Research Paper

Variation in responses to interspecific vocalizations among sister taxa of the Sittidae: imminent extinction of a cryptic species on Grand Bahama Island?

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ABSTRACT. We conducted playback-response experiments to assess whether the Brown-headed Nuthatch (*Sitta pusilla*) population found on Grand Bahama Island might be a distinct and critically endangered species. In one experiment, Brown-headed Nuthatch individuals in north Florida were presented with calls from: (1) a male conspecific in North Carolina; (2) a male recorded on Grand Bahama Island; (3) a male Pygmy Nuthatch (*S. pygmae*), a western congener; and (4) a male House Wren (*Troglodytes aedon*), which occurs in a different avian family (Troglodytidae). Vocalizations were broadcast at 20 locations, and detection and the proximity with which individuals approached the speaker were quantified. Nuthatches were detected at 0.72 (± 0.02; mean ± standard deviation) of trials where conspecific vocalizations were used, but were only detected half as frequently 0.27–0.30 (± 0.04) when Bahama Nuthatch and Pygmy Nuthatch vocalizations were used. Detections were least likely when House Wren vocalizations were used (0.15 ± 0.11). Nuthatches also approached the playback device more closely when North Carolina vocalizations were used. In a second playback assessment conducted in the Bahamas, males were three times more likely to respond when calls of a Bahama male were used versus calls of males in Florida. We also analyzed spectrograms of the two-syllable call notes produced by Bahama (*N* = 1) and continental (*N* = 10) males. The Bahama call has a higher peak frequency (6.1 vs. 4.8 kHz ± 0.6) and a slurred descent that extends over a broader frequency range (4.5 vs. 2.0 kHz). Results suggest that vocalizations of the Bahama population have diverged significantly and may affect interactions if the populations were to come into contact. Other genetic and morphological assessments also point to significant differences and support recognition of the Bahama Nuthatch as an independent species that may now be extinct.

Variation des réponses aux vocalisations interspécifiques parmi les taxons parents des Sittidae : disparition imminente d'une espèce cryptique sur l'île de Grand Bahama ?

RÉSUMÉ. Nous avons mené des expériences de réponses à des enregistrements de chant pour évaluer si la population de Sittelles à tête brune (*Sitta pusilla*) présente sur l'île de Grand Bahama pourrait être une espèce distincte et en voie de disparition critique. Comme première expérience, nous avons fait jouer les enregistrements suivants à des individus de Sittelle à tête brune du nord de la Floride : (1) un mâle conspécifique de Caroline du Nord; (2) un mâle enregistré sur l'île de Grand Bahama; (3) une Sittelle pygmée mâle (*S. pygmae*), un congénère occidental; et (4) un Troglodyte familier mâle (*Troglodytes aedon*), qui fait partie d'une famille aviaire différente (Troglodytidae). Les enregistrements ont été diffusés à 20 sites, et la détection et la proximité avec laquelle les individus se sont approchés du haut-parleur ont été quantifiées. Les sittelles ont été détectées dans une proportion de 0,72 (± 0,02; moyenne ± écart type) lors d'essais où des enregistrements de conspécifiques ont été utilisés, mais ont été détectées deux fois moins souvent, soit 0,27-0,30 (± 0,04) lorsque des enregistrements de sittelle des Bahamas et de Sittelle pygmée ont été utilisés. La proportion de détections était plus faible lorsque des enregistrements de troglodytes étaient utilisés (0,15 ± 0,11). Les sittelles se sont également rapprochées davantage du haut-parleur lorsque des enregistrements de Caroline du Nord étaient utilisés. Lors d'une deuxième expérience effectuée aux Bahamas, les mâles ont été trois fois plus susceptibles de répondre aux enregistrements d'un mâle des Bahamas qu'à ceux d'un mâle de Floride. Nous avons aussi analysé les spectrogrammes des cris de deux syllabes produits par les mâles des Bahamas (N = 1) et du continent (N = 10). Le cri des Bahamas a une fréquence de crête plus élevée (6,1 vs. 4,8 kHz ± 0,6) et une descente qui s'étend sur une gamme de fréquences plus large (4,5 vs. 2,0 kHz). Nos résultats laissent entendre que les vocalisations de la population des Bahamas ont divergé de manière importante et pourraient affecter les interactions si les populations entraient en contact. D'autres évaluations génétiques et morphologiques indiquent aussi des différences considérables et soutiennent la reconnaissance de la sittelle des Bahamas comme une espèce indépendante qui pourrait maintenant être disparue.

