ABUNDANCE AND DISTRIBUTION OF BREEDING BIRDS IN THE PINE FORESTS OF GRAND BAHAMA, BAHAMAS

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Abstract: Grand Bahama's pine forests are home to a unique but largely unstudied avifauna. No recent comprehensive survey has been conducted in these forests and little is known about the abundance and distribution of the island's pineland birds. This lack of information hinders efforts to monitor avian population trends, identify and protect areas important for bird conservation, and manage existing protected areas. We addressed this information gap by conducting line-transect surveys throughout the pinelands of Grand Bahama during April 2007 with the objective of providing updated information on the abundance and distribution of its resident birds. Of the species that rely primarily or exclusively on pine forest for breeding habitat, Olive-capped Warblers (*Setophaga pityophila*) and Pine Warblers (*S. pinus*) were nearly ubiquitous in distribution and had large estimated population sizes. The remaining pineland species for which we estimated abundance—Hairy Woodpecker (*Picoides villosus*), Loggerhead Kingbird (*Tyrannus caudifasciatus*), and Bahama Warbler (*S. flavescens*)—were far less abundant and had very patchy distributions. We encountered too few La Sagra's Flycatchers (*Myiarchus sagrae*), Cuban Pewees (*Contopus caribaeus*), and Brown-headed Nuthatches (*Sitta pusilla*) to estimate abundance. The scarcity of Brown-headed Nuthatches stood in stark contrast to their relative abundance in the late 1960s, and follow-up surveys for this species are of critical importance. We recommend additional surveys in the future, both to refine the findings presented here and to begin to generate estimates of population trends. Our results also suggest that the priority for conservation and management efforts should be those forest stands that support populations of Bahama Warblers and Brown-headed Nuthatches.

Key words: avian conservation, Bahama Warbler, Brown-headed Nuthatch, Grand Bahama, *Setophaga flavescens*, *Sitta pusilla insularis*

Resumen: ABUNDANCIA Y DISTRIBUCIÓN DE LAS AVES ANIDANTES EN LOS PINARES DE GRAN BAHAMA, BAHAMAS. Los bosques de pinos de Gran Bahama son hogar de una avifauna única y muy poco estudiada. Ningún censo exhaustivo se ha conducido recientemente y se conoce muy poco sobre la abundancia y distribución de las aves de pinares isleños. Esta falta de información obstaculiza los esfuerzos para el seguimiento de las tendencias poblacionales, para la identificación y protección de áreas importantes para la conservación de las aves y para el manejo de las áreas protegidas existentes. Enfocado en llenar éste vacío de información se condujeron muestreos por medio de transectos de línea a través de los pinares de Gran Bahama, durante abril del año 2007, con el objetivo de adquirir información actualizada acerca de la abundancia y distribución de sus aves residentes. De las especies que dependen primaria o exclusivamente de los pinares como hábitat de cría, *Setophaga pityophila* y *S. pinus* se distribuyeron de manera casi ubícua y con grandes tamaños poblacionales estimados. El resto de las especies de pinares para las cuales se estimó la abundancia—*Picoides villosus*, *Tyrannus caudifasciatus* y *Setophaga flavescens*—fue mucho menos abundante y tuvieron distribuciones muy fragmentadas. Se encontraron muy pocos *Myiarchus sagrae*, *Contopus caribaeus* y *Sitta pusilla* como para hacer un estimado de abundancia. La rareza de *Sitta pusilla* resalta con marcado contraste por su elevada abundancia relativa en la década de 1960 y seguimientos posteriores de esta especie serán de crítica importancia. Se recomiendan muestreos adicionales, tanto para refinar los resultados obtenidos como para comenzar a generar estimaciones de las tendencias poblacionales. Los resultados sugieren que la prioridad para la conservación y los esfuerzos de manejo deben enfocarse en las zonas boscosas que albergan las poblaciones de *Setophaga flavescens* y *Sitta pusilla*.

