

12-2000

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Recommended Citation

Herb Jr., A. and D.B. Burt. 2000. Influence of habitat use-patterns on cooperative breeding in the Brown-headed Nuthatch. *Bulletin of the Texas Ornithological Society* 33:25-36.

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BULLETIN OF THE
TEXAS ORNITHOLOGICAL SOCIETY

Vol. 33, No. 3.

December, 2000

Pages 25–36

**INFLUENCE OF HABITAT USE-PATTERNS ON COOPERATIVE
BREEDING IN THE BROWN-HEADED NUTHATCH**

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ABSTRACT.—We document the habitat use patterns of the Brown-headed Nuthatch (*Sitta pusilla*). We describe how its habitat use patterns contribute to ecological constraints that may maintain cooperative breeding in this species. Brown-headed Nuthatches are pine specialists. In particular, Brown-headed Nuthatches forage primarily on the bark and cones in the top distal portions of mature pines. Breeding territories differ considerably in pine density. We suggest that differences in pine density are an indicator of habitat and territory quality. We predict that additional studies will document that helpers are more common on relatively small territories with high tree densities and in habitats with few suitable nest sites.

The Brown-headed Nuthatch (*Sitta pusilla*) is a non-migratory passerine distributed throughout the pine and mixed pine-hardwood forests of the southeastern United States (Withgott and Smith 1998). Brown-headed Nuthatches occur in greater densities in open forests dominated by older (35–45+ year) pines with few hardwoods (Morse 1970; Meyers and Johnson 1978; Dickson et al. 1980; Conner et al. 1983; Hamel 1992). More specifically, individuals prefer foraging in open pine stands with a low basal area of hardwoods (O'Halloran and Conner 1987). The Brown-headed Nuthatch is, therefore, in general terms, a pine habitat specialist.

Surprisingly few behavioral studies have been conducted on this species. Information on how this species adapts to human induced habitat alteration is virtually unstudied. This paucity of information is particularly surprising given its commonness in appropriate habitats and given that it breeds cooperatively. In a cooperative breeding system, certain individuals (helpers) regularly provide some degree of parental care to young that are not their own offspring (Brown 1987). Several other North American cooperative breeding species have been the foci of detailed, long-term studies (Red-cockaded Woodpecker—*Picoides borealis*, Walters 1990; Acorn Woodpeckers—*Melanerpes formicivorus*, Koenig and Stacey 1990; Pinyon Jays—*Gymnorhinus cyanocephalus*, Marzluff and Balda 1990; Mexican Jays—*Aphelocoma ultramarina*, Brown and Brown 1990; Florida Scrub Jays—*Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1990). Many hypotheses that attempt to explain why helpers provide this apparently altruistic behavior center on the concept of ecological constraints. For example, some ecological

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variable or variables may make immediate natal dispersal prohibitively costly (habitat saturation hypothesis—Selander 1964; Brown 1974, marginal habitat model—Koenig and Pitelka 1981; Emlen 1982; Woolfenden and Fitzpatrick 1984). Alternatively, certain individuals may benefit from delayed dispersal if this tactic increases their chance of gaining control of a critical resource for breeding (benefits-of-philopatry hypothesis—Stacy and Ligon 1987; 1991). Ecological constraints might include a lack of suitable breeding territories, a lack of suitable nesting areas, or even a lack of marginal habitats that could allow pre-breeding dispersal and floating.

This study addresses four fundamental questions related to habitat use patterns and cooperative breeding in Brown-headed Nuthatches. We first quantify the degree of Brown-headed Nuthatch preference for pine in a mixed pine-hardwood habitat. Second, we examine the behaviors and microhabitat preferences of this species. Third, we analyze the relationship between breeding territory size and vegetation composition. Fourth, we examine the location of nest cavities within breeding territories. We explore the possibility that ecological constraints may exist due to the pine-specialist foraging behaviors in this species. Availability of snags and dead branches for excavation of nests may be an additional ecological factor constraining breeding in Brown-headed Nuthatches. These constraints may at least partially explain the maintenance of cooperative breeding in this species.