Key Words: *allopatric populations; Bahama Nuthatch; Brown-headed Nuthatch; conspecific recognition; island populations; playback experiment; species limits*

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INTRODUCTION

Responses to recorded vocalizations are regularly used to assess species limits for closely related avian taxa (Freeman and Montgomery 2017, Isler et al. 2007). Avian vocalizations are a key component of mate acquisition and territory defense, and even subtle differences in the vocalizations produced by individuals in a population have the capacity to reduce conspecific recognition and enhance reproductive isolation (Irwin et al. 2001). Compared to sympatric populations, geographically isolated bird populations consistently exhibit stronger divergences in their responses to recorded songs from other isolated populations. Distinctive vocalizations have also been shown to prevent hybridization in closely related taxa that are otherwise capable of producing viable offspring (Baker and Boylan 1999).

The Sittidae of North America includes three closely related taxa that inhabit pine forests in disjunct regions. The Pygmy Nuthatch (*Sitta pygmae*) and Brown-headed Nuthatch (*S. pusilla*) occupy western and eastern pine forests of the continental United States, respectively. These taxa are listed as conspecifics in some treatments (e.g., Mayr and Short 1970) and distinct species in others (Banks et al. 2006) based on differences in morphology, ecology, vocalizations, and behavior (Norris 1958). The third disjunct taxon inhabits Grand Bahama Island and exhibits quantitative differences in morphology that some researchers have argued warrant recognition of the island population as a species (*S. insularis*) distinct from the Brown-headed Nuthatch (Hayes et al. 2004). Banks et al. (2006) argue that the data available were inconclusive on this question, whereas del Hoyo et al. (2014) list the island population as a distinct species (*S. insularis*). Given the critically endangered status of the Grand Bahama population (Hayes et al. 2004), new evaluations of this question are urgently needed.

We conducted behavioral experiments to assess the responses of continental and island populations of the Brown-headed Nuthatch to the vocalizations these populations produce. We also assessed the responses of the continental population to other related taxa. In the first assessment, we quantified the responses of nuthatches on Grand Bahama Island to recorded male vocalizations from the island population and from a continental nuthatch population. This assessment was limited to three distinct nuthatch groups discovered on Grand Bahama Island during an attempt to collect DNA in 2012 (Han et al. 2019). In a second assessment, we quantified responses of a nuthatch population in north Florida in winter to four different vocalizations: (1) conspecific male vocalizations from a geographically distinct nuthatch population in North Carolina; (2) male Pygmy Nuthatch vocalizations; (3) male vocalizations from the nuthatch population on Grand Bahama Island; and (4) vocalizations from a male House Wren (*Troglodytes aedon*), a winter visitor in the study area that is distantly related to nuthatches (all taxa are members of the superfamily Certhioidae). The members of the Sittidae assessed here are aggregated phylogenetically into a distinctive subgenus (Micrositta) that contains small, Holarctic nuthatches that inhabit coniferous forests (Matthysen 1998). Accordingly, we use Micrositta throughout to refer collectively to Pygmy Nuthatches and the continental and island populations of Brown-headed Nuthatch.

We also analyzed a suite of acoustic traits using spectrograms of recorded male vocalizations from 10 continental populations of the Brown-headed Nuthatch and compared them with similar measurements of the male vocalization recorded from the island population. This assessment included vocalizations from several populations in east-central Florida (approximately 80.98 W, 28.50 N) that were < 250 km from the Bahama population. Spectrograms from different parts of a species' range can also help to assess species limits, especially when the range is fragmented or includes island populations (Payne 1986).

METHODS

Study areas

Our assessment of the Bahama nuthatch population took place in Lucaya Estate on Grand Bahama Island (78.54 W, 26.60 N) from 12–23 July 2012. Lucaya Estates is a large (~13,000 ha) real estate venture with an extensive network of lime-rock roads but very few structures. The area is dominated by mature Caribbean pine (*Pinus caribbean*), southern bracken fern (*Pteridium aquilinum*), poisonwood (*Metopium toxiferum*), and silver palm (*Coccothrinax argentata*).

