NEST SITE SELECTION
OF THE BROWN-HEADED NUTHATCH IN VIRGINIA

A Thesis

Presented to

The Faculty of the Department of Biology

The College of Williams and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

---

by,

Valerie A. Weiss

1999

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

____

Author

Approved, July 1999

____

Martha Case

____

Daniel Cristol

____

Paul Heideman

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

The writer wishes to express appreciation to the Colonial National Historic Parks, Eastern Bird Banding Association, Virginia Society of Ornithologists, and Williamsburg Bird Club for providing grants to fund this research. Sincere thanks also to the kind staff of Chincoteague National Wildlife Refuge, Colonial National Historic Parks, Hog Island Wildlife Management Area, and Plum Tree Island Wildlife Refuge, for permitting this research and providing substantial logistical support for the work completed at each location. The author expresses deep appreciation to graduate advisor Dr. Daniel Cristol for guidance and advice throughout this investigation, and to Dr. Cristol and Dr. Christopher Bailey for providing equipment essential to this research. Special thanks to Shaun Boren, Brandi Jenks, Jodi Stephenson, and Bob and Mabel Lou Weiss for invaluable assistance in the field. The author is also indebted to graduate committee members Dr. Martha Case and Dr. Paul Heideman for their careful reading and criticism of the manuscript.

LIST OF TABLES

Table

LIST OF FIGURES

Figure

ABSTRACT

The brown-headed nuthatch (*Sitta pusilla*), a cavity nesting bird endemic to the pine forest system of the southeastern United States, is experiencing population declines. Though alteration or loss of habitat may be responsible for brown-headed nuthatch declines, specific details regarding their habitat requirements are not well known. In order to evaluate whether loss or alteration of habitat was responsible for population declines, I examined three aspects of brown-headed nuthatch nesting habitat: nest site selection at the forest patch level, potential competition with other cavity nesting birds, and nest site characteristics in Virginia relative to historical data.

In 1997 and 1998 I located 29 active nests, carried out forest sampling to investigate nest site selection, and recorded nest site characteristics for comparison with historical data. I conducted point counts at nest sites in 1998 in order to evaluate the potential for competition with other cavity nesting birds.

Occupied forest patches had significantly less oak basal area than unoccupied patches, and nest plots had significantly higher sapling basal area and a significantly lower distance to the nearest mature pine than random plots. No significant differences between nest and random plots were detected for deciduous tree basal area in the canopy or subcanopy, nor in the basal area of snags in the subcanopy. Nest sites did not appear to be more similar to one another than would be expected based on available habitat. No relationship was found between the number of cavity nesting birds present and the apparent quality of a nest site. Characteristics of brown-headed nuthatch nest sites in Virginia differed from previously reported data, with cavities occurring at greater heights and in a wider variety of tree types than expected.

The results of this study suggest that brown-headed nuthatches are not highly restricted in terms of nesting habitat, that competition with other cavity nesting birds is not decreasing the quality of brown-headed nuthatch nest sites, and that brown-headed nuthatch nests in Virginia occur in a wider range of conditions than historical data would lead one to expect. Differences between nest sites and available habitat may exist that were not detected due to low statistical power, and subtle aspects of competition with specific cavity nesting species could exist that were not detectable when all cavity nesting birds were considered. Further study is needed to rule out nest site limitation as an explanation for local population declines.

NEST SITE SELECTION
OF THE BROWN-HEADED NUTHATCH IN VIRGINIA

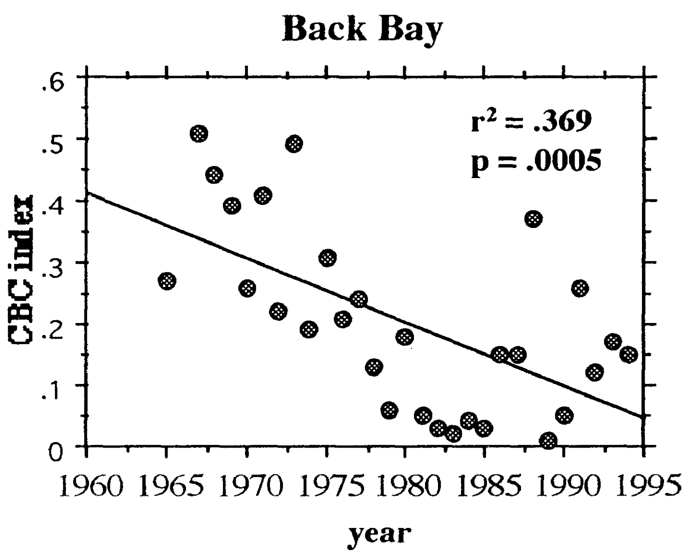
INTRODUCTION

Deforestation and the resulting loss or fragmentation of habitat is often responsible for avian population declines (Newton 1998). Loss of appropriate nesting habitat may be particularly problematic for cavity-nesting species because of their need for specific excavation or cavity-defense conditions. The brown-headed nuthatch (*Sitta pusilla*) is a cavity-nesting bird endemic to the southeastern United States that appears to be experiencing population declines. Breeding Bird Survey data from 1966 to 1995 show a range wide annual population decrease of 1.8% (Withgott and Smith 1998). I analyzed twenty-nine years of Christmas Bird Count data (1965 - 1994) from the nine counts in Virginia which regularly reported brown-headed nuthatches: Back Bay, Cape Charles, Chincoteague, Danville, Little Creek, Matthews, and Wachapreague. Four other counts in Virginia have reported brown-headed nuthatches (J. H. Kerr Reservoir, Martinsville, Philpott Reservoir, and Banister River Wildlife Management Area), but fewer than ten years of data were available for these counts, so they were not included in the analysis. My analysis showed significant declines at two locations (Back Bay: $r^2 = 0.369$ and $p = 0.0005$, Cape Charles: $r^2 = 0.503$ and $p < 0.0001$, Figure 1) and non-significant negative trends at three others (Chincoteague, Danville, and Newport News, Figure 2).

Loss of pine habitat has been linked to brown-headed nuthatch population declines in southern Florida (Slayter 1997) and on Grand Bahama Island (Smith and Smith 1994). Reduction in the southern pine forest system due to logging and development could be having a direct negative effect on local bird populations. However, even areas where large tracts of pine forest remain may be experiencing population declines due to changes in forest character resulting from fire suppression,

FIGURE 1

CHRISTMAS BIRD COUNTS SHOWING SIGNIFICANT DECLINES (1965-1994)



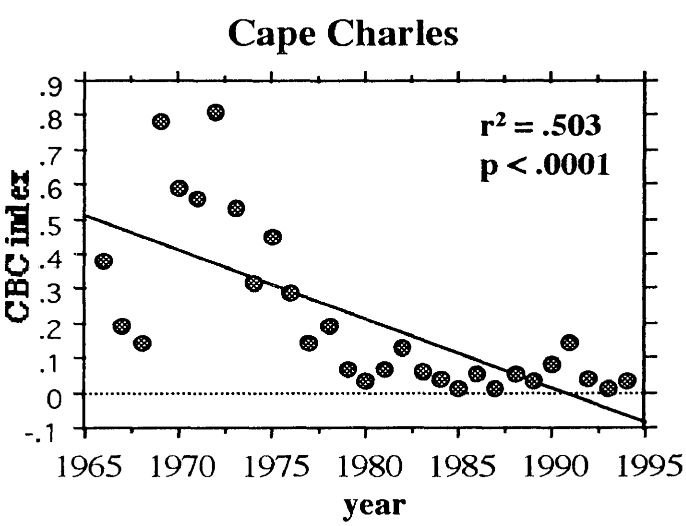
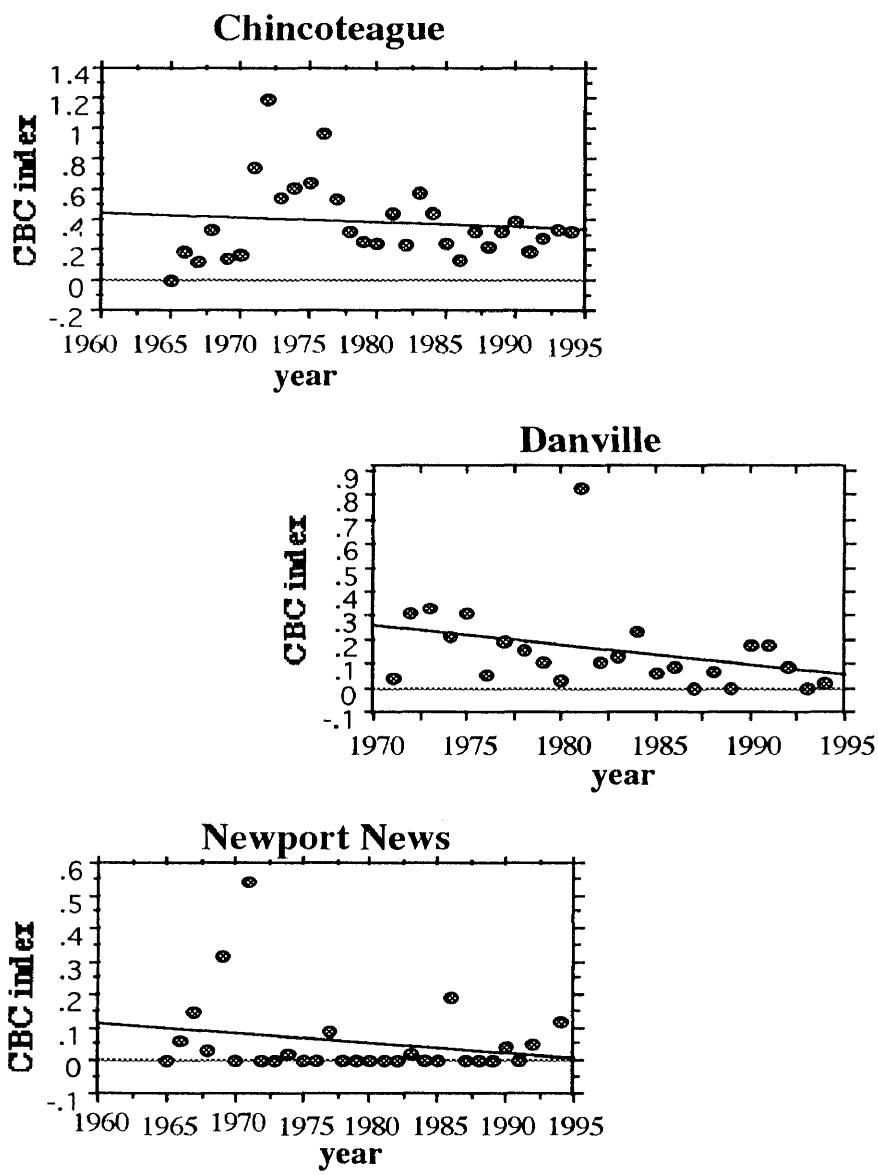