METHODS

This study took place on the campus of Stephen F. Austin State University in Nacogdoches, Texas. The campus represents a mixed hardwood-pine habitat. Brown-headed Nuthatches were captured in mist nets and banded with Fish and Wildlife Service leg bands and an individual-specific combination of two colored leg bands. Each bird was aged as adult or juvenile. Females were identified by the presence of a brood patch during the breeding season. Individuals without brood patches during the breeding season were assumed to be male. Determination of sex by behavioral differences was necessary in some cases.

Herb collected data from November 1997 through October 1998. Bird activity and behaviors were recorded to the nearest second in 15 minute sampling sessions or until the bird was lost from sight. Behavior perceived to be influenced by the presence of the observer was excluded. The behaviors were categorized as feeding, inactive, preening, territorial, excavating, or other (begging, copulating, vocalizing, activities related to the care of young, etc.). The specific location of foraging behaviors was categorized as bark, leaves or needles, cones/buds, bird feeder, or unknown. Substrates occupied were categorized as pine, hardwood, or other (lightpost, building, etc.). Location within trees (top, middle, and lower; proximal, distal, and trunk) was also recorded. Data were collected between a half-hour after sunrise and a half-hour before sunset. We attempted to observe all marked individuals equally.

Throughout the study, the location and movement of banded individuals was recorded and overlaid on a pre-existing GIS database of the campus using ArcView version 3.0. The nest site of each group during the 1998 breeding season was mapped. In instances where a group did not lay eggs, the last cavity substantially excavated was mapped. Territory boundaries were determined by drawing a polygon around observed locations of each family group. The family group included the breeding pair, fledglings, and any helpers present. Suspected outliers were excluded from the polygon. Points were identified as outliers when the identification of an individual was uncertain or when the location of the focal individual was clearly outside its normal range. The following parameters for each territory were determined: size, density of trees, proportion of pines and hardwoods, nest location, and distance from nest to the closest mature pine.

The time Brown-headed Nuthatches used pines versus hardwoods was compared to the expected use. The expected use pattern assumes no preference for either vegetation type. Expected use of pines and hardwoods was calculated by multiplying the total time observed by the proportion of pine and hardwoods available on campus. The actual number of hardwoods and pines found on

campus was determined using the GIS database. A G-test was used to test for a significant difference from the null hypothesis of proportional vegetation type use. Time-budget data were also used to examine whether Brown-headed Nuthatches showed specific microhabitat preferences within each vegetation type. Times spent within each microhabitat location were compared using a Mann-Whitney multiple comparison test (Sokal and Rohlf 1995).

RESULTS

We recorded a total of 206 episodes of time-budget activity. From these trials we accumulated 24 hrs, 46 minutes, and 58 seconds of data. Trial duration averaged 7.2 minutes (SE = 4.6, n = 206) before the bird was lost from sight. We attempted to record data evenly throughout the day; however, the majority of the data was collected in the morning hours. This data collection pattern occurred because most focal individuals were located by sound and Brown-headed Nuthatches are most vocal during the morning hours. This observation bias has the potential to skew the behavior data to non-sedentary activities if individuals were inactive more in the afternoon. However, our records of Brown-headed Nuthatches during the afternoon showed similar behaviors, other than vocalizations, to those in the morning.

Of the 2329 total trees on campus, 1099 (47%) were *Pinus* sp. and the remaining 1230 (53%) were hardwoods. Of the 75908 seconds that Brown-headed Nuthatches were observed in vegetation, 62208 s (82%) were in pines and 13700 s (18%) were in hardwoods. Assuming that Brown-headed Nuthatches show no vegetation preference and use each type according to availability, the expected usage times are 35677 s (47%) for pines and 40231 s (53%) for hardwoods. In order to have independent data points for a G-test; we used the number of trials dominated by use of a particular substrate instead of total seconds. The transformed data show the same trend of an overwhelming amount of time spent in pines. Brown-headed Nuthatches in this study used pines significantly more than expected ($G_{adj} = 60.71$, $\chi^2_{.05(1)} = 3.841$, $p \ll 0.001$).

