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Cover: The Bahama Yellow-throated Warbler (*Dendroica "dominica" flavescens*) shown foraging on Caribbean Pine in native forests in the Bahamas. Bark foraging is one of many genetic, plumage and behavioral features used by McKay et al. (pages 932–939) to argue for species status for the Bahama Yellow-throated Warbler. Mixed media painting © H. Douglas Pratt 2010.



EVIDENCE FOR THE SPECIES STATUS OF THE BAHAMA YELLOW-THROATED WARBLER (*DENDROICA "DOMINICA" FLAVESCENS*)

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ABSTRACT.—The Bahama subspecies of the Yellow-throated Warbler (*Dendroica dominica flavescens*) was originally described as a species. However, it was later reclassified as a subspecies, in part because the trinomial was considered useful for demonstrating relationships. Although *flavescens* has been widely reported as diagnostic in plumage and distinctive in ecology, it has remained a subspecies of *D. dominica*, perhaps because of the notion that its song is similar to that of continental *dominica*. We investigated the taxonomic status of *flavescens* by examining morphological, song, and genetic data. We found statistically significant differences between *flavescens* and continental *dominica* in wing chord and in bill, tarsus, and tail lengths. Discriminant function analysis correctly predicted 100% of *flavescens* individuals using morphological characters. Contrary to earlier accounts, we also found the ascending song of *flavescens* to be diagnosable from the descending song of continental *dominica*. Mitochondrial control-region sequence data revealed fixed differences and a 1.0% divergence between *flavescens* and continental *dominica*. Phylogenetic analysis indicated that *flavescens* samples form a monophyletic group and that continental *dominica* is paraphyletic with respect to *flavescens*. This is consistent with a scenario of peripatric speciation: complete lineage sorting in the *flavescens* population but incomplete lineage sorting in the much larger continental *dominica* population. We conclude that *flavescens* be reclassified as a separate species, the Bahama Warbler (*Dendroica flavescens*). *Received 23 July 2009, accepted 13 January 2010*.

Key words: Bahama Warbler, Dendroica dominica flavescens, species limits, systematics, taxonomy, Yellow-throated Warbler.

Evidencia del Estatus de Especie para Dendroica "dominica" flavescens

RESUMEN.—La subespecie de Las Bahamas *Dendroica dominica flavescens* fue descrita originalmente como una especie. Sin embargo, fue reclasificada más tarde como una subespecie, en parte porque el trinomio fue considerado útil para demostrar relaciones. A pesar de que *flavescens* ha sido extensamente reconocida por su diferenciación en el plumaje y su ecología, ha permanecido como una subespecie de *D. dominica*, tal vez debido a la noción de que su canto es similar al de las poblaciones continentales de *D. dominica*. Investigamos el estatus taxonómico de *flavescens* examinando datos morfológicos, de canto y genéticos. Encontramos diferencias estadísticamente significativas entre *flavescens* y las poblaciones continentales de *dominica* en la longitud del ala, el pico, el tarso y la cola. Un análisis de función discriminante basado en datos morfológicos clasificó correctamente el 100% de los individuos de *flavescens*. De manera contraria a los hallazgos previos, también encontramos que el canto ascendente de *flavescens* es distinguible del canto descendente de las poblaciones continentales de *dominica*. Los análisis filogenéticos indicaron que las muestras de *flavescens* forman un grupo monofilético y que la forma continental de *dominica* es parafilética con relación *flavescens*. Esto concuerda con un escenario de especiación peripátrica: con purificación completa de linajes en *flavescens* pero incompleta en la población continental de *dominica*, que es mucho mayor. Concluimos que *flavescens* satisface el requerimiento de tanto el concepto biológico como el concepto filogenético de especia distina, pendroica flavescens.

CONSERVATION BIOLOGY DEPENDS critically on good taxonomy to properly list, prioritize, and manage biodiversity, and as we enter into the sixth mass extinction in Earth's history, there has never been a greater need for taxonomic study. Subspecies are considered objects of conservation (Haig et al. 2006), but it is well known that subspecies are often arbitrary divisions of character clines rather than discrete entities (Wilson and Brown 1953). This is particularly true of bird subspecies, and it can make them misleading

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targets for conservation (Zink 2004). In light of increasing threats to biodiversity, there is a pressing need to reexamine avian subspecies to ensure that they correspond to discrete entities. If they are found to be good subspecies, the next step should be to determine whether they warrant species status on the basis of generally accepted criteria. This is especially important for threatened taxa because the conservation priority of a taxon is higher if it is named a species rather than a subspecies.