Our second playback study took place on the Wakulla unit of St. Marks National Wildlife Refuge (Wakulla County, Florida; 84.13 W, 30.14 N) from October 2017 to March 2018. The Wakulla unit consists primarily of mature pine flatwoods with accompanying hardwood swamps, coastal marshes, and riverine forests. Pine flatwoods support large numbers of nuthatches (Cox et al. 2012) and are dominated by slash pine (*Pinus elliottii*) intermixed with scattered hardwoods such as sweet gum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*), and a dense understory dominated by saw palmetto (*Serenoa repens*) and gallberry (*Ilex glabra*).

Vocalizations and field assessments on Grand Bahama Island

We located nuthatches on Grand Bahama Island using the same disyllabic male Bahama nuthatch vocalization used in the trials conducted in Florida. The vocalization was played at 120 locations visited from 8:00 AM to 2:00 PM during an 8-day survey period. Sampling locations were separated by ≥ 1 km, georeferenced, and reviewed each evening to determine new areas to sample the following day. We located seven individuals in total distributed across three locations that were separated by ≥ 2 km. The individuals observed were two adult males and one adult female (first location), a single adult male (second location), and an adult male-female pair with a dependent juvenile (third location). The disyllabic Bahama nuthatch vocalization was also used in attempts to net individuals and secure DNA samples. Samples for four males were secured; samples for the females and lone juvenile were not obtained despite making repeated attempts. We marked the adult males using uniquely numbered metal bands (2.1 mm internal diameter), took basic measurements (weight and wing, bill, and tarsal lengths), and placed the bands on opposite legs for the two males captured at the first location. We then returned to each location to assess the detection of nuthatches using three different vocalizations: (1) disyllabic notes of a continental male, (2) the *schwee* call reported as distinct for the Bahama population (Hayes et al. 2004), and (3) the male Bahama

Nuthatch vocalization. Four trials using the different vocalizations were performed at each location (*N* = 12). Assessments could not be performed on separate days given the limited field time available. However, we did allow ≥ 2 h to elapse between each sampling event.

Vocalizations and field assessments in north Florida

All vocalizations (*S. pusilla, S. pygmaea,* and *T. aedon*) except the Bahama Nuthatch were downloaded from xeno-canto (https://www.xeno-canto.org/). Vocalizations of the Bahama male were extracted from a video collected on Grand Bahama Island in 2012 (P. Merritt, Hobe Sound, Florida). The Micrositta vocalizations used in playback experiments were limited to the typical disyllabic "rubber ducky" notes produced by males (Matthysen 1998). Female vocalizations for continental Micrositta can be distinguished from those of males by pitch, harshness, and the frequency with which staccato "chip" notes are used (Norris 1958, Haarap and Quinn 1996, Benedict 2008; J. Cox, *personal observation*). Sex-specific calls have not been confirmed for Bahama nuthatches based on the behavioral and DNA information used with continental populations (Benedict 2008, Cox et al. 2019), but our observations in the Bahamas suggest that similar differences exist.

Given our use of a single male recording from the Bahamas, we also used a single vocalization for other taxa in the trials conducted in north Florida. The other vocalizations were recorded in North Carolina (continental Brown-headed Nuthatch), Wyoming (Pygmy Nuthatch), and New York (House Wren). The recordings used for each trial were standardized to −3 dB using Audacity 2.2.2 software (https://www.audacityteam.org/). Vocalizations were further edited to provide consistent presentations across all taxa. The individual playback files we created each consisted of 10 s of silence (which allowed observers to prepare for encounters) followed by three iterations of 45 s of vocalizations and 15 s of silence (total sampling time = 3 min 10 s). Vocalizations were broadcast using a wireless handheld speaker placed near the base of a pine, and a detection was recorded when a nuthatch came within 30 m. All nuthatches were observed even though many were initially detected aurally.