FIGURE 2

CHRISTMAS BID COUNTS SHOWING NON-SIGNIFICANT DECLINING TRENDS (1965-1994)



forest management techniques that lead to even-aged stands, and short rotation times that reduce the age and complexity of the forest (Adkisson 1988, Land 1986). In an Arkansas study of the effect of different management regimes on forest bird populations, unburned (control) forest plots had dense hardwood midstories, sparse ground cover, and a greater canopy cover than burned plots (Wilson et al. 1995). The highest densities of brown-headed nuthatches in this study were found in burned treatment plots (Wilson et al. 1995), supporting the idea that fire suppression may be contributing to changes in forest character and having a negative impact on brown-headed nuthatches

Changes in forest character could be particularly problematic for cavity nesting birds such as brown-headed nuthatches if they lead to a reduction in the number or the quality of available nest sites. Concurrent declines in populations of different cavity nesting species suggest that there may be a link between these declines and nesting habits. Population declines of four other cavity-nesting birds have been reported in the same region of Florida as brown-headed nuthatch declines (eastern bluebird [*Sialia sialis*], southeastern American kestrel [*Falco sparverius paulus*], red-cockaded woodpecker [*Picoides borealis*], and hairy woodpecker [*Picoides villosus*], Slayter 1997). Their specific nest site requirements may make cavity nesting birds susceptible to habitat changes, as numerous habitat variables appear to impact the nesting success of these birds. For example, snag density is commonly considered a limiting factor for cavity nesting birds (Conway and Martin 1993, Li and Martin 1991, Zarnowitz and Manuwal 1985). The number of snags in a forest is positively correlated with age of the forest (Newton 1998), so short timber rotations are likely to lead to a reduction in snags. More subtle changes in the forest can also have an effect on nesting success. Even with adequate snags or cavity sites, increased deciduous cover resulting from fire suppression could lead to reduced breeding success, as observed in an Oregon study

(Li and Martin 1991). Thus, it is possible that changes in the southeastern pine forest are closely linked to population declines of the brown-headed nuthatch in Virginia.

Characteristics of brown-headed nuthatch habitat have been broadly defined, but specific details are lacking. Brown-headed nuthatches are found in mature pine woodlands with open understories (Morris 1982, Haney 1981, Withgott and Smith 1998). Because they excavate their own nests, brown-headed nuthatches require partially rotted wood in their habitat (McNair 1984). In the upper coastal plain, they are generally found in forests of the loblolly-shortleaf (*Pinus taeda -P. echinata*) pine association, while in the lower coastal plain they are generally found in forests of the longleaf-slash (*P. palustris -P. elliottii*) pine association (Withgott and Smith 1998). However, some published accounts of brown-headed nuthatch habitat requirements are contradictory. Brown-headed nuthatches have been described as preferring pine woods but also inhabiting cypress swamps and mixed pine-hardwood forests (Bent 1948, Haney 1981, Slayter 1997). In other publications they are characterized as being restricted to mature pine woods (Conner et al. 1983, Hamel 1992, Johnston and Odum 1956). Brown-headed nuthatches are reported to exhibit a strong preference for pole-stage pines (Conner et al. 1983, Johnston and Odum 1956). They have also been described as particularly well adapted to marginal habitat between forest and swamp with nests at a distance from foraging locations (Bent 1948) and reported as more abundant in developed residential areas than in undisturbed forest locations (Yaukey 1992). Some of these differences may reflect seasonal or geographic variation in population dynamics. In order to evaluate the situation of brown-headed nuthatches in Virginia, I needed habitat information specific to populations in Virginia. My study had three goals: to examine brown-headed nuthatch nest site selection at the forest patch level, to investigate the potential for competition with other cavity nesting birds, and to compare nuthatch nest site characteristics in Virginia with published descriptions.

Forest patch

A starting point for avian habitat studies is often to compare chosen habitat with the available habitat to determine whether the birds are being selective. A study in Texas (O'Halloran and Conner 1987) found that brown-headed nuthatch foraging areas were distributed non-randomly, and that foraging sites tended to have less hardwood midstory and lower overstory pine basal area than random sites. This finding of selectivity for foraging sites led me to hypothesize that brown-headed nuthatches would exhibit similar selectivity for nest sites. If nuthatches select nest sites based on certain characteristics which have become less common due to development or timber management practices, then a lack of appropriate nesting habitat could be contributing to brown-headed nuthatch population declines.

My first step was to test the hypothesis that nest patches differed from available habitat. The next step was to determine whether there was a consistent suite of characteristics that defined a brown-headed nuthatch nest site. I predicted that brown-headed nuthatch nest plots would differ significantly from random plots within each of my study locations. Further, I predicted that the characteristics of nest plots should be more similar between study locations than would be expected given the degree of similarity of random plots in the different study locations. This would support my hypothesis that brown-headed nuthatches are selecting specific forest patch attributes when choosing a nest site.

Nest site

Historical data suggest that brown-headed nuthatches tend to nest low (< 3 m) in snags or stumps that are in an advanced state of decay (McNair 1984). Nest heights reported in previous studies are: median height of 1.21 m in Georgia (Norris 1958), mean height of 2.3 m in Louisiana (Morse 1977), and mean height of 2.09 m rangewide (McNair 1984). A pilot study I carried out in 1997 suggested that brown-headed nuthatch nests in Virginia occur in a wider range of situations than expected from historical data. All of the nests I found in 1997 were over 3 m from the ground, and only 50% occurred in snags lacking bark and branches, characteristics indicative of an advanced decay state (Raphael and White 1984, Schreiber and deCalesta 1992, Connor et al. 1975, Cline et al. 1980, Manan et al.1980). Similar differences in nest height and cavity tree characteristics were recently reported for southern Florida (Slater 1997).

Previous studies depended largely on data from amateur ornithologists who encountered nests haphazardly, rather than on data systematically collected by field researchers. It is possible that the current understanding of brown-headed nest site characteristics is skewed by dependence on casual observations, as low nests in "classic" snags would be more likely to be spotted by a casual observer than would a nest in a dead branch near the top of a tall tree. In support of this explanation for biased historical records, the mean nest height observed by Morris (1982) was 3.5 m, while the mean height he calculated from museum records was 1.5 m (Morris 1982). My objective was to evaluate how well characteristics of nests in Virginia match historical descriptions in terms of cavity height, cavity tree condition, and immediate nest environment.

Competition

Another possible limiting factor for brown-headed nuthatch populations is competition with other birds for suitable cavity sites. Cavity-nesting bird population densities have been positively correlated with snag density (Land 1986, Zarnowitz and Manuwal 1984), suggesting nest site limitation at low snag densities. Even with abundant snags, the quality of potential nest sites may vary substantially. In southern Florida, cavity nesting bird diversity increased as numbers of broken-topped snags increased and as percent bark cover on available snags decreased, suggesting that snags in an advanced state of decay may be a limiting factor (Land 1986). An advanced state of decay is indicated by the following characteristics: broken tops, few remaining branches, and reduced bark cover (Raphael and White 1984, Schreiber and deCalesta 1992, Connor et al. 1975, Cline et al. 1980, Manan et al.1980).

Factors other than state of decay may also be important in cavity site selection and breeding success. Competition with other primary cavity nesters could be forcing brown-headed nuthatches to excavate their cavities in sub-optimal locations, leading to greater nest predation and reduced breeding success. In an Arizona study of the closely-related pygmy nuthatch (*Sitta pygmaea*), failed nests were significantly lower in height and had significantly greater foliage cover than successful nests (Li and Martin 1991). A negative correlation between understory height and cavity nesting bird diversity in Florida (Land 1986) also suggests that foliage around the cavity is an undesirable nest site condition. If competition with other cavity nesting birds is restricting cavity placement for brown-headed nuthatches, nuthatch nest quality, as indicated by characteristics such as cavity height and foliage cover, should decrease as the number of potential competitors in the area increases.

METHODS

Study Areas

This study was carried out at five locations in eastern Virginia: Chincoteague National Wildlife Refuge (Accomack County), Jamestown Island National Historic Park (James City County), Hog Island Wildlife Management Area (Surry County), Guinea (Gloucester County), and Plum Tree Island Wildlife Management Area (Poquoson City). Each study location contained areas of pine dominated woodlands bordered by marshes, a habitat type which is recognized as typical of the brown-headed nuthatch (Withgott and Smith 1998). I selected study areas where brown-headed nuthatches were known to be present and in which I would have access to large forested areas. Because I sampled habitat at five distinct locations, my results should be generalizeable to the entire region.

Nest/territory searches

I carried out nest searches from March through June in 1997 and 1998. Nests were located by listening for vocalizations while walking through the forest and then following birds to the cavity. The time required to find a nest ranged from forty-five minutes to several days, with a mean search time per nest of 8.3 hours. There were eight brown-headed nuthatch territories in 1997 and 11 in 1998 in which I was unable to locate a nest but repeatedly observed birds foraging. In 1997, I sampled vegetation at the eight non-confirmed breeding territories in addition to six confirmed breeding territories. In 1998 I did not gather data at non-confirmed territories. Nests which I found during excavation were visited repeatedly until I observed birds making regular feeding visits to the cavity.