While in pines, individuals spent a majority of their time foraging on bark (50.4%) and cone substrates (16.9%). Brown-headed Nuthatches use hardwoods with similar behavioral patterns. While in hardwoods, individuals spent a majority of their time foraging on the bark substrate (54.2%).

Figure 1A shows the time that Brown-headed Nuthatches spent in different regions within trees. Brown-headed Nuthatches spent significantly more time in the top distal portions of the trees than any other area (Fig. 1B). There was also a significant preference for the middle distal and top proximal portions of trees over the middle trunk, bottom trunk and bottom proximal parts of trees (Fig. 1C and D). Additionally, nuthatches spent significantly less time in the top trunk portion of trees than in top distal, top proximal, middle proximal, and middle distal portions (Fig. 1E).

Six Brown-headed Nuthatch groups maintained territories on the campus (Table 1, map in Herb 1999). These territories were occupied year around. Most of the territory borders were within the campus. The exception was the UPD group. This territory was probably larger than recorded (5.3 ha) because focal individuals were not mapped off campus where they may have spent most of their time. The mean territory size was 7.4 ha (4.4 ha–16.2 ha) when including the UPD group. When this group is excluded, the mean size was 8.0 ha.

Nests were located in natural and artificial cavities. Only half of the groups nested successfully, all in artificial cavities. Two nests were located in the top of light posts where a hole was available in the side and the top was covered. One of these nesting groups bred cooperatively with one helper. The third successful artificial nest was located in an electrical box atop a pole. One additional group built a nest in a light pole with an open top. This group laid and incubated eggs but abandoned the nest prior to fledging. Heavy construction occurred directly adjacent to this pole. Two groups excavated into dead portions of living trees. One group excavated a dead pine branch in a relatively dense area of trees. The other group excavated a dead portion of a hickory. Neither of these groups with natural cavities appeared to lay eggs before the cavities were abandoned. These groups did not appear to nest elsewhere.

The distance of nests from the closest foraging tree averaged 26.7 m (4.9 m–54.7 m). All nests