Palabras clave: conservación de las aves, Gran Bahama, *Setophaga flavescens*, *Sitta pusilla insularis*

Résumé : ABONDANCE ET DISTRIBUTION DES OISEAUX NICHEURS DANS LES FORÊTS DE PINS DE GRAND BAHAMA, BAHAMAS. Les forêts de pins de Grand Bahama abritent une avifaune unique mais très peu étudiée à ce jour. Aucune étude complète n'ayant été récemment menée dans ces forêts, l'abondance et la distribution des oiseaux inféodés à ces milieux sont mal connues. Le suivi des tendances des populations d'oiseaux, l'identification et la protection de zones importantes pour la conservation des oiseaux ainsi que la gestion des aires protégées existantes sont freinés par ce manque d'information. Pour pallier cette absence de données, nous avons réalisé des relevés par line-transect dans toute la pinède de Grand Bahama en avril 2007, avec pour objectif l'actualisation des informations sur l'abondance et la distribution de ses oiseaux sédentaires. Parmi les espèces qui dépendent principalement ou exclusivement de la pinède pour leur habitat de nidification, la Paruline à calotte verte (*Setophaga pityophila*) et la Paruline des pins (*S. pinus*) étaient presque omniprésentes. La taille de leurs populations a été estimée comme im-

portante. Les autres espèces pour lesquelles nous avons estimé l'abondance—Pic chevelu (*Picoides villosus*), Tyran tête-police (*Tyrannus caudifasciatus*) et Paruline des Bahamas (*Setophaga flavescens*)—étaient beaucoup moins communes et présentaient des distributions très morcelées. Nous avons rencontré trop peu de Tyran de La Sagra (*Myiarchus sagrae*), de Moucherolle tête-fou (*Contopus caribaeus*) et de Sittelle des Bahamas (*Sitta pusilla insularis*) pour en estimer l'abondance. La rareté de la Sittelle des Bahamas contraste fortement avec son abondance relative à la fin des années 60 et la mise en place d'un suivi de l'espèce apparait essentielle. Nous recommandons la réalisation d'études complémentaires pour affiner les résultats présentés ici et pour pouvoir estimer les tendances des populations. Nos résultats suggèrent également que les efforts de conservation et de gestion devraient prioritairement être orientés vers les massifs forestiers qui accueillent des populations de Paruline à gorge jaune et de Sittelle des Bahamas.

Mots clés : conservation des oiseaux, Grand Bahama, Paruline des Bahamas, *Setophaga dominica*, *Sitta pusilla insularis*, Sittelle des Bahamas

The Caribbean pine (*Pinus caribea*) forests of Grand Bahama support a distinctive avifauna, including endemic species such as Bahama Yellowthroat (*Geothlypis rostrata*), Bahama Warbler (*Setophaga flavescens*), and Bahama Swallow (*Tachycineata cyaneoviridis*), as well as endemic subspecies of Brown-headed Nuthatch (*Sitta pusilla insularis*; Bond 1931) and Western Spindalis (*Spindalis zena zena*; Garrido *et al*. 1997). 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. Such data 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 addressed these information gaps by conducting line-transect surveys in the pinelands of Grand Bahama during the spring of 2007 and by using these data to estimate abundance, density, and distribution of singing birds. Our objectives were twofold: first, to provide updated information on the abundance and distribution of pineland birds across Grand Bahama, and second, to evaluate potential changes in this avifauna through qualitative comparisons with the results presented in Emlen (1977).

STUDY AREA AND METHODS

LINE TRANSECT SURVEYS

Between 15–25 April 2007, we conducted line-transect surveys along the network of abandoned logging tracks that occur throughout 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 might 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 (Buckland *et al*. 2001). 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 yr, were fairly narrow, ranging from about 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 scope of inference might be limited (Buckland *et al*. 2001). The logging tracks on Grand Bahama were systematically established across all of the island's pine forests: main north–south tracks occurred every 1–2 km across the island, and shorter, perpendicular spurs were 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), and 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 our concerns 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 15–25 April 2007. Surveys began within 15 min of sunrise and were completed by 1000. We did not conduct surveys during inclement weather (rain or high wind). We conducted surveys by walking slowly (~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 26–100 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.

