TAXONOMY AND POPULATION SIZE OF THE BAHAMA NUTHATCH

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EXECUTIVE SUMMARY

The Caribbean pine (*Pinus caribea*) forests of Grand Bahama support a rich assemblage of birds, including several endemic species and subspecies. One of the most enigmatic is the Brown-headed Nuthatch (*Sitta pusilla*), which, unlike any of the other avian inhabitants of the pine forests, is found only on Grand Bahama and is absent from the pine forests on the neighboring islands of Andros and Abaco. The form that inhabits Grand Bahama was originally described as a subspecies (*S. p. insularis*) by pioneering ornithologist James Bond (Bond 1931, *Proc. Acad. Nat. Sci. Philadelphia* 83: 389), on the basis of morphological measurements obtained from two individuals. Subsequent studies have both challenged this distinction and sought to amplify it: Smith and Smith (1994, *Bahamas Journal of Science* 1:22-26) suggested that additional specimens revealed that Bond's analysis overestimated the degree of difference between *insularis* and the nominate subspecies (*S. p. pusilla*) from the United States, whereas Hayes et al. (2004, *Bahamas Journal of Science* 12:21-28) presented new morphological data and argued that *insularis* should be considered a distinct species. As the taxonomy of the Brown-headed Nuthatch was argued, its numbers on Grand Bahama appeared to plummet. Common as recently as the late 1960s (Emlen 1977, *Ornithological Monographs* 24:1-129), surveys in 1993 and 2004 yielded only a handful of individuals in a single tract of forest (Smith and Smith 1994, Hayes et al. 2004). The best available evidence therefore suggested that Brown-headed Nuthatches on Grand Bahama were in a perilous situation and at risk of extinction, but precise estimates of population size were lacking. At the same time, due to taxonomic uncertainties, it remained unclear what the loss of nuthatches from Grand Bahama would represent. Were they simply a peripheral population of a common North American species or, as others argued, a distinct species, new to science?

In this report, we present the results of research aimed at resolving the taxonomy of Brown-headed Nuthatches on Grand Bahama and estimating the distribution and size of the remaining population. Using two genetic markers from mitochondrial DNA (mtDNA), we estimated that the average level of sequence divergence between individuals collected on Grand Bahama and in the United States was 1.37%. This level of divergence, although somewhat less than is typically seen between sister species, suggests that *insularis* and the nominate subspecies diverged from a common ancestor approximately 685,000 years ago. Given the geologic history of the northern Bahamas, including at least two periods in the last 100,000 years during which the pine islands were completely inundated by rising sea level, *insularis* almost certainly colonized Grand Bahama after it had begun diverging from the common ancestor that it shared with *S. p. pusilla*. This novel finding challenges conventional wisdom about the evolution of Grand Bahama's pineland avifauna. Furthermore, our results show clearly that Brown-headed Nuthatches on Grand Bahama are a genetically distinct evolutionary lineage and, at the very least, constitute a unique subspecies. As with previous studies, we also found that Brown-headed Nuthatches have become exceedingly rare and localized on Grand Bahama. We detected only two individuals during line-transect surveys of the entire island, although we found 21 additional individuals (14 adults and 7 juveniles) using *ad hoc* survey methods that involved broadcasting recorded vocalizations of Brown-headed Nuthatches. Because we had to rely on an *ad hoc* approach, we were unable to generate rigorous estimates of population size. However, our results were comparable to the findings of previous surveys that estimated less than 2,000 individuals remained. All of the individuals detected were found in Lucaya Estates (the same was true of the surveys reported by Hayes et al. 2004), a subdivision in the center of the island that has yet to be built-out. Because it appears to support the only remaining population of *insularis*, this area is vital to the persistence of this unique piece of the Bahamas natural heritage. Residential development of Lucaya Estates will almost certainly lead to the extinction of *insularis*. Thus, we recommend the protection of these pine forests as the first and most important step in the development of a more comprehensive strategy for the conservation of Brown-headed Nuthatches on Grand Bahama.

CHAPTER 1: GENETIC ANALYSIS

Mitochondrial DNA diversity in the Brown-headed Nuthatch of the southeastern United States (*Sitta pusilla*) and on Grand Bahama, Bahamas (*Sitta pusilla insularis*): effects of climate, geology and sea-level changes on genetic variation

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"A genetically distinct evolutionary lineage": Grand Bahama is home to a unique subspecies of Brown-headed Nuthatch (*Sitta pusilla insularis*), which new data show may have split from its more common American cousin 685,000 years ago. This individual was captured in 2007, along with its mate, at a nest on the island.

Introduction

Molecular genetic studies have revealed the presence of numerous cryptic species that exhibit substantial genetic divergence from related species without corresponding morphological differentiation (Zink 2004). The decoupling of genetic and morphological evolution poses a significant problem for biodiversity conservation: if ecologically or evolutionarily significant variation cannot be recognized, it cannot be conserved. The challenges of protecting cryptic species are compounded because not only are they difficult to recognize but, once recognized, the basic ecological information necessary for developing conservation plans is rarely available.

The Brown-headed Nuthatch (*Sitta pusilla*) on Grand Bahama, Bahamas, provides an outstanding example of the challenges of conserving cryptic sources of biodiversity. Brown-headed Nuthatches on Grand Bahama long have been considered a subspecies (*S. p. insularis*) of the nominate form (*S. p. pusilla*) found in the United States (Bond 1931), but a recent morphometric and behavioral study suggests that full species status is warranted (Hayes et al. 2004). If *S. p. insularis* is indeed a distinct species, it is one of the most threatened bird species in the world. Once fairly common (Emlen 1977), *S. p. insularis* is now perilously close to extinction (Hayes et al. 2004, Smith and Smith 1994, Chapter 2 of this report), likely a consequence of its close association with Caribbean pine (*Pinus caribaea*) forests, which were heavily logged on Grand Bahama Island, and remain one of the most critically threatened and least protected habitats in the Caribbean. Ongoing threats to this habitat include renewed timber harvest, increased residential development, and more frequent and intense hurricanes. Given the rapidity of their decline over the past several decades, Brown-headed Nuthatches are almost certain to disappear from Grand Bahama Island absent a vigorous conservation effort and with them will vanish a unique piece of biological diversity and evolutionary potential. Yet, largely because ornithologists and conservationists have assumed that *S. p. insularis* is no different from the common and widely distributed mainland form, they are virtually unstudied on Grand Bahama Island.

The degree to which Brown-headed Nuthatches on Grand Bahama Island have diverged from mainland populations has yet to be addressed in a rigorous fashion. Particularly lacking are genetic analyses that examine molecular variation. To this end, we examined two genetic markers from mitochondrial DNA (mtDNA) collected from individuals in mainland populations (North Carolina, Georgia, Alabama, Florida, Louisiana and Texas) and from Grand Bahama. Genes from the mitochondrion should show initial evidence of population structure and geographic differentiation because the haploid nature and maternal inheritance of the genome reduces effective population size to a greater degree than nuclear DNA (Birkey et al. 1983, Moore 1995). In addition to resolving the question of degree of genetic isolation of island nuthatches from mainland populations, biogeographic analysis of genetic diversity could shed light on the geographic origin of the Brown-headed Nuthatch and its dispersal from mainland to island habitat.

Materials and Methods

Data collection. We analyzed DNA sequences from 33 Brown-headed Nuthatches throughout the species range (Table 1). At least three individuals were sampled from each location. Southern Florida samples were provided as blood in buffer by G. L. Slater and were collected between January 1997 and April 1998. Northern Florida samples were provided as extracted whole DNA by Rebecca Kimball and Sarah Haas (University of Florida); collection dates were not given for these samples. Texas samples were provided as blood in buffer by Brent Burt (Stephen F. Austin State University) and were collected between January and August 2007. Louisiana samples were downloaded directly from GenBank. The remaining mainland samples were collected as whole birds by T. Benson (Alabama and Georgia) or G. L. Slater (North Carolina) between June and September 2008. These birds were prepared as study skins and are deposited in the San Bernardino County Museum (Redlands, CA). Samples from Grand Bahama were provided as blood in buffer and were collected by G. L. Slater and

T. Benson in April 2007. Three Pygmy Nuthatch (*Sitta pygmaea*) samples, each representing different haplotypes, were downloaded directly from GenBank and included for outgroup analysis.

Total DNA was extracted in one of three methods: 1) using standard phenol-chloroform-isoamyl extractions, followed by precipitation with sodium acetate and ethanol, 2) using Qiagen DNA extraction kits (Qiagen, Inc.), or 3) using the Quickgene-810 nucleic acid isolation system (FujiFilm). A 958 bp sequence of mitochondrial DNA, composed of 2 non-contiguous fragments, was amplified and sequenced for all samples. This sequence consisted of a 447-bp fragment from NADH dehydrogenase 6 (ND6), and a 511-bp fragment from the control region (D-loop). We chose these 2 fragments based on extensive analysis of variable regions in Pygmy Nuthatch. Primers used for PCR amplification are described in Table 2. PCR reactions were carried out using Eppendorf MasterTaq Kit (Brinkmann Instruments, Inc.) in 50 µL volumes: 5.0 µL template DNA (approximately 0.2 µg/mL; the template volume would vary accordingly to reach this concentration), 1.0 µL each primer (5.0 mM), 0.5 µL polymerase, 5.0 µL dNTPs, 5.0 µL buffer, and 10.0 µL TaqMaster. The profile for ND6 PCR reactions was: initial denaturation at 94ºC for 2 minutes; 35 cycles of denaturation at 94ºC for 50 seconds, annealing at 50ºC for 1 minute, and extension at 72ºC for 2 minutes; and final extension at 72ºC for 2 minutes. The profile for D-loop PCR reactions was: initial denaturation at 94ºC for 2 minutes; 35 cycles of denaturation at 94ºC for 50 seconds, annealing at 55ºC for 1 minute, and extension at 72ºC for 1.5 minutes; and final extension at 72ºC for 2 minutes. PCR products were purified using ExoSAP-IT (USB Corporation). Cycle sequencing reactions were performed using Sequitherm EXCEL II DNA Sequencing Kit-LC (Epicentre) in 20 µL volumes: 1.0 µL purified PCR product (this amount would be adjusted depending on the quality and yield of the PCR amplification), 1.0 µL each standard M13 forward (ND6 and D-loop) and reverse primers or LCR4 (5'-ttcgggtatgtggttctgca-3') and M13 reverse primers (D-loop), 7.2 µL buffer, 1.0 µL polymerase, and 8.8 µL distilled water. Cycle sequencing products were sequenced on a LI-COR 4300 automated

sequencer. Double-stranded sequences were constructed with AlignIR version 2.0 software (LI-COR, Inc.) and aligned in ClustalX (Larkin et al. 2007).

