SONG CHARACTERISTICS AND SINGING BEHAVIOR OF THE MANGROVE WARBLER (*DENDROICA PETECHIA BRYANTI*)

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Abstract.—Based on recordings and observations from the Yucatan Peninsula, I present the first formal description of the song characteristics and singing behavior of the Mangrove Warbler. Male Mangrove Warblers sing multiple song types with immediate variety, and song types are shared between neighbors. Responses from a playback experiment suggested that Mangrove Warbler song functions in an intrasexual territory defense context. I compared the fine structural characteristics of songs from one subspecies of Mangrove Warbler (*Dendroica petechia bryanti*) to that of a widely studied Northern Yellow Warbler subspecies (*D. p. aestiva*). Songs from these two subspecies are significantly different in length frequency and syllabic characteristics, and principal components analysis separates their songs entirely. These results, when taken together with geographical and morphological evidence, suggest a great separation between Mangrove Warblers and Northern Yellow Warblers.

CARACTERÍSTICAS Y CONDUCTA DEL CANTO DE *DENDROICA PETECHIA BRYANTI*

Sinopsis.—Basado en grabaciones y observaciones llevadas a cabo en la Península de Yucatán, presento la descripción formal, características y conducta del canto de *Dendroica petechia bryanti*. Los machos ejecutan múltiples tipos de canto con variación inmediata y tipos de cantos compartido entre vecinos. La respuesta a grabaciones sugiere que la función del canto es una de contexto de defenza intrasexual del territorio. Comparé las características estructurales del canto del *D. p. bryanti*, con la del muy estudiado *D. p. aestiva* y encontré diferencias significativas en la longitud, frecuencia y características de las sílabas. El análisis de los componentes principales, separa ambas canciones en su totalidad. Estos resultados, cuando son tomados en conjunto con evidencia geográfica y morfológica, sugieren una amplia separación entre estos dos tipos de parúlidos.

The Yellow Warbler (*Dendroica petechia*) complex comprises a remarkably diverse group of 43 subspecies distributed throughout North America and the northern half of South America (Dunn and Garrett 1997). These subspecies, which were first combined as a single species in 1942, are presently classified into three groups on the basis of plumage characteristics (Browning 1994; American Ornithologists' Union 1998). The Mangrove Warbler group includes 16 tropical subspecies resident in mangrove forests on both Atlantic and Pacific coasts of North and South America.

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Most adult male Mangrove Warblers have an unmistakable chestnut colored hood. The Golden Warbler group encompasses 18 Caribbean resident subspecies in most of which the male's chestnut coloring is restricted to a crown patch on an otherwise yellow head. The Northern Yellow Warbler group contains nine migratory subspecies which breed throughout continental North America; most males of the Northern Yellow group lack chestnut coloring on the head (Browning 1994). While Northern Yellow Warblers have been widely studied, particularly with reference to their song system, much less is known about their tropical counterparts.

In this study I present the first formal description of song characteristics and singing behavior of the Mangrove Warbler. I compare the song system of one Mangrove Warbler subspecies (*D. p. bryanti*) to that of a widely distributed and well-studied Northern Yellow Warbler subspecies (*D. p. aestiva*). Comparisons of fine structural song characteristics are based on detailed spectrographic analysis of songs from both subspecies. To characterize patterns of song use, I present results from a playback experiment and compare songs given in response to playback to those given outside of playback. My aim was to determine whether these Yellow Warbler subspecies, as characterized by Browning (1994) on the basis of visual characteristics, show similar differences in their song characteristics and singing behavior.

METHODS

From 23 to 26 February 1999 I recorded 135 songs from seven Mangrove Warblers (15 to 35 songs from each male) in a forest of black mangrove (*Avicennia germinans*) in Celestun, Mexico. At least six of the seven focal males were paired with females, and all males were actively defending contiguous territories from neighboring individuals. Five of these males were caught and banded with unique color combinations. The two unbanded males were identified by territory location alone. Because none of the banded males was ever observed leaving his territory, I am confident that identification of unbanded individuals by location was reliable. All recordings were made between 0700 and 1300 h with an Audio-technica directional microphone (model AT815a) attached to a Sony Professional Walkman stereo cassette recorder (model WM D6C) through a Saul Mineroff pre-amplifier (model BA3).

