BROWN-HEADED NUTHATCH OCCUPANCY IN CENTRAL FLORIDA AND ITS RELATIONSHIP TO FOREST TYPE, FOREST STRUCTURE, AND THE PRESENCE OF RED-COCKADED WOODPECKERS

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Abstract. The Brown-headed Nuthatch (*Sitta pusilla*) is listed as a species of conservation concern throughout most of its range. Forest conditions that support the imperiled Red-cockaded Woodpecker (*Picoides borealis*) are thought to provide excellent habitat for the nuthatch, but ambiguity exists because the nuthatch has disappeared from some areas where the woodpecker persists. We studied Brown-headed Nuthatches in two forest types that spanned an environmental gradient in central Florida and also differed in terms of forest structure and the presence of woodpeckers. Sandhill forests had mature timber that supported a large woodpecker population (~70 territories); flatwood forests were dominated by younger pines and supported no Red-cockaded Woodpeckers. We used repeated surveys incorporating broadcast vocalizations and patch-occupancy analysis to assess variation in nuthatch occupancy and detection in relation to forest type, four structural covariates (snag density, basal area of pines and hardwoods, and pine diameter), and proximity to Red-cockaded Woodpecker territories. In our best model, occupancy and detection varied in relation to forest type and pine basal area. Occupancy and detection probabilities were higher in the younger flatwood forests and averaged 0.96 and 0.75 as compared to 0.56 and 0.37, respectively, in older sandhill forests. Occupancy and detection were not influenced by proximity to Red-cockaded Woodpecker territories. The higher encounter rates recorded in younger flatwood forests likely stemmed from differences in habitat quality, while variation attributable to forest structure and woodpecker distribution warrants further study.

Key words: *Brown-headed Nuthatch, habitat quality,* Picoides borealis, *occupancy, Red-cockaded Woodpecker,* Sitta pusilla.

Ocupación de *Sitta pusilla* en el Centro de Florida y su Relación al Tipo de Bosque, la Estructura del Bosque y la Presencia de *Picoides borealis*

Resumen. *Sitta pusilla* está listada como una especie con estado de conservación preocupante a lo largo de casi todo su rango de distribución. Se piensa que las condiciones del bosque que alberga a la especie en peligro *Picoides borealis* brindan un hábitat excelente para los trepadores, pero existe ambigüedad debido a que los trepadores han desaparecido de algunas áreas donde los carpinteros han persistido. Estudiamos a *S. pusilla* en dos tipos de bosque que se extienden en un gradiente ambiental en el centro de Florida y que también difieren en términos de la estructura del bosque y la presencia de carpinteros. Los bosques de las dunas tenían bosque maduro que albergaba una gran población de carpinteros (~70 territorios); los bosques de áreas planas estaban dominados por pinos más jóvenes y no albergaban individuos de *P. borealis*. Empleamos muestreos repetidos incorporando la emisión de vocalizaciones y el análisis de la ocupación de parches para evaluar la variación en la ocupación de los trepadores y en la detección con relación al tipo de bosque, a cuatro covariables estructurales (densidad de tocones, área basal de pinos y maderas duras y diámetro de los pinos) y a la proximidad a los territorios de *P. borealis*. En nuestros mejores modelos, la ocupación y la detección variaron con relación al tipo de bosque y al área basal de pino. Las probabilidades de ocupación y detección fueron más altas en los boques de áreas planas más jóvenes y promedió 0.96 y 0.75 en comparación a 0.56 y 0.37, respectivamente, en los bosques más viejos de las dunas. La ocupación y la detección no fueron influenciadas por la proximidad a los territorios de *P. borealis*. Las tasas de encuentro más altas registradas en los bosques más jóvenes de áreas planas probablemente se debieron a diferencias en la calidad del hábitat, mientras que las variaciones atribuibles a la estructura del bosque y a la distribución de los carpinteros requieren estudios posteriores.