Sequence analysis. Prior to analysis the reverse complement of the ND6 sequence was obtained using MacClade 4.01 (Maddison and Maddison 2000) to analyze the protein-coding strand in both the separate and concatenated analyses. A partition homogeneity test was conducted in Paup* 4.10b (Swofford 2003) to determine if the two mitochondrial gene fragments could be combined into a single sequence for analysis. Genetic variation for each locus (ND6, D-loop, and the concatenated sequences) is described using basic descriptive statistics including nucleotide frequency, number of haplotypes, number of polymorphic sites, number and type of substitutions, number of transitions (Ti) and transversions (Tv), Ti/Tv ratio, and genetic distances among haplotypes. Descriptive statistics were calculated using Arlequin (Schneider et al. 2000) or were done by hand.

Phylogenetics and population genetics. Evolutionary relationships among haplotypes and phylogenetic inferences were estimated using Bayesian maximum likelihood analyses. Analyses were implemented using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001) for ND6, Dloop and the concatenated sequence. The amino acid coding sequence was partitioned by 1st, 2nd, and 3rd position for ND6 (1-447), and as non-coding for the control region (448-958). Four chains were run for 30 million generations sampling every 1000th generation with a burn-in of 3000 sampled generations. We used the HKY+G (Hasegawa et al. 1985) nucleotide substitution model of evolution as recommended by Modeltest (Posada and Crandall 1998), with a gamma distribution for rate heterogeneity across the partitions.

Patterns of historical gene flow across the range of the species were also inferred using Minimum Spanning Trees generated with TCS 1.21 (Clement et al. 2000) for ND6, D-loop and the concatenated sequence.

Fu's F_S, nucleotide diversity (Π), and percentage of variable sites were calculated as measures of intrapopulation variability in Arlequin 2.0 (Schneider et al. 2000). Fu's F_S can be used to detect

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population expansion (Sgariglia and Burns 2003). To further examine population expansion, we examined the mismatch distribution of haplotypes for non-significance using Harpending's raggedness index as implemented in Arlequin 2.0 (Schneider et al. 2000).

Results

Sequence analysis. We obtained ND6 sequence for 32 of the 33 Brown-headed Nuthatch samples; we were unable to amplify this locus in one of the three samples from Grand Bahama. Among the 32 samples we found 15 haplotypes: seven mainland haplotypes were represented once, one haplotype was represented twice, three haplotypes were found thrice, one was represented four times, and one haplotype was found eight times. The 2 Bahamian samples each represented a unique haplotype. Base frequencies for the ND6 sequence were A=0.125, T=0.389, C=0.094, and G=0.391. There were 19 polymorphic sites (all transitions): sixteen 3rd-position substitutions were synonymous, while one 2nd and two 1st-postion substitutions were non-synonymous. The average uncorrected pairwise distance among all Brown-headed Nuthatch haplotypes was 0.66%, and the average uncorrected pairwise distance among mainland Brown-headed Nuthatch haplotypes was 0.53%.

We obtained D-loop sequence for 31 of the 33 Brown-headed Nuthatch samples; 2 of the Louisiana samples obtained from GenBank were partial sequences and were discarded from the analysis. Among the 31 samples we found 11 haplotypes: one mainland haplotype was represented by 21 individuals and seven haplotypes were represented by single individuals. The 3 Bahamian samples each represented a unique haplotype. Base frequencies for the concatenated sequence were A=0.278, T=0.274, C=0.287, and G=0.161. There were 13 polymorphic sites including 10 transitions and 3 transversions. The average uncorrected pairwise distance among all Brown-headed Nuthatch haplotypes was 0.29%, and the average uncorrected pairwise distance among mainland Brown-headed Nuthatch haplotypes was 0.11%.

We obtained concatenated sequence for 30 of the 33 Brown-headed Nuthatch samples; one

Bahamas sample and 2 Louisiana samples were excluded from the analysis for reasons noted above.

Among the 30 samples we found 20 haplotypes: twelve mainland haplotypes were represented once,

three haplotypes were represented twice, two haplotypes were found thrice, and one was represented

four times. The 2 Bahamian samples each represented a unique haplotype. Base frequencies for the

concatenated sequence were A=0.207, T=0.328, C=0.197, and G=0.268. There were 32 polymorphic

sites (described above). The average uncorrected pairwise distance among all Brown-headed Nuthatch

haplotypes was 0.45%, and the average uncorrected pairwise distance among mainland Brown-headed

Nuthatch haplotypes was 0.32%. Nucleotide diversity was 0.003 among mainland birds and 0.004

among the two Bahamian samples.

Phylogenetics and population structure. Bayesian analysis of the ND6, D-loop, and

concatenated sequences each produced unrooted consensus trees with similar topologies (Figs. 1-4).

Bayesian analysis of the concatenated sequences using Pygmy Nuthatch to root the phylogeny (100%

posterior probability) produced a phylogram (Fig. 1) congruent with the unrooted Brown-headed

Nuthatch phylograms (Figs. 2-4) with the root being placed in a large basal polytomy of all Brown-

headed Nuthatch haplotypes. Within this basal polytomy there are six individual haplotypes and four

more derived groupings. Among these more derived groupings, only one grouping (the 2 Bahamas

haplotypes) shows strong geographic specificity and monophyly (100% posterior probability), and the

remaining groupings each contain haplotypes that are widely distributed across the mainland (posterior

probabilities ranging from 67-73%). The unrooted phylogram of the concatenated sequences (Fig. 2)

recapitulates the structure of the rooted cladogram showing strong geographic structure (100%

posterior probability) of the Bahamas haplotypes but not among mainland haplotypes. The unrooted

ND6 phylogram (Fig. 3) shows an expected reduction in haplotype diversity but maintains a similar

topology to the unrooted concatenated phylogram, namely a lack of geographic structure among

mainland haplotypes and strongly supported (100% posterior probability) grouping of the 2 Bahamas

haplotypes. The unrooted D-loop phylogram (Fig. 4) is characterized by a further reduction in haplotypes diversity and structure, with 7 of the 8 mainland haplotypes collapsing into a star polytomy and the 3 Bahamas haplotypes forming a well-separated and strongly supported (100% posterior probability) grouping.

Minimum spanning trees were created for ND6, D-loop, and the concatenated sequences (Figs. 5-7). As with the phylogenetic trees, all three trees showed similar topologies with decreasing haplotype diversity and structure in the concatenated, ND6, and D-loop trees, respectively. The primary difference among the minimum spanning trees is the absolute number of mutational steps among haplotypes. In the concatenated MST (Fig. 5), the nearest Bahamas and mainland haplotypes are separated by 9 unsampled mutational steps. Mutational steps among mainland haplotypes range from 1 to 7, with only 4 unsampled haplotypes and no more than 2 unsampled haplotypes between nearest neighbors. The ND6 (Fig. 6) and D-loop (Fig. 7) MSTs show 4 and 3 unsampled mutational steps between the closest Bahamas and mainland haplotypes, respectively. Mutational steps among mainland haplotypes range from 1 to 7 in the ND6 MST with 2 unsampled haplotypes, and range from 1 to 3 in the D-loop MST with only 1 unsampled haplotype.

We obtained values of Fu's F_S and Harpending's raggedness index to test for population expansion within the mainland population. The values of Fu's F_S were calculated by Arlequin as -5.76 (P = 0.001), -6.87 (P < 0.001), and −12.31 (P < 0.001) for ND6, D-loop, and the concatenated sequence, respectively. The value for the raggedness index (0.036) was not significant.

Discussion

The Grand Bahama Brown-headed Nuthatch (*S. p. insularis*) showed significant geographic differentiation and long-term isolation from the nominate *S. p. pusilla* found in the United States. Our phylogenetic analyses revealed significant and relatively long-term genetic differentiation of

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haplotypes between the Bahamas and populations sampled in the United States. In strong contrast, there was no apparent geographic structure of haplotypes among United States populations. This lack of mainland geographic structure in the phylogenetic analyses, combined with the relatively low haplotype diversity, the lack of missing mainland haplotypes in the MST, and population-genetic analyses indicated that mainland populations of Brown-headed Nuthatch have recently and rapidly expanded from a single source population.

Sequence analysis. Analysis of both the D-loop and ND6 sequences revealed low levels of genetic variation within mainland populations and across all Brown-headed Nuthatches sampled. The levels of genetic variation, as well as the nucleotide composition and substitution data, were consistent with other passerines at the intraspecific level, including other nuthatches and West Indian endemics (Spellman and Klicka 2006, Spellman and Klicka 2007, Lovette et al. 1998, Baker and Marshall 1997). The high proportion of 3rd-position, synonymous substitutions within the coding region (ND6) is also consistent with recently diverged birds (Moore and DeFilippis 1997). However, there were two informative non-synonymous mutations between Grand Bahama and mainland populations, whereas there is only a single non-informative amino acid substitution across the entire mainland group, further supporting a long-term isolation of the Grand Bahama population of nuthatches from populations in the United States.