Island taxa are particularly vulnerable to extinction because they typically have relatively small distributions and population sizes (Şekercioğlu et al. 2004). In birds, molecular studies have shown that island subspecies are significantly more likely to correspond to historical lineages or "phylogroups" than temperate continental subspecies (Phillimore and Owens 2006). Thus, island subspecies should be a priority for taxonomic reappraisal. The Bahama archipelago hosts several distinct forms of species that inhabit continental North America, and although some of these are considered subspecies, few have been subjected to modern analysis.

The Bahama subspecies of the Yellow-throated Warbler (Dendroica dominica flavescens) is among the most distinctive Bahamian subspecies. Endemic to the islands of Abaco and Grand Bahama, this taxon was originally described by Todd (1909) as a new species, the Yellow-breasted Warbler (D. flavescens). However, it was later incorporated into D. dominica by Bond (1930), who felt that the trinomial was useful in revealing a close relationship between the island and continental forms. Although subsequent authors have followed Bond's taxonomy, it has been recognized that *flavescens* differs markedly from continental *D. dominica* in morphology, behavior, and ecology (Curson et al. 1994, Hall 1996). It has been widely reported, however, that *flavescens* sings a song similar to that of dominica (Todd and Worthington 1911, Curson et al. 1994), and this is perhaps a primary reason why *flavescens* has not been elevated to species status. McKay (2008b, 2009) recently showed that the three continental subspecies of the Yellowthroated Warbler are not discrete entities and, therefore, are not defensible subspecies. Here, we investigate whether *flavescens* differs discretely from continental D. dominica (hereafter "dominica" refers to all three continental subspecies) and consider whether it should be elevated to species status. We begin by reviewing the plumage and ecological differences between *flavescens* and *domi*nica and then present new analyses of morphometrics, song, and genetics.

Plumage.—Curson et al. (1994) and Hall (1996) both noted that *flavescens* can be unambiguously distinguished from *dominica* by plumage alone. The yellow on the throat of *flavescens* extends through the belly, giving it a mostly uniform yellow ventral surface. This is in contrast to the strong demarcation between white belly and yellow breast in continental *dominica* (Fig. 1). In head pattern, the supraloral is thinner and paler yellow, on average, in *flavescens* than in *dominica*. The white neck patch of *flavescens* is smaller (sometimes reduced to a thin line) and dull white, which generates a less contrasted and more subdued face pattern. The supercilium is thin, shortened, and frequently broken. Dorsal portions of the adult's head and back are dull gray tinged with brown, and the back and flanks of immatures and fresh-plumaged adults are tinged with buff. The forehead of adult male *flavescens* shows less black than *dominica*. The wing bars are shorter, thinner,



FIG. 1. Photograph of three *Dendroica dominica flavescens* (left) and three continental *D. dominica* (right) specimens illustrating plumage differences of the throat and belly. In *D. d. flavescens* the yellow extends into the belly, where it fades, whereas in *D. dominica* the yellow comes to a clean demarcation forming a distinct border with the white belly.

and less contrasting. The undertail coverts are more strongly and consistently streaked, and the inner webs of the rectrices have much less white than in *dominica*. Like many subtropical woodwarblers, *flavescens* is less sexually dimorphic in plumage than the temperate *dominica*.

Ecology.—Ecologically, *dominica* regularly breeds in several habitats, including Loblolly Pine (*Pinus taeda*), bald cypress (*Taxodium* spp.), and sycamore (*Platanus* spp.) forests (Hall 1996). By contrast, *flavescens* appears to be much more specialized and breeds only in mature Caribbean Pine (*Pinus caribaea*) forests, though the variety of distinct habitats is more limited on the Bahamas. Caribbean Pine forests consist of an open overstory and a low understory of woody shrubs with small areas of mixed broadleaf coppice throughout (Correll and Correll 1982), and *flavescens* appears to be confined to the pine trunks and overstory. Furthermore, *flavescens* remains in Caribbean pine forests year-round. This is in contrast to wintering *dominica* in the Bahamas, which is not restricted to pines and is found throughout the West Indies in various habitats, including forests, mangroves, landscaped areas, and stands of planted Coconut Palms (*Cocos nucifera*).