STATISTICAL ANALYSES

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 five of the 21 breeding species that we surveyed met this criterion; 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 most 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*), Cuban Pewee (*Contopus caribaeus*), Thick-billed Vireo (*Vireo crassirostris*), Bahamas Warbler, Olive-capped Warbler (*S. pityophila*), Pine Warbler (*S. pinus*), Bahama Yellowthroat, and Northern Mockingbird (*Mimus polyglottos*). 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 Gnatcatch-

er, 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 Thrushes (*Turdus plumbeus*), on the other hand, were detected mostly 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). We adjusted density and abundance estimates for species in which only singing males were included in the analyses using the multiplier function in Program Distance. We did so to allow for comparisons of density and abundance with species in which both sexes were included in analyses, and in doing so 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 breed in pine forests (Table 1). The remaining species were either Nearctic-Neotropical migrants or species associated with other habitats. There was substantial uncertainty as to the best detection function for each group (Table 2), justifying our use of model-averaged estimates of density. However, as is often the case with distance sampling, estimated detection probabilities were robust to variation in
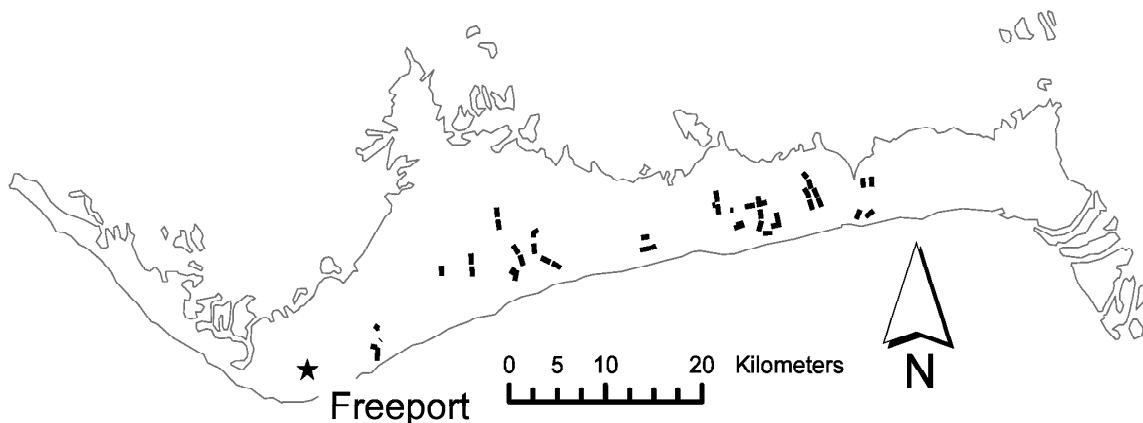

Fig. 1. Map of Grand Bahama showing locations of line transects (bold lines) where breeding birds were surveyed during April 2007.

model specification (Table 2).

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 were rarely detected in our samples, most likely 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 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 unpubl. 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 (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 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

Table 1. Total number of detections recorded during avian surveys along 46 line transects in the pine forests of Grand Bahama, Bahamas, in April 2007.