Phylogenetics and population genetics. The highly negatively significant Fu's F_S and the non-significant estimate of raggedness suggest that the lack of geographic structure was due to the recent expansion of the mainland population as a whole (Slatkin and Hudson, 1991, Rodgers and Harpending, 1992). This is congruent with a pattern of population expansion from glacial refugia during approximately the last 20,000 years. Although the Brown-headed Nuthatch is a sedentary species, the geographic signature from both population and phylogenetic analyses showed a lack of lineage sorting among populations ranging from southern Florida, north to North Carolina, and west to Texas. There was strong to moderate support for some clade structure in the phylogenetic analyses of D-loop, ND6

and the two genes combined. The most striking characteristic of these trees was that all clades were organized around haplotypes lacking geographic association, except for the strongly supported clade of haplotypes from Grand Bahama. Another finding was that most of the haplotypes in each analysis were associated with unresolved polytomies and star-shaped haplotypic relationships characteristic of recent expansions from a bottlenecked population (Avise 2000). In addition, there were no haplotypes or geographic regions that can be considered as ancestral in the Bayesian maximum likelihood reconstruction. The root of the tree, in the concatenated phylogenetic analysis, is within a large basal polytomy consisting of individuals, haplotypes, and clades from all sampling locations, except for the single Louisiana haplotype which is in the most derived (but still geographically unstructured) clade.

The MST analyses of the two loci and the concatenated sequences recapitulated the lack of geographic structure and the rapid mainland expansion from the phylogenetic analysis, and further highlighted the long-term isolation of the birds on Grand Bahama. The MST of the D-loop haplotypes is dominated by a star-shaped cluster of haplotypes, centered on a single geographically widespread haplotype. This star-like cluster of mainland haplotypes is characterized by one missing haplotype, whereas there are three unsampled haplotypes to the nearest Bahamian haplotype. There was only a single missing haplotype among island samples. This could be due to either incomplete sampling, which is likely with three individuals sampled and three haplotypes found, or loss of that haplotype from the island. It is far less likely that sampling error produced the missing haplotypes between the mainland and the island, as will be explained below.

There was more variation among ND6 haplotypes due primarily to the higher substitution rate at third positions. Consequently, there were 13 mainland haplotypes, with a somewhat more complicated relationship. The salient features of the ND6 MST were similar to the D-loop MST: a few central widespread haplotypes with a star-like structure, no more than one missing haplotype between any two mainland haplotypes, and five mutational steps to the nearest Bahamian haplotype with four of those steps represented as missing haplotypes in the tree. The concatenated MST is similar in form,

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although there was more complexity to the MST among mainland haplotypes: there were nine missing mutational steps between the nearest mainland and the island haplotypes.

Biogeographic analysis of S. p. insularis. The phylogenetic and population genetic analyses of Bahamian Brown-headed Nuthatches showed the island haplotypes are both unique within the species and well-separated from haplotypes of mainland birds. These results suggest two hypotheses concerning the origin of Brown-headed Nuthatches on Grand Bahama Island: 1) a common ancestral haplotype dispersed to Grand Bahama Island from the mainland during a single colonization event, and the current island haplotypes evolved on Grand Bahama Island with intermediate haplotypes (on the island and/or the mainland) lost to genetic drift (e.g., a population bottleneck), or 2) a common ancestral haplotype dispersed to an intermediate location(s), haplotypes evolved at these intermediate locations and then colonized Grand Bahama Island, followed by intermediate locations (and haplotypes) lost to a stochastic event(s). We believe that second hypothesis more likely reflects the true evolutionary history of the Brown-headed Nuthatch on Grand Bahama.

Mainland and island haplotypes were separated by 1.37% mean sequence divergence. Based on an estimated molecular clock of approximately 2% sequence divergence per million years (Shields and Wilson 1987, Fleischer et al. 1998, Lovette et al. 1998), mainland and island haplotypes diverged from a common ancestor about 685,000 years ago. During the late Pleistocene Grand Bahama underwent dramatic climatic and ecological changes (Pregill and Olson, 1981, Hearty and Neuman 2001, Olson and Hearty 2003). The general pattern of climatic change during this time has been the expansion of island area as sea level drops during glacial periods and the reduction of island area as sea level rises during interglacial periods (Pregill and Olson 1981, Hearty and Neuman 2001). Geologic evidence indicates that Grand Bahama has been inundated numerous times during the late Pleistocene, including two recent inundations approximately 7,500 and 125,000 years ago (Digerfeldt and Henry 1986, Hearty and Kaufman 2000, Hearty and Neuman 2001). These inundations, and the subsequent uninhabitability of the island, make it unlikely that a population of Brown-headed Nuthatches has continuously

occupied Grand Bahama following a single colonization event by a common ancestral haplotype. Furthermore, the distribution of genetic variation among mainland and island haplotypes does not support repetitive or recent colonization of Grand Bahama Island from mainland populations.

The second hypothesis requires that the ancestor to *S. p. insularis* initially dispersed from the mainland to other locations before colonizing Grand Bahama. This scenario is consistent with the inferred evolutionary histories of several birds and other vertebrates in the West Indies (Pregill and Olson 1981, Lovette et al. 1998), and Emlen (1977) discussed three avian species which subspeciated on Greater Antillean islands before dispersing north to the Bahamas. That levels of genetic diversity in the island population were comparable to the mainland suggested only a recent reduction in population size. This is consistent with geological evidence that suggests that during and before the most recent glacial period (approximately 20,000 - 60,000 years ago) the sea level was much lower, with the Bahamas (including Grand Bahama) and other Antillean islands coalescing into fewer larger islands (Pregill and Olson 1981, Hearty and Kaufmann 2000). These "super-islands" could have provided more extensive habitat for a much larger Brown-headed Nuthatch population on the Bahamas (or on more extensive Antillean Islands to the south), allowing for the maintenance of greater genetic diversity. Sea levels have risen during the current interglacial period, islands and available habitat has been reduced, yet we still see levels of genetic diversity of Brown-headed Nuthatch on the Grand Bahama comparable to the mainland levels, suggesting that the loss of habitat, and a corresponding drop in population size, have been relatively recent. The low numbers of existing individuals (see Chapter 2) still maintain a level of mitochondrial genetic variation comparable to other passerines (Spellman and Klicka 2006, Spellman and Klicka 2007, Lovette et al. 1998, Baker and Marshall 1997). These historical climatic and ecological changes in and around the Bahamas favor an indirect colonization pathway to Grand Bahama from the mainland rather than a single, recent colonization from the mainland as hypothesized by Emlen (1977).

Conclusions

The population of Brown-headed Nuthatches (*S. p. insularis*) on Grand Bahama comprises a genetically distinct evolutionary lineage within this species. While geological evidence suggests that Grand Bahama has been colonized only recently, mainland and island haplotypes diverged from a common ancestor several hundred thousand years ago with much of the genetic diversity separating these two populations lost to stochastic events and genetic drift. Due to the unique mitochondrial genetic makeup of *S. p. insularis* and its long-term isolation from the mainland, we recommend that *S. p. insularis* be considered a distinct taxon. We also advocate that *S. p. insularis* be given priority for further research, particularly with regard to its specific status (e.g., through more extensive sampling and analysis of nuclear genetic markers). Furthermore, due to the extremely small size of the Grand Bahama population, genetic drift and the probability of stochastic events (e.g., population bottlenecks due to hurricanes) will continue to reduce genetic diversity in the Brown-headed Nuthatch population on Grand Bahama Island. Therefore, we urge that *S. p. insularis* be given immediate conservation priority.

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Table 1. Collection locations for *Sitta pusilla* specimens used in the genetic analyses.

Study ID#	Location	Other ID[1]
Spus101	FL	FWS band 99028
Spus102	FL	
Spus103	FL	
Spus104	FL	
Spus105	FL	
Spus106	Bahamas, Grand Bahama I.	
Spus107	Bahamas, Grand Bahama I.	
Spus108	Bahamas, Grand Bahama I.	
Spus109	GA, Putnam Co., Oconee National Forest	SBCM 60057
Spus110	GA, Greene Co., Oconee National Forest	SBCM 60058
Spus111	GA, Greene Co., Oconee National Forest	SBCM 60059
Spus112	GA, Putnam Co., Oconee National Forest	SBCM 60060
Spus113	GA, Putnam Co., Oconee National Forest	SBCM 60061
Spus114	AL, Butler Co., Greenville	SBCM 60062
Spus115	AL, Butler Co., Greenville	SBCM 60063
Spus116	AL, Butler Co., Greenville	SBCM 60064
Spus117	AL, Butler Co., Greenville	SBCM 60065
Spus118	AL, Butler Co., Greenville	SBCM 60066
Spus119	TX, Nacogdoches Co., Nacogdoches	SFA 94639
Spus120	TX, Nacogdoches Co., Nacogdoches	SFA 94640
Spus121	TX, Nacogdoches Co., Nacogdoches	SFA 94641
Spus122	FL, Leon Co., Tallahassee	TTRS 32450
Spus123	FL, Leon Co., Tallahassee	TTRS 59568
Spus124	FL, Leon Co., Tallahassee	TTRS 03081
Spus125	FL, Leon Co., Tallahassee	TTRS 03100
Spus126	FL, Leon Co., Tallahassee	TTRS 59590
Spus127	NC, Moore Co., Weymouth Woods	SBCM
Spus128	NC, Harnett Co., TNC Long Valley Farm	SBCM
Spus129	NC, Harnett Co., TNC Long Valley Farm	SBCM
Spus130	NC, Harnett Co., TNC Long Valley Farm	SBCM
Spus131	LA, St. Tammany Parish	DQ154007
Spus132	LA, St. Tammany Parish	DQ153994
Spus133	LA, St. Tammany Parish	DQ153995
S. pygmaea	CA	DQ194980
S. pygmaea	CA	DQ194302
S. pygmaea	CA	DQ194298

[1] Abbreviations used in this table: FWS – United State Fish and Wildlife Service, SBCM – San Bernardino County Museum, SFA – Stephen F. Austin State University, TTRS – Tall Timbers Research Station (University of Florida), TNC – The Nature Conservancy.