INTRODUCTION

Populations of the Brown-headed Nuthatch (*Sitta pusilla*) have declined to the point that the nuthatch is listed as a species of conservation concern in most states in which it occurs (Cox and Widener 2008). The Brown-headed Nuthatch is a member of a distinctive avifauna associated with open pine forests of the southeastern U.S. (Johnston and Odum 1956, Engstrom 1993). The imperiled Red-cockaded Woodpecker (*Picoides borealis*), another member of this group, occurs

regularly with the Brown-headed Nuthatch in mature pine forests of the region (Engstrom 1993). Both species excavate roosting and nesting cavities that are used by other animals (Blanc and Walters 2008), both prey upon arboreal insects on limbs and boles (Nesbitt and Hetrick 1976, Hanula and Horn 2004), and both breed cooperatively in groups that contain >2 adults (Walters et al. 1988, Cox and Slater 2007).

Because of its need for a larger area (≥100 ha per territory) and use of old (≥80 years) living pine trees as a substrate for nest and roost cavities, habitat management for the Red-cockaded Woodpecker is thought to encompass the habitat needs of the Brown-headed Nuthatch and other members of the regional avifauna (Hunter et al. 1994). Several studies suggest the woodpecker may serve in this manner (Wilson et al. 1995, Plentovich et al. 1998, Conner et al. 2002), but Simberloff (2004) cautioned that use of "umbrella species" such as the Red-cockaded Woodpecker is a blunt tool at best and may have limitations. The Brown-headed Nuthatch appears to fare well in many settings where it occurs with the Red-cockaded Woodpecker, but three observations point to distinctive habitat needs: (1) the nuthatch disappeared from sites in Missouri nearly 40 years before the Red-cockaded Woodpecker did (Robbins and Easterla 1992); (2) Kale et al. (1992) did not find nuthatches in three conservation areas in Florida that each supported >30 woodpecker territories; and (3) nuthatches can be found in young pine forests that do not support Red-cockaded Woodpeckers (Hamel 1992, Wilson and Watts 1999).

Pine forests that support the Brown-headed Nuthatch and Red-cockaded Woodpecker span broad environmental gradients that range from xerophytic forests on well-drained soils to mesophytic forests bordering wetlands (Mitchell et al. 1999). Some occupied areas are dominated by a single species of pine (Lloyd and Slater 2007), while others are forested with two or three codominant species (Cox and Slater 2007). The Red-cockaded Woodpecker has been studied across many of these ecological gradients (Costa and Daniels 2004), but information on the Brown-headed Nuthatch has been collected from fewer forest types and often has been based on multispecies surveys that may not adequately account for the effects that cooperative breeding behavior (i.e., ≥2 adults per territory) may have on abundance estimates (e.g., Wilson et al. 1995, Conner et al. 2002, Allen et al. 2006). Nuthatches also nest early in the year with many young fledging by late April (McNair 1984, Cox and Slater 2007). Multi-species counts in May and June thus may include counts of independent offspring as well as of adults.

The purpose of our study was to assess variation in patch occupancy and the probability of detecting the nuthatch in two types of pine forests that spanned an edaphic and elevation gradient in central Florida. The pine forests also differed in terms of the associated Red-cockaded Woodpecker populations they supported. The first forest type was dominated by

longleaf pine (*Pinus palustris*) and occurred on sandy, well-drained soils on prominent ridges. The Florida Natural Areas Inventory (FNAI 2010) classified such areas as "sandhill" forests, and the sandhill forests we studied contained mature timber that supported approximately 70 Red-cockaded Woodpecker territories (C. Sekerak, U.S. Forest Service, unpubl. data). The second forest type, classified as "mesic flatwoods" (FNAI 2010), occupied poorly drained soils at lower elevations and was dominated by slash pine (*P. elliottii*) and intermittent patches of pond pine (*P. serotina*). The mesic flatwoods we studied contained younger timber that did not support Red-cockaded Woodpeckers (C. Sekerak, U.S. Forest Service, unpubl. data).

We used playback vocalizations, repeated sampling, and patch-occupancy analysis (MacKenzie et al. 2002) to evaluate variation in occupancy and probability of detection of the nuthatch within these distinctive forest types in central Florida. Occupancy and detection often serve as good surrogates for abundance (MacKenzie et al. 2002), and patch-occupancy analysis is well suited to species like the Brown-headed Nuthatch that occupy year-round territories and live in social groups with 1–5 adults per territory (Cox and Slater 2007). We assessed whether nuthatch occupancy varied in relation to forest type and proximity to Red-cockaded Woodpecker territories. We also evaluated structural covariates (basal area of pines and hardwoods, tree girth, and snag density) that have been linked to variation in nuthatch abundance in other studies. Understanding the effects that forest type and the presence of a putative umbrella species may have on Brown-headed Nuthatch occupancy should assist in efforts to conserve and manage this declining passerine.