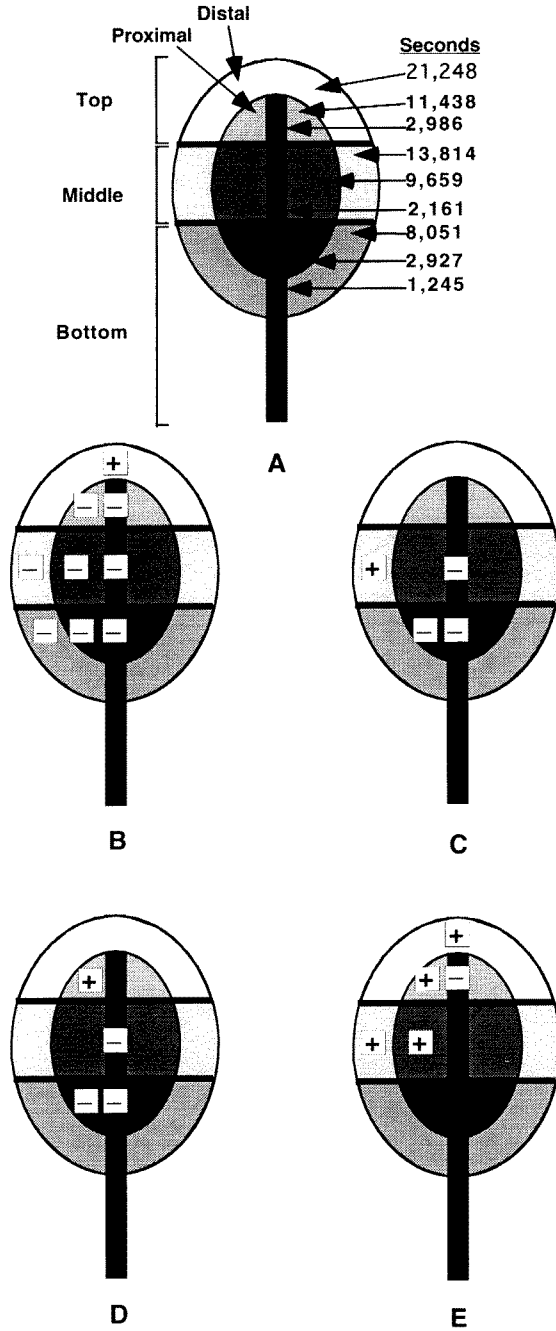


Fig. 1. Time in seconds for each location where Brown-headed Nuthatches were seen (A). A Mann-Whitney multiple comparison test shows several patterns of differential tree location use. Individuals showed significantly more use of top distal locations compared to all other tree locations (B). Individuals also showed significantly more use of top distal locations compared to all other tree locations (B).
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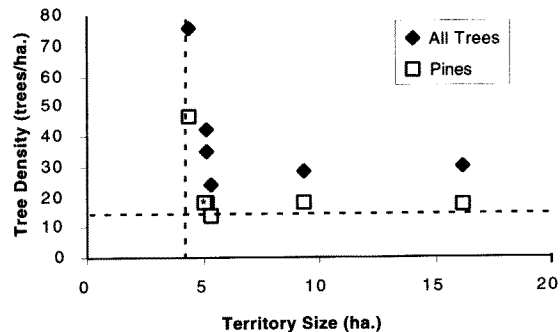


Fig. 2. Brown-headed Nuthatches appear to have a minimum territory size (dashed vertical line), and require both a minimum density of pines (dashed horizontal line) and total trees. Territories with greater densities are probably higher quality. Additionally, small territories of a particular density are of higher quality than are large territories. Asterisk indicates 2 overlapping pine data points.

but one were located in relatively open areas. We observed no apparent pattern of nest placement relative to territory boundaries. The availability and distribution of artificial cavities and dead branches likely plays a large role in nest placement.

DISCUSSION

Brown-headed Nuthatches are pine specialists. In particular they require territories with numerous pines for foraging. Individuals primarily concentrate foraging on bark and cones in the top distal portions of pines. These preferences have also been documented in previous studies. Many studies have noted that Brown-headed Nuthatches occur in a mature pine dominated forest with an open understory (Johnston and Odum 1956, Mose 1970, Meyers and Johnson 1978, Dickson and Segequist 1979, Haney 1981, Johnson and Landers 1982, Conner et al. 1983, O'Halloran and Conner 1987). Some authors have also noted a preference for the top portion of trees (Norris 1958, Morse 1970, O'Halloran 1984, Yaukey 1997).

While our sample size is small, we suspect that territory size varies in relation to tree density (Fig. 2), with a minimum territory size of approximately 4.5–5.0 hectares. These territories differ considerably in tree density (Fig. 2, Table 1). We suggest that this difference in tree density, particularly pine density, may indicate habitat and territory quality. The importance of pine density in Brown-headed Nuthatches territories has been reported previously (O'Halloran and Conner 1987). We suggest there is a relationship between territory size and tree density in this species. In Ovenbirds (*Seiurus aurocapillus*), territory size is inversely related to habitat quality (Smith and Shugart 1987). Habitat quality in the case of Ovenbirds relates to prey density. Brown-headed Nuthatch habitat quality may relate to prey density as well. In this case, the prey source occurs in mature pines. Territories with relatively dense pine composition provide more foraging substrate for individuals. These high quality territories may allow increased foraging efficiency and greater reproductive success.

Territory formation appears to require a minimum tree density. Three low-density territories varied considerably in size (Fig. 2, Table 1). We suggest that size differences of territories of comparable tree densities also indicate territory quality differences. Relatively large territories for

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more use of middle distal (C) and top proximal (D) locations than middle and bottom trunk and bottom proximal locations. Individuals showed significantly less use of top trunk regions than all top and middle branch locations (E).

Table 1. Quantitative data for six Brown-headed Nuthatch territories on the Stephen F. Austin State University campus.