Table 2. Primer sequences used in the genetic analyses.

Primer	Sequence	Gene amplified	Strand	Source
LPRO[1]	ggaatttttattaaactact	ND6	Light	This study
HGLU[1]	ggagagaggccaggtggga	ND6	Heavy	Benson thesis
LGLU[1]	attcccaacctggcctctctcc	Partial D-loop	Light	Benson thesis
LCR4	ttcgggtatgtggttctgca	Partial D-loop	Light	This study
HCR4[1]	ccatccccaagcaaatgtat	Partial D-loop	Heavy	This study

[1]Light and heavy strand primers were prepended with standard M13 forward and reverse primer sequences, respectively, to facilitate sequencing reactions.
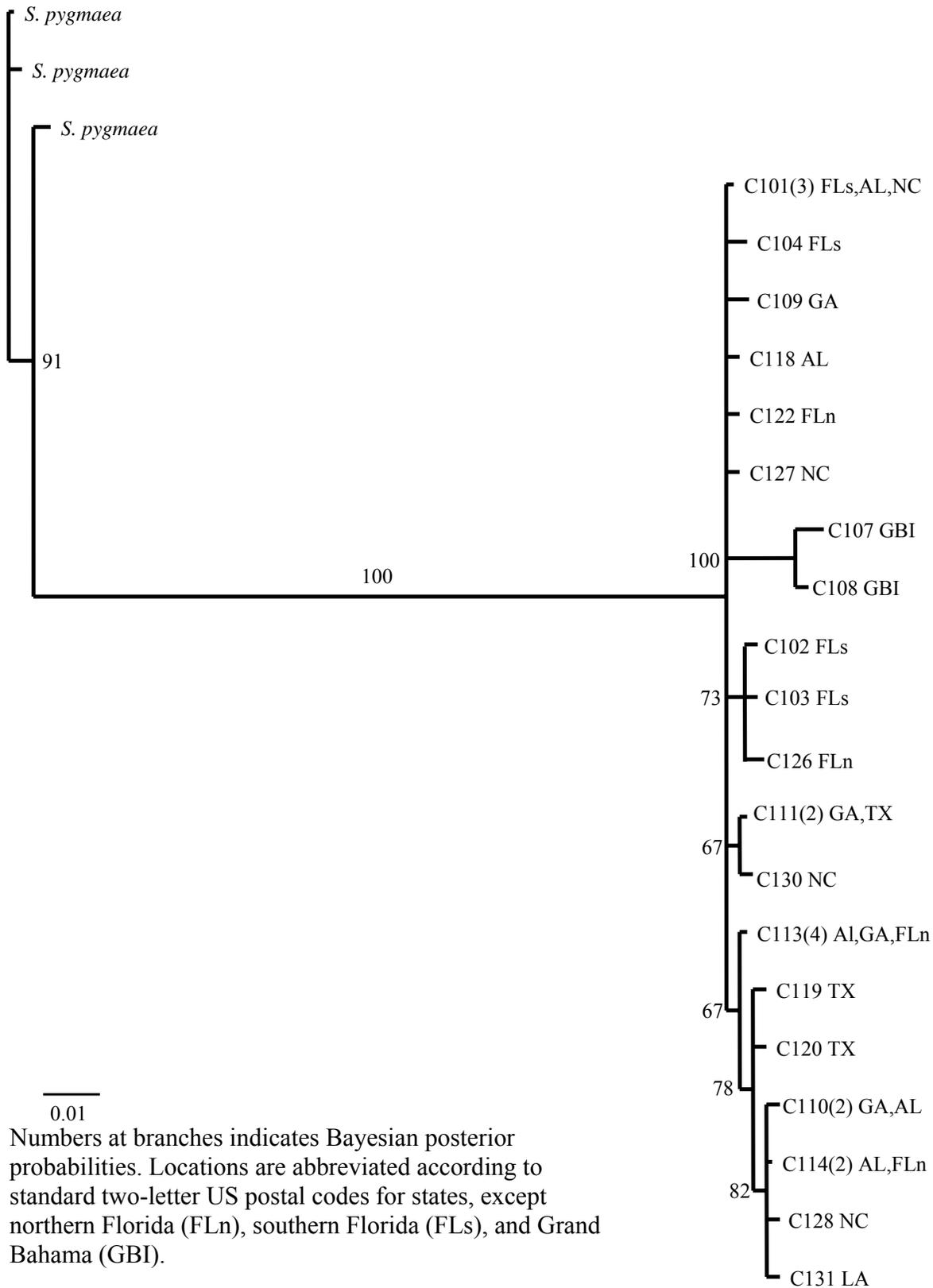
Figure 1. Rooted phylogram of concatenated haplotypes.

S. pygmaea

S. pygmaea

S. pygmaea

91

100

C101(3) FLs,AL,NC

C104 FLs

C109 GA

C118 AL

C122 FLn

C127 NC

100

C107 GBI

C108 GBI

73

C102 FLs

C103 FLs

C126 FLn

67

C111(2) GA,TX

C130 NC

67

C113(4) Al,GA,FLn

C119 TX

C120 TX

78

82

C110(2) GA,AL

C114(2) AL,FLn

C128 NC

C131 LA

0.01

Numbers at branches indicates Bayesian posterior probabilities. Locations are abbreviated according to standard two-letter US postal codes for states, except northern Florida (FLn), southern Florida (FLs), and Grand Bahama (GBI).