METHODS

Morphometrics.—Bill length, bill width, bill depth, tarsus length, wing chord, and tail length were measured from *flavescens* study skins from Abaco (n = 9) and Grand Bahama (n = 12) following the protocol of McKay (2008b). These data were compared with the same measurements taken from 98 specimens of *D. dominica* collected from across the continental range (these are the same specimens from McKay 2008b). The *dominica* specimens are deposited in the J.F. Bell Museum of Natural History at the University of Minnesota (BMNH46327–415). Information on the *flavescens* specimens used can be found in the Acknowledgments. B.D.M. took all the measurements used in our study.

Principal component analysis was used to describe morphological differences between *flavescens* and continental *dominica*. Male samples were grouped as either continental *dominica* or *flavescens*, and *t*-tests for each of the six characters were performed. We also applied a stepwise discriminant function analysis using all six morphological characters. Prior probabilities were computed from group sizes. The leave-one-out method was used to cross-validate the accuracy of group assignments. We used SPSS, version 17.0 (SPSS, Chicago, Illinois), for Windows for all analyses and considered $P \ge 0.05$ statistically significant.

Song.-We purchased recordings of dominica from the Borror Laboratory of Bioacoustics (The Ohio State University, Columbus) and the Macaulay Library (Cornell Lab of Ornithology, Ithaca, New York). We obtained our own recordings of *flavescens* from Grand Bahama and Great Abaco, Bahamas. Additional flavescens recordings from Grand Bahama were provided by the Macaulay Library and Mark W. Oberle (University of Washington, Seattle). We used only those recordings that unambiguously belonged to the purported taxon and, on the basis of date and location, appeared to be distinct individuals. Because recordings were made using a wide range of microphones and recorders, some unknown to us, we do not provide equipment details here. Our final sample of 69 songs varied considerably by time of year (dominica well represented across the continental range, n = 58, March-November; *flavescens*, n = 11, January–July) and time of day; thus, the songs analyzed presumably encompassed a wide range of variation. Type B songs (Spector 1992) exist in continental dominica, though they are rare (McKay 2008a); we restricted our analysis to the common Type A songs.

We used RAVEN, version 1.2.1 (Cornell Lab of Ornithology), for Windows to produce oscillograms and spectrograms of individual songs and to analyze quantitative characters. Recordings were viewed on a scale of either 0–22 or 0–24 kHz, always at onehalf the original sampling frequency to avoid aliasing. Analysis was limited to the first song on each track that was distinguishable from other bird vocalizations and background noise. Sound files were opened with a 512-point transformation and Hann analysis window. Sonograms were visualized at 50% brightness and contrast with averaging. For consistency, one of us (M.B.J.R.) generated all spectral measurements.

For each song, we measured a suite of spectrographic characters. We visually examined the nature of individual syllables, which could be broadly classified as simple (a single note or element), complex-joined (multiple notes or elements joined into a single continuous tracing that formed a repeated unit), or complex-detached (multiple notes separated by silence but forming a repeated unit). We counted the number of syllables per song and number of phrases per song; repeated syllables of similar appearance constituted a single phrase, and many songs consisted of two or more phrases (i.e., different repeated syllable types). For the entire song, we recorded the lowest and highest frequencies (Hz) and computed delta frequency (Hz), the difference between the two frequencies. We also recorded the lowest and highest frequencies of the first syllable. We determined the duration (in seconds) of the entire song and the mean duration (in seconds) of all syllables, of all intervals between syllables, and of all syllables plus their subsequent interval. Pitch typically changed during successive syllables, and we measured this as a dichotomous character

(ascending or descending) for the entire song, using calculation of slopes (positive or negative) derived from the middle frequency of successive syllables. Because the pitch frequently changed in the opposite direction for the final one or two syllables, we excluded those syllables when computing slopes for any songs that had such a change. We recorded whether or not the pitch changed in the final one or two syllables as a trichotomous character (ascending, no change, descending), which we determined by simultaneous visual spectrographic and auditory examination. Finally, tempo changes across the entire song were recorded as a dichotomous character (accelerating or decelerating) on the basis of separately calculated slopes (decreasing or increasing) for duration of successive syllables and for duration of intervals between syllables. We chose not to analyze number or presence or absence of harmonics because recording quality (loudness) had a substantial effect.

