMGO) and American Robins (AMRO). Note that palmetto is actually a floristic component, but is included here for comparative purposes. Standard errors for each β value are included on Table 2.
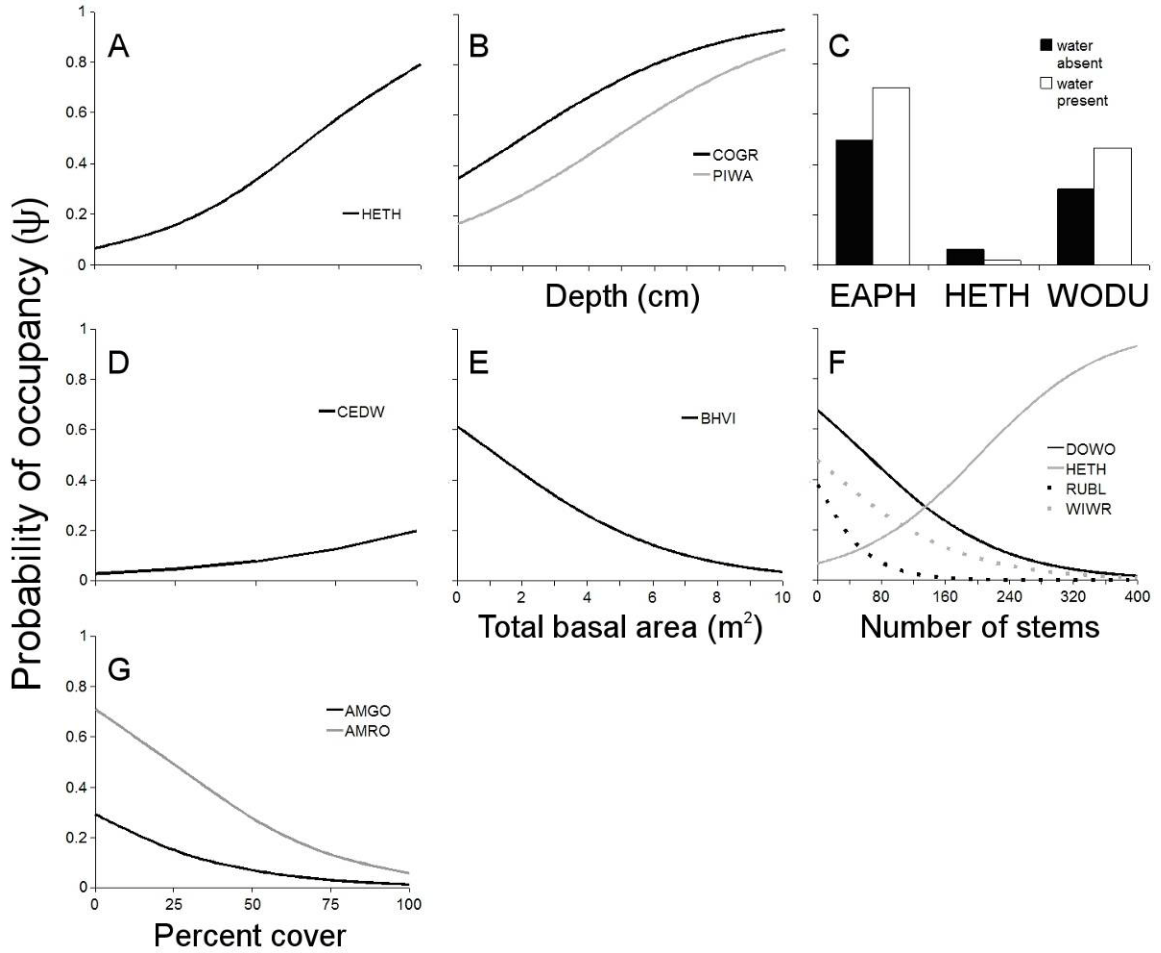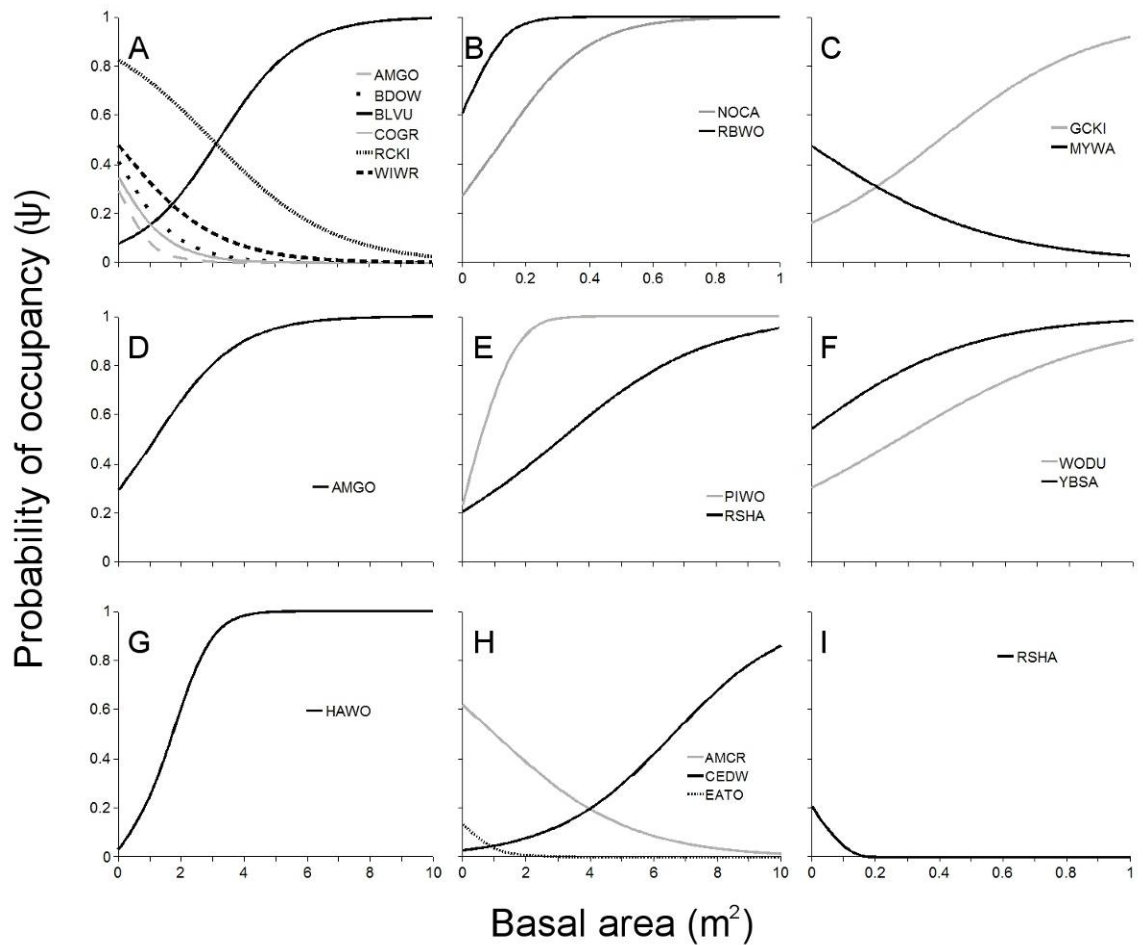
Figure 5. Effects of floristic characteristics on occupancy in an assessment of habitat selection by wintering birds in the Choctawhatchee River Basin, Florida. Modeled effects are (A) tupelo on American Goldfinches (AMGO), Barred Owls (BDOW), Black Vultures (BLVU), Common Grackles (COGR), Ruby-crowned Kinglets (RCKI) and Winter Wrens (WIWR), (B) holly on Northern Cardinals (NOCA) and Red-bellied Woodpeckers (RBWO), (C) pine on Golden-crowned Kinglets (GCKI) and Yellow-rumped Warblers (YRWA), (D) Sweetgum on American Goldfinches, (E) oak-gum-cypress on Pileated Woodpeckers (PIWO) and Red-shouldered Hawks (RSHA), (F) hickory on Wood Ducks (WODU) and Yellow-bellied Sapsuckers (YBSA), (G) maple on Hairy Woodpeckers (HAWO), (H) oak-hickory on American Crows (AMCR), Cedar Waxwings (CEDW), and Eastern Towhees (EATO), (I) elm on Red-shouldered Hawks. Note that although palmetto is a floristic covariate, palmetto is included with physiognomic characteristics in Fig. 4 for comparative purposes. Standard errors for each β value are included on Table 2.