Figure 2. Unrooted phylogram of concatenated haplotypes. Numbers along branches indicate Bayesian posterior probabilities. See Figure 1 for abbreviations.
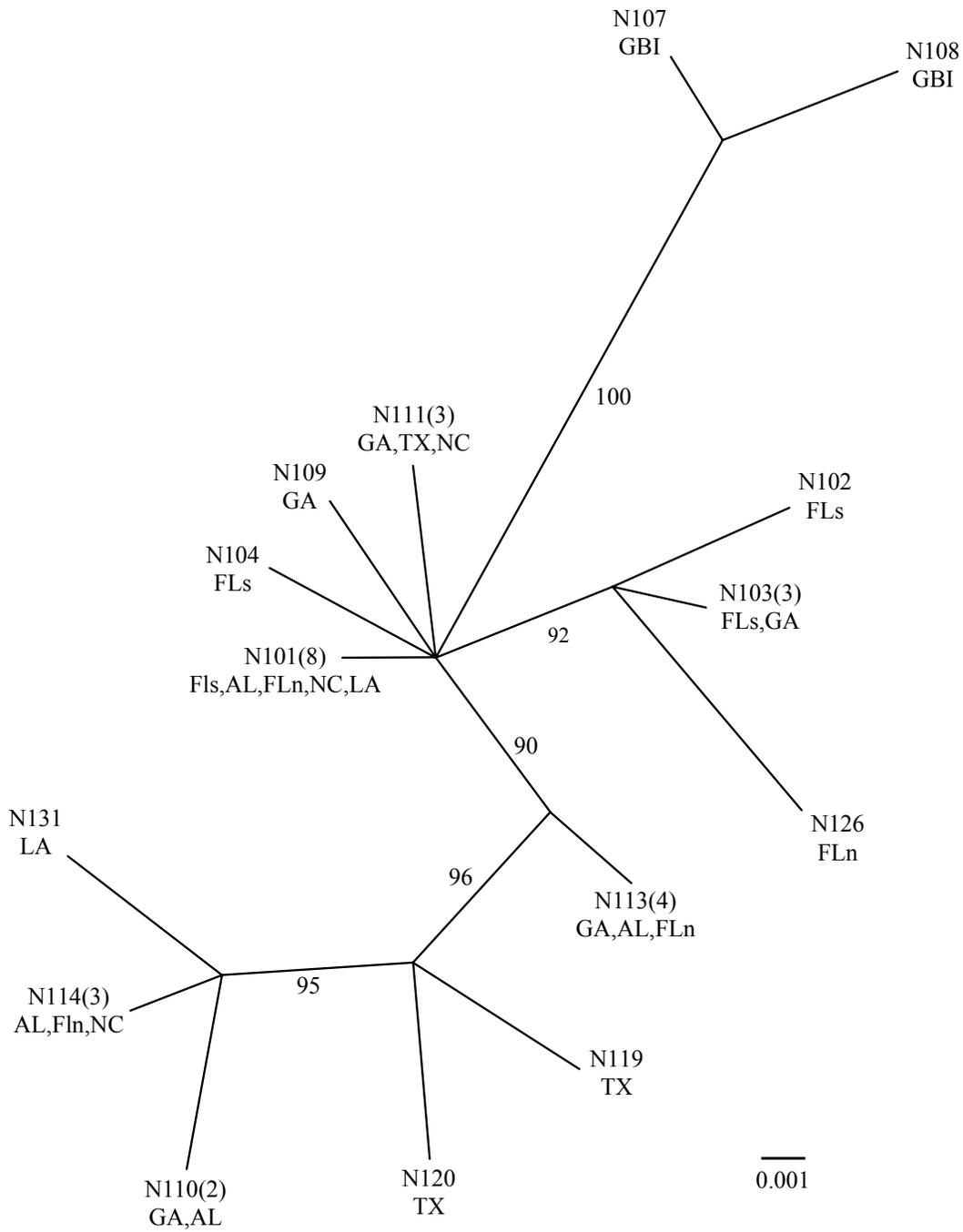
Figure 3. Unrooted phylogram of ND6 haplotypes. Numbers along branches indicate Bayesian posterior probabilities. See Figure 1 for abbreviations.
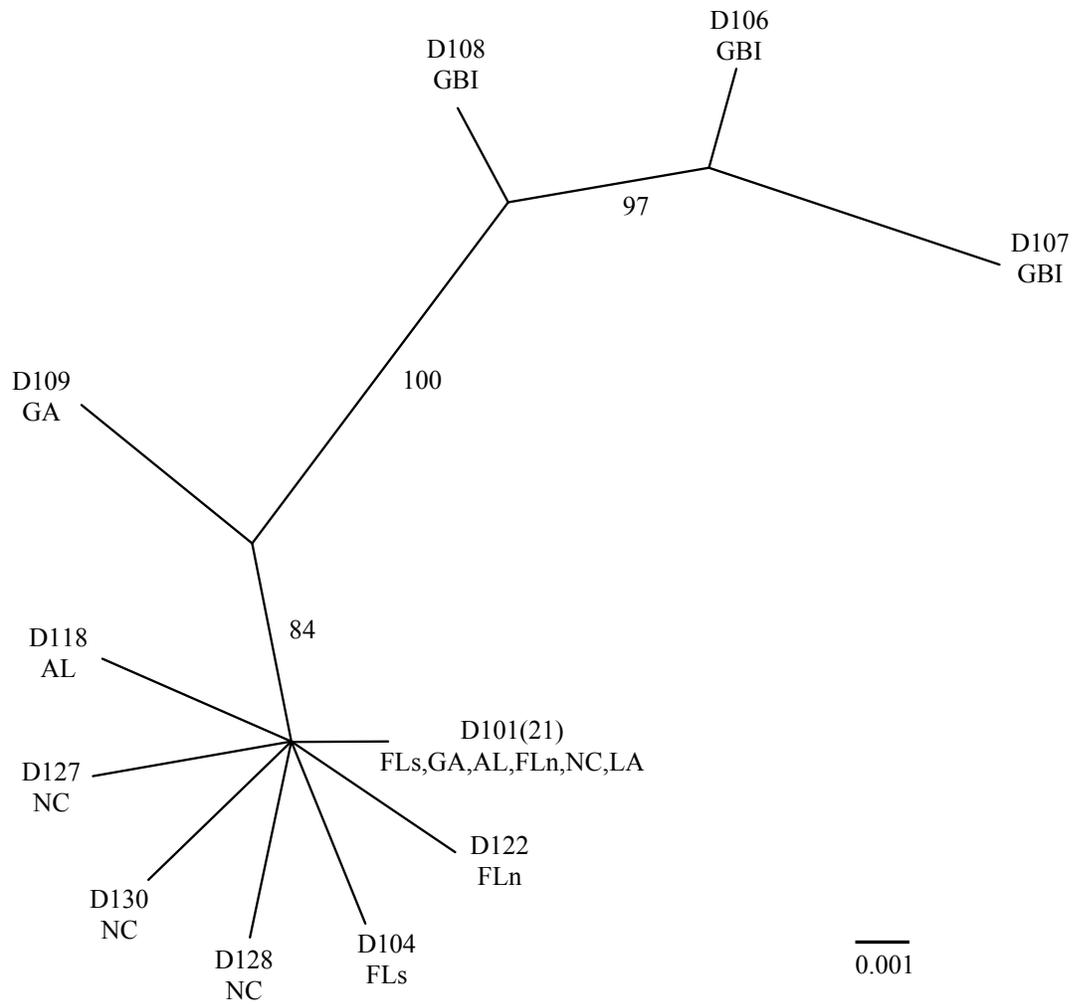
Figure 4. Unrooted phlogram of D-loop haplotypes.   Numbers along branches indicate Bayesian posterior probabilities. See Figure 1 for abbreviations.
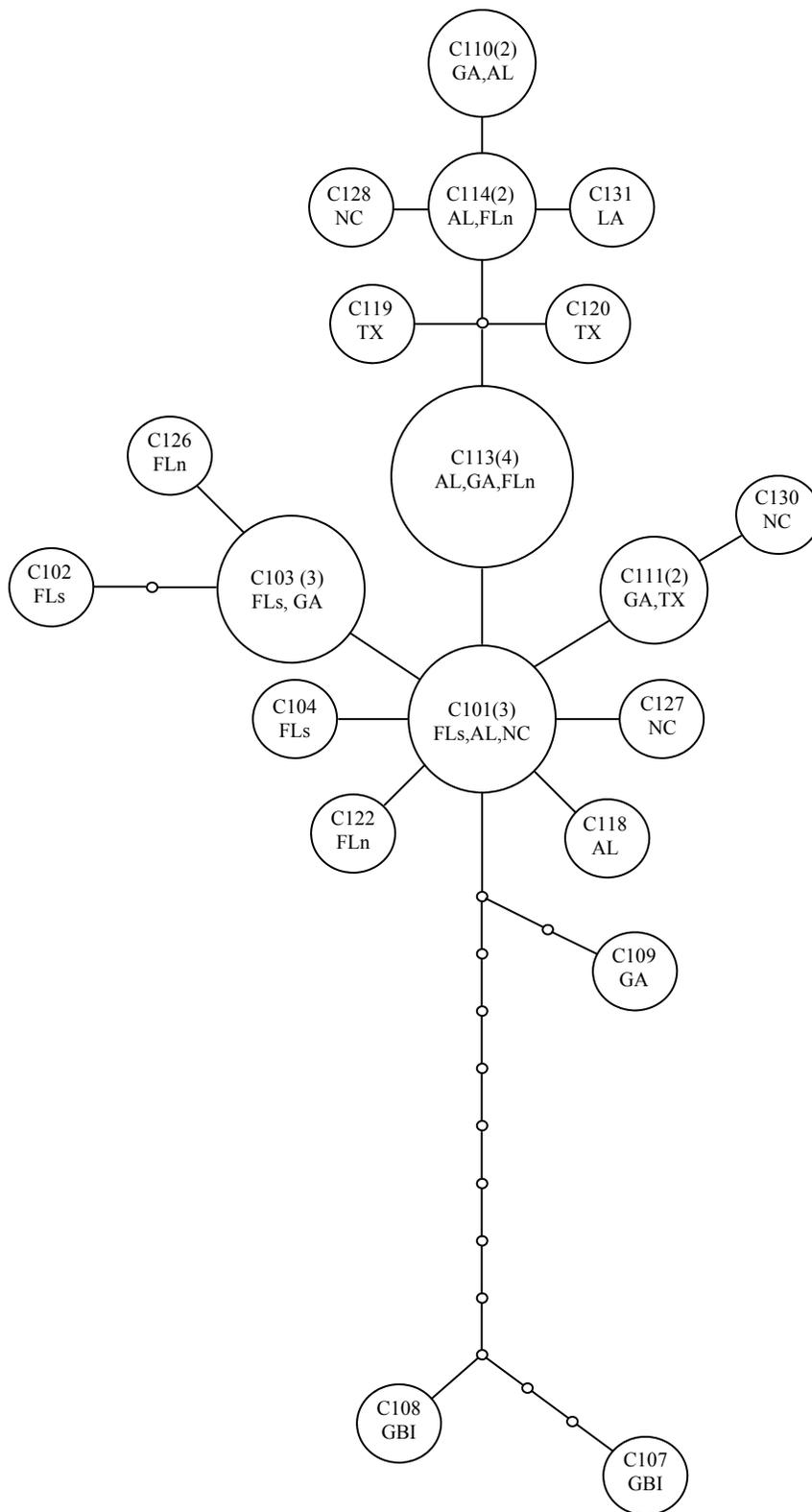
Figure 5. Minimum spanning tree of concatenated haplotypes. Circle size is relative number of individuals per haplotype; the smallest unlabeled circles represent unsampled haplotypes. See Figure 1 for abbreviations.
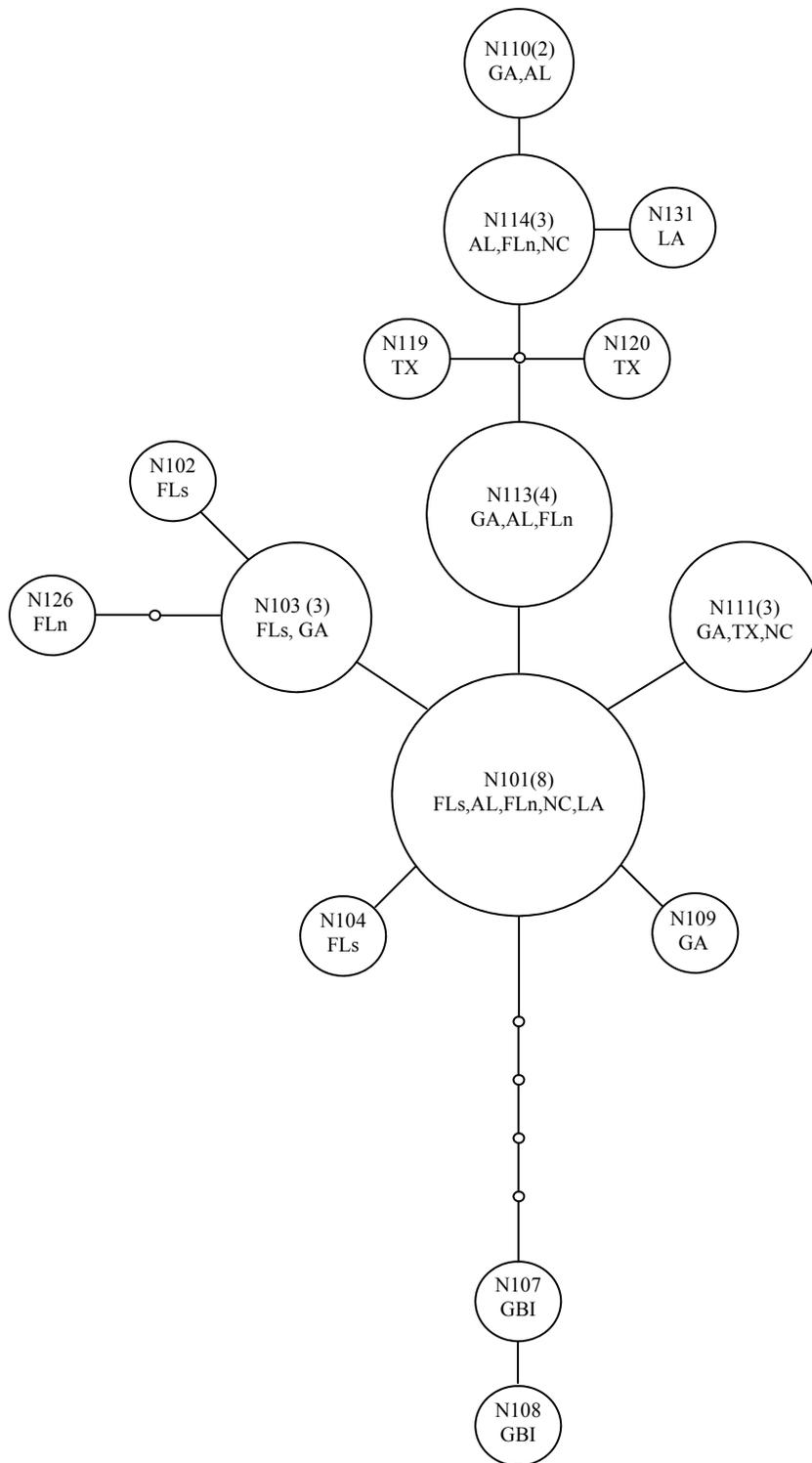
Figure 6. Minimum spanning tree of ND6 haplotypes. Circle size is relative to number of individuals per haplotype; the smallest unlabeled circles represent unsampled haplotypes. See Figure 1 for abbreviations.
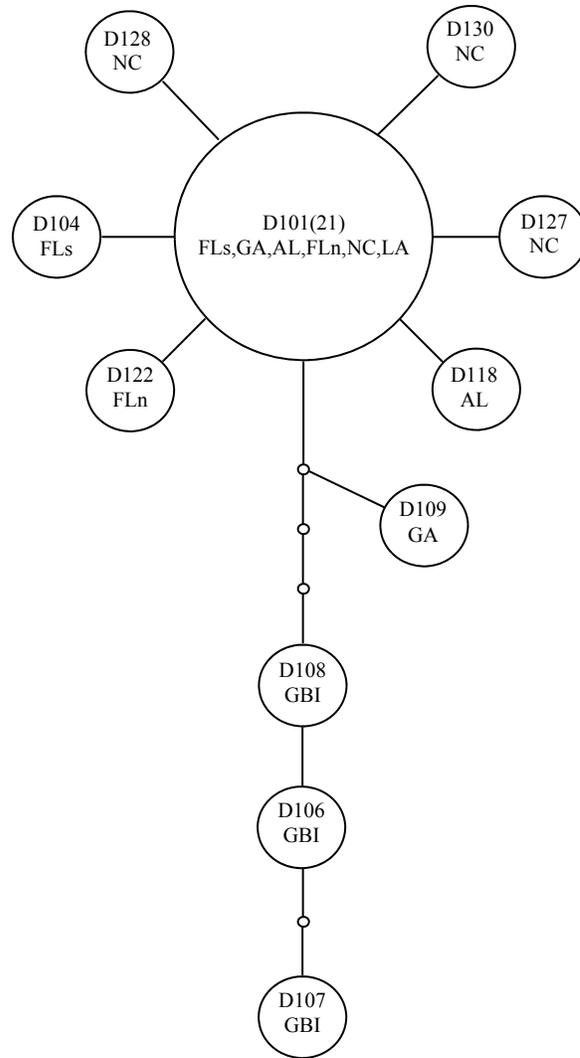
Figure 7. Minimum spanning tree of D-loop haplotypes. Circle size is relative to number of individuals per haplotype; the smallest unlabeled circles represent unsampled haplotypes. See Figure 1 for abbreviations.

