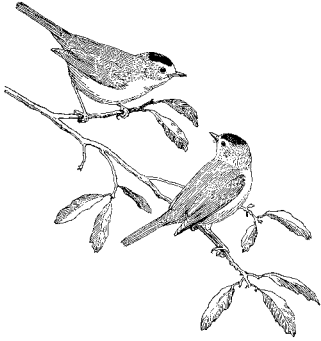




FRONTISPIECE. This is a reproduction of an original watercolor by George M. Sutton painted in 1952 as an illustration for the book, *Georgia Birds*, written by Thomas D. Burleigh and published by University of Oklahoma Press. The original paintings for the book were given in friendship to Herbert Stoddard and are part of the Stoddard Collection at Tall Timbers Research Station & Land Conservancy.

“When I made this painting, the nuthatches were not moving through the pine tops in noisy family groups, as they often do, but nesting quietly. This pair had a nest in a small hollowed-out cypress knee placed for them on a fence post. I looked a long while before finding exactly the right shortleaf pine branch for the picture. I wanted the branch, as well as the birds, to be interesting.”



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COOPERATIVE BREEDING IN THE BROWN-HEADED NUTHATCH

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ABSTRACT.—We monitored two color-marked populations of the Brown-headed Nuthatch (*Sitta pusilla*) for ≥ 5 years and collected data on survival, dispersal, territoriality, and cooperative breeding. Adults ($n = 284$) were sedentary, maintained long-term pair bonds, and had higher apparent annual survival (66–78%) than previously reported. Territories monitored ($n = 347$) contained up to five adults; the percentage of territories containing >2 adults averaged $\sim 20\%$ but varied widely. Most groups with >2 adults consisted of a breeding pair and a male helper related to at least one breeding adult ($n = 8$), but several exceptions were noted. The presence of helpers did not improve nest productivity. Apparent annual survival for females was lower than apparent survival for males in one population and may have influenced cooperative breeding. In the other population, apparent survival was similar between males and females. We suggest food resources and other environmental factors may have influenced cooperative breeding in this setting. Received 19 January 2006. Accepted 21 July 2006.

Cooperative breeding in the Brown-headed Nuthatch (*Sitta pusilla*) has received little attention since the behavior was first described by Norris (1958). Presumably non-breeding adult nuthatches spend large amounts of time assisting in nest construction, feeding nestlings, and defending territories (Norris 1958, Thompson 2000), but recent studies of cooperative breeding in this species are limited to two unpublished theses (Slater 1997, Thompson 2000) and a study based on 15 territories (Miller and Jones 1999).

The Brown-headed Nuthatch is a primary cavity-nesting species (McComb et al. 1986)

that inhabits open pine (*Pinus* spp.) forests in the southeastern United States and the Bahamas. Populations have declined steadily throughout much of the species' range (Sauer et al. 2005) as a result of habitat loss from human development and habitat degradation through fire suppression and logging (Withgott and Smith 1998). The species also has exhibited range contraction in some regions (e.g., South Florida and Missouri), and Withgott and Smith (1998) noted that nuthatches disappeared from some areas before the endangered Red-cockaded Woodpecker (*Picoides borealis*; U.S. Department of Interior 2003) disappeared from those same areas. Accordingly, the Brown-headed Nuthatch has been designated a species of management concern in several evaluations (Hunter et al. 1993, Carter et al. 1998, U.S. Department of Interior 2002), and the Bahamian subspecies

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(*S. p. insularis*; Bond 1931) is thought to be highly imperiled (Smith and Smith 1994, Hayes et al. 2004).

Characteristics of social breeding systems have been used to develop management programs for some cooperative breeders that have undergone population declines (Walters et al. 1992, Mumme and Below 1999). Information on cooperative breeding in the Brown-headed Nuthatch could have a similar role and also broaden our understanding of social breeding systems (Boland and Cockburn 2002); however, data regarding the extent and frequency of cooperative breeding, gender of auxiliary adults, territory establishment and maintenance, and adult and natal dispersal are generally lacking (Norris 1958, Withgott and Smith 1998).

The objectives of our study were to (1) quantify and compare demographic parameters, population densities, and characteristics of cooperative breeding between two populations of Brown-headed Nuthatch in Florida, (2) develop hypotheses for factors influencing cooperative breeding in this species, and (3) consider how our information regarding cooperative breeding and other life history traits may contribute to population conservation and management.