APPENDIX I.
All birds detected during surveys, their sample sizes, along with the number of habitat covariates tested. Habitat covariates are further divided into physiognomic and floristic covariates tested. Total number of detections includes detections at all distances. Number of sites is truncated at 100 m unless indicated otherwise.

Genus species	Common Name	Detections	Sites present	Physiognomic	Floristic	Total covariates
Corvus brachyrhynchos	American Crow*	259	43	3	4	7
Carduelis tristis	American Goldfinch	403	40	7	4	11
Turdus migratorius	American Robin	555	40	5	4	9
Scolopax minor	American Woodcock**	1	1	-	-	-
Mniotilta varia	Black-and-white Warbler**	8	7	-	-	-
Strix varia	Barred Owl*	66	37	5	5	10
Megaceryle alcyon	Belted Kingfisher**	15	9	-	-	-
Polioptila caerulea	Blue-gray Gnatcatcher**	14	9	-	-	-
Vireo solitarious	Blue-headed Vireo	77	47	4	4	8
Cyanocitta cristata	Blue Jay	70	27	4	5	9
Coragyps atratus	Black Vulture*	31	15	2	5	7
Certhia americana	Brown Creeper	24	14	2	6	8
Poecile carolinensis	Carolina Chickadee	360	26	7	5	12
Thryothorus ludovicianus	Carolina Wren	972	26	5	7	12
Bombycilla cedrorum	Cedar Waxwing*	18	11	2	6	8
Quiscalus quiscula	Common Grackle*	246	20	5	5	10
Accipiter cooperii	Cooper's Hawk**	1	1	-	-	-
Geothlypis trichas	Common Yellowthroat**	12	7	-	-	-
Picoides pubescens	Downy Woodpecker	207	43	7	5	12
Sialia sialis	Eastern Bluebird*	30	19	3	3	6
Sayornis phoebe	Eastern Phoebe	181	46	4	7	11
Megascops asio	Eastern Screech-Owl**	2	2	-	-	-
Pipilo erythrophthalmus	Eastern Towhee*	16	9	4	4	8
Contopus virens	Eastern Wood-pewee**	3	2	-	-	-
Baeolophus bicolor	Tufted Titmouse	471	37	5	8	13
Corvus ossifragus	Fish Crow*	40	23	2	3	5
Ardea herodias	Great Blue Heron**	1	1	-	-	-
Regulus satrapa	Golden-crowned Kinglet	22	16	4	6	10
Dumetella carolinensis	Gray Catbird**	1	1	-	-	-
Ardea alba	Great Egret**	2	2	-	-	-
Picoides villosus	Hairy Woodpecker	15	10	6	8	14

* denotes that this species was analyzed but unlimited distance point counts were used. ** denotes that the species was detected at least once but an insufficient sample size was obtained for analyses.

APPENDIX I. continued.