Forest patch

Forest plots

One objective of this study was to investigate nuthatch nesting habitat selection at the level of the forest patch, to see if differences in forest structure existed between sections of pine woods in which nuthatches were present and absent. I compared 14 nuthatch territories (six confirmed nest sites and eight non-confirmed breeding sites) with 11 non-territories in 1997. The criteria for selection of a non-territory (unoccupied site) was three visits to an apparently appropriate forest area in which no brown-headed nuthatch activity was observed. These territories and non-territories were located in Guinea, Hog Island Wildlife Management Area, or Jamestown Island National Historic Park. Vegetation characteristics were measured in four 10-m diameter circular plots (0.00785 hectare) evenly spaced along a 60-m long transect. All woody stems >3.2 cm in diameter were identified and measured for diameter at breast height (DBH), with stems less than 10 cm DBH classed as shrubs/saplings layer and stems >10 cm DBH classed as trees.

Nest plots

I examined the immediate environment around each nest (n = 29) in order to test the hypothesis that brown-headed nuthatches were selecting specific nest site characteristics, investigate the possibility that competition with other cavity nesters was forcing nuthatches into sub-optimal nest locations, and test the hypothesis that characteristics of nest sites in Virginia differed from those previously reported. Vegetation characteristics of the immediate nest environment were measured in 10-m diameter circular plots (0.00785 hectare) centered on the nest tree. For all woody stems >3.2 cm in diameter, diameter at breast height (DBH) and genus were recorded. I grouped stems into three size classes: shrub/sapling (3.2-10 cm DBH), subcanopy and canopy (both >10 cm DBH). Canopy closure was determined by estimating percent foliage cover through a sighting tube in each of the cardinal directions at 1 m increments moving outward from the center point. The twenty values for each plot were then averaged to give a mean canopy closure value. Ground cover was determined by taking readings through a sighting tube in the four off-cardinal directions at 1 m increments moving outward from the center point. The type of ground cover (leaves, pine needles, dead wood, water, bare ground, vegetation) that composed the majority of the field of view was recorded as the ground cover at that reading, and twenty readings per plot were grouped by type to represent ground cover in that plot. Ground-level vegetation density was measured in each of the cardinal directions using a half-sighting board (Bibby et al. 1992), and an average of the four values was taken as an index of ground-level vegetation density for the plot. I measured the distance from each nest tree, or the center point of the random plots, to the nearest cone-bearing pine as an estimate of distance to the nearest foraging site.

Random plots

Ten random plots were chosen for sampling in each of the four locations studied in 1998 (Chincoteague National Wildlife Refuge, Jamestown National Historic Park, Hog Island Wildlife Management Area, and Plum Tree Island Wildlife Management Area) in order to allow the data set to be balanced (ten nests was the maximum number found at any location). GPS coordinates for random plot centers were determined using 7 1/2 minute topographic maps, and a hand-held GPS unit was used to navigate to the center point. Woody vegetation was sampled in the same manner as in nest plots. Canopy closure, ground cover, ground-level vegetation density, and distance to the nearest mature pine were also measured following the procedures described above.

Nest site

In order to test the hypothesis that nest sites in Virginia differed from what would be expected based on historical data, the following characteristics were recorded at each nest. Tree condition (alive or dead), height, DBH, number of branches remaining (in five classes: 0, <5, 5-10, 10-20, >20), state of tree top (broken or intact), percent bark cover (0, 25, 50, 75, 100), presence of other cavities, and distance to the nearest mature pine were recorded for each nest tree. Cavity shape, height of the cavity, cavity orientation, and vegetative cover around the cavity were also recorded for each nest.

Seven nest site characteristics (tree condition, number of branches remaining, state of tree top, percent bark cover, presence of other cavities, cavity height, and vegetative cover around cavity) were evaluated by testing the observed patterns against a binomial distribution. Midpoints for the binomial tests were established *apriori* based, when possible, on published statements about brown-headed nuthatch nest sites and on published data from other cavity-nesting birds when details specific to brown-headed nuthatches were not available. I tested two predictions specific to brown-headed nuthatches: that the majority of nests would be less than 3 m high (McNair 1984, Morris 1977) and that cavities would occur primarily in snags of advanced decay (McNair 1984). Indicators of an advanced state of decay in a snag are: having a broken top, few branches (<5), low percent bark cover (<50%), and other cavities present (Land 1986, Mannan et al 1980, Raphael and White 1984). A third prediction based on general cavity-nesting bird biology was that cavity entrances would be free of vegetative cover (Li and Martin, 1991).

Presence of competitors

If competition with other cavity nesting birds is forcing brown-headed nuthatches to nest in low quality locations, there should be a negative correlation between the number of potential competitors present at a nest site and the quality of that site. In order to test the hypothesis that nest site quality would decrease as the number of local cavity nesting birds increased, I carried out ten-minute, fixed-radius point counts at each of the 1998 nest sites (Bibby et al. 1992). Center points for the counts were set at 10 m from the nest tree in a randomly selected direction (to minimize disturbance of active nests). I used a rangefinder to select 4 reference points each at 25 and 50 m from the nest. After selecting reference points, 2 minutes were allowed to pass before beginning the count. All point count sessions began 30 minutes after sunrise and were completed within 4 hours. Each nest area was surveyed twice between June 12 and June 25, with count order within a study location chosen randomly.

I created a scale (range: 0-7) for evaluating quality of nest-sites, using characteristics which have been found to be positively correlated with cavity-nesting bird diversity and/or nesting success as indicators of quality. A high score was considered indicative of a high quality nest site. Nests were ranked in the following ordinal categories: state of tree (live = 1, dead = 0), bark cover (0-25% = 1, 25-75% = 0.5, 75-100% = 0), remaining branches (0-10 = 1, 10-20 = 0.5, >20 = 0), broken top (yes = 1, no = 0), vegetation around cavity (open = 1, partially occluded = 0.5, occluded = 0), presence of other cavities (yes = 1, no = 0), and cavity height (> 5 m = 1, 3-5 m = 0.5, < 3 m = 0).

Statistics

Forest plot, nest plot, and random plot data were tested for normality (Shapiro-Wilk W test) and heterogeneity of variances (Browne-Forsythe test). Forest plot data were log transformed to eliminate heterogeneous variance and reduce non-normality, and univariate analysis of variance (ANOVA) was used to examine differences in basal area index (transformed basal area) of tree classes in nuthatch territories and non-territories. Nest plot and random plot data (1998) were non-normal but did not exhibit heterogeneous variance. As ANOVA is robust to non-normality, I did not transform the data from 1998. In order to have a nearly-balanced data set for the nest site analysis, I randomly eliminated four random plots from each site, one nest site from Hog Island, and four nest sites from Chincoteague. This left six random plots and six nest plots per site, with the exception of Jamestown Island where there were only three nest sites. Two-way ANOVA with site and plot type as factors was used to compare vegetation characteristics between nest plots and random plots. All analyses within one forest layer were considered a family of tests, and the Bonferroni adjustment was used to maintain the experimentwise error at 0.05 (Krishnaiah 1980).

RESULTS

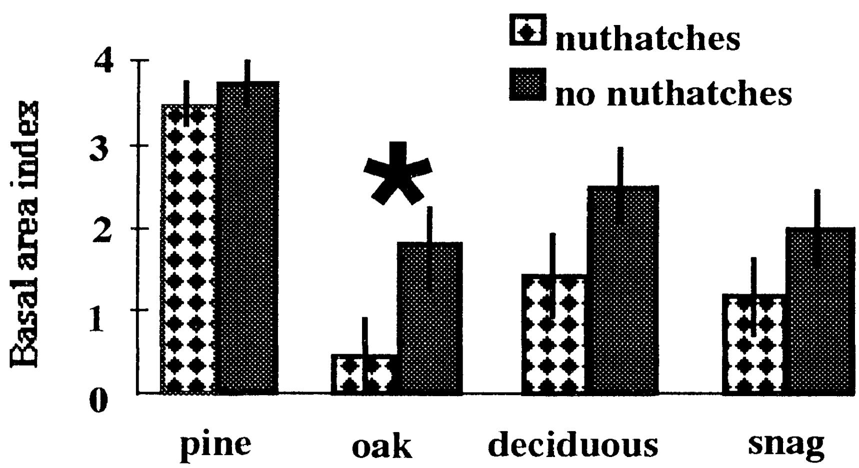
Forest patch

I compared total basal area of pines (*Pinus* sp.), oaks (*Quercus* sp.), all deciduous trees (including oaks), and snags between breeding territories and non-territories (1997). Basal area of oaks in the forest plots was significantly higher in non-territories than in territories ($p = 0.04$, Figure 3). No difference was found between nest sites and random sites (1998) in basal area of deciduous trees ($p = 0.165$) in the canopy, nor was a difference detected in the subcanopy for basal area of deciduous trees ($p = 0.824$) or snags ($p = 0.425$). There was a significant interaction effect between site and plot type for subcanopy deciduous tree basal area ($p = 0.02$). Basal area of saplings in nest plots was significantly higher than in random plots ($p = 0.02$, Figure 4). The distance to the nearest mature pine was significantly higher in random plots than in nest plots ($p = 0.03$, Figure 5).