We employed *t*-tests to compare means of the quantitative characters for the two taxa. Some characters failed to meet parametric assumptions, so nonparametric Mann-Whitney *U*-tests were also computed, but these always yielded identical results. Qualitative characters were subjected to chi-square tests. Although most chi-square tests had >20% of cells with expected frequency <5, the large samples gave us confidence in the results.

Genetics.-We obtained blood, other tissue, or toepad shavings from museum skins from seven individuals of *flavescens*. Three samples came from Abaco, and four samples came from Grand Bahama. For fresh tissue samples, we extracted whole genomic DNA following a standard phenol-chloroform protocol. We amplified and sequenced domain I of the mitochondrial control region following McKay (2009). Toepad shavings from four museum skins were obtained from the Louisiana State University Museum of Natural Science. To minimize the possibility of contamination, we extracted toepad samples in a separate building (away from any avian research) using the DNeasy Tissue Kit (Qiagen, Valencia, California). Toepad samples were amplified for a smaller (230 base pair [bp]) fragment of domain I of the control region using the primers Passerine ContRegFor (5'-TAC CTA GGA GGT GGG CGA AT-3') and Passerine ContRegRev (5'-CCC AAA CAT TAT CTC CAA AA-3'; both designed by R. T. Brumfield). We cleaned polymerase-chain-reaction products with ExoSAP-IT (USB, Cleveland, Ohio) and sequenced them with the amplification primers on an ABI 3700 automated sequencer using BigDye kit version 3.0 according to recommended protocols (Applied Biosystems, Carlsbad, California). All DNA sequences were sequenced in both directions and complementary strands were unambiguously aligned and edited using SEQUENCHER, version 4.6 (Gene Codes, Ann Arbor, Michigan). Sequences were inspected individually using the raw spectrograph data, and every point mutation was checked for authenticity. These sequences have been deposited in GenBank (GU560058-64).

We combined our seven *flavescens* sequences with continental *dominica* mtDNA sequences from a phylogeographic study of this species (McKay 2009) that included 109 individuals from 10 widely distributed geographic localities and all described continental subspecies. A maximum-likelihood phylogeny was constructed using an online implementation of PHYML, version 3.0 (Guindon et al. 2005). We used the general-time-reversal substitution model with a proportion of invariable sites and a gammadistributed rate heterogeneity of four rate categories (GTR+I+G₄).



FIG. 2. A bivariate plot of principal components 1 and 2 from a principal component analysis that describes morphological variation of the *flavescens* and *dominica* forms of the Yellow-throated Warbler. The three continental subspecies of *flavescens* are labeled separately to demonstrate that they are indistinguishable in principal component space (solid circles, *Dendroica dominica dominica*; solid squares, *D. d. albilora*; stars, *D. d. stoddardi*).

All parameter values were estimated. Clade stability was estimated with 1,000 replicates of nonparametric bootstrapping. Published *D. coronata* sequences (GenBank accessions DQ855191 and DQ855190) were included as outgroups because *D. coronata* is thought to be closely related to *D. dominica* (Lovette and Bermingham 1999).

RESULTS

Morphometrics.—Principal component analysis yielded two components that explained 63% of the total variance. There was no overlap between *flavescens* and continental *dominica* for the first principal component (Fig. 2). The first principal component (eigenvalue = 2.24) explained 37.3% of the variance, and the factor loadings indicated that birds with positive scores had long bills, tarsi, and tails, but short wing chord and narrow bills (Table 1). The second principal component (eigenvalue = 1.53) explained 25.5% of the variance and described an increasing gradient of bill length and width with tail length (Table 1). Four measurements differed significantly between *dominica* and *flavescens* (Table 2). Discriminant function analysis produced a final model with three functions (eigenvalue = 0.053) and included bill length, tarsus length, wing cord, and tail length. The overall Wilks's lambda was significant (λ = 0.232, *P* < 0.001). Classification and cross-validation both

TABLE 1. Factor loadings for the first two principal components (PC) derived from morphological measurements of the *flavescens* and *dominica* forms of the Yellow-throated Warbler.