Genus species	Common Name	Detections	Sites present	Physiognomic	Floristic	Total covariates tested
Catharus guttatus	Hermit Thrush	19	14	5	7	12
Dendroica coronata	Yellow-rumped Warbler	224	34	4	7	11
Cardinalis cardinalis	Northern Cardinal	121	43	5	8	13
Vermivora celata	Orange-crowned Warbler**	9	5	-	-	-
Dendroica pinus	Pine Warbler	109	39	6	5	11
Dryocopus pileatus	Pileated Woodpecker	210	49	6	9	15
Sitta canadensis	Red-breasted Nuthatch**	1	1	-	-	-
Melanerpes carolinus	Red-bellied Woodpecker	750	22	7	7	14
Regulus calendula	Ruby-crowned Kinglet	441	40	6	8	14
Buteo lineatus	Red-shouldered Hawk	355	33	4	7	11
Euphagus carolinus	Rusty Blackbird*	45	11	5	6	11
Agelaius phoeniceus	Red-winged Blackbird*	91	38	-	-	-
Melospiza melodia	Song Sparrow**	7	2	-	-	-
Melospiza georgiana	Swamp Sparrow**	35	8	-	-	-
Cathartes aura	Turkey Vulture*	82	43	4	6	10
Vireo griseus	White-eyed Vireo**	17	9	-	-	-
Meleagris gallopavo	Wild Turkey**	3	3	-	-	-
Troglodytes troglodytes	Winter Wren	72	41	8	8	16
Aix sponsa	Wood Duck	629	18	3	8	11
Sphyrapicus varius	Yellow-bellied Sapsucker	522	34	4	8	12
Colaptes auratus	Northern Flicker	425	36	6	6	12
Dendroica dominica	Yellow-throated Warbler**	1	1	-	-	-

* denotes that this species was analyzed but unlimited distance point counts were used. ** denotes that the species was detected at least once but an insufficient sample size was obtained for analyses.

APPENDIX II.

Individual species and their corresponding best detectability models (ΔQAIC = 0). Also shown are occupancy (ψ) and detectability (p) intercepts' β values alongside detectability covariates' β values. These models can be used along with software such as GENPRES to estimate detection probabilities and sampling effort needed to complete future research goals.

Species	Model	QAIC weights	Parameters		Detectability covariates				
			ψ (SE)	p (SE)	Date (SE)	Time (SE)	Temp (SE)	Wind (SE)	Observer (SE)
American Crow	ψ(oak-hickory), p(date+wind)	0.30	0.48 (0.25)	-0.36 (0.16)	0.65 (0.11)			-0.45 (0.11)	
American Goldfinch	ψ(tupelo+sweetgum+ground), p(date+temp)	0.40	-0.88 (0.47)	-2.14 (0.32)	0.60 (0.20)		-0.44 (0.21)		
American Robin	ψ(ground), p(time)	0.33	0.89 (0.31)	-1.43 (0.14)		-0.62 (0.11)			
Barred Owl	ψ(tupelo), p(date+wind)	0.26	-0.36 (0.37)	-1.74 (0.32)	0.51 (0.17)			-0.35 (0.19)	
Blue-headed Vireo	ψ(BA), p(date+wind)	0.37	0.46 (0.56)	-1.38 (0.29)	0.53 (0.16)			-0.39 (0.17)	
Blue Jay	ψ(.), p(.)	0.50	-1.61 (0.23)	-1.02 (0.21)					
Black Vulture	ψ(tupelo), p(date+temp)	0.38	-2.50 (0.39)	-1.92 (0.38)	-1.33 (0.40)		0.53 (0.28)		
Brown Creeper	ψ(.), p(observer+ wind)	0.24	-2.19 (0.38)	-4.01 (1.05)				0.65 (0.38)	2.71 (0.75)
Carolina Chickadee	ψ(.), p(date+temp)	0.33	0.13 (0.17)	-0.80 (0.11)	0.22 (0.09)		0.37 (0.10)		
Carolina Wren	ψ(.), p(date+wind)	0.28	1.00 (0.20)	-0.30 (0.12)	0.22 (0.08)			-0.33 (0.09)	
Cedar Waxwing	ψ(oak-hickory+ canopy), p(date)	0.37	-3.56 (0.83)	-2.25 (0.55)	0.80 (0.38)				
Common Grackle	ψ(tupelo+leaf litter), p(time)	0.23	-0.64 (0.44)	-2.05 (0.27)		-0.35 (0.17)			
Downy Woodpecker	ψ(stems), p(time)	0.21	0.73 (0.35)	-1.32 (0.14)		-0.32 (0.12)			
Eastern Bluebird	ψ(.), p(date+observer)	0.45	-1.25 (0.42)	-2.18 (0.52)	1.29 (0.37)				-2.58 (0.81)
Eastern Phoebe	ψ(water), p(wind+observer)	0.15	0.00 (0.30)	-0.86 (0.28)				-0.37 (0.15)	-0.45 (0.26)
Eastern Towhee	ψ(oak-hickory), p(.)	0.39	-1.88 (0.53)	-1.62 (0.50)					
Tufted Titmouse	ψ(.), p(date+wind)	0.31	0.13 (0.19)	-0.72 (0.15)	0.53 (0.11)			-0.36 (0.11)	
Fish Crow	ψ(.), p(date)	0.31	-1.66 (0.32)	-1.76 (0.35)	0.77 (0.30)				
Golden-crowned Kinglet	ψ(pine), p(date+observer)	0.78	-1.64 (0.46)	-3.62 (0.67)	0.73 (0.29)				1.63 (0.60)