METHODS

Study Areas.—We studied nuthatches at Tall Timbers Research Station (TTRS; 30.66° N, 84.22° W) in north Florida (2001–present) and at two sites in south Florida (1998–2003): Big Cypress National Preserve (BCNP; 26.03° N, 81.20° W) and Everglades National Park (ENP; 25.37° N, 80.59° W). TTRS encompasses 1,630 ha and is dominated by upland pine habitats consisting primarily of loblolly (*Pinus taeda*) and shortleaf pines (*P. echinata*). Dominant trees are >100 years old, and prescribed burns are conducted from March to April at two-year return intervals. Historically, upland forests at TTRS were dominated by longleaf pine (*P. palustris*), but the original forests were cleared for agriculture many decades ago (Frost 1993). In south Florida, the BCNP site is associated with an old-growth slash pine (*P. elliotii* var. *densa*) forest surrounded by a cypress (*Taxodium* sp.) mosaic. ENP contained even-aged slash pines interspersed with hardwood forests and grassy

glades. Nuthatches disappeared from ENP in the early 1940s apparently as a result of extensive logging (Robertson and Kushlan 1984), and data collected here stemmed from a reintroduction program initiated in 1997. Most prescribed burns in BCNP and ENP were conducted during the early wet season (May–Jun) at 3 to 5-year return intervals.

Fieldwork and Data Analysis.—Area searches were initiated in February to locate territories and find nests. Nests were identified by worn or freshly exposed wood at cavity entrances, observing birds excavating cavities, or by finding completed nests with eggs or young. Nest locations were geographically referenced using hand-held global positioning systems. Dispersal distances, nest displacements, and territory densities were estimated using ArcView (ESRI 1998) and the straight-line distance between nest locations.

Nests were visited every 3–4 days to ascertain status and gather information on adults associated with nests. Nest height at TTRS generally was <3 m and nesting status was monitored using step ladders, flash lights, and dental mirrors. In south Florida, nest height averaged >10 m and status was monitored using behavioral observations (typically <30 min/visit). A breeding attempt was defined as the presence of eggs or behavioral cues indicating nesting was underway (used for tall nests).

Nestlings were banded 13–16 days after hatching at TTRS by removing the front of nesting cavities using a small saw. The cavity face was secured after banding using wood putty, staples, and masking tape. A single federal band was affixed to nestlings. All adults were color banded. The height of nests in South Florida precluded banding of young, and data on dispersal for second-year (SY) birds and nestlings stemmed exclusively from the TTRS population. We compared productivity between pairs and cooperative groups within populations using (1) the number of nestlings banded per nest (TTRS) and (2) the number of fledglings counted on at least two visits (south Florida) less than two weeks after young left the nest.

Most adults were captured using mist nets placed near nests, but a few individuals were lured into mist nets using recorded vocalizations of nuthatches or Eastern Screech-owl

TABLE 1. Data for color-marked populations of the Brown-headed Nuthatch in Florida.

Study area	North Florida	South Florida
Study length (years)	5	6
Territories monitored	152	195
Territories with helpers (%) ^a	22.7 ± 11.4	17.3 ± 16.1
Maximum group size	5	4
Territories with nests (%) ^a	85.2 ± 9.2	83.2 ± 22.4
Adults banded	148	136
Females	66	57
Males	62	57
Unknown	20	22
Nestlings banded	246	
SY ^b in natal territories	8	
SY ^b Dispersed	8	
Apparent annual survival ^c		
Females (%) ^a	66.1 ± 5.3	68.7 ± 13.1
Males (%) ^a	77.8 ± 4.7	69.3 ± 15.8

^a Mean ± SD.

^b Second Year (SY) individuals banded as nestlings and recaptured the next breeding season.

^c Estimates obtained from Program MARK (White and Burnham 1999).

(*Otus asio*). Gender was assigned based on the presence (female) or absence (male) of a brood patch on breeding birds, behavioral observations of color-banded birds (e.g., copulation), and presence of a cloacal protuberance (male; Norris 1958, Pyle 1997). Wing length was used to assign gender for some SY helpers captured at TTRS if other traits were equivocal. Wing length averaged 2.5 mm longer for males than females among individuals whose gender was assigned using other criteria (t -test = -9.657 , $P < 0.01$; all measurements by JAC). Wing length also appeared to vary with age, so gender of some SY birds was assigned only when observed in subsequent breeding seasons.

Adults were fitted with three plastic color bands and an aluminum federal band (two bands per leg; federal permits 22446 [JAC] and 22932 [GLS], state permit WB04060a). Plastic bands were sealed using acetone. Except where noted, results were based on color-banded individuals and banded nestlings recaptured as adults.