	PC1	PC2
Bill length	0.814	0.268
Bill width	-0.596	0.612
Bill depth	-0.296	0.844
Tarsus length	0.659	0.338
Wing chord	-0.685	0.095
Tail length	0.481	0.496

indicated that 100% of *flavescens* individuals were assigned correctly. This was true whether or not females were included.

Song.—Representative songs are depicted in Figure 3, in which the song of a closely related congener in the Bahamas is also provided for comparison. Songs consisted of a series of 6 to 14 syllables in 1 to 5 evenly spaced phrases within the range of 2,400–8,510 Hz. The songs of most individuals of both taxa consisted entirely of complex–joined syllables, though several *flavescens* individuals had primarily complex–detached syllables, and one or several complex–detached or simple syllables were occasionally present in both taxa. Initial syllables were relatively quiet, and subsequent syllables usually increased in loudness, though this was not quantified.

Eight of the 11 quantitative characters (Table 3) differed significantly between taxa ($P \ge 0.020$). One of these characters, highest frequency of the first syllable, was diagnostic for *flavescens* in that it was always lower-pitched than, and did not overlap, that of *dominica*. The songs of *flavescens* were generally of shorter duration and included fewer syllables that were briefer in duration and of lower frequencies.

Three of the four qualitative characters (Table 3) also differed between taxa. Successive syllables of *flavescens* always ascended in pitch, whereas those of *dominica* always descended in pitch (P< 0.001); thus, this character was also diagnostic. The change in pitch during the song often reversed in the final syllable or two (Fig. 3). For *dominica*, roughly half of the songs abruptly increased in pitch, with the final syllables being higher or the final syllable slurring markedly upward, or both. By contrast, the final syllable or two of Bahamas *flavescens* usually decreased in pitch, leading to a marked subspecies difference (P < 0.001). The majority of songs, regardless of taxon, accelerated in tempo (Table 3). Both

TABLE 2. Comparisons of morphological character measurements (mm; means \pm SE) of male *dominica* (including all three continental subspecies) and *flavescens* specimens of the Yellow-throated Warbler.

Character	dominica $(n = 88)$	flavescens $(n = 10)$	t	Р
Bill length	9.59 ± 0.08	11.49 ± 0.22	-7.65	<0.001
Bill width	3.04 ± 0.04	2.87 ± 0.04	1.38	0.724
Bill depth	3.28 ± 0.02	3.40 ± 0.05	-1.63	0.873
Tarsus length	16.8 ± 0.05	18.1 ± 0.28	-6.06	< 0.001
Wing chord	67.3 ± 0.25	64.0 ± 0.66	6.05	< 0.001
Tail length	49.4 ± 0.15	52.7 ± 0.66	-6.46	< 0.001

TABLE 3. Song characters (means \pm SE and range, or proportion) of continental *dominica* (including two continental subspecies) and *flavescens* forms of the Yellow-throated Warbler. Changes in pitch (ascending or descending) and tempo (increasing or decreasing) are dichotomous characters; change in pitch of final syllable is trichotomous.