To test the hypothesis that nest sites were more similar to each other than would be expected based on the similarity of available habitat, coefficients of variation of nest sites and random sites were compared for measurements of forest structure and nest-site characteristics. Basal area of pines, deciduous trees, and snags were compared in the canopy (Table 1), and basal area of pines, deciduous trees, snags, and shrubs were compared in the subcanopy and sapling layers (Tables 2 and 3). The only cases in which there was less variation for nest sites than for random sites was for pine basal area in the canopy and subcanopy, and deciduous tree basal area in the canopy. Lower variance in three out of eleven categories is not a sufficient departure from a random distribution to support the hypothesis that nest sites are more similar than random sites. I also compared coefficients of variation for a variety of nest site characteristics (Table

FIGURE 3

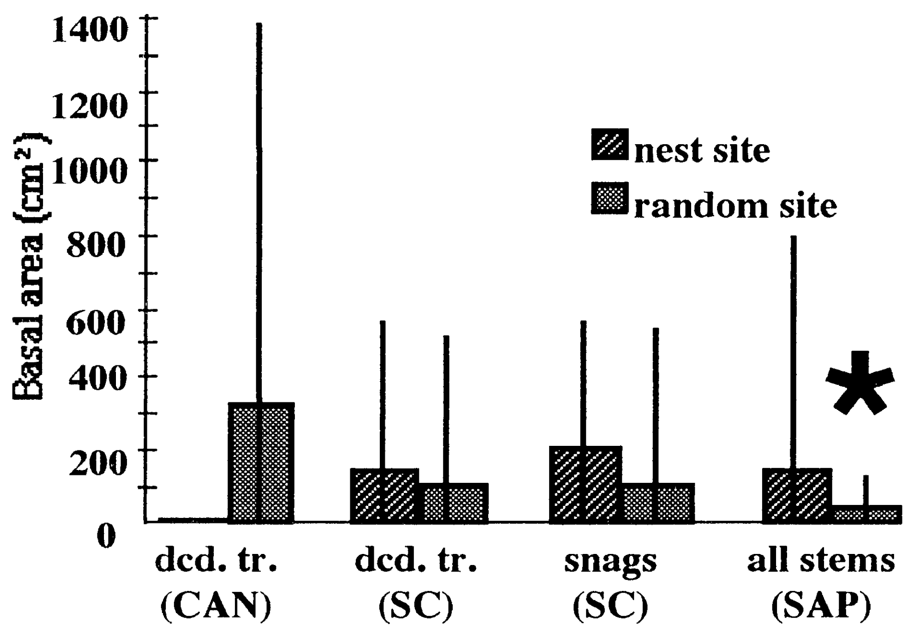
BASAL AREA OF SELECTED STEM TYPES IN BREEDING TERRITORIES VS. NON-TERRITORIES.



Basal area of stem types in brown-headed nuthatch territories vs. apparently suitable habitat with no brown-headed nuthatches present. Notice the significantly lower basal area of oaks in nuthatch territories. Data were log transformed to eliminate heterogeneity of variance and non-normality.

FIGURE 4

BASAL AREA OF STEMS IN DIFFERENT LAYERS OF THE FOREST IN NEST PLOTS VS. RANDOM PLOTS



Basal area of stem types in different levels of the forest (CAN=canopy, SC=subcanopy, SAP=shrub/sapling layer) in nest plots versus random plots. Notice the significantly higher basal area of the shrub/sapling layer in nest plots.

FIGURE 5

**DISTANCE TO NEAREST PINE
FOR NEST SITES VS RANDOM SITES**

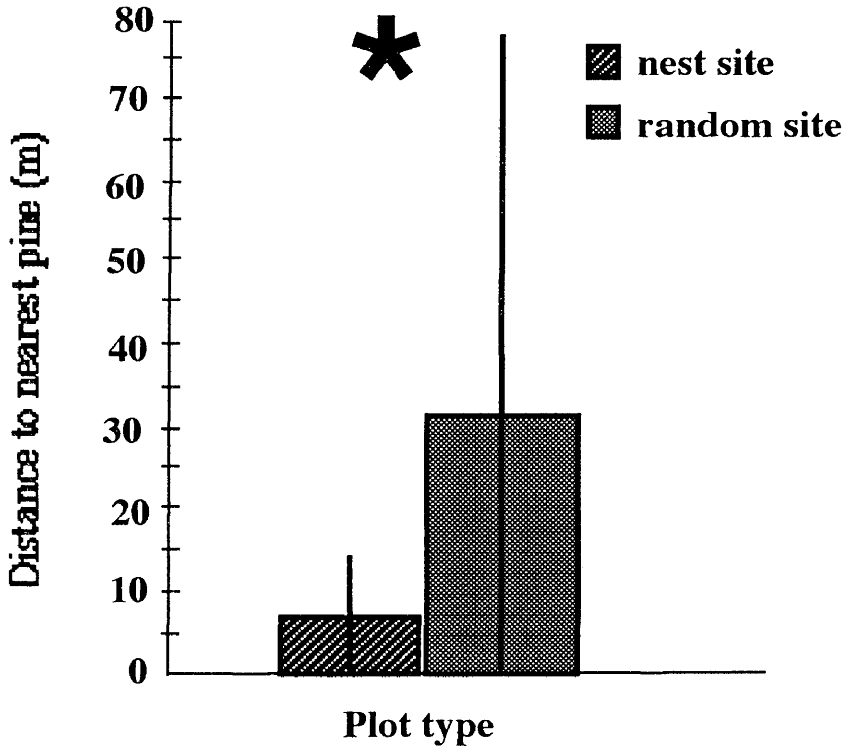


TABLE 1

COMPARISON OF COEFFICIENTS OF VARIATION FOR THE CANOPY LAYER IN NEST PLOTS AND RANDOM PLOTS

		NEST PLOT			RANDOM PLOT		
		pine	snag	dcd. tr.[1]	pine	snag	dcd. tr.[1]
STUDY SITE	JT[2]	173.20	0.00	0.00	191.61	0.00	156.90
	PO[3]	169.25	168.49	0.00	170.03	244.95	0.00
	HI[4]	87.63	164.45	0.00	154.93	0.00	0.00
	CH[5]	110.74	244.94	0.00	172.78	0.00	0.00

[1] dcd. tr. = deciduous trees [2]JT = Jamestown [3]PO = Poquoson [4]HI = Hog Island [5]CH = Chincoteague

TABLE 2

COMPARISON OF COEFFICIENTS OF VARIATION FOR THE SUBCANOPY LAYER IN NEST PLOTS AND RANDOM PLOTS

		NEST PLOT				RANDOM PLOT			
		pine	snag	dcd. tr.[1]	shrub	pine	snag	dcd. tr.[1]	shrub
STUDY SITE	JT[2]	0.00	92.10	0.00	0.00	244.96	244.96	159.17	0.00
	PO[3]	154.92	124.09	0.00	0.00	165.37	244.90	0.00	0.00
	HI[4]	197.02	164.14	0.00	244.87	244.95	0.00	245.05	0.00
	CH[5]	0.00	244.95	103.78	244.94	244.98	217.85	0.00	245.00

[1] dcd. tr. = deciduous trees [2] JT = Jamestown [3] PO = Poquoson [4] HI = Hog Island [5] CH = Chincoteague

TABLE 3

COMPARISON OF COEFFICIENTS OF VARIATION FOR THE SHRUB/SAPLING LAYER IN NEST PLOTS AND RANDOM PLOTS

		NEST PLOT				RANDOM PLOT			
		pine	snag	dcd. tr.[1]	shrub	pine	snag	dcd. tr.[1]	shrub
STUDY SITE	JT[2]	0.00	122.93	0.00	126.47	244.59	244.91	0.00	198.24
	PO[3]	0.00	188.15	0.00	173.46	245.00	0.00	245.02	0.00
	HI[4]	244.96	114.01	0.00	148.70	0.00	244.99	245.01	0.00
	CH[5]	0.00	244.97	165.96	155.05	244.96	244.78	0.00	209.22

[1] dcd. tr. = deciduous trees [2]JT = Jamestown [3]PO = Poquoson [4]HI = Hog Island [5]CH = Chincoteague

4). No consistent patterns of differences in variation were observed for distance to nearest pine, canopy closure, dead wood ground cover, or ground level vegetation density.

Competition

No relationship was found between the mean number of cavity nesting birds detected at each nest site and nest quality (r^2 = 0.03, p = 0.37, Figure 6). I carried out *post hoc* analyses of the point count data in which I looked for a relationship between nest site quality and the number of primary cavity nesting birds and secondary nesting birds. No relationship was found (primary: r^2 = .0007, p = .90, secondary: r^2 = .07, p = .21, Figure 7). Further *post hoc* analysis showed no relationship between nest site quality and the number of small cavity nesting birds (r^2 = .04, p = .34), medium cavity nesting birds (r^2 = .03, p = .40), and large cavity nesting birds (r^2 = .003, p = .79, Figure 8). Birds classed as small were the Carolina chickadee (*Parus carolinensis*), Carolina wren (*Thryothorus ludovicianus*), house wren (*Troglodytes aedon*), and tree swallow (*Tachycineta bicolor*). Medium birds were the downy woodpecker (*Picoides pubescens*), eastern bluebird (*Sialia sialis*), European starling (*Sturnus vulgaris*), great crested flycatcher (*Myarchus crinitus*), hairy woodpecker (*Picoides villosus*), house finch (*Carpodacus mexicanus*), and tufted titmouse (*Parus bicolor*). Large birds were the northern flicker (*Colaptes auratus*), pileated woodpecker (*Dryocarpus pileatus*), red-bellied woodpecker (*Melanerpes carolinensis*), and red-headed woodpecker (*Melanerpes erythrocephalus*). The mean number of potential competitors at a nest site ranged from 1.8 birds at Jamestown to 5.2 birds at Hog Island (Table 5).