METHODS

STUDY AREA

Our study took place on the Ocala National Forest (ONF; Lake, Marion, and Sumter counties, Florida) where Hamel (1992) suggested high nuthatch densities could be expected. The area's terrain consists of gently rolling hills with elevations ranging from 3 to 55 m. The ONF encompasses the largest area of sandhill forest remaining in peninsular Florida (~16 000 ha) and includes sites such as Riverside Island that have served as ecological reference points for this forest type (Laessle 1958). Early settlers referred to patches of sandhill forest within the ONF as "islands" because the forest patches were isolated by intervening areas of sand pine (*P. clausa*) scrub (a forest type not used by nuthatches; Hamel 1992). We sampled Kerr, Norwalk, Riverside, and Syracuse islands in the ONF, and the distances separating sandhill islands ranged from 11 to 60 km.

Mesic flatwood forests encompassed approximately 13 500 ha of the ONF, and we sampled three distinct areas of flatwood forest that each encompassed >3500 ha. The

flatwood forests we sampled were separated >25 km and their isolation paralleled that of the sandhill forests as a result of intervening areas of unsuitable nuthatch habitat (i.e., scrub, riverine forests, and urban areas). Flatwood and sandhill forests both were burned regularly (fire-return intervals ≤4 years) and had an open midstory. Ground-cover conditions in the two forest types differed: sandhill forests were dominated by wiregrass (*Aristida stricta*), while flatwood forests were dominated by saw palmetto (*Serenoa repens*) and gallberry (*Ilex glabra*).

FIELD METHODS

To identify survey sites, we merged the centers of Red-cockaded Woodpecker territories (C. Sekerak, U.S. Forest Service, unpubl. data), roads and trails, and a classified Landsat image (Stys et al. 2003) depicting dominant forest types within the ONF in ArcView GIS (version 3.2, ESRI, Redlands, CA). We established 45 potential survey points in both forest types ($n = 90$) that met the following conditions: (1) land cover within 200 m of each survey point had to be dominated (>80% of areal extent) either by sandhill or mesic flatwood forest; (2) each survey point had to be ≥800 m from the nearest neighboring point; and (3) points had to be easily accessed by dirt roads and trails. We visited candidate points to confirm their appropriateness (i.e., open pine forests with little midstory), and we relocated six points <300 m because of poor road conditions or the absence of appropriate habitat as a result of recent logging or inaccurate land-cover classification. Final survey points were broadly distributed among the different timber stands and burn units used to manage pine forests in the ONF, were separated >900 m, and spanned a 40 × 90 km area. A nuthatch's home range typically extends 200–300 m (Cox and Slater 2007), so the distance separating the points ensured we sampled independent territories.

We visited each survey point three times from January to March 2011 at times when rain was absent and wind as measured by the Beaufort scale was ≤3 (Sauer et al. 2011). We played a 6-min recording of nuthatch vocalizations during each visit and recorded the total number of individuals observed. Broadcast of recordings improves the probability of detection of species like the nuthatch that do not defend territories with song (Withgott and Smith 1998). The recorded vocalizations (available from the first author) included aggressive calls and contact and foraging notes (Norris 1958) that alternated with 15 sec of silence at the end of each 1-min interval. We played the vocalizations with an MP3 player and battery-powered external speakers with volume held constant at 90 decibels. Surveys took place between 08:00 and 16:30 at times varied so that sites were visited both early and late in the day. Nuthatches respond aggressively to conspecific vocalizations throughout the year and during all daylight hours (J. Cox, pers. obs.), but our surveys coincided with the early part of the breeding season when territorial aggression was likely to provide strong responses.

We quantified forest structure at three locations established 50 m from survey points along compass bearings ~120° apart. We used a 5-factor prism to quantify the basal area of pines and hardwoods and tree calipers to measure the diameter at breast height (dbh) of the six pines closest to the point of sampling. Pines' dbh is correlated with their maturity, but the slope and strength of this correlation varies by species and site. Slash pines on mesophytic soils grow faster and increase girth more rapidly than do longleaf pines on xerophytic soils (Alavalapati et al. 2002), and these differences need to be considered when the maturity of the timber in our samples is compared. We used a range finder to measure the distance to the nearest snag in four quadrants and used point-center quarter methods (Cottam and Curtis 1956) to convert these distances to a density estimate. For each survey point we calculated averages for pine dbh (cm), basal area of pines and hardwoods (m^2 ha^{-1}), and snag density (ha^{-1}) and used the averages as covariates in statistical analyses.