Song character	dominica $(n = 58)$	<i>flavescens</i> ($n = 11$)	Test statistic	Р
Number of syllables	9.0±0.2 (6-14)	7.3 ± 0.3 (6-9)	t = 3.28, df = 67	0.002
Number of phrases	$2.7 \pm 0.2 (1-5)$	$2.1 \pm 0.1 \ (2-3)$	t = 1.68, df = 67	0.099
Song lowest frequency (Hz)	2,912 ± 30 (2,409–3,574)	2,999 ± 82 (2,400-3,295)	t = -1.13, df = 67	0.262
Song highest frequency (Hz)	7,057 ± 66 (5,643-8,510)	5,519 ± 154 (4,741–6,188)	t = 9.26	< 0.001
Song delta frequency (Hz)	4,142 ± 72 (2,865–5,754)	2,556 ± 199 (1,729–3,688)	t = 8.49, df = 67	< 0.001
First syllable lowest frequency (Hz)	4,262 ± 67 (3,177-6,162)	3,124 ± 117 (2,227–3,803)	t = 7.05, df = 67	< 0.001
First syllable highest frequency (Hz)	6,479 ± 60 (5,479–7,782)	4,140 ± 88 (3,790-4,668)	t = 16.30, df = 67	< 0.001
Song duration (s)	$2.258 \pm 0.048 (1.529 - 3.261)$	1.730 ± 0.063 (1.373-2.011)	t = 4.63, df = 67	< 0.001
Mean duration of syllables (s)	$0.198 \pm 0.004 \ (0.143 - 0.291)$	$0.177 \pm 0.008 (0.136 - 0.220)$	t = 2.38, df = 67	0.020
Mean interval between syllables (s)	$0.062 \pm 0.002 \ (0.038 - 0.097)$	$0.075 \pm 0.004 (0.053 - 0.107)$	t = -2.72, df = 67	0.008
Mean duration of syllables and subsequent intervals (s)	$0.264 \pm 0.004 \ (0.197 - 0.353)$	$0.257 \pm 0.006 \ (0.224 - 0.283)$	t = 0.73, df = 67	0.468
Pitch descending (by middle frequency [%])	100.0	0.0	$\chi^2 = 69.00$, df = 1	< 0.001
Pitch change in final 1 or 2 syllables			, , , , , , , , , , , , , , , , , , ,	
Ascending pitch (%)	53.4	0.0		
No change (%)	46.6	54.5	$\chi^2 = 32.37$, df = 2	< 0.001
Descending pitch (%)	0.0	45.5		
Tempo accelerating by				
Syllables (%)	69.0	81.8	$\chi^2 = 0.74$, df = 1	0.389
Intervals between syllables (%)	98.3	81.8	$\chi^2 = 6.02$, df = 1	0.014



FIG. 3. Representative song spectrograms of continental (*Dendroica dominica dominica*, BLB 4997) and Bahamas (*D. d. flavescens*, WKH GB-06-34) Yellow-throated Warblers and the Bahamas population of Olive-capped Warblers (*D. pityophila*, WKH GB-06-54). Individual syllables are indicated by letters corresponding to type; syllables of the same type constitute a phrase. Note the lower first-syllable frequency of *flavescens* compared with *dominica* and the ascending rather than descending pitch of successive syllables, the tendency toward pitch changes in the final one or two syllables (*dominica* ascending, *flavescens* descending), the tendency toward increased loudness and accelerating tempo, and the similarity of continental *dominica* and *D. pityophila*. (Song sources: BLB = Borror Laboratory of Bioacoustics, WKH = William K. Hayes collection.)

the syllables and the intervals between syllables usually became briefer as the song progressed, but only the latter differed significantly between taxa (P = 0.014). The intervals of *dominica* nearly always accelerated, whereas those of *flavescens* accelerated less often. Syllables and syllable intervals often had contrasting patterns in both *dominica* and *flavescens*; in 19 cases (27.5%) the syllables decelerated while the intervals accelerated, and in two cases (2.9%) the syllables accelerated while the intervals decelerated.

Genetics.—We obtained 399 bp of control-region sequence from the three fresh samples and 230 bp of control-region sequence from the four toepad samples. A single haplotype was uncovered for all individuals. This *flavescens* haplotype differed from *dominica* haplotypes by four fixed nucleotide positions (1.0%). No polymorphisms were shared between *flavescens* and *dominica*. Maximum-likelihood analysis produced a tree largely characterized by unresolved branches and low overall bootstrap support. However, the seven *flavescens* sequences formed a highly supported clade that was embedded within the continental *dominica* sequences, rendering *dominica* paraphyletic with respect to *flavescens* (Fig. 4).