Trials were conducted at 20 sampling stations established along a dirt road in St. Marks National Wildlife Refuge. A single random sampling station was established in suitable habitat along the road using a geographic information system. Additional stations were then added in suitable habitat ≥ 500 m apart to ensure that unique individuals were targeted (typical territory extents are 100–150 m; Cox and Slater 2007). Sampling stations were visited 12 times each between October 2017 and March 2018. Presentations of the recordings of the four taxa rotated such that each station received three presentations of each recording. The vocalization presented at the first trial conducted at a location was determined using a random number generator, and the other vocalizations presented differed on each visit such that adjacent points did not receive the same vocalizations on the day of each visit by using a preloaded sequence of vocalizations. No points were sampled after 11:30 AM. We also recorded wind speed (Beaufort scale) and cloud cover at each sample using criteria established for Breeding Bird Surveys.

We created an approach score for the individuals observed in north Florida ranging from 1 (distant) to 4 (close). The score served as a proxy for aggression and was based on the closest distance an individual approached the playback speaker. Similar response metrics in other songbirds have proven to be good surrogates for aggression (Searcy et al. 2006). The scores were: (1) the individual remained ≥ 8 m from the speaker; (2) the individual approached within 8 m of the speaker; (3) the individual descended the bole of the tree and approached within 3 m of the speaker; and (4) the individual flew directly over or landed within 1 m of the speaker.

Statistical analyses

We used single-season occupancy models to assess variation in detection probabilities in north Florida (MacKenzie et al. 2002). We removed from the analyses two sites where no nuthatches were detected to limit assessments to occupied sites. We created a set of candidate occupancy models using the package "unmarked" in R and performed analyses using RStudio (RStudio Team 2020). We specified constant occupancy in our models and allowed detection to vary in relation to three covariates: playback type, wind speed, and time of year. All covariates were treated as fixed effects. We used an information-theoretic approach to evaluate models and rank them based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Models with ΔAIC values ≤ 2 typically represent the most supported model among the candidate set (Arnold 2010). In the Bahamas, detection probabilities were based simply on the number of encounters that occurred across all visits.

We also recorded the maximum approach score elicited by the playback for each trial where nuthatches were detected in Florida. Because nuthatches are year-round residents, the individuals encountered likely were not unique, and the approach scores recorded could have been for one of the dominant males in each group. To account for this possibility, we averaged scores among trials per playback type. For example, if a bird received an approach score of 2 on one visit and an approach score of 3 on another visit, the average of 2.5 was used for this individual average score. These data were not normally distributed and were assessed for differences in the approach scores derived for different playback vocalizations using a nonparametric Kruskal-Wallis test (Kruskal and Wallace 1952). We then used a post-hoc nonparametric Dunn's multiple comparison test to assess differences between vocalization types.

The recording of the male Bahama nuthatch used here is the only such call known to us. Other nuthatch recordings from Grand Bahama Island (e.g., MC163289, Macaulay Library, Cornell University; Gerbracht 2011) have qualities similar to calls of continental females. Although we could not assess individual variation in calls from the Bahamas, we downloaded 10 disyllabic male calls from xeno-canto to assess variation in continental calls. Field playbacks had not been used in any of these recordings (Appendix 1). The continental vocalizations were collected from eight states and included three populations in central Florida. We quantified (1) the total length of the two-syllable phrase(s), (2) the lengths of each individual phrase, and (3) the interval of silence between the phrases for each vocalization. We also determined the peak frequency for each phrase using Audacity 2.2.2. Results for the multiple samples obtained from continental

populations are presented as the mean ± 1 standard deviation. We used the R package "warbleR" (Araya-Salas and Smith-Vidaurre 2017) to create spectrograms for one of the male nuthatches recorded in central Florida (XC417815) and the male recorded on Grand Bahama.

RESULTS

Grand Bahama samples
Detection of Bahama nuthatches was three times more likely to occur when the recorded voices of a Bahama male were presented compared to the recording of a conspecific male from Florida (0.83 vs. 0.25). We did not encounter Bahaman individuals when the *schwee* call described by Hayes et al. (2004) was presented. Individuals also responded more aggressively to the male Bahama vocalization, often creeping down the bole of the tree to within 1 m of the playback device. This response was consistent even though all four males had been netted and banded recently using the same vocalization.