STATISTICAL ANALYSES

For descriptive statistics and statistical comparisons of forest structure we used Systat (version 12.00.08, Chicago). Values reported are means ± SD unless otherwise noted. We assessed forest-structure variables for normality with the Shapiro–Wilk statistic. Snag density and pine basal area deviated from normality, but log transformations corrected these deviations. We used log-transformed variables in statistical tests comparing differences in snag density and pine basal area in different forest types, but, to facilitate comparisons with other studies, descriptive statistics presented for these variables are based on untransformed data. Tests and descriptive statistics for other forest structure variables are based on untransformed data, and correlation analysis suggests collinearity among the structural measurements was low ($|r| < 0.15$).

We used the program PRESENCE (http://www.mbr-pwrc.usgs.gov/software/presence.html) to model variation in nuthatch occupancy (ψ) and detection probabilities (p) in relation to corresponding variation in forest type, basal area of pines and hardwoods, pine dbh, and snag density. We transformed the four continuous covariates (basal area of pines and hardwoods, pine dbh, and snag density) to Z-scores before modeling to standardize ranges and variances. We began by constructing models that predicted ψ or p from each covariate singly as well as a model in which ψ and p were held constant. We then evaluated additive and interactive models in which we assessed variation in ψ and p with combinations of covariates. A global model considered variation in ψ and p in relation to forest type and four covariates and was evaluated for goodness of fit according to MacKenzie and Bailey (2004). The evaluation suggested data were overdispersed, so we applied a variance-inflation factor ($\hat{c}$) of 1.1. We evaluated

the models' with differences in the quasi Akaike information criterion (ΔQAIC), and our confidence set comprised models with ΔQAIC ≤2 of that of the highest-ranking model (Burnham and Anderson 2002).

We used two procedures to assess potential relationships between nuthatch occupancy and the presence of Red-cockaded Woodpeckers. First, we compared estimated nuthatch occupancy at sample points within 0.8 km of active woodpecker territories to estimated occupancy among samples >0.8 km from territory centers. The 0.8-km distance is used by public land managers to define zones where habitat is managed for the benefit of the Red-cockaded Woodpecker (USFWS 2003). Second, using GIS, we calculated the distance between a sample point and the center of the nearest woodpecker territory. We then assessed the relationship between this distance (log-transformed to satisfy normality assumptions) and estimated nuthatch occupancy at the sample point by linear regression analysis. Flatwood forests did not support Red-cockaded Woodpeckers, and all flatwood sample points were >5 km from active woodpecker territories, so these analyses were restricted to samples obtained from sandhill forests ($n = 45$).

RESULTS

Brown-headed Nuthatches responded aggressively to broadcast vocalizations in both forest types, but we recorded them at only 18 sample points in sandhill forests (40%) as compared to 42 sample points in mesic flatwoods (93%). Our naïve detection estimate derived from the program PRESENCE was 0.20 ± 0.28 for sandhill forests and 0.72 ± 0.31 for mesic flatwoods. The average number of nuthatches we observed among flatwood samples (2.1 ± 1.1) was approximately five times the number observed among sandhill sites (0.4 ± 0.7) and also less variable (CV = 0.5 vs. 1.7).

Forest structure in mesic flatwoods differed in several ways from that in sandhills. Average pine dbh (cm) was smaller in mesic flatwoods (25.1 ± 6.6) than in sandhill forests (30.5 ± 6.4; $F_{1,88} = 14.81$; $P <0.01$), while snag densities (ha^{-1}) were higher in flatwoods (3.8 ± 5.7) than in sandhills (1.4 ± 0.7; $F_{1,88} = 7.20$; $P <0.01$). As noted, snag-density measurements were skewed, so median values (1.6 for mesic flatwoods and 1.2 for sandhill sites) may reflect central tendencies for this structural component more accurately. Pine basal area (m^2 ha^{-1}) did not differ significantly by habitat type ($F_{1,88} = 1.76$; $P = 0.19$) and averaged 11.5 ± 4.6 in mesic flatwoods versus 10.4 ± 3.3 in sandhill sites. Hardwood basal area was higher in sandhill forests ($F_{1,88} = 13.7$; $P <0.01$) where it averaged 1.1 ± 1.3 vs. 0.3 ± 0.7 in mesic flatwoods.