Nest site

Nest site analysis was carried out on all nests from 1997 and 1998 (n = 29, Table 6). Significant departures from the binomial distribution were found for cavity

TABLE 4

COMPARISON OF COEFFICIENTS OF VARIATION FOR NEST SITE CHARACTERISTICS IN NEST PLOTS AND RANDOM PLOTS

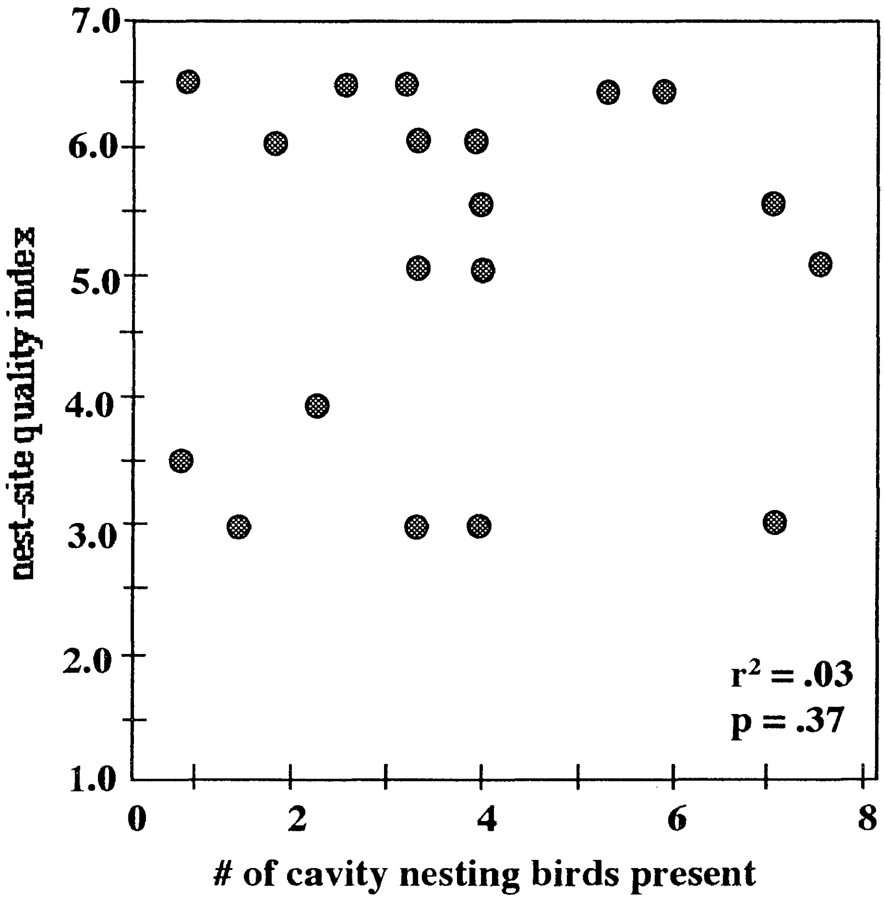
		NEST PLOT				RANDOM PLOT			
		PD[1]	CC[2]	DW[3]	GVD[4]	PD[1]	CC[2]	DW[3]	GVD[4]
STUDY SITE	JT[5]	119.59	90.07	89.20	121.81	115.64	44.39	29.94	47.89
	PO[6]	24.69	109.20	100.34	82.62	118.78	124.70	109.60	67.93
	HI[7]	54.03	38.92	112.40	67.91	113.28	164.07	109.60	91.86
	CH[8]	75.64	47.28	84.33	76.36	116.28	123.71	83.70	52.69

[1]PD = pine distance [2]CC = canopy closure [3]DW = dead wood ground cover [4]GVD = ground- level vegetation density

[5]JT = Jamestown [6]PO = Poquoson [7]HI = Hog Island [8]CH = Chincoteague

FIGURE 6

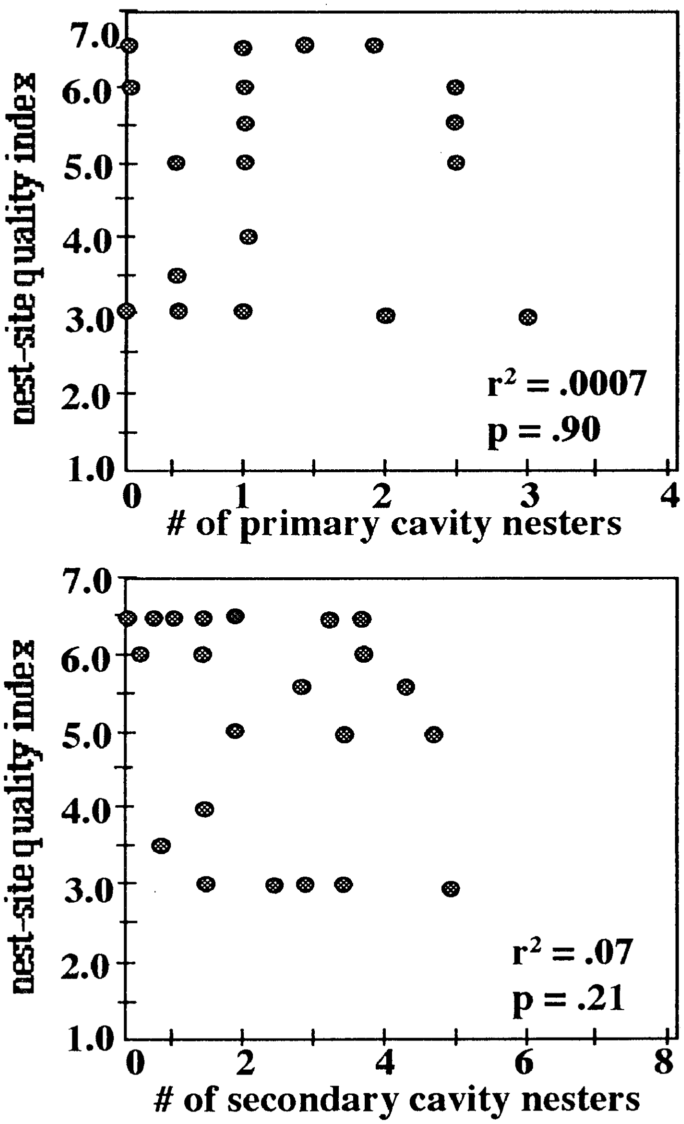
REGRESSION ANALYSIS OF NEST SITE QUALITY AND PRESENCE OF POTENTIAL COMPETITORS.



Regression analysis of nest site quality versus the number of cavity nesting birds present at a nest site showed no relationship between the two.

FIGURE 7

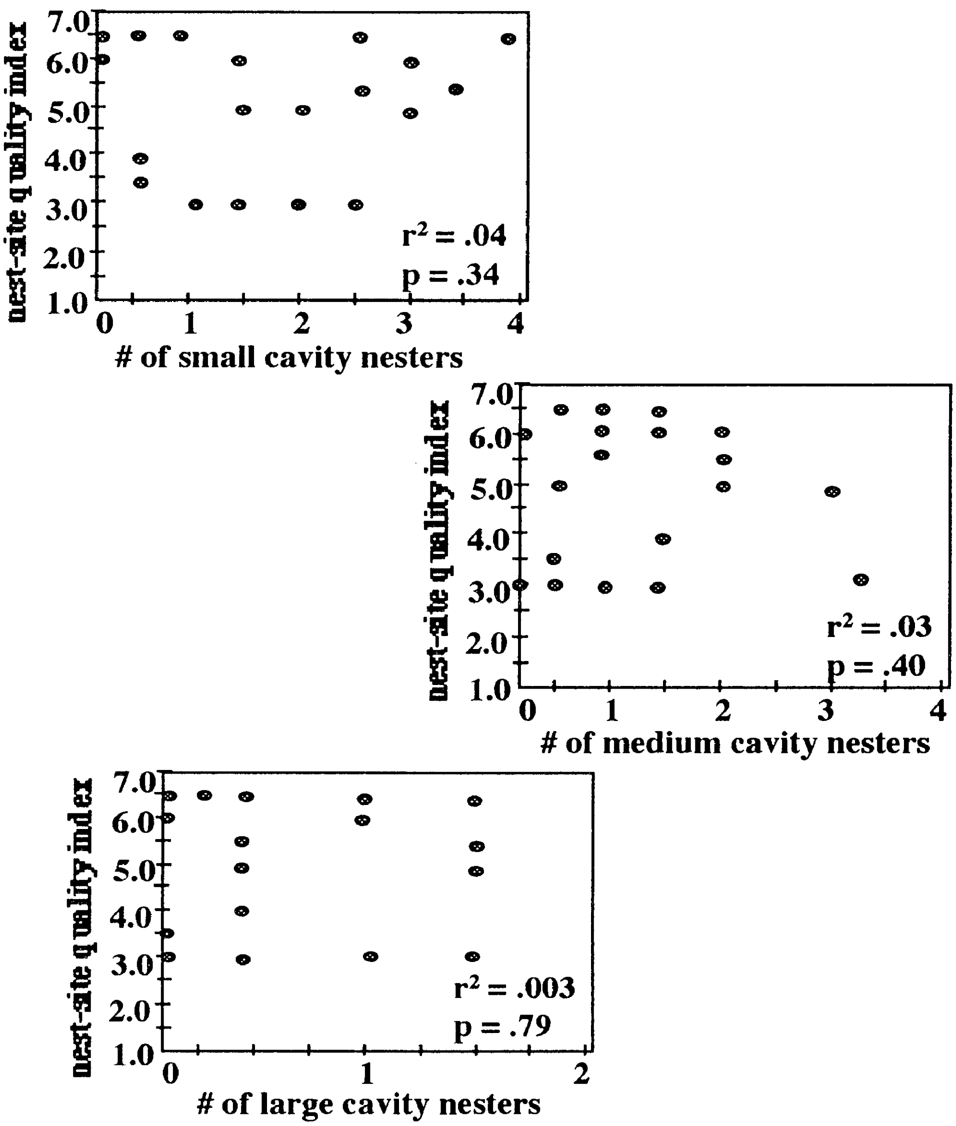
REGRESSION ANALYSIS OF NEST SITE QUALITY AND PRESENCE OF PRIMARY AND SECONDARY CAVITY NESTING BIRDS



Regression analysis showed no relationship between nest site quality and the number of primary or secondary cavity nesting birds present.

FIGURE 8

REGRESSION ANALYSIS OF NEST SITE QUALITY AND PRESENCE OF SMALL, MEDIUM, AND LARGE CAVITY NESTINGBIRDS



Regression analysis showed no relationship between nest site quality and the number of primary or secondary cavity nesting birds present.