North Florida samples
We detected Brown-headed Nuthatch individuals on 25.8% (N = 62) of the 240 trials conducted in north Florida. Of five candidate detection models, two had ΔAIC ≤ 2.0: playback type (w_i = 0.55), followed by the global model (w_i = 0.45), which contained all covariates (Table 1). The naive occupancy estimate derived from a null model with constant detection and occupancy was 0.36 ± 0.03. Brown-headed Nuthatch detection estimates were highest when the playback from the continental population was used (0.72 ± 0.02), followed by Pygmy Nuthatch (0.30 ± 0.04), Bahama Nuthatch (0.27 ± 0.03), and House Wren (0.15 ± 0.11; Fig. 1). Playback type also significantly affected approach scores (χ^2 = 16.7, df = 3, P < 0.001). Brown-headed Nuthatch consistently came closest and responded most aggressively toward conspecific vocalizations (2.1 ± 0.16), followed by Bahama Nuthatch (1.4 ± 0.19), House Wren (1.1 ± 0.13), and Pygmy Nuthatch (1.0 ± 0.00; Fig. 2). Significant differences in approaches occurred between conspecific vocalizations and all other exemplars.

Table 1. Ranked candidate models of factors affecting Brown-headed Nuthatch detection in north Florida.

| Rank	Description	Number of parameters	AIC[†]	ΔAIC	Weight	Cumulative weight
1	Playback type	5	248.6	0.00	0.55	0.55
2	Global	7	249.0	0.42	0.45	1.00
3	Wind	3	284.2	36.7	0.00	1.00
4	Null	2	286.6	38.0	0.00	1.00
5	Time of year	3	288.4	40.0	0.00	1.00

[†]Akaike Information Criterion.

Vocalization assessments
The disyllabic notes produced by Bahama and continental nuthatches differ in pitch, phrasing, and other qualities (Fig. 3). The total length of the disyllabic vocalization for the Bahama male (0.27 s) was similar to that of continental populations (0.25 ± 0.04 s), but the first syllable in the Bahama population is longer (0.16 vs. 0.12 ± 0.03 s), higher pitched (peak frequency 6.1 vs. 4.8 ± 0.6 kHz), and includes a slurred descent that extends throughout

the first phrase (Fig. 3). The interval between disyllabic phrases is similar (0.04 vs. 0.05 ± 0.01 s in continental populations), but the second syllable also has a higher peak frequency in the Bahama population (6.4 vs. 4.6 ± 0.6 kHz).

Fig. 1. Percent of Brown-headed Nuthatch responses to vocalizations of four taxa (N = 62 total detections for all taxa). Vocalizations of each taxon were broadcast 54 times, and bars represent the percentage of positive detections (± standard error) elicited by the taxon-specific vocalization. Taxa are arranged on the x-axis based on their relatedness to *Sitta pusilla* (close to more distant).
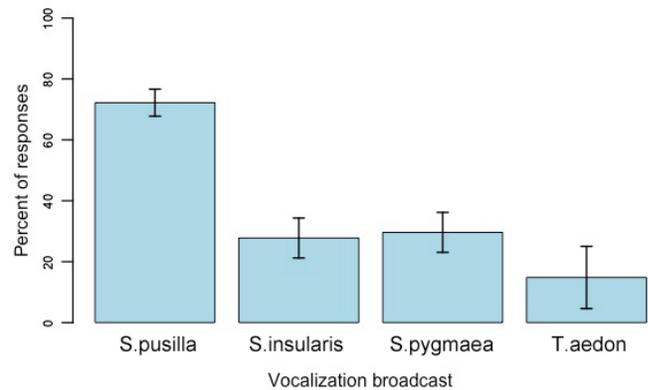
Fig. 2. Boxplot of approach scores for all positive detections of Brown-headed Nuthatch individuals to taxon-specific vocalizations (N = 62 responses). The midline represents the median approach score; lower and upper lines represent the first and third quartiles, respectively. Vertical lines represent the maximum and minimum values, and the dots indicate outliers.
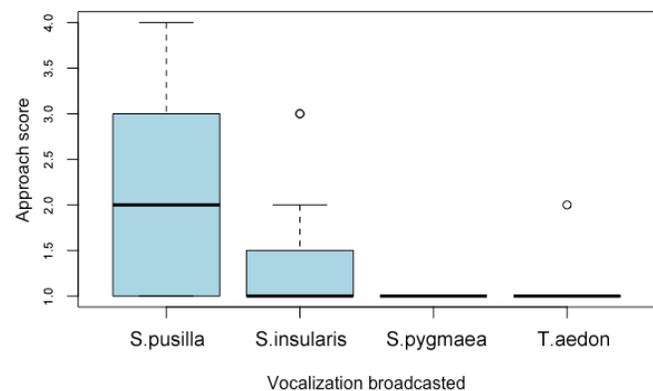