The top-ranked model (Table 1) evaluated with program PRESENCE was an additive model that linked variation in ψ and p to habitat type (sandhill vs. flatwoods) and pine basal area. The next highest-ranking model was an additive model that linked variation in ψ and p to the basal area of pines and hardwoods and to pine dbh (Table 1). The second-ranked model had low support compared to the top-ranked model and was not part of our confidence set. None of the remaining models that we considered had greater support, including models that incorporated habitat type, pine dbh, snag densities, and pine basal area independently as well as in various combinations (Table 1).

The estimated probability of patch occupancy for our top model averaged 0.96 (SE = 0.07) in mesic flatwoods and 0.56 (SE = 0.27) in sandhill forests. The estimated probability of detection averaged 0.75 (SE = 0.05) in mesic flatwoods and 0.37 (SE = 0.04) in sandhill forests. The modeled relationship for patch occupancy and pine basal area was negative (Fig. 1a), while the relationship between estimated detection probabilities and pine basal area was positive (Fig. 1b).

The occupancy estimated for the Brown-headed Nuthatch within habitat-management zones established for the Red-cockaded Woodpecker averaged 0.53 ± 0.24 among sample points ($n = 26$). Estimated probabilities of occupancy among sample points ($n = 19$) outside foraging zones were similar ($t_{1,43} = 0.13$; $P = 0.89$) and averaged 0.54 ± 0.2. The distance separating

TABLE 1. Model rankings derived from program PRESENCE. Only the top five models used to estimate occupancy (ψ) and detection probabilities (p) for the Brown-headed Nuthatch in the Ocala National Forest are presented. Ranks are based on QAIC$_c$ (Akaike's information criterion adjusted for lack of model fit), and habitat covariates (in parentheses) were forest type (type), basal area of pines and hardwoods (pnba and hwba, respectively), pine diameter at breast height (dbh), and snag densities (snag). ΔQAIC$_c$ represent the change in QAIC$_c$ units between the top-ranked model and remaining models. QAIC$_c$ weight (w_i) measures the relative support in the data for a model, likelihood the evidence ratio, and K the number of parameters.

Model	K	ΔAIC_c	w_i	Likelihood
ψ(type + pnba), p(type + pnba)	6	0.00[a]	0.461	1.000
ψ(type + pnba + hwba), p(type + pnba + hwba)	8	3.01	0.102	0.222
ψ(type × hwba), p(type × hwba)	8	3.25	0.091	0.197
ψ(pnba + snag + dbh), p (pnba + snag + dbh)	8	3.51	0.080	0.173
ψ(type), p(type)	4	4.35	0.052	0.114

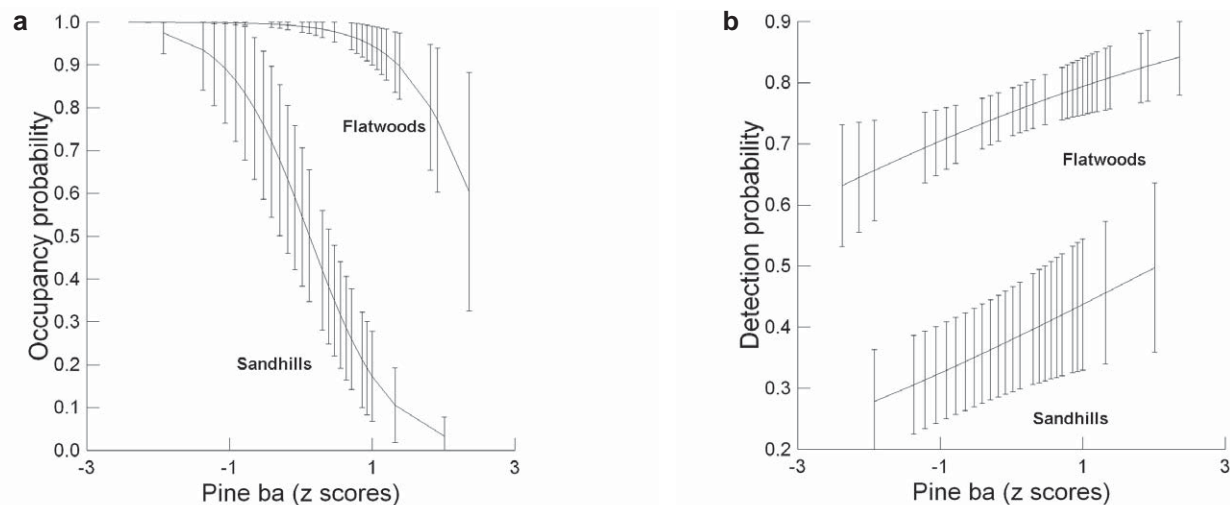[a]Minimum QAIC$_c$ for this set of models was 289.37.