TABLE 5

CAVITY NESTING BIRDS AT BROWN-HEADED NUTHATCH NEST SITES
(in order of abundance at each location)

location	Hog Island	Poquoson	Jamestown	Assateague
mean #	5.2 individuals/count	3.9 individuals /count	1.8 individuals /count	2.6 individuals /count
species recorded	Carolina wren *(Thryothorus ludovicianus)* northern flicker *(Colaptes auratus)* eastern bluebird *(Sialia sialis)* Carolina chickadee *(Parus carolinensus)* downy woodpecker *(Picoides pubescens)* great crested flycatcher *(Myarchus crinitus)* hairy woodpecker *(Picoides villosus)* tree swallow *(Tachycineta bicolor)* European starling *(Sturnus vulgaris)* house finch *(Carpodacus mexicanus)* tufted titmouse *(Parus bicolor)*	Carolina wren *(Thryothorus ludovicianus)* house wren *(Troglodytes aedon)* Carolina chickadee *(Parus carolinensus)* downy woodpecker *(Picoides pubescens)* tufted titmouse *(Parus bicolor)* hairy woodpecker *(Picoides villosus)* northern flicker *(Colaptes auratus)* tree swallow *(Tachycineta bicolor)* eastern bluebird *(Sialia sialis)* pileated woodpecker *(Dryocopus pileatus)* red-bellied woodpecker *(Melanerpes carolinus)* great crested flycatcher *(Myarchus crinitus)*	northern flicker *(Colaptes auratus)* downy woodpecker *(Picoides pubescens)* great crested flycatcher *(Myarchus crinitus)* Carolina wren *(Thryothorus ludovicianus)* house finch *(Carpodacus mexicanus)* European starling *(Sturnus vulgaris)* tufted titmouse *(Parus bicolor)* Carolina chickadee *(Parus carolinensus)*	house wren *(Troglodytes aedon)* downy woodpecker *(Picoides pubescens)* northern flicker *(Colaptes auratus)* European starling *(Sturnus vulgaris)* Carolina wren *(Thryothorus ludovicianus)* Carolina chickadee *(Parus carolinensus)* tree swallow *(Tachycineta bicolor)* red- headed woodpecker *(Melanerpes erythrocephalus)* red-bellied woodpecker *(Melanerpes carolinus)* house finch *(Carpodacus mexicanus)* tufted titmouse *(Parus bicolor)* great crested flycatcher *(Myarchus crinitus)*

TABLE 6

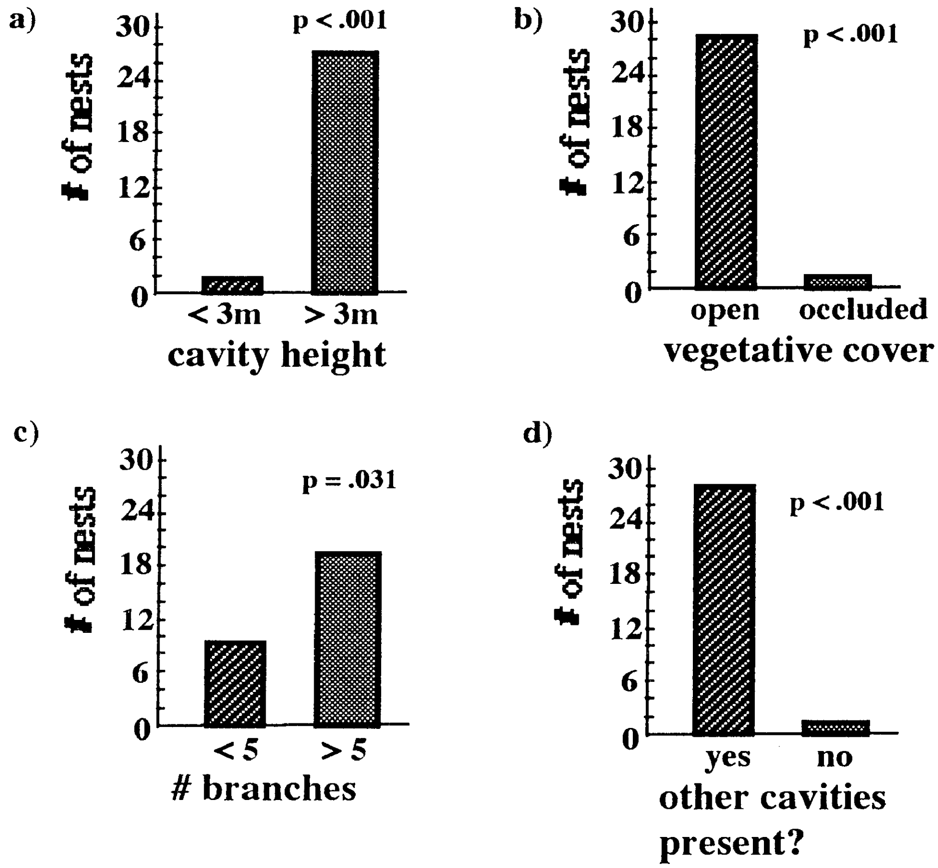
NEST SITE CHARACTERISTICS COMPARED TO AN EXPECTED BINOMIAL DISTRIBUTION
(see text for explanation of expected values)

category	number above and below expected	deviates from binomial distribution?	p
cavity height	<3 m: 2 >3 m: 27	YES	< .001
vegetative cover	open: 28 occluded: 1	YES	< .001
number of branches	<5 : 9 >5: 20	YES	= .031
other cavities	yes: 28 no: 1	YES	< .001
tree condition	live: 10 dead: 19	NO	= .068
bark cover	<50%: 16 >50%: 13	NO	= .356
broken top	yes: 19 no: 10	NO	= .068

height (greater than 3 m, $p < 0.001$), vegetative cover around cavity entrance (open, $p < 0.001$), number of branches remaining on the cavity tree (>5, $p = 0.031$), and presence of other cavities (yes, $p < 0.001$, Figure 9). No significant departures from the binomial distribution were found for whether the cavity tree was alive or dead ($p = 0.07$), percent bark cover ($p = 0.356$), or if the cavity tree had a broken top ($p = 0.07$, Figure 10).

FIGURE 9

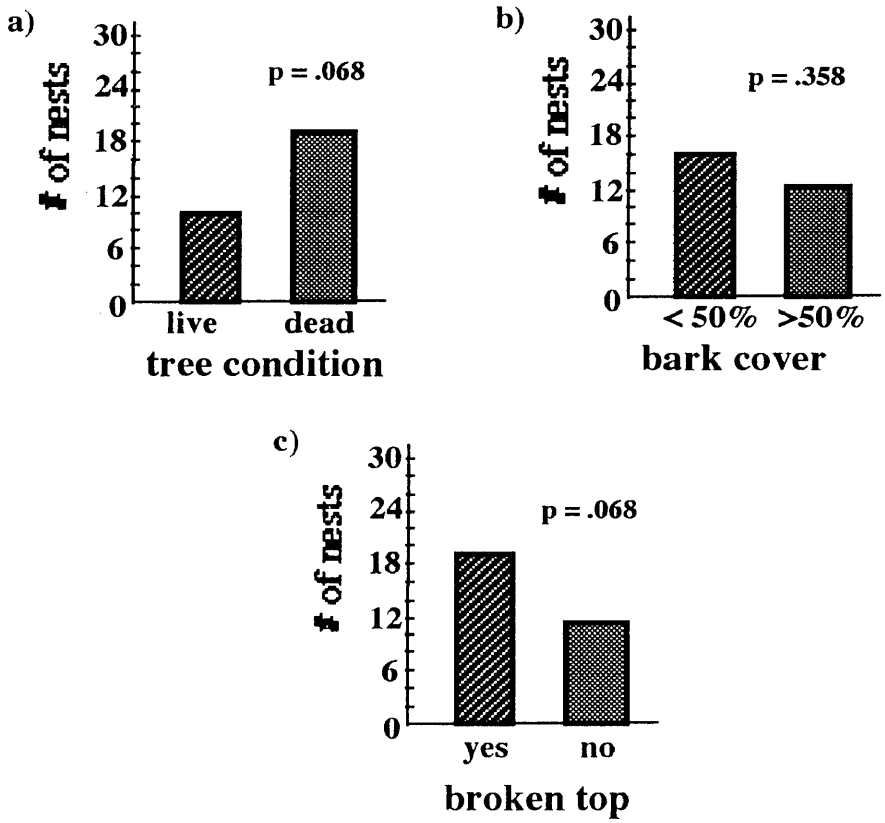
NEST SITE CHARACTERISTICS DEVIATING SIGNIFICANTLY FROM A BINOMIAL DISTRIBUTION



Predictions based on published literature were that (a) the majority of nests would be less than 3 m high, (b) cavity entrances would be free of vegetation, (c) cavity trees would have few branches, and (d) other cavities would be present in the cavity tree. Note that data for nest height and number of branches remaining deviate from the predicted pattern.

FIGURE 10

NEST SITE CHARACTERISTICS NOT DEVIATING SIGNIFICANTLY FROM A BINOMIAL DISTRIBUTION



Predictions based on published literature were that (a) the majority of nests trees would be dead, (b) with less than 50% bark cover remaining and (c) broken tops. Note that the predicted significant departures from a binomial distribution were not observed.

DISCUSSION

Forest patch

The finding that basal area of oaks was significantly higher in non-territory forest plots than in territory forest plots is consistent with O'Halloran and Conner's (1987) finding of higher hardwood basal area in random plots than in foraging plots. I had only two size classes in 1997: shrub/sapling and tree. Because all of the forest plots had a pine-dominated canopy, it is likely that the difference in oak basal area was driven by differences in the subcanopy. However, without having distinguished between canopy and subcanopy trees during data collection, I cannot confirm this. More informative differences may have been detected if I had partitioned the tree data into canopy and subcanopy classes during data collection.