DISCUSSION

Species limits are rarely simple
A recent assessment by Barrowclough et al. (2016) suggests that the taxonomic methods applied to birds could underestimate the diversity of species by a factor of two or more. Avian systematics,

Fig. 3. Spectrograms of the disyllabic vocalizations of the Brown-headed Nuthatch produced by a male on Grand Bahama Island (A) and a male in east central Florida (B).
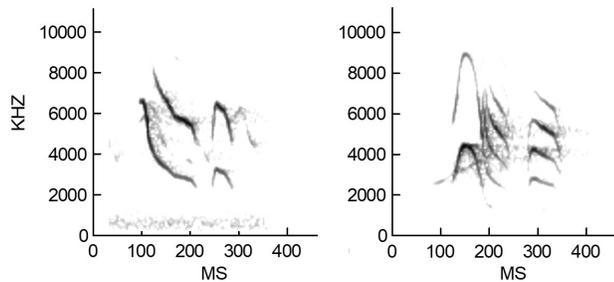
including assessments of the Bahama nuthatch population (Banks et al. 2006), have relied heavily on reproductive isolation (biological species concept) to distinguish unique species; other methods consider the presence of a common ancestor coupled with statistical differences in genetic structure, morphology, and ethology (phylogenetic species concept). Variation in the methods used for designating unique species have far-reaching implications and have led some researchers to suggest that conflicting methods may cause anarchy in efforts to conserve rare birds (Garnett and Christidis 2017).

Reproductive isolation is difficult to prove for these members of the Micrositta, but differences in morphology, genetics, and vocalizations documented for the Bahama nuthatch population are similar to those used to distinguish the two continental populations (American Ornithologists' Union 1983). Nuthatches in the Bahamas have shorter wings and longer bills than other Micrositta in North America (Hayes et al. 2004). A reduction in wing length occurs regularly among island birds and has been used elsewhere to ascribe island populations with distinctive taxonomic status (Wright et al. 2016). Similar morphological differences also were used recently to recognize the Bahama Warbler (*Setophaga flavescens*) as a distinct species (McKay et al. 2010) from the continental Yellow-throated Warbler (*S. dominica*).

Consistent differences among three Micrositta

The variation in responses of Brown-headed Nuthatch individuals in north Florida also followed a taxonomic gradient that was (1) generally weakest in response to a distantly related wren, (2) weak to modest in response to disjunct populations of Micrositta, and (3) strongest in response to another continental population of *S. pusilla*. Similar to Hayes et al. (2004), we also found a weak response among a small number of Bahama individuals when vocalizations of a continental Brown-headed Nuthatch were presented in addition to similar morphometric differences among the birds we captured. Our procedures suffered from some unavoidable pseudoreplication given the single male vocalization we used for the Bahama population, but recent evaluations suggest that this issue often changes the magnitude but not the direction of responses (Parker et al. 2018). We did not observe a strong response to the *schwee* call when it was presented

to Bahama nuthatches. This could reflect unknown seasonal factors or the context in which it was presented. This call also may not be distinctive because it sounds similar to juvenile begging notes and solicitation vocalizations that have been observed in one well-studied continental population (Cox and Slater 2007, Cox et al. 2019).

Significant genetic differences have also been documented for the Bahama nuthatch population. Han et al. (2019) reported moderate to high levels of genetic differentiation when comparing Bahama populations to 12 populations in Florida. Heterozygosity was lower in the Bahama population (0.39 vs. 0.75), and pairwise estimates of allelic differentiation (Jost's *D*; Han et al. 2019) showed moderate to high levels of differentiation in pairwise comparisons with the mainland populations (0.38 ± 0.02 for Bahama samples vs. 0.15 ± 0.02 for the most distinct mainland populations). In a separate assessment of mitochondrial DNA, mean sequence divergence between the two populations was found to be 1.4%, with two nonsynonymous substitutions (Lloyd et al. 2008).