The size of breeding groups was estimated by observing the number of adults engaged in nesting activities (i.e., cavity excavation, nest building, or providing food for young or incubating females) on >2 occasions during the breeding season. Recorded nuthatch vocalizations played near nests were used to solicit territorial responses during some visits. Vo-

calizations, copulation, incubation, and dominance (Norris 1958) were used to categorize breeding status either as breeding adult or an auxiliary helper; however, individuals described as helpers may have been breeders (Richardson et al. 2001).

Apparent adult survival was estimated with Program MARK (White and Burnham 1999) using observations of color-banded adults during subsequent breeding seasons (Feb–Jul). Data for north and south Florida were analyzed separately because of differences in years of study and number of populations monitored. Global models that included variation in apparent survival and recapture probabilities based on gender, site (south Florida only), and year were considered initially. Nested models for north and south Florida were evaluated using information-theoretic methods (Anderson et al. 2000).

RESULTS

Group Size and Frequency; Gender and Influence of Helpers.—The largest breeding group contained 5 adults, but most (>70%) groups with >2 adults contained 3 adults. The frequency of territories with >2 adults ranged from 10 to 32% and appeared to be more variable in south Florida (CV = 0.93) than at TTRS (CV = 0.50; Table 1). Most helpers were SY males that assisted at the nest of at least one parent ($n = 8$), but we also found

males that assisted parents for at least 3 years ($n = 2$). A female helper (gender based on observations in later years) was recorded in south Florida and assisted with incubation.

The presence of helpers had no apparent effect on the number of young produced. In north Florida, we banded an average of 4.35 (SD = 1.11) nestlings in nests tended by >2 adults ($n = 34$) and 4.16 (SD = 1.45) nestlings in nests tended by pairs ($n = 117$; t -test = -0.534 ; $P = 0.541$). In south Florida, territories with helpers ($n = 17$) averaged 2.94 fledglings per successful nest (SD = 1.19), while territories consisting of pairs ($n = 139$) averaged 2.90 fledglings per successful nest (SD = 1.07; t -test = -0.147 ; $P = 0.883$). However, dead nestlings were found buried in some nests tended by pairs ($n = 5$) and suggested brood reduction occurred. Body mass differences among nest mates also frequently exceeded 1.5 g (~20% nestling mass in the later stages of development).

We observed six cases where adult males provided assistance at neighboring nests following the failure of their nests (i.e., facultative helping). Two males provided assistance at a neighboring nest 3–5 days after they lost their nests (and presumably their mates). The remaining four cases involved breeding males that assisted other nests in subsequent breeding seasons.

Variation in Apparent Survival and Nesting Attempts.—The most parsimonious model selected from Program MARK for south Florida included variation in apparent survival by site (BCNP vs. ENP) but held apparent survival and recapture probabilities ($P = 1.0$) constant by gender and year. The most parsimonious model for TTRS incorporated variation in apparent survival due to gender but held recapture probabilities ($P = 0.93$) and survival rates within gender constant among years. Apparent annual survival was >65% for both populations but appeared to be more variable in south Florida (CV > 0.15; Table 1). Males in north Florida had the highest apparent survival (Table 1), while females in north Florida had the lowest apparent survival (Table 1). We also observed new sources of adult mortality: five females tending nests at TTRS were killed either by red ratsnakes (*Elaphe guttata*) or small mammals.

Breeding attempts were observed in >80%

of the territories monitored each year with considerable variation among study sites and years (range = 33–100%). South Florida study sites exhibited greater variation in the proportion of active territories, and annual nesting attempts were <65% in some years (Table 1). In south Florida, group size was identified in 27 of 42 territories without breeding attempts. The majority of groups consisted of pairs ($n = 18$), followed by single birds (likely males; $n = 6$), and groups of three individuals ($n = 3$). In north Florida, territories without observed nesting attempts appeared to consist of single males ($n = 3$) or groups of males ($n = 2$ based on color-banded individuals) that either failed to attract mates or lost mates before eggs were laid.

The primary sources of nest failures at TTRS were depredation (24%) and cavities burned by prescribed fires (21%). In south Florida, most nest failures (37%) appeared to stem from nest depredation based on the cavity damage observed. We also recorded a new egg predator at two nests: broad-headed skink (*Eumeces laticeps*).

Pair-bond and Site Fidelity.—Pair bonds extending over several years were common, and approximately 50% of the territories consisted of individuals paired the previous year. Pair bonds became established at almost any time of the year. Two juveniles banded in the same area in July were paired as breeders the following breeding season. In contrast, a male that completed a cavity in mid-March did not attract a mate until mid-April. We also observed unpaired males ($n = 5$) excavating cavities and maintaining territories throughout the breeding season.