FIGURE 1. Relationships among estimated patch occupancy (ψ; a), detection (p; b) probabilities, and pine basal area for Brown-headed Nuthatches occurring in flatwood and sandhill forests of the Ocala National Forest, Florida. Values for basal area of pines (pine ba) were converted to Z-scores prior to modeling. Bars represent the SE for parameter estimates.

sample points and the center of the nearest woodpecker territory averaged 431 m ± 167 (median = 439) for points within woodpecker-foraging zones and 2924 m ± 2004 (median = 2656) for points outside foraging zones. There was no linear relationship between estimated nuthatch occupancy and the distance separating sample points and the centers of Red-cockaded Woodpecker territories ($F_{1,43} = 0.114$; $P = 0.74$).

DISCUSSION

In the ONF, we encountered Brown-headed Nuthatches more frequently in younger flatwood forests that did not support Red-cockaded Woodpeckers. In the sandhill forests where the Brown-headed Nuthatch and Red-cockaded Woodpecker occurred jointly, there was no relationship between nuthatch occupancy and the proximity of sample points to woodpecker territories. These results deviate from those of other studies that found positive relationships between nuthatch abundance, woodpecker management, and mature timber (Johnston and Odum 1956, Conner et al. 1983, O'Halloran and Conner 1987). On the basis of previous work, Tirpak et al. (2009) defined the nuthatch's preferred conditions as mature pine stands where pine dbh averaged ≥25.6 cm. In the ONF, we found probabilities of site occupancy and detection to be higher in younger mesic flatwoods where pine dbh averaged ≤25.6 cm at half the sites sampled. Meanwhile, we encountered nuthatches less commonly in mature sandhill forests where pine dbh averaged >25.6 cm in >75% of the samples.

Differences in nuthatch occupancy in the forest types we studied point to marked differences in the quality of habitat provided by flatwood and sandhill forests. We hypothesize that differences in habitat quality could be linked to a site's productivity, nutrient and food availability, and ecosystem

functions rather than the forest-structure components highlighted in previous studies. Net primary productivity in flatwoods can exceed that in sandhill forests by ≥200% (Gholz et al. 1991, Mitchell et al. 1999), while potentially limiting resources such as calcium also occur at higher concentrations in mesic flatwoods and may influence the quality of the nuthatch's food (James et al. 1997, Hainds et al. 1999). In addition, flatwood forests in the ONF are dominated by slash pine, which produces seeds more consistently than does longleaf pine (Fowells 1965). Morse (1967) found pine seeds to be an important winter staple for the Brown-headed Nuthatch, and Cox and Slater (2007) suggested that differences in seed production influence the nuthatch's population dynamics in some settings. If these factors act in the manner hypothesized, we should expect nuthatch populations residing in sandhill and flatwood forests to differ in clutch size, territory extent, cooperative breeding behavior, and other traits correspondingly.

Previous work on the nuthatch's habitat preferences also stressed the importance of hardwood basal area and snag densities (Conner et al. 1983, Wilson and Watt 1999). In the ONF, occupancy and detection probabilities were not strongly influenced by hardwood basal area, but our results are consistent with those reported previously because hardwood basal area in the ONF was well below the maximum values the nuthatch tolerates elsewhere (4.6 m^2 ha^{-1}; Wilson and Watts 1999, Tirpak et al. 2009). Conversely, snag densities in the ONF were generally lower than those recommended by McComb et al. (1986; ≥2.3 ha^{-1}) and Tirpak et al. (2009; ≥8 ha^{-1}). However, we found that snag densities bore no strong relationship with ψ and p and suggest other factors had greater importance in this setting. Approximately 68% of the sites sampled in mesic flatwoods had estimated snag densities <2.3 ha^{-1}, while probabilities of detection and occupancy at these sites were high (>80%).