DISCUSSION

Consistent differences in morphology, song, and genetics distinguish *flavescens* from *dominica*. In morphology, several characters differ significantly between *flavescens* and *dominica*. For example, bill length is longer in *flavescens* and, indeed, *flavescens* has the longest bill of any Parulid warbler. In continental *dominica*, bill length increases clinally from west to east (McKay 2008b), despite the fact that there is likely high gene flow across the continental population (McKay 2009). This suggests that selection acts against



FIG. 4. Maximum-likelihood analysis of Yellow-throated Warbler controlregion sequences that demonstrate that individuals of *flavescens* form a highly supported clade that is embedded within continental *dominica*. Black circles represent continental individuals (of the subspecies *dominica, albilora, or stoddardi*); gray squares represent individuals of the Bahama endemic subspecies *flavescens*. Branch lengths are proportional to sequence divergence. Only bootstrap values >70 are shown. The bold arrow at the base of the tree leads to the outgroup.

the homogenizing forces of gene flow to maintain bill-length differences in *dominica*. Bill length may also be under strong selection in *flavescens*. The bill of the Brown-headed Nuthatch (*Sitta pusilla*) on Grand Bahama is also much longer than that of continental populations (Hayes et al. 2004). Therefore, in both species a long bill is perhaps an adaptation to the more specialized requirements of foraging in the Caribbean pine forest. Wing length is significantly shorter in *flavescens*, possibly in association with its nonmigratory habits (Mönkkönen 1995). Tail length and tarsus length are both significantly longer in *flavescens*, and this may be related to foraging on the trunks of trees (Emlen 1981). The two taxa did not overlap in principal component space, because of their complete separation on the first principal component. The second principal component, which was correlated mainly with bill depth and width and tail length, showed broad overlap of *flavescens* and *dominica*. These results indicate that the primary morphological differences between the taxa arise from the long and narrow bill, larger body size (as indicated by tarsus length), and proportionately shorter wings of *dominica*.

Contrary to early published reports (Todd and Worthington 1911), we found the song of *flavescens* to be distinct and 100% diagnosable from the song of *dominica*. Most notably, the song of flavescens ascends in pitch whereas the song of dominica descends in pitch. We think that the misunderstanding may have stemmed from a simple misidentification. The Olive-capped Warbler (D. pityophila) is a close relative of dominica and flavescens (Lovette and Bermingham 1999) that also inhabits the Caribbean Pine forests of the Bahamas. The Olive-capped Warbler sings a descending song that resembles the one sung by continental dominica (Fig. 3). In fact, we initially attempted to capture *flavescens* using playback of dominica's song but never succeeded. Only when we used its own song were we eventually successful. Interestingly, however, in four of five attempts we lured pityophila into our nets using dominica's song, which demonstrates how similar the local pityophila's song is to the continental dominica's. We suspect that early researchers in the Caribbean forest, without the aid of binoculars, mistook the song of *pityophila* for that of *flavescens*.

We found fixed differences between *flavescens* and *dominica* in mtDNA. The sequence data also shed light on the mode of speciation and suggest a scenario of peripatric speciation. Peripatric speciation occurs when a small peripheral population speciates from a larger ancestral species. Peripatric speciation could be expected to yield a paraphyletic pattern (Avise 2000). Because the effective population size of the daughter species is much smaller than that of the ancestral species, gene lineages should coalesce faster in the daughter than in the ancestral species. Thus, for a period of time following isolation the daughter species will show gene-tree monophyly but could be embedded within the ancestral species, whose gene lineages would not have had time to sort (Avise 2000). This is exactly the pattern that we observed between flavescens and dominica. Todd and Worthington (1911) speculated that *flavescens* was derived from members of *dominica* that failed to migrate and instead became resident breeders. Although current distributions and migratory patterns may be a poor predictor of past distributions, the scenario put forth by Todd and Worthington is appealing and is also a suggested mechanism of speciation in some Neotropical orioles (Kondo et al. 2008)

Taken together, differences in plumage, ecology, morphology, song, and mtDNA indicate that *flavescens* is a distinct taxonomic unit. Therefore, *flavescens* should be considered, at minimum, a good subspecies, and thus an object of conservation. This is in contrast to the three continental subspecies of Yellow-throated Warbler that were not found to be discrete entities in morphology (McKay 2008b) or mtDNA (McKay 2009). Having established that *flavescens* differs discretely from other Yellow-throated Warblers, it is important to consider whether *flavescens* should be elevated to species status. The two most commonly employed species concepts in ornithology are the phylogenetic and biological species concepts. The phylogenetic species concept requires species to be diagnosable lineages (Cracraft 1983), whereas the biological species concept requires species to be reproductively isolated (Mayr 1942). *Dendroica d. flavescens* is 100% diagnosable in plumage, song, and mtDNA and therefore qualifies as a phylogenetic species.