In 1998 I compared the habitat that was available to the birds (random plots) with the habitat in which they nested (nest plots) to test the hypothesis that brown-headed nuthatches were selecting specific nest-site characteristics. The occurrence of a greater shrub/sapling basal area in nest plots than in random plots is consistent with the positive correlation found between ground-cover density and occurrence of brown-headed nuthatches in a North Carolina study (Wilson and Watts 1999). Increased foraging substrate for insectivores may be a benefit of dense understory vegetation (Dickson and Segelquist 1979), and this could be particularly important to brown-headed nuthatches during the breeding season. The finding that nest plots were significantly closer to mature pines than random plots is not unexpected, and confirms that these nuthatches tend to nest close to the important food resource provided by cone-bearing pine trees.

Because I found numerous nest trees in marshes and meadows beyond the forest edge, I did not require that random plots fall in the forest. This allowed a true comparison of available habitat to nesting habitat. However, the fact that some random plots fell in densely forested areas while others fell in completely open areas led to a high degree of variance in the random plot data. The two-way ANOVAs on canopy and subcanopy deciduous tree density and subcanopy snag density had very low power: 0.09, 0.07, and 0.06 respectively to detect a 20% difference in basal area between random and nest plots, and only 0.29, 0.20, and 0.16 respectively to detect a 50% difference. This indicates that differences may exist that were not detected because of the high variance. Increased sample size could lead to greater power and more informative results. Alternatively, requiring that random plots fall within the forest could reduce variance and increase power, but that would have required an adjusted hypothesis that nest sites in the forest differed from available forest patches. For this comparison to be valid, nests that occurred beyond the forest edge would need to be excluded. Brown-headed nuthatch nests do not always occur within the forests in which they forage (Norris 1958), and in this study 9 out of 29 nests were located beyond the forest edge. Limiting analysis to forested plots would not allow an accurate assessment of brown-headed nuthatch nesting habitat. A paired design in which each random plot was selected from the same habitat as a matched nest plot would have provided increase power without requiring an unreasonably large sample size.

A second comparison I made between nest and random plots was of the degree of similarity between plot types for a given variable, such as basal area of deciduous trees in the canopy or distance to the nearest mature pine. I hypothesized that random plots would exhibit higher variability in these variables than would nest plots. I compared coefficients of variation of the forest layers for basal area of pines, deciduous trees, snags, and shrubs (in the subcanopy and sapling layer) as well as for distance to the nearest pine, canopy closure, and percent ground cover composed of dead wood.

In three of the comparisons, pine basal area in both canopy and subcanopy layer and deciduous tree basal area in the canopy, nest plots had lower coefficients of variation than random plots at all four study locations. In twelve of the fifteen comparisons there was no consistent pattern. However, because there were many zero values in these data, standard errors were often close in value to means, causing the standard deviation to be approximately 2.45 times the mean. Coefficients of variation calculated from these data tended to be near 245, resulting in the large number of values in Tables 1 - 3 that are close to 245. The large number of zero values make my results very sensitive to the occurrence of one or a few stems in all plots in a given category. Thus, the comparison of coefficients of variation is probably of low power. Further study with larger sample sizes is needed before conclusions can be drawn about the relative difference between nest and random plots.

Nest site

Nest characteristics observed in 1997 and 1998 were quite different than those predicted from data in previous studies. In marked contrast to reports that the majority of brown-headed nuthatch nests occur lower than 3 m, only two of my nests were less than 3 m above the ground. My mean height of 10.01 m (range: 2.2 m - 29.3 m, Table 7) was much closer to a recently reported mean of 10.9 m for southern Florida (Slayter 1997).

It is widely accepted that brown-headed nuthatches require snags in an advanced state of decay (McNair 1984). Indicators of such "soft" snags include the presence of other cavities, broken tops, few remaining branches, and little bark remaining. I expected to find brown-headed nuthatches nesting in low pine snags with few branches and bleached white trunks without bark. In fact, the majority of my nest trees did not fit this search image. Ten of twenty-nine nests were not in snags, but were in dead portions of live trees (with three of these being deciduous trees). This is

TABLE 7

NEST TREE CHARACTERISTICS

NEST TREE MEASUREMENT	MEAN VALUE (±SD)
cavity height	10.01 m (± 6.78)
tree height	15.25 m (± 9.17)
tree DBH	37.92 cm (±15.67)

an important difference, as previous accounts indicated that the vast majority of nests would occur in snags. Also in contrast to expectation, almost half of the cavity trees had more than 50% bark cover remaining. However, it is possible that percent bark cover may not be a reliable indicator of decay state. Personal observation revealed that snags with bark often had softer wood than those without bark, suggesting that excavation into a bark-covered snag could be preferable to excavating into the tough weathered outer layer of wood on a barkless snag. Two other areas in which observations differed from expectations based on previous research were: fewer of the cavity trees than expected had broken tops and more of them than expected had greater than five branches remaining. Departures from the binomial distribution which were expected based on previous literature were observed in two categories. Only one nest tree did not have other cavities present, and only one cavity had an entrance that was not free of vegetative cover.

Snags are often considered a limiting factor for populations of cavity nesting birds (Conway 1993, Li and Martin 1991, Zarnowitz and Manuwal 1985), and a reduction in the number of available snags can result from both fire suppression and intensive timber management of forest. However, 34% of nests in this study were found in dead portions of live trees, suggesting that that traditional snags may not be a resource critical to brown-headed nuthatches. Snags were available near each of the nest sites in this study. It may be that those snags were not chosen because of some shortcoming of snag or location, or it may be that brown-headed nuthatches need dead wood for nest excavation and do not differentiate between dead wood in a snag or dead wood in a live tree. In support of this explanation, 17% of nests found in south Florida were in live trees or dead portions of live trees (Slayter 1997). A study of cavity nesting birds in Colorado found no evidence of nest site limitation in a cottonwood bottomland, with the majority of nests occurring in dead limbs of living trees (Sedgwick and Knopf 1986). The small size of brown-headed nuthatches (length 105 -

110 mm, Withgott and Smith 1998) may allow them to nest more readily in branches and small diameter snags, in contrast to woodpeckers which require snags with a DBH of at least 20-30 cm (Conner et al. 1975). Again, further study of this species is necessary to pinpoint important habitat resources.

Competition

The fact that no correlation was found between number of cavity nesting birds at a nest site and apparent nest quality does not mean that competition with other cavity-nesting birds does not affect nest site choice in brown-headed nuthatches. It may simply be that the indicators of a quality nest site which have been demonstrated for other species do not hold for the brown-headed nuthatch. None of the estimators of quality used in this study have been shown to be related to nest success in brown-headed nuthatches. Determination of indicators of cavity-site quality specific to brown-headed nuthatches would be a good next step. Further evaluation of species abundance of potential competitors could reveal informative patterns, as could carrying out point counts throughout the entire breeding season. My point counts were done once all brown-headed nuthatch nests were active, but competitors present only during excavation or later in the breeding season may have been missed.

There is evidence that competition with other cavity nesting species does occur. Nest-site usurpations have been reported by both primary cavity nesters (red-bellied woodpeckers, *Melanerpes carolinus*) and secondary cavity nesters (eastern bluebirds) (Slayter 1997). On several occasions I observed aggressive encounters between other cavity-nesting birds and a nuthatch on or near the nuthatch nest tree. Generally these encounters were with red-bellied woodpeckers, but I also observed two conflicts between tree swallows and nuthatches. It is possible that the incidence of nest site competition may be reduced by the relatively early nesting phenology of the brown-headed nuthatch (Slayter 1997), allowing them to leave the nest before potential competitors begin nesting.

Conclusions

Because brown-headed nuthatches are endemic to the southern pine forest system to which the endangered red-cockaded woodpecker is restricted (Ligon et al. 1986), it is tempting to draw comparisons between the situations of the two birds. Though brown-headed nuthatches have been shown to benefit from management practices in the red-cockaded woodpecker recovery effort (Wilson et al. 1995), consideration must be given to notable differences in life-history traits. The brown-headed nuthatch has been described both as "one of three species restricted to southern pines" (Johnston and Odum 1956) and as a highly adaptable species that can be found in marginal habitat and is common in residential areas (Norris 1958, Yaukey 1996). While red-cockaded woodpecker cavity construction is limited to pines over seventy years old which are infected with heart-rot fungus, brown-headed nuthatch nests have been found in at least nine species of tree (Bent 1948, Haney 1981, Morse 1977), as well as fence posts and, in one case, a plank leaning against a tree (McNair 1984). One of the nest cavities I found was located in a support post of an old duck blind in the James River. Excavation of a red-cockaded woodpecker cavity is a very energy-expensive endeavor (Ligon et al. 1986), while brown-headed nuthatches frequently excavate multiple cavities before choosing one in which to nest (Bent 1948, McNair 1984, Morse 1977).

My data suggest that brown-headed nuthatches are not highly restricted in terms of nesting habitat. I did not find a consistent suite of characteristics that defined a "classic" brown-headed nuthatch cavity site. Nor did I find substantial differences between nest plots and random plots, which suggests that there is not a shortage of suitable available nesting habitat. However, several previous studies have shown that densities of brown-headed nuthatches, both breeding and foraging, are negatively correlated with an increase in mid-story hardwoods. My data may have failed to show a similar trend because of low statistical power. If so, my results could lead to a false sense of security about the habitat status of this species. Another possible explanation for my finding of no significant differences between nest plots and random plots is that the basal area of midstory hardwoods was low in all of my plots. Support for this idea is given by the fact that mean basal area for pine, deciduous trees, and snags for nest sites and random sites in this study were both comparable to or lower than the mean basal areas reported for occupied forest patches in Texas (O'Halloran and Conner 1987, see Table 8). However, further study is needed to rule out nest-site limitation as an explanation for local population declines.

Future study

There are many potential areas for further study regarding habitat of brown-headed nuthatches. It would be valuable to look more closely at breeding success in different areas and to examine how vegetation and nest site characteristics are correlated with nest successes. A related line of inquiry would be to look specifically at correlations between causes of nest failure (usurpation, predation, structural failure) and nest site characteristics. Looking more closely at nest site characteristics, such as the prevalence of living nest trees in this study, could provide valuable information regarding nest site selection. For example, comparing the relative volume or surface area of dead wood available in snags and dead portions of living trees with the sites used for nesting could answer the question of whether brown-headed nuthatches actually prefer to nest in snags, in dead wood in live trees, or simply in any dead wood regardless of location.