Breeding pairs frequently excavated their nests within 100 m of nests excavated the previous year. Some breeding groups ($n = 5$) excavated nesting cavities in the same snag for ≥ 2 years. Site fidelity also was evident when individuals remained in their territories following the apparent loss of parents ($n = 2$) or mates ($n = 7$). Most individuals that retained territories successfully attracted new mates in subsequent breeding seasons, but more complex scenarios also occurred. In one case, two male siblings that hatched a year apart (the older sibling was a helper when the younger sibling was a nestling) remained in their natal territory following disappearance of their par-

ents. These males attracted an unbanded female and initiated a nest in the territory held by their parents the following breeding season. Two years later, the younger sibling was observed assisting at a neighboring territory while the older sibling had disappeared.

Territory Proximity and Dispersal.—Nuthatch densities were higher in north Florida than in south Florida. The distances between nearest neighboring nests was significantly lower at TTRS (mean = 198.5 m, SD = 90.7) than in south Florida (mean = 394.9 m, SD = 242.8; t -test = 12.86, $P < 0.001$). Nearest neighbor distances at TTRS also generally were more consistent from year to year. Average distances at TTRS ranged from 199 to 216 m annually (CV = 0.04), while average distances in south Florida ranged from 370 to 550 m (CV = 0.169). Nearest neighbor distances suggest densities of 0.33 territories/ha at TTRS and 0.08 territories/ha in south Florida.

Most observed dispersal events spanned short distances. Seven SY males established territories or assisted at territories within 300 m of the territory held by their parents (i.e., generally the nearest neighboring nest to the natal territory). In two cases, the SY males were nest mates that each attracted unbanded females and initiated nesting attempts within 100 m of their natal nest. In a third case, two SY siblings were associated with a single female and initiated a nest within 300 m of their natal nest. In a fourth case, a SY male was captured assisting at a territory adjacent to his natal territory. The territory was held by a male banded the previous breeding season, while the father of the SY male was engaged in a nesting attempt <150 m away and assisted by a nest mate of the SY male at the neighboring nest. Two males also established territories next to territories of the breeding adults they assisted during a previous breeding season.

Four SY males were recaptured ≥ 2 territories from natal territories. Dispersal averaged 1,358 m for males dispersing ≥ 2 territories. The limited data primarily demonstrate that some males disperse and attempt to breed (successfully [$n = 2$]) in their first year, while others stay and help. Dispersal of older individuals (after their SY) ≥ 2 territories also occurred infrequently ($n = 3$). Two breeding fe-

males relocated 586 and 1,020 m, respectively, while a male associated with a four-adult breeding group in 2003 became a breeder in a territory 2,080 m away in 2004. There were no recaptures of SY females at TTRS.

DISCUSSION

The extent of cooperative breeding we observed (~20%) is similar to that reported in Georgia (Norris 1958), north Florida (Miller and Jones 1999), and Texas (Thompson 2000) and demonstrates cooperative breeding occurs consistently throughout the range of this species. Although the behavior is widespread, Ligon and Burt (2004) noted the potential benefits and constraints that favor the behavior have not been identified. Our data suggest potential direct benefits include acquisition of the territory of a parent or neighbor (Woolfenden and Fitzpatrick 1984, Walters 1990) as well as assistance provided by offspring that are helped (Hannon et al. 1985). Helpers also may benefit through other means that we did not assess, including extra-pair fertilizations, egg-dumping (Richardson et al. 2001), and increased survival or productivity.

Arnold and Owens (1998) reported high annual survival was an important factor favoring the expression of cooperative breeding in many avian lineages. Our estimate for annual survival for the Brown-headed Nuthatch (66–78%) is high for a small passerine (Martin 1995) and markedly higher than the estimate of 54% reported by Norris (1958). We also found gender-based differences in survival in north Florida and believe this influenced cooperative breeding. Skutch (1961) originally suggested a shortage of female nuthatches might constrain breeding opportunities for males (based on sex ratios reported in Norris 1958), and we found additional support for this hypothesis in the discovery ($n = 5$) of breeding females consumed by ratsnakes and small mammals in nesting cavities.

Lower survival among females may be related to the strong nest attentiveness exhibited during incubation and brooding coupled with the low height (<3 m) of cavities used at TTRS (and elsewhere; McNair 1984). Females rarely flushed when nests were inspected at TTRS, and we suspect this behavior reduced egg depredation (Dornak et al. 2004) by small lizards or nest usurpation by cavity

competitors (e.g., Carolina Chickadee, *Poecile carolinensis*). This behavior leads to higher predation risks for females (Martin and Li 1992), especially later during the breeding season when warmer ambient temperatures lead to increased snake activity (Neal et al. 1993, Weatherhead and Blouin-Demers 2004).