CHAPTER 2: POPULATION SURVEYS

Abundance and distribution of breeding birds in the pine forests of Grand Bahama, Bahamas

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Pine-rockland forest at Lucaya Estates, Grand Bahama: the last refuge of the unique Bahamas Brown-headed Nuthatch (*Sitta pusilla insularis*).

Introduction

The Caribbean pine (*Pinus caribea*) forests of Grand Bahama support a distinctive avifauna, including endemic species such as Bahama Yellowthroat (*Geothlypis rostrata*) and Bahama Swallow (*Tachycineata cyaneoviridis*) as well as endemic subspecies of Yellow-throated Warbler (*Dendroica dominica flavescens*; Hall 1996), Brown-headed Nuthatch (*Sitta pusilla insularis*; Bond 1931, Chapter 1 of this report), and Western Spindalis (*Spindalis zena zena*; Garrido et al. 1998). Yet, with few exceptions, most notably the surveys conducted by John Emlen in 1968-1969 (Emlen 1971, 1977, 1981; see also Allen 1996), this avian assemblage has escaped ornithological inquiry, and as a consequence even the most basic information, such as abundance, density, and distribution, is either lacking or outdated for most of the constituent species. This lack of information constitutes a significant obstacle to efficient conservation planning, which will be increasingly important as residential development expands into the pinelands and as large-scale timber harvest once again becomes economically viable. For example, additional data on abundance and distribution will be useful in identifying species of concern and areas that are important for their conservation. It may also prove useful in developing management plans for existing protected areas, such as national parks, for example by allowing for the development of quantitative goals for population size.

We sought to address these information gaps by providing updated information on the abundance and distribution of pineland birds across Grand Bahama. We also sought to evaluate potential changes in this avifauna through qualitative comparisons with the results presented in Emlen (1977). We addressed these objectives by using line-transect surveys conducted throughout the pinelands of Grand Bahama during the spring of 2007 to estimate abundance, density, and distribution of breeding birds.

Methods

      We conducted line-transect surveys along the network of abandoned logging tracks that blanket the pine forest of Grand Bahama. Conducting surveys along roads or trails introduces two potential sources of bias. First, the presence of roads or trails may directly or indirectly (i.e., through effects on structure and composition of the plant community) influence bird abundance, and thus yield biased estimates of abundance when inference is drawn about the forest as a whole. In this case, we felt that any edge effect associated with the logging tracks was likely to be minimal: the logging tracks, which have been abandoned for approximately 40-60 years, were fairly narrow, ranging from c.a. 1.5 – 4 m in width, most were overgrown with thatch palm (*Thrinax morrissi*) and young pine trees, and many had an unbroken pine canopy overhead. Surveys along existing roads or trails can also be problematic because they generally do not constitute a random sample of the study area, and thus the generality of results is limited. The logging tracks on Grand Bahama were systematically established and were nearly ubiquitous in the island's pine forests: main north/south tracks occur every 1-2 km across the island, and shorter, perpendicular spurs are located every 0.25 km along the main tracks. A random sample of systematically placed transects should be sufficient to yield relatively unbiased parameter estimates (Buckland et al. 2001, Morrison et al. 2001). Thus, we concluded that using abandoned logging tracks as transects was unlikely to introduce substantial bias into our estimates of abundance and distribution. At the same time, surveying line transects along abandoned logging tracks greatly improved the efficiency of our surveys. The pine forests of Grand Bahama grow on exposed limestone outcrops, and the forest floor is typically composed of jagged, loose piles of limestone interspersed with solution holes. As a consequence, foot travel is difficult and slow. In contrast, the old logging tracks were created by scraping the exposed rock to create a mostly level and smooth surface. Thus, conducting surveys along these tracks allowed us to complete more surveys and also obviated concerns

that we had about the ability of observers to detect birds and accurately estimate distances while navigating difficult terrain.

We established transects by first identifying all potentially suitable (i.e., within pine forest) 1 km segments of abandoned logging tracks using 1:25,000 scale maps provided by the Department of Land and Surveys. We then randomly chose 46 of these transects to survey, with the constraints that transects had to fall entirely within pine forest, as identified on the maps, and that all transects were separated from one another by at least 500 m. We used a Global Positioning System (GPS) receiver to record the starting and ending location of each transect, and calculated the length of each transect from these coordinates. We surveyed each transect once between 15 April 2007 and 25 April 2007. Surveys began within 15 minutes of sunrise and were completed by 10:00. We did not conduct surveys during inclement weather (rain or high wind). We conducted surveys by walking slowly (c.a. 1 km hr^{-1}) along the transect and recording all individual birds heard or seen. We estimated whether each detected individual was within 25 m of the transect, between 26 and 100 m from the transect, or >100 m from the transect. We also recorded the sex of each individual when possible and whether the detection was auditory or visual.

We estimated density and abundance of birds using distance sampling as implemented by program Distance (Thomas et al. 2006). Distance sampling is one of several methods that can be used to adjust counts of birds to address imperfect detectability. As a rule of thumb, Buckland et al. (2001) recommended that at least 60 detections are needed to estimate reliably the detection function, which in turn is used to estimate the average probability of detecting an individual given that it is present and can be seen or heard. Only 5 of the 21 breeding species that we surveyed met this criterion, and thus we decided to pool species into groups and estimate a common detection function for each group, which was then applied to counts for each species to generate species-specific estimates of density and abundance. The validity of this approach hinges on the assumption that a common detection function can accurately estimate detection probability for different species. Although we cannot formally test

this assumption, theoretical and empirical support exists for this approach (e.g., Alldredge et al 2007).