Territory	Size (ha)	Tree density (#/ha)	Density of pines (#/ha)	Density of hardwoods (#/ha)	Distance to closest foraging tree (m)	Number fledged
Tennis	16.2	29.7	17.8	11.9	52.4	2
Forestry	9.3	28.6	18.3	10.3	54.7	4
UPD	5.3	23.8	13.5	10.2	17.1	0
Alumni	5.1	34.7	18.4	60.31	19.3	0
Griffith	5.1	42.4	19.1	23.3	11.8	2
Birdwell	4.4	75.7	46.9	28.8	4.9	0

a given tree density may incur greater energetic costs due to increased travel distances for territory defense and foraging behaviors. The larger territories in this study included large expanses of parking lots and may represent an ecological condition not seen in birds in more natural settings.

This territory size to tree density pattern fits conditions of the benefits-of-philopatry hypothesis (Stacey and Ligon 1987, 1991). Helpers should be more common on high quality territories (high tree density, relatively small territory size) than on low quality territories (low tree density, relatively large territory size). Helpers on high quality territories delay dispersal and use natal territory resources, while waiting for a breeding opening on a high quality territory. Individuals gain no benefit from delaying dispersal on low quality natal territories. These individuals should choose immediate dispersal into higher quality territories, if possible. If high quality territories are saturated, these individuals still fare better occupying open lower quality habitats in which they either become a breeder or non-breeding floater.

Despite intuitive appeal, limited data on helper distribution and reproductive success among territories in this study do not support the benefits-of-philopatry hypothesis (Table 1). We need more data to adequately address this issue.

Given the composition of the manicured habitat of the campus with removal of snags and dead limbs, it is possible that suitable nest sites are at a premium and may be an additional limiting factor for territory establishment. Brown-headed Nuthatches may also have microhabitat preferences for cavities in open areas. McNair (1984) observed that Brown-headed Nuthatches frequently selected nest sites in clear cuts, along roadsides, in wind breaks, over ponds, and in fields. Morris (1982) noted a strong preference to nest over or near water. Burleigh (1958) documented one nest as 460 m from the nearest woods.

This study addresses potential ecological factors *maintaining* cooperative breeding behavior in an urban population of Brown-headed Nuthatches. This study cannot, however, directly address the ecological influences that led to the *evolution* of cooperative breeding in the Brown-headed Nuthatch. In fact, cooperative breeding likely evolved in the common ancestor of the Brown-headed Nuthatch and the, also cooperative Pygmy Nuthatch (*Sitta pygmaea*). To understand the evolution of this trait will require detailed comparative data on the behavior ecology of both of these species living in more natural habitats. For the Brown-headed Nuthatch this means studying the species in pine habitats closer to those of the pre-Columbian southern pine ecosystem. This ecosystem was dominated by contiguous open stands of mature southern pine that received regular burning of the understory. This pattern of regular burning likely made snags suitable for excavation of nests a limiting resource. Limited nesting sites may have played a significant role in the evolution of cooperative breeding in this species. However, the degree of territory quality variation and the suitability of the benefits-of-philopatry hypothesis in this pre-settlement ecosystem are unknown. Studies in expansive pine forests maintained with prescribed burning are needed to address these issues.

We are collecting additional data to address whether tree density and territory size truly is related to habitat quality and nesting success. If this pattern is supported, young fledged on high quality territories may benefit by delaying dispersal and helping until a high quality territory becomes available for

breeding. This life history strategy may partially explain the maintenance of cooperative breeding in this pine specialist species, at least in fragmented urban populations. Future studies will also examine habitat size, habitat composition, reproductive success, and frequency of cooperative breeding groups of Brown-headed Nuthatches in more natural pine habitats. These data will allow a better understanding of the behavioral flexibility of Brown-headed Nuthatches to different ecological circumstances.

ACKNOWLEDGMENTS

We thank Karen Herb, Heather Podlipny, Valerie Shafer and Tamara Thompson for assistance in the field. The Arthur Temple College of Forestry at Stephen F. Austin State University provided access to the campus vegetation GIS database. Financial assistance was provided through a Faculty Research Grant to DBB from the Stephen F. Austin State University Research Council. Keith Arnold, Tim Brush, Dick Conner and Paul Hamel provided helpful comments on an earlier manuscript.

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Received 24 May 2000; accepted 15 July 2000