Other indirect measures also suggest that a long period of reproductive isolation has elapsed. If gene flow were taking place with any regularity, we might expect populations along the east coast of Florida to be most similar to nuthatches in the Bahamas based on their closer proximity (approximately 200 km). Based on allelic diversity, the closest mainland population assessed by Han et al. (2019) on the east coast of Florida was the least similar to Bahama nuthatches. Furthermore, if dispersal or immigration were common, we might also expect nuthatches to have colonized other islands in the Bahamas instead of showing the opposite trend of disappearing from every island except Grand Bahama (Steadman and Franklin 2015).

Taxonomic assessments perforce attempt to assess a complex continuous process (speciation) in a dichotomous manner, but recognition of *S. insularis* as a distinct species (del Hoyo et al. 2014) seems to be supported as well as the recognition of *S. pygmae* and *S. pusilla* (American Ornithologists' Union 1983). All taxa have distinctive voices and behaviors, recognizable morphological and genetic differences, and have been isolated for long periods. Furthermore, the Bahama population warrants greater attention soon because its evolutionary history may be coming to an end. Emlen (1977) found the nuthatch to be common in the mid-1970s, but fewer than eight individuals have been seen in recent surveys (this study; M. Zeko, *personal communication*). North America's Micrositta also exhibit complex behaviors that include cooperative breeding (Norris 1958), tool usage (Gray et al. 2016), social grooming (Cox 2012), seed caching (Norris 1958), communal roosting (Norris 1958), and male:female duets (Benedict 2008; J. Cox, *personal observation*). Little is known about how novel environments of the Bahamas have affected these and other complex behaviors, but behavioral variation likely exists as well. Some Micrositta also excavate cavities annually that are used by secondary cavity-nesting birds. The potential extinction of a small, primary excavator could influence dynamics of the cavity-nesting community on the island.

Forest conditions on Grand Bahama Island have changed since our visit in 2012 following the passage of several devastating hurricanes, but conditions during our visit looked similar to the conditions that Emlen (1977) described years earlier. We noted

recent storm damage to pines over approximately 15% of Lucaya Estates in 2012, but several thousand hectares looked much like the photos provided by Emlen (1977) and suggested to us that suitable habitat was still available over large areas. The precarious status of the Bahama population could relate instead to the nuthatch's specialized habitat needs, limited dispersal capabilities, and susceptibility to stochastic events, rather than the anthropogenic changes often adduced for avian extinctions. Emlen (1977) listed the nuthatch and four other Bahama species as habitat specialists. The nuthatch is the only specialist among those five species that currently is restricted to a single island. Loss of the nuthatch and other pineland specialists also has occurred on other islands in the archipelago. Based on fossil records, Steadman and Franklin (2015) found that the nuthatch, Eastern Bluebird (*Sialis sialis*), and Pine Warbler (*Dendroica pinus*) disappeared from Abacco before humans arrived on the archipelago (Steadman and Franklin 2017).

The International Union for Conservation of Nature recognizes the nuthatch population on Grand Bahama as critically endangered, and legal definitions of endangered species regularly include populations and subspecies (Haig et al. 2006). Designation of the Bahama Nuthatch as a distinct species is not a requirement for stronger conservation efforts, but it should help underscore the need for additional work on a unique population that has experienced a distinct and separate evolutionary history. New surveys should be implemented as soon as possible to determine the current population status and habitat conditions following the record-breaking hurricane that devastated Grand Bahama Island in September 2019. If territorial pairs are discovered, efforts should be taken to make any nesting attempts as successful as possible. At the same time, husbandry techniques could be assessed using the Brown-headed Nuthatch as a surrogate. A working group should also be organized to address future conservation and monitoring needs.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1646

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Appendix 1. Xeno-canto files used to quantify characteristics of the disyllabic male vocalizations of continental Brown-headed Nuthatches (*Sitta pusilla*).

Catalog Number	Location	State
XC192108	Hal Scott Preserve	FL
XC314876	Cottonton	AL
XC182614	Liberty County	GA
XC173363	Tosohatchee Wildlife Management Area	FL
XC135504	Cove Park	TN
XC102138	Three Lakes Widlife Management Area	FL
XC64533	Splinter Bog State Forest	AL
XC33526	Ouachita National Forest	AK
XC543265	Lawrence	AL
XC543265	Piedmont National Wildlife Refuge	GA