Brown-headed nuthatches are cooperative breeders, one of only three species of nuthatches worldwide that do so. Only a handful of North American birds breed

TABLE 8

COMPARISON OF MEAN BASAL AREA (m^2/ha) IN TERRITORIES AND NON-TERRITORIES BETWEEN TWO STUDIES

	PRESENT STUDY		O'HALLORAN &CONNER 1987	
	NEST	RANDOM	OCCUPIED	RANDOM
CANOPY	pine: 12.14± 16.42	pine: 12.08± 20.97	pine: 11.94± 5.40	pine: 14.41± 4.90
	snag: 2.37± 5.04	snag: 0.21± 1.01	snag: 0.18± 0.40	snag: 0.15± 0.40
	dcd.tr.: 0.00± 0.00	dcd.tr.: 4.08 ±13.96	dcd.tr.: 0.31 ±0.60	dcd.tr.: 1.88± 2.50
SUBCANOPY	pine: 0.71± 2.28	pine: 0.96± 2.04	pine: 3.10± 3.30	pine: 3.32 ±3.10
	snag: 2.38± 4.55	snag: 1.48± 5.17	snag: 0.37± 0.70	snag: 0.94± 1.20
	dcd.tr.: 2.00± 4.87	dcd.tr.: 1.49± 4.99	dcd.tr.: 1.09± 2.30	dcd.tr.: 6.29±3.6

dcd. tr. = deciduous trees

cooperatively, and very little is known about cooperative breeding in the brown-headed nuthatch. Cooperative breeding was reported at 18% of nests in a Georgia study (Norris 1958) and at 60% of nests in a Florida study (Slater 1997). Significantly higher breeding success was found at nests with helpers than at regular nests in southern Florida, with 70% success for nests with helpers and 48% success for nests without helpers as calculated by the Mayfield method (Slater 1997). Habitat characteristics may be important to helping behavior in the brown-headed nuthatch, as a relationship has been demonstrated between the occurrence of helping behavior and measures of habitat quality in both the red-cockaded woodpecker (Walters et al. 1992) and Seychelles warbler (*Acrocephalus sechellensis*) (Komdeur et al. 1995). Further study on the relationships between habitat characteristics, cooperative breeding, and nesting success could allow more targeted population management efforts for the brown-headed nuthatch.

Brown-headed nuthatches are regarded as being very sedentary, exhibiting little population movement even in response to local fluctuation in food abundance (Morse 1977). Low recolonization of areas could pose problems for nuthatch populations, even with restoration of former habitat to mature pine woods. Long term tracking of local populations to determine habitat use patterns, cooperative breeding patterns, and the potential for population expansion would be valuable to future conservation efforts. For example, habitat restoration could prove useless if the restored habitat is out of the dispersal range of existing brown-headed nuthatch population.

Conservation

Declines throughout the range of the brown-headed nuthatch provide cause for concern about the species. However, the apparent adaptability of this species in terms of nesting behavior suggests that managing forests for recovery of brown-headed nuthatch populations could be a relatively simple task. Unlike the red-cockaded woodpecker which requires very specific cavity tree conditions, brown-headed nuthatches appear to be able to nest in a wide range of circumstance as long as there is excavateable wood. Brown-headed nuthatch populations have already been shown to benefit from habitat management for the endangered red-cockaded woodpecker (Wilson et al. 1995). Wider application of procedures such as thinning of the hardwood midstory and prescribed burns might provide further benefit to brown-headed nuthatch populations. Retaining snags of different stages of decay could provide a benefit to brown-headed nuthatches, and certainly to other cavity nesting birds (Zarnowitz and Manuwal 1985). Further careful analysis of the nesting habitat requirements of this species will allow us to focus management efforts and prevent further declines in populations of the brown-headed nuthatch and other cavity nesting species.

LITERATURE CITED

Adkisson, C. S. 1988. Cavity-nesting birds of North America: Past history, present status, and future prospects. In *Bird Conservation*, Jackson, J. A. (ed.) University of Wisconsin Press, Madison, WI.

Bent, A. C. 1948. *Life histories of North American nuthatches, wrens, thrashers, and their allies*. U.S. National Museum Bulletin, **195**.

Bibby, C. J., Burgess, N. D., and Hill, D. A. 1992. *Bird Census Techniques*. Academic Press Inc., San Diego, CA.

Cline, S. P., Berg, A. B., and Wight, H. M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management, **44**, 773-786.

Conner, R. N., Dickson, J. G., Locke, B. E., and Segelquist, C. A. 1983. Vegetation characteristics important to common songbirds in East Texas. Wilson Bulletin, **95**, 349-361.

Conner, R. N., Hooper, R. G., Crawford, H. S., and Mosby, H. S. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. Journal of Wildlife Management, **39**, 144-150.

Conway, C. J., and Martin, T. E. 1993. Habitat suitability for Williamson's sapsuckers in mixed-conifer forests. Journal of Wildlife Management, **57**, 322-328.

Dickson, J. G., and Segelquist, C. A. 1979. Breeding bird populations in pine and pine-hardwood forests in Texas. Journal of Wildlife Management, **43**, 549-555.

Hamel, P. B. 1992. *Land manager's guide to birds of the South*. The Nature Conservancy, Chapel Hill, NC, and U.S. Forest Service, Southern Region, Atlanta, GA.

Haney, J. C. 1981. The distribution and life history of the brown-headed nuthatch (*Sitta pusilla*) in Tennessee. Migrant, **52**, 77-86.

Harrap, S. and Quinn, D.. 1995. *Chickadees, tits, nuthatches and treecreepers*. Priceton University Press, Princeton, NJ.

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

Komdeur, J. 1995. Transfer experiment of Seychelles warblers to new islands: changes in dispersal and helping behavior. Animal Behavior, **49**, 695-708.

Krishnaiah, P. R., ed. 1980. *Analysis of Variance*. North-Holland Publishing Company, New York, NY.

Land, E. D. 1986. Snag characteristics and their relationship to cavity nesting birds in slash pine plantations of north-central Florida. Masters thesis, University of Florida, Gainesville.

Li, P., and Martin, T. E. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. The Auk, **108**, 405-418.

Ligon, L., Stacey, P. B., Conner, R. N., Bock, C. E., and Adkisson, C. S. 1986. Report of the American Ornithologists' Union Committee for the Conservation of Red-cockaded Woodpecker. The Auk, **103**, 848-854.

Mannan, R. W., Meslow, E. C., and Wight, H. M. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. Journal of Wildlife Management, **44**, 787-797.

McNair, D. B. 1984. Clutch-size and nest placement in the brown-headed nuthatch. Wilson Bulletin, **69**, 296-301.

Morris, S. M. 1982. Nesting activities of the Brown-headed Nuthatch in Louisiana. Master's thesis, Louisiana Tech. University, Ruston.

Newton, I. 1998. *Population Limitation in Birds*. Academic Press Limited, London, U.K.

Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches (*Sitta pygmaea* and *Sitta pusilla*). University of California Publications in Zoology, **56**, 119-300.

O'Halloran, K. A., and Conner, R. N. 1987. Habitat used by Brown-headed Nuthatches. Bulletin of the Texas Ornithological Society, **20**, 7-13.

Schreiber, B., and deCalesta, D. S. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecology and Management, **50**, 299-316.

Sedgwick, J. A., and Knopf, F. L. 1986. Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. Journal of Wildlife Management, **50**, 247-256.

Slater, G. 1997. Brown-headed Nuthatches and Eastern Bluebirds in southern Florida pinelands: breeding biology, nest-site selection, and the influence of habitat on nesting success. Master's thesis, University of Florida, Gainesville.

Smith, P. W., and Smith, S. A. 1994. A preliminary assessment of the Brown-headed Nuthatch in the Bahamas. Bahama Journal of Science, **1**, 22-26.

Walters, J. R., Copeyon, C. K., and Carter, J. H. 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. Auk, **109**, 90-97.

Williams, J. B. 1969. Competition among bark foraging birds. 1969. Condor, **81**, 122-132.

Williams, J. B. 1979. Interspecific competition and niche shifts. 1979. Wilson Bulletin, **91**, 400-411.

Wilson, C. W., Masters, R. E., and Bukenhofer, G. A. 1995. Breeding bird response ro pine-grassland community restoration for Red-cockaded Woodpeckers. Journal of Wildlife Management, **59**, 56-67.

Wilson, M. D., and Watts, B. D. 1999. Response of Brown-headed Nuthatches to thinning of pine plantations. Wilson Bulletin, **3**, 56-60.

Withgott, J. H. and Smith, K. G. 1998. Brown-headed Nuthatch. In: *Birds of North America, Species Accounts*.. The Birds of North America, Inc., Philadelphia, PA.

Yaukey, P. H. 1992. The Effect of Residential Development on Interspecific Grouping in the Brown-headed Nuthatch. PhD dissertation, University of Georgia, Athens.

Yaukey, P. H. 1996. Patterns of avian population density, habitat use, and flocking behavior in urban and rural habitats during winter. Professional Geographer, **48**, 70-81.

Zarnowitz, J. E., Manuwal, D. A. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management, **49**, 255-263.

VITA

Valerie Anne Weiss

Valerie Weiss was born in Staunton, Virginia on February 28, 1970. She graduated from Robert E. Lee High School in Staunton, Virginia, in June 1988, and headed west to Minnesota for college. Graduating from Carleton College in Northfield, Minnesota in June 1992 with a B.A. and a major in Biology, she returned to the East Coast to work in outdoor education on the shores of the Chesapeake Bay for two years. Next, it was back to the midwest for two years of teaching math and science in a Granville, Ohio middle school. She returned to Virginia and to the life of a student, entering the College of William and Mary as a graduate assistant in the Department of Biology in January 1997.