Because *flavescens* is allopatric, reproductive isolation cannot be directly tested, which makes it impossible to determine whether or not *flavescens* conforms to the standard for recognition as a biological species. However, in cases of allopatry, indirect evidence may be used to infer reproductive isolation. For example, song is considered a strong premating reproductive barrier in birds, so behavioral responses to song playback can be used to infer biological species status (Alström and Ranft 2003). We found that *flavescens* did not respond to playback of continental dominica's song, which suggests that female *flavescens* would not respond to the advertising songs of *dominica* if the two were to come into sympatry. This is confirmed in nature: overwintering dominica in the Bahamas begin to sing before the start of migration (B. D. Mc-Kay et al. pers. obs.). Both taxa seem to ignore each other's song during this period. Reproductive isolation between resident and overwintering populations has also been reported between D. coronata nigrifrons and D. c. auduboni in western Mexico (Milá et al. 2007). Another method of assessing the biological species status of allopatric taxa is to compare the amount of divergence between allopatric taxa with the amount of divergence between closely related sympatric species (Helbig et al. 2002). Although they are not currently listed as species, recent work has suggested that the Audubon's (D. c. auduboni) and Myrtle (D. c. coronata) subspecies of Yellow-rumped Warbler are reproductively isolated (Breisford and Irwin 2009). These two subspecies are apparently more closely related to each other (having diverged ~16,000 years ago; Milá et al. 2007) than *flavescens* is to continental *dominica*. The amount of plumage divergence within each of these pairs of taxa is comparable. Therefore, *flavescens* could be considered a biological species using the comparative method of Helbig et al. (2002).

The common name "Yellow-breasted Warbler," given by Todd (1909), might be confusing in that there is an Old World warbler, *Seicercus montis*, with that name. Therefore, given its endemism in the Bahamas, we suggest "Bahama Warbler" as an appropriate common name for *D. flavescens*.

Recent attention to Bahamian avifauna has suggested previously overlooked diversity. In addition to the Bahama Warbler, species or subspecies splits have been proposed for endangered Bahamian populations of the Cuban Parrot (*Amazona leucocephala*; Reynolds and Hayes 2009), Brown-headed Nuthatch (Hayes et al. 2004, Lloyd et al. 2008), and Greater Antillean Oriole (*Icterus dominicensis*; Price and Hayes 2009, Sturge et al. 2009). The Bahama Warbler joins these species as another bird of conservation concern. With density estimates of 3.5 individuals km⁻² (for detectability of 0.54; Lloyd et al. 2008) to 17.1 individuals km⁻² (for detectability of 0.20; Emlen 1977) on Grand Bahama, and with roughly 900–1,000 km² of pine forest remaining on Grand Bahama and Abaco combined (Allen 1996, Myers et al. 2004), one could estimate a population of 3,150–17,100 individuals. The more recent density estimate, which Lloyd et al. (2008) obtained from some of the better remaining habitat, suggests a population of no more than 3,150–3,500 individuals. The Bahama Warbler is therefore of potential conservation concern.

The Brown-headed Nuthatch, the Bahama Warbler, and the Abaco population of the Cuban Parrot are all highly dependent on the Caribbean Pine forests (Hayes 2006), which also host wintering populations of the endangered Kirtland's Warbler (*D. kirtlandii*; Haney et al. 1998) and other Neotropical migrants (Emlen 1977; Lee 1996a, b). These forests remain at high risk of further development and renewed logging. The endemic Bahama Warbler makes the need to preserve the pine forests more imperative and should reinforce ongoing efforts to conserve the Caribbean Pine ecosystem.

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