Species	Number Detected
Olive-capped Warbler*	314
Pine Warbler*	225
Bahama Yellowthroat*	111
Black-faced Grassquit*	85
Western Spindalis*	67
Cuban Emerald*	30
Thick-billed Vireo*	28
Red-legged Thrush*	24
Yellow-throated Warbler*	21
Northern Mockingbird*	16
Hairy Woodpecker*	15
Palm Warbler (*Setophaga palmarum*)	13
Loggerhead Kingbird*	12
Blue-gray Gnatcatcher*	12
Cuban Pewee*	11
Cape May Warbler (*Setophaga tigrina*)	8
Red-winged Blackbird (*Agelaius phoeniceus*)	6
Gray Catbird (*Dumetella carolinensis*)	6
Turkey Vulture (*Cathartes aura*)	5
Mourning Dove (*Zenaida macroura*)*	5
Zenaida Dove (*Z. aurita*)*	5
Black-and-white Warbler (*Mniotilta varia*)	4
Bobolink (*Dolichonyx oryzivorus*)	4
La Sagra's Flycatcher (*Myiarchus sagrae*)*	4
Prairie Warbler (*Setophaga discolor*)	3
Red-tailed Hawk (*Buteo jamaicensis*)	3
Greater Yellowlegs (*Tringa melanoleuca*)	2
Blackpoll Warbler (*Setophaga striata*)	2
Brown-headed Nuthatch*	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*	1
Indigo Bunting (*Passerina cyanea*)	1

*Species potentially breeding in pinelands.

distribution and relatively high densities throughout the pine forests of Grand Bahama. Olive-capped Warbler was the most abundant species surveyed by Emlen (1977). He reported an average density nearly three times greater than ours. Some of this discrepancy may be explained by changes in forest structure, including residual effects of hurricanes Frances (2004), Jeanne (2004), or Wilma (2005);

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 best model in the candidate set. Probability of detection is the probability of detecting an individual, given that it was present and available (i.e., singing) for detection.

Model[a]	Probability of Detection	ΔAIC_c	w
Group 1			
Hazard rate	0.54	0	0.56
Uniform + simple polynomial	0.54	1.75	0.23
Uniform + cosine	0.53	2.75	0.14
Half normal + hermite polynomial	0.52	5.55	0.03
Half normal + cosine	0.52	5.68	0.03
Half normal	0.47	13.16	0
Uniform	1.00	240.94	0
Group 2			
Half normal	0.11	0	0.73
Hazard rate	0.14	2	0.27
Uniform	1.00	255.71	0
Western Spindalis			
Half normal	0.23	0	0.45
Uniform + simple polynomial	0.31	1.17	0.25
Hazard rate	0.25	1.98	0.17
Uniform + cosine	0.28	2.42	0.13
Uniform	1.00	58.65	0
Red-legged Thrush			
Uniform	1.00	0	0.58
Half normal	0.77	1.31	0.31
Hazard rate	0.80	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.

differences in the timing of surveys (Emlen's surveys began in January); or differences in the areas surveyed (Emlen's surveys were limited to the western half of the island), but much of the difference was 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 than our's (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). However, we estimated a higher probability of detection for these three species than Emlen (1977) used, and thus they would have appeared less common in our sample regardless of changes in population size. Nonetheless, irrespective of any methodological effect, estimated population sizes of all three species were small and their distribution was patchy, suggesting that they 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 sea-

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

Species	% Incidence	Probability 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 in which 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 (Hayes *et al*. 2004).

son, 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. This species, a known obligate of pine forests, was in the midst of breeding during our surveys (we located one nest containing an unknown number of nestlings, observed five separate family groups in which two or three adults were feeding dependent juveniles that we estimated ranged in age from < 3 d to > 2 wk post-fledging, and observed a single independent juvenile that we estimated to be > 30 d post-fledging) 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 10 days of intensive area searches coupled with broadcast playbacks of recorded vocalizations. All of the individuals were located in or adjacent to Lucaya Estates, a subdivision in the center of the island that contains extensive road networks but that has yet to be 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 (A. Metcalf, J. D. Lloyd, and G. L Slater, unpubl. data) divergence from the nominate subspecies in the United States.