To create groups of species with similar detection functions, we first decided which detections to include in the analysis. For most species, we considered only detections of singing males because these were the most common form of detection. In these cases, we excluded all visual detections and all auditory detections of females because the detection functions for these encounters were almost certainly different from detection functions generated from encounters with singing males. When this sort of heterogeneity is present, the resulting detection function can produce unreliable estimates of density and thus it is generally preferable to estimate densities of singing males only (Buckland 2006). For three species, however, we considered all detections: Hairy Woodpecker (*Picoides villosus*), Cuban Emerald (*Chlorostilbon ricordii*) and Blue-gray Gnatcatcher (*Polioptila caerulea*). We did so for Hairy Woodpeckers and Blue-gray Gnatcatchers because all individuals were detected by calls that are given by both sexes (Ellison 1992, Jackson et al. 2002) and thus we saw no reason to censor any observations. Likewise, we did not censor any detections of Cuban Emeralds because all individuals were detected visually, within 25 m of the transect, typically in territorial interactions with other individuals.

Once we had determined which, if any, detections to censor, we examined plots of the number of detections as a function of distance from the transect. Based on these histograms, we created three groups of species for analysis. The first group consisted of species with a bell-shaped distribution of detections, with the majority of detections occurring from 26-100 m from the transect and the remainder divided evenly between the other distance intervals. Included in this group (Group 1) were Hairy Woodpecker, Loggerhead Kingbird (*Tyrannus caudifasciatus*), Crescent-eyed Pewee (*Contopus caribaeus*), Thick-billed Vireo (*Vireo crassirostris*), Yellow-throated Warbler (*Dendroica dominica*), Olive-capped Warbler (*D. pityophila*), Pine Warbler (*D. pinus*), Bahama Yellowthroat (*Geothlypis rostrata*), and Northern Mockingbird (*Mimus polyglottus*). The second group (Group 2) consisted of species in which >90% of individuals were detected with 25 m of the transect, and included Cuban

Emerald, Blue-gray Gnatcatcher, and Black-faced Grassquit (*Tiaris bicolor*). Finally, we estimated

separate detection functions for two species that did not fall into either of the above groupings.

Detections of singing, male Western Spindalis (*Spindalis zena*) were concentrated in the first two

distance intervals and very few detections were noted beyond 100 m. Red-legged Thrush (*Turdus*

plumbeus), on the other hand, were mostly detected in the two outer distance intervals, and relatively

few were detected near the transects. We did not attempt to model detectability or estimate abundance

for species with <10 observations because we could not reliably place these species into any of the

above groups.

Following Buckland et al. (2001), we modeled detection functions using one of three key

functions (uniform, half normal, and hazard rate). In addition, we examined whether changing the

shape of each key function via a series expansion term (cosine, simple polynomial, or hermite

polynomial) improved the ability of the model to describe the detection function. We were limited to

models with ≤ 2 parameters because our data were in three intervals, which precluded any adjustments

to the hazard-rate key function. We evaluated the strength of support for each model using Akaike's

Information Criteria, as adjusted for small sample size (AIC_c) and normalized Akaike weights (w_i).

However, rather than relying on a single model to draw inference about density and abundance, we

used model-averaged estimates of density, in which a weighted average was calculated using the

species-specific density estimates for each model and w_i as a weighting factor (Burnham and Anderson

2002). We then calculated an unconditional estimate of variance (Burnham and Anderson 2002:162)

and an approximate 95% confidence interval around the model-averaged estimate of density using the

formula in Buckland et al. (2001:77). Abundance estimates were based on an estimate of

approximately 60,000 ha of pine forest on Grand Bahama (Hayes et al. 2004). Where necessary, we

adjusted both density and abundance estimates to include both sexes; in cases where density estimates

were based on singing males, we assumed a population sex ratio of 1:1.

Results

We surveyed a total of 36.5 km along 46 line transects across Grand Bahama's pinelands (Fig. 1). Although the target length for each transect was 1 km, some were shortened because they crossed into different vegetation types or because the tracks that we used as survey lines were shorter than indicated on the maps. We detected 37 species, 21 of which were likely breeding in the pine forests (Table 1). The remaining species were either neotropical migrants or species associated with other habitats.

There was substantial uncertainty as to the best detection function for each group (Table 2), and so we used model-averaged estimates of abundance and density (Table 3). The pineland bird assemblage was dominated numerically by three species: Black-faced Grassquit, Olive-capped Warbler, and Pine Warbler (Table 3). Of these three, Olive-capped and Pine Warblers, which forage and nest in pine trees on Grand Bahama, were widespread and abundant, whereas Black-faced Grassquits, which are edge-associated throughout their range and nest in understory plants such as thatch palm, were detected on just over half of the transects but occurred at very high densities when present. We observed Cuban Emerald, Bahama Yellowthroat, and Western Spindalis, all of which occur commonly in vegetation types other than pine forest (e.g., coppice (Emlen 1977)), at moderate densities (Table 3). The eight remaining species for which we estimated abundance – Hairy Woodpecker, Blue-gray Gnatcatcher, Thick-billed Vireo, Yellow-throated Warbler, Red-legged Thrush, Northern Mockingbird, Cuban Pewee, and Loggerhead Kingbird – occurred at low densities and were detected on relatively few transects (Table 3). Seven other species were detected with such infrequency that we did not attempt to estimate density. Most of these species appeared rare in our sample only because pine forest is not a preferred vegetation type for foraging or nesting or, in the case of the Bahama Swallow, because our sampling methodology was inadequate. However, one obligate resident of the pine forest was notably rare: the Brown-headed Nuthatch, of which we detected only

two individuals during line-transect surveys (we located 14 additional adults, and seven juveniles, using intensive area searches coupled with broadcast playbacks of recorded vocalizations; J. D. Lloyd and G. L. Slater, unpublished data).

Discussion

The assemblage of birds inhabiting the pine forests of Grand Bahama includes eight species that rely primarily or exclusively on pine forest for breeding habitat (Olive-capped Warbler, Pine Warbler, Yellow-throated Warbler, Hairy Woodpecker, Brown-headed Nuthatch, La Sagra's Flycatcher, Cuban Pewee, and Loggerhead Kingbird) and many more that are found in a variety of settings across the island. From the standpoint of conservation, our results are most useful for these species limited to pine forest, as the estimates presented here reflect the best assessment of their current island-wide status. Populations of Olive-capped Warbler and Pine Warbler appeared secure, with a nearly ubiquitous distribution and relatively high densities throughout the pine forests of Grand Bahama. Olive-capped Warblers were the most abundant species surveyed by Emlen (1977), but he reported an average density nearly 3 times greater than that we estimated. Some of this discrepancy may be explained by changes in forest structure, including residual effects of Hurricanes Frances (2004), Jeanne (2004), or Wilma (2005), or differences in the areas surveyed (Emlen's surveys were limited to the western half of the island), but most of the difference was likely a consequence of different analytical methods. Emlen (1977) used 0.25 as the probability of detection for Olive-capped Warblers, whereas we estimated the probability of detection to be 0.54; as a consequence, without any difference in the number of individuals counted, our estimates of density would be less than 50% of that estimated by Emlen (1977). The estimated density of Pine Warblers in the present study, on the other hand, was nearly identical to that reported by Emlen (1977), although again Emlen's probability of detection was lower (0.30 vs. 0.54).

The remaining pine-forest species for which we estimated abundance – Yellow-throated Warbler, Hairy Woodpecker, and Loggerhead Kingbird – were found on relatively few transects and at low densities, and all were far less abundant than reported by Emlen (1977). The apparent scarcity of Loggerhead Kingbirds may be an artifact of sampling prior to the onset of their breeding season; Brudenell-Bruce (1975) reported that this species was common outside of the pine forest until late spring, at which point it withdrew to the pines and commenced breeding. Brudenell-Bruce (1975) also reported an observation of an active nest in July, suggesting that we may have sampled too early to draw reliable inferences about this species. Yellow-throated Warbler and Hairy Woodpecker likely appeared less common in our sample than reported by Emlen (1977) due to differences in how detectability was modeled. Nonetheless, irrespective of any methodological effect, estimated population sizes of both species were small and their distribution was patchy, suggesting that both species may be especially vulnerable to future habitat loss.

We were unable to generate estimates of abundance for La Sagra's Flycatcher, Cuban Pewee, or Brown-headed Nuthatch because we detected so few individuals. The apparent rarity of La Sagra's Flycatcher and Cuban Pewee may have been a result of sampling outside of the main breeding season, use of other habitats, or inherent scarcity on Grand Bahama (Emlen (1977) also found these species to be uncommon). None of these factors explain the near-absence of Brown-headed Nuthatches on our transects, however. This species, a known obligate of pine forests, was in the midst of breeding during our surveys (we located nests and observed pairs and groups building nests and feeding young) and was relatively common during the surveys conducted by Emlen (1971, 1977). We detected only two individuals during line-transect surveys. We located 14 additional adults, and seven juveniles, during ten days of intensive area searches coupled with broadcast playbacks of recorded vocalizations. All of the individuals were located in or adjacent to the Lucaya Estates subdivision (Fig. 1), which has extensive road networks but has not yet been built-out. The increased rate of detection that accompanied use of the recorded vocalizations suggested that passive survey methods, such as distance

sampling, were inefficient in sampling this species, but nonetheless the absolute scarcity of Brown-headed Nuthatches was striking (see also Smith and Smith 1994, Hayes et al. 2004). This apparent decline in numbers of Brown-headed Nuthatches on Grand Bahama is especially troubling given recent evidence of morphological (Hayes et al. 2004) and genetic (Chapter 1 of this report) divergence from the nominate subspecies in the United States.