Species	Model	QAIC weights	Parameters				Detectability covariates		
			ψ (SE)	p (SE)	Date (SE)	Time (SE)	Temp (SE)	Wind (SE)	Observer (SE)
Hairy Woodpecker	ψ(maple), p(date)	0.38	-3.49 (0.56)	-1.42 (0.50)	-0.64 (0.38)				
Hermit Thrush	ψ(sawpalmetto+water+stems), p(.)	0.39	-2.67 (1.00)	-2.39 (0.50)					
Yellow-rumped Warbler	ψ(pine), p(date)	0.38	-0.10 (0.20)	-1.25 (0.15)	0.90 (0.13)				
Northern Cardinal	ψ(holly), p(time+observer)	0.37	-0.99 (0.28)	-2.70 (0.37)		-0.69 (0.20)			1.51 (0.36)
Pine Warbler	ψ(leaf litter), p(date)	0.37	-1.61 (0.37)	-2.27 (0.38)	1.46 (0.27)				
Pileated Woodpecker	ψ(oak-gum-cypress), p(temp+wind+observer)	0.46	-1.19 (0.42)	-3.56 (0.92)			-0.57 (0.25)	-0.65 (0.38)	1.97 (0.86)
Red-bellied Woodpecker	ψ(holly), p(.)	0.37	0.44 (0.18)	-0.49 (0.08)					
Ruby-crowned Kinglet	ψ(tupelo), p(observer)	0.27	1.55 (0.24)	-0.84 (0.11)					0.59 (0.14)
Red-shouldered Hawk	ψ(elm+oak-gum-cypress), p(temp+wind+observer)	0.44	-1.35 (0.38)	-0.27 (0.68)			-0.47 (0.28)	-0.94 (0.39)	-1.60 (0.65)
Rusty Blackbird	ψ(stems), p(date+wind)	0.23	-0.50 (0.95)	-1.83 (0.73)	-0.71 (0.35)			-1.43 (0.52)	
Turkey Vulture	ψ(.), p(date+time)	0.40	-0.16 (0.33)	-2.41 (0.26)	-0.43 (0.16)	0.88 (0.19)			
Winter Wren	ψ(tupelo+stems), p(temp+observer)	0.33	-0.09 (2.43)	-2.43 (0.37)			-0.34 (0.18)		1.22 (0.37)
Wood Duck	ψ(hickory+water), p(observer)	0.26	-0.83 (0.31)	-3.26 (0.34)					2.86 (0.35)
Yellow-bellied Sapsucker	ψ(hickory), p(date)	0.11	0.17 (0.21)	-0.21 (0.08)	0.28 (0.08)				
Northern Flicker	ψ(.), p(.)	0.47	0.15 (0.20)	-1.18 (0.13)					