In considering how to apply the findings presented here it is important to recognize that we made several important assumptions in the analysis and interpretation of our results. First, we assumed that species could be placed into groups for the purposes of estimating detection functions. Ideally, this assumption could be tested by comparing relative support for models that estimate pooled versus species-specific detection functions. We had insufficiently large sample sizes to do so, and thus we may have specified a poor detection function for some species, which would bias our estimates of density and abundance. However, in our experience, estimates of density produced by distance sampling

tend to be robust to variation in the specified detection function, and so misspecification of the detection function might not produce substantial bias. We also note that theoretical and empirical support exists for the practice of pooling species for the purpose of estimating detection functions (Alldredge *et al.* 2007), but acknowledge that future studies of this avifauna might benefit by increasing sample size so that the assumption of a common detection function can be tested directly.

Second, we assumed that we were sampling the breeding population of each species (with the exception of Nearctic-Neotropical migrants or species not known to breed in the pine forests). However, we found incontrovertible evidence that individuals were breeding during the course of our surveys for only one species: Brown-headed Nuthatch. Breeding dates for most species on Grand Bahama are poorly documented, although our surveys fell within the breeding season identified for most species by Brudenell-Bruce (1975) and corresponded to the beginning of the breeding season in the similar pine-rocklands ecosystem of southern Florida (G. L. Slater unpubl. data). Nonetheless, the onset of breeding may vary annually due to weather conditions; for example, in the pine rocklands of Florida, birds tend to breed later following winters that are cool and relatively wet (e.g., in El Niño years), and earlier when winters are warm and dry (G. L. Slater unpubl. data). The winter of 2007 on Grand Bahama did not feature any exceptional patterns in either temperature or precipitation. The breeding season of birds on Grand Bahama also may be shaped by the timing of the transition between wet and dry seasons. Birds in a dry forest on Puerto Rico did not initiate breeding until after the arrival of wet-season rains (Faaborg and Arendt 1995; W. J. Arendt pers. comm.). In 2007, significant rainfall heralding the end of the dry season was not recorded until early June (based on provisional METAR records for station MYGF at the Grand Bahama International Airport; available online at www.wunderground.com/history/airport). Thus, if pineland birds on Grand Bahama initiate breeding to coincide with the arrival of the wet season, then we may have conducted our surveys too early and consequently underestimated densities of breeding birds (although not for Brown-headed Nuthatch, which was clearly in the middle of its breeding season). Finally, breeding seasons in this system may reflect the divergent origins of the avifauna. Species with a relatively recent North American origin, such as Brown-headed Nuthatch, may initiate breeding in response

to the same proximate factors that trigger the onset of reproduction in similar North American species, whereas species with an Antillean affinity, such as Western Spindalis, may initiate breeding in response to an entirely different suite of environmental forces. Much remains unknown about avian breeding seasons in Caribbean pine forests, and refining the optimal sampling time for surveying breeding populations of pineland birds is a prerequisite for future efforts at population monitoring.

Third, we did not conduct surveys in the pine forests on the west end of the island (i.e., those areas west of Freeport). Approximately 2,000–3,000 ha of pine forest occur west of Freeport. These pine forests have been fragmented by roads and residential development, and their structure and composition affected by altered fire regimes, human activity, and hurricanes. These pine forests are generally considered to support relatively low abundances of pineland bird species, although no published data are available to support this contention. By extending results obtained in the more intact eastern pinelands to the west end pinelands, we may have introduced bias into our estimates of population size—presumably overestimating total population size by assuming that densities obtained in the eastern pinelands applied to the west end. However, given that pinelands west of Freeport account for a relatively small proportion of the island's total area of pineland, we suspect that any bias introduced by excluding west end pinelands is small.

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 Bahama Warbler and Brown-headed Nuthatch, should be the focus of conservation and management efforts. Unfortunately, based on present knowledge, the remaining population of Brown-headed Nuthatches on Grand Bahama is concentrated within the central portion of the island's pine forests, which are also slated for large-scale residential development.

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