The estimates of density and abundance presented here should be useful both as a baseline for comparison with future population monitoring, with the caveat that the populations we sampled may still bear the mark of the damaging hurricanes of 2004 and 2006, and as a preliminary assessment of the current status of Grand Bahama's pineland bird assemblage. In general, the pine-forest avifauna is similar in structure to that described by Emlen (1977). Only Olive-capped Warbler and Pine Warbler were abundant and widely distributed; the remaining species were relatively scarce and patchy in their distribution. As such, stands that support populations of the less-abundant species, especially Yellow-throated Warbler and Brown-headed Nuthatch, should be the focus of conservation and management efforts. Unfortunately, based on present knowledge (see similar findings in Hayes et al. 2004), the remaining population of Brown-headed Nuthatches on Grand Bahama is limited to Lucaya Estates in the central portion of the island's pine forests, which is also slated for large-scale residential development. Should this area ultimately be built-out as planned, it will almost certainly result in the extinction of *Sitta pusilla insularis*. As such, protection of these pine forests should be the first step in any conservation effort targeted at Brown-headed Nuthatches on Grand Bahama. Future efforts should include the development of a comprehensive conservation strategy, including guidelines for the management of Grand Bahama's pine forests. Pressing research needs include more rigorous estimates of population size, an examination of why Brown-headed Nuthatches appear limited to Lucaya Estates, and demographic studies that might explain the ongoing population decline.

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Table 1. Total number of individuals detected during surveys of 46 line transects in the pine forests of Grand Bahama, Bahamas during April 2007.

Species[a]	No. detected
Olive-capped Warbler (*Dendroica pityophila*)	314
Pine Warbler (*Dendroica pinus*)	225
Bahama Yellowthroat (*Geothlypis rostrata*)	111
Black-faced Grassquit (*Tiaris bicolor*)	85
Western Spindalis (*Spindalis zena*)	67
Cuban Emerald (*Chlorostilbon ricordii*)	30
Thick-billed Vireo (*Vireo crassirostris*)	28
Red-legged Thrush (*Turdus plumbeus*)	24
Yellow-throated Warbler (*Dendroica dominica*)	21
Northern Mockingbird (*Mimus polyglottos*)	16
Hairy Woodpecker (*Picoides villosus*)	15
Palm Warbler (*Dendroica palmarum*)	13
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	12
Blue-gray Gnatcatcher (*Polioptila caerulea*)	12
Cuban (Crescent-eyed) Pewee (*Contopus caribaeus*)	11
Cape May Warbler (*Dendroica tigrina*)	8
Red-winged Blackbird (*Agelaius phoeniceus*)	6
Gray Catbird (*Dumatella carolinensis*)	6
Turkey Vulture (*Cathartes aura*)	5
Mourning Dove (*Zenaida macroura*)	5
Zenaida Dove (*Zenaida aurita*)	5

Table 1. Continued.

Black-and-white Warbler (*Mniotilta varia*)	4
Bobolink (*Dolichonyx oryzivorous*)	4
La Sagra's Flycatcher (*Myiarchus sagrae*)	4
Prairie Warbler (*Dendroica discolor*)	3
Red-tailed Hawk (*Buteo jamaicensis*)	3
Greater Yellowlegs (*Tringa melanoleuca*)	2
Blackpoll Warbler (*Dendroica striata*)	2
Brown-headed Nuthatch (*Sitta pusilla*)	2
Scarlet Tanager (*Piranga olivacea*)	2
Common Ground Dove (*Columbina passerina*)	1
American Redstart (*Setophaga ruticilla*)	1
Barn Owl (*Tyto alba*)	1
Yellow-billed Cuckoo (*Coccyzus americanus*)	1
Bahama Mockingbird (*Mimus gundlachii*)	1
Bahama Swallow (*Tachycineta cyaneoviridis*)	1
Indigo Bunting (*Passerina cyanea*)	1

[a] Breeding species in bold.

Table 2. Model-selection results for analysis of candidate models of detection functions for species surveyed on 46 line transects in the pine forests of Grand Bahama, Bahamas during April 2007. ΔAIC_c is the difference between a given model and the model with the lowest AIC_c score and AIC_c weight (w) reflects the relative support for each model being the actual best model in the candidate set.

Model[a]	ΔAIC_c	w
Group 1		
Hazard rate	0	0.56
Uniform + single polynomial	1.75	0.23
Uniform + cosine	2.75	0.14
Half normal + hermite polynomial	5.55	0.03
Half normal + cosine	5.68	0.03
Half normal	13.16	0
Uniform	240.94	0
Group 2		
Half normal	0	0.73
Hazard rate	2	0.27
Uniform	255.71	0
Western Spindalis		
Half normal	0	0.45
Uniform + simple polynomial	1.17	0.25
Hazard rate	1.98	0.17
Uniform + cosine	2.42	0.13
Uniform	58.65	0

Table 2. Continued.

Red-legged Thrush		
Uniform	0	0.58
Half normal	1.31	0.30
Hazard rate	3.27	0.11

[a] Series expansion terms were included only when they resulted in a lower AIC_c value than the key function alone.

Table 3. Percent incidence and model-averaged estimates of detection probability, density (individuals ha^{-1}), and total abundance of birds in Grand Bahama pinelands detected during surveys on 46 line transects in the pine forests of Grand Bahama, Bahamas during April 2007. Confidence intervals are based on unconditional variance estimates.

Species	% Incidence	Prob. of detection	Density[a] (95% CI)	Abundance[b] (95% CI)
Black-faced Grassquit	59	0.12	0.464 (0.304 – 0.710)	27,845 (18,208 – 42,583)
Olive-capped Warbler	89	0.54	0.436 (0.348 – 0.546)	26,139 (20,869 – 32,739)
Pine Warbler	96	0.54	0.410 (0.328 – 0.516)	24,645 (19,647 – 30,914)
Cuban Emerald	43	0.12	0.270 (0.156 - 0.466)	16,243 (9,404 – 28,056)
Bahama Yellowthroat	78	0.54	0.188 (0.132 – 0.272)	11,326 (7,881 – 16,277)
Western Spindalis	48	0.26	0.160 (0.094 – 0.272)	9,611 (5,674 – 16,278)
Blue-gray Gnatcatcher	20	0.12	0.058 (0.014 – 0.234)	3,440 (843 – 14,030)
Yellow-throated Warbler	41	0.54	0.036 (0.020 – 0.060)	2,116 (1,239 – 3,614)
Hairy Woodpecker	30	0.54	0.032 (0.014 – 0.048)	1,867 (1,094 – 3,183)
Thick-billed Vireo	35	0.54	0.026 (0.013 – 0.055)	1,618 (790 – 3,316)
Red-legged Thrush	39	0.91	0.018 (0.010 – 0.038)	1,118 (559 – 2,235)
Northern Mockingbird	28	0.54	0.012 (0.006 – 0.030)	746 (309 – 1,803)
Cuban Pewee	20	0.54	0.006 (0.002 – 0.036)	373 (66 – 2,112)
Loggerhead Kingbird	22	0.54	0.004 (0.002 – 0.022)	249 (45 – 1,363)

[a]For species where only males were included in modeling of detection function, density estimates were adjusted based on the assumption of 1:1 population sex ratio.

[b]Abundance estimates are based on an estimate of 60,000 ha of pine forest remaining on Grand Bahama.
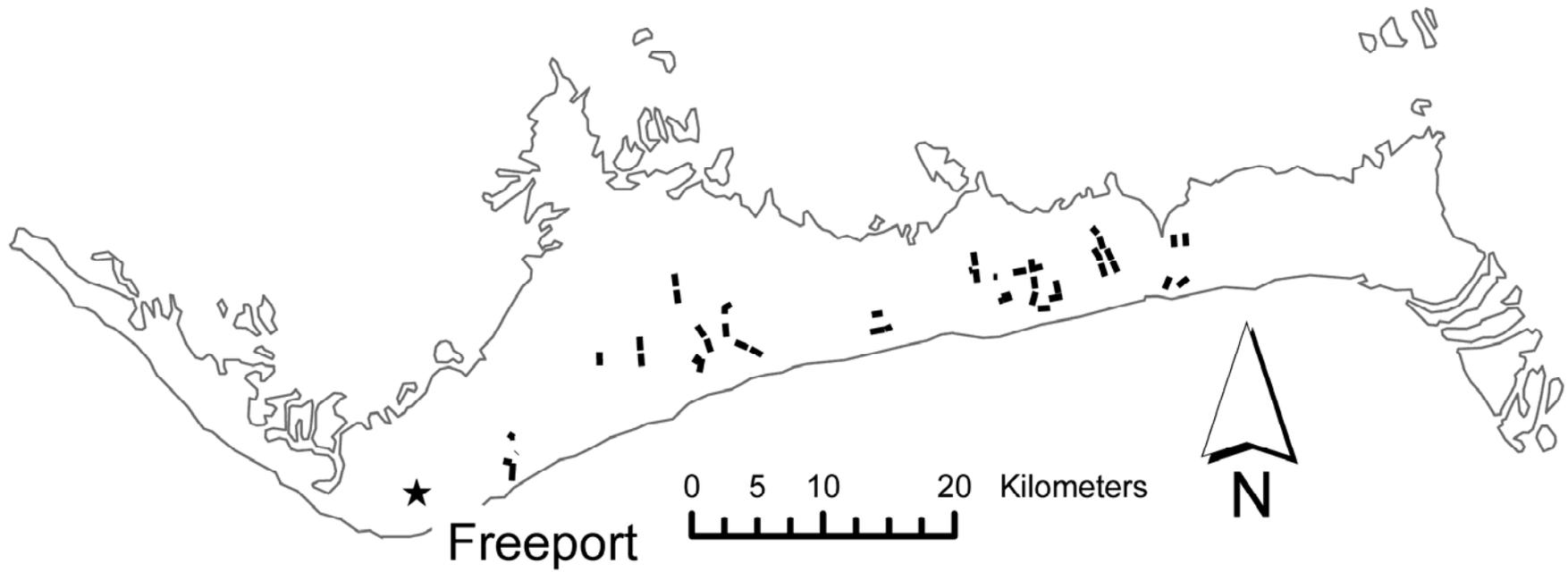
Figure 1. Map of Grand Bahama showing locations of line transects (bold lines) where breeding birds were surveyed during April 2007.