The Brown-headed Nuthatch exhibits limited dispersal in many settings (Lloyd and Slater 2009, Haas et al. 2010), so patch isolation coupled with variation in the nuthatch's abundance in different forest types could influence patch occupancy. For example, one sandhill site (Norwalk Island; $n = 6$ points) encompassed 2645 ha of potential nuthatch habitat but was >5 km from other patches of potential habitat. Another sandhill site (Syracuse Island; $n = 12$ points) encompassed 1550 ha of suitable habitat and was contiguous with a large block of flatwood forest (3350 ha). Post-hoc evaluations based on the distance between sandhill sampling points and the nearest patch of flatwood forest suggested ψ and p in sandhill forests were not influenced by proximity to flatwood forests; however, more extensive sampling should be pursued. The number of sandhill sites where nuthatches were detected was small ($n = 18$) while variation in estimated occupancy was high (CV = 0.43 for sandhill sites vs. 0.10 for flatwood sites). Variation in habitat quality should lead to fine-scale variation in population stability, abundance, and growth. If so, patch occupancy among the sandhill islands of the ONF could have links to source–sink and dispersal dynamics (Dunning et al. 1992).

Results from our single-year study might be biased if our sampling followed a catastrophe that temporarily decreased nuthatch abundances in sandhill forests (Lloyd and Slater 2007). Independent breeding-season point counts in sandhill forests of the ONF suggest this was not the case (U.S. Forest Service, unpubl. data). Brown-headed Nuthatches have been observed on only 2% of the 200 10-min counts made annually since 2001. No corresponding data exist for flatwood forests in the ONF, but, during similar passive point counts (10 min) within 2200 ha where Cox and Slater (2007) estimated a density of 0.3 nuthatch territories ha^{-1}, our probabilities of detection have been much higher (~0.6 annually). The passive point counts affirm the low abundance of the Brown-headed Nuthatch in sandhill forests in the ONF, but we also caution that these counts may not detect downward population trends (should they occur).

Although habitat requirements for the Brown-headed Nuthatch and Red-cockaded Woodpecker in central Florida obviously differ, it would be premature to suggest that forest conditions suitable for the woodpecker are not also suitable for the nuthatch. The Red-cockaded Woodpecker was absent from flatwood forests in the ONF primarily because of an absence of trees suitable for its cavities. If suitable trees were present in flatwood forests, the patterns of distribution and occupancy of the Red-cockaded Woodpecker might resemble those of the nuthatch because the arthropods on which these species feed overlap broadly (Hanula and Horn 2004, Nesbitt and Hetrick 1976). In addition, maintenance of mature pine forests containing trees suitable for Red-cockaded Woodpecker cavities could be essential for sustaining the Brown-headed Nuthatch in sandhill forests that appear to be of lower quality.

Contrary to results obtained elsewhere, habitat suitability for the nuthatch in central Florida should not be inferred from the presence of putative umbrella species such as the Red-cockaded Woodpecker. In the ONF, we found habitat quality to be higher in younger flatwood forests that often were ≥10 km from mature sandhill forests that supported stable woodpecker populations. Our results also should heighten conservation concerns for the Brown-headed Nuthatch in peninsular Florida. Results presented by Kale et al. (1992) suggest the nuthatch does not occur in many of the conservation areas in peninsular Florida that are dominated by sandhill forests. Better information on the nuthatch's habitat requirements and demography in the sandhill forests of the ONF are needed because the data could help to clarify the limiting factors operating in sandhill forests and lead to development of better management guidelines for that habitat. The contrasting positive/negative relationships we found for pine basal area and ψ and p (Fig. 1) suggest habitat suitability may decrease both at the lower and upper ends of the range of pine basal area found in the ONF. Expanded sampling in the sandhill forests of the ONF could improve detection probabilities, lower variation in estimated occupancy, and allow this relationship to be modeled more accurately.

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