In contrast, the absence of gender-based survival differences in south Florida suggests factors such as food resources (Koenig and Stacey 1990) or habitat features (Walters 1990) may constrain breeding opportunities in this region. This hypothesis is consistent with our data suggesting that habitat quality is lower in south Florida (e.g., lower territory densities, greater variation in annual breeding effort, and greater variation in adult survival; Table 1). Nest productivity also appeared to be lower in south Florida than at TTRS and elsewhere (Morris 1982, Miller and Jones 1999, Thompson 2000). McNair (1984) also noted reduced clutch sizes for nuthatches in south Florida and suggested the reductions stemmed from environmental factors.

Nuthatches in south Florida select nest territories with a greater proportion of large pines (Slater 1997), and the density and diversity of large pine trees might affect food resources and habitat quality (Koenig and Haydock 1999). Large pines produce proportionally more seeds than smaller pines (W. J. Platt, pers. comm.), and nuthatches cache and rely heavily upon pine seeds during the winter (Yaukey 1995). We did not measure pine seed production, but we suspect it is more variable in south Florida where only one species of pine occurs (slash pine). TTRS supports four species, including two consistent seed-producers (loblolly and short-leaf pines; Cain and Shelton 2001). Large pines also have greater surface area, providing more foraging space.

Helpers appeared to be closely related to breeders, and alloparental care may include indirect benefits (Brown 1978). Even for situations where individuals provided assistance at neighboring nests, the short dispersal distances we recorded suggested neighbors often were closely related. Three adjacent territories monitored in 2004 consisted of (1) a father, (2) a son born in 2002, and (3) a son born in 2003. In addition, the father was assisted in 2004 by a male offspring born in 2003. We observed six other cases where adjacent ter-

ritories were held by siblings or parent-offspring combinations. Helpers also may lighten feeding responsibilities for females and enable them to initiate second clutches (Thompson 2000). Helpers also may serve as sentinels (McGowan and Woolfenden 1989) and decrease female (and in most cases maternal) susceptibility to predators.

Cooperative breeding in the Brown-headed Nuthatch is similar to Pygmy Nuthatch (*S. pygmae*) behavior and suggests this trait was present in a shared ancestor (Ligon and Burt 2004). Helping behavior is observed in about 15–30% of the annual territories of both species (Norris 1958, Miller and Jones 1999, Kingery and Ghalambor 2001) and less frequently reaches frequencies as high as 40% (Slater 1997, Miller and Jones 1999, Kingery and Ghalambor 2001). Facultative helping occurs infrequently (Sydeman 1991) and, while breeding groups may include up to five adults, they more typically contain either two or three adults (Sydeman et al. 1988). Cooperative behavior in the Pygmy Nuthatch has been linked both to skewed sex ratios (Norris 1958, Skutch 1961) and environmental features (Sydeman et al. 1988).

The life-history characteristics we documented in association with cooperative breeding suggest that management of small, isolated populations of Brown-headed Nuthatches deserves special attention. This species is relatively sedentary and appears to disperse short distances. Accordingly, it is unlikely to re-colonize isolated areas should populations disappear (Walters et al. 2004). This phenomenon has already occurred in south Florida (Robertson and Kushlan 1984) and other areas where the species' range has contracted. Management should focus on retention of mature, seed-bearing pine trees, particularly in situations where pine basal area is low and only 1–2 species of pines exist. Retaining sufficient snag resources also should alleviate competition for nesting sites (McComb et al. 1986) and reduce nest depredation (Li and Martin 1991). Timing of prescribed burns also deserves attention where small, isolated populations exist. Frequent prescribed burning is essential for maintaining suitable habitat conditions (Engstrom et al. 1984), but burns conducted during the nesting season destroy nests

and shift re-nesting to periods with warmer ambient temperatures.

Our study suggests that cooperative breeding in the Brown-headed Nuthatch is a fluid behavior that should be amenable to experimental manipulation. For example, female survival in north Florida may be improved by protecting nesting cavities from predators (e.g., Withgott et al. 1995). This treatment should lead to fewer breeding groups consisting of >2 adults (unless the habitat becomes saturated). Supplemental food (e.g., Egan and Brittingham 1994, Yaukey 1995) could be provided in south Florida to learn if group size increases in territories with better food resources (Koenig and Stacey 1990).

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