Song Analysis.—All Mangrove Warbler songs that I recorded in the field plus seven Northern Yellow Warbler songs from the Stokes Field Guide to Bird Songs discs (Elliot et al. 1997) and 18 Northern Yellow Warbler songs from the Cornell Laboratory of Ornithology tapes (Borror and Gunn 1985; Northern Yellow Warbler recordings from northeastern U.S.A., and Manitoba and Ontario, Canada) were digitized at a sampling rate of 22050 Hz using Syrinx sound analysis software (John Burt, Ithaca, New York; Mennill and Ratcliffe 2000). For each song I measured total number of syllables, number of different types of syllables (see below), maximum and minimum frequencies, frequency of maximum amplitude (FMA) for the entire song, time from beginning of song to the point of

maximum amplitude, FMA of the last syllable, FMA of the last repetition of the first syllable, length of the entire song and length of the last syllable. Measurements were made using time and frequency cursors in Syrinx and CoolEdit 96 (Syntrillium, Phoenix, Arizona) software, and FMA measurements were made using the frequency analysis function of CoolEdit 96. For maximum and minimum frequency measurements I used a filter bandwidth of 7 Hz, and for time measurements I used a filter bandwidth of 118 Hz. This method of analysis produced the same values as measurements taken on a Kay Elemetrics DSP Sona-Graph Model 5500.

To categorize song types, I first created a library of all syllable types in the Mangrove Warbler recordings. The few syllables that were not easily categorized by visual discrimination were distinguished only if the maximum or minimum frequency range differed by ≥1000 Hz. The 40-syllable library was then used to assign each song a series of numbers representing the syllables within each song (e.g., song type A in Fig. I was represented at ''4-4-4-4-12-12-1-13-29-10''). All songs were then sorted into song types based on their syllabic composition and sequence. Songs that did not have identical syllabic composition were considered to be variations of the same song type only if the first syllable was repeated a different number of times between songs, or if multiple songs were identical except for the omission of one syllable.

Song Playback Experiment.—I conducted a playback experiment on 25 and 26 February 1999 to characterize Mangrove Warbler singing behavior and test for the presence of Type I (male-female communication) and Type II (male-male communication; Spector 1991) song categories. Fifteen playback songs were recorded from one of the five banded males who was then excluded from the playback experiment. I played the 3.0-min., 15-song stimulus to each of the remaining six males between 0700 and 1000 h, the period when most natural countersinging interactions were observed. I placed a Sony Sports speaker (model SRS-T50) halfway between the center and the edge of focal males' territories and avoided playing back to any male within an hour of playing back to his neighbor. I recorded the vocal responses of each focal male and made detailed behavioral observations of territorial males and females for 15 minutes following playback. Behavioral measures included number of playback songs given prior to the focal male's approach to within 1 meter of the speaker, time from the focal male's approach to his first song, and post-playback song rate of the focal male. I compared the first fifteen songs given by each male after playback to songs that were recorded when no other males were detected nearby or countersinging from afar.

Comparison Between Subspecies.—No differences in fine structure were found between the Northern Yellow Warbler songs sampled from the Cornell library and the Stokes field guide (one-way ANOVA; $P > 0.15$), so these data were pooled. I used principal components analysis (PCA; James and McCulloch 1990) based on the variance-covariance matrix of non-transformed data to compare all measured song features of Mangrove Warblers and Northern Yellow Warblers. Using the eigenvectors gener-

ated through this analysis, I produced principal component scores for all song measurements and plotted the values for the first two principal components. I plotted 95% confidence ellipses for Mangrove and Northern Yellow Warbler songs, which provide a graphical representation of the total variance of all song features from both groups. Based on the results from the PCA, I tested for the same direction pattern using one-tailed *t*–tests for all frequency, length, and syllable characteristics of Mangrove Warbler songs against average values for Northern Yellow Warbler songs from three other studies for which raw data were not available (Bankwitz and Thompson 1979; Spector 1991; Wittam 1995). All statistical analyses were conducted using JMP 3.2 and StatView 5.0 software. Unless otherwise indicated, all comparisons are with one-way ANOVA and average values are means ±SD.

RESULTS

Song analysis.—Features of Mangrove Warbler song are presented in Table 1. In my sample of 135 songs from seven Mangrove Warblers I found a total of 20 different song types. Two of these song types were shared between five males, four song types were shared between three males, six song types were shared between two males, and eight song types were sampled from only one male each. The average number of song types per number of songs sampled from each male was 0.34 ± 0.16, and the largest repertoire size was 10 song types from a sample of 35 songs from one individual. However, a plot of the number of songs sampled versus the number of novel song types encountered reveals that my sample size was too small to represent accurately the total repertoire size of any one individual or of the entire population. Within song bouts, song types were repeated an average of 2.04 ± 1.47 times before singing males switched song types, and the longest bout of a single song type was seven songs. The maximum song rate recorded was 4.2 songs per minute.

Curson et al. (1994) suggest that all Mangrove Warbler songs end with a higher pitched, upslurred terminal syllable except for the songs of the Galapagos subspecies (*D. p. aureola*), which terminate with a downslurred syllable. However, I found 10 song types with upslurred terminal syllables (e.g., song types C and E in Fig. 1) and 10 song types with downslurred terminal syllables (e.g., song types A, B, D and F in Fig. 1). There were six significant differences between songs with upslurred terminal syllables and those with downslurred terminal syllables ($n = 5$ males for which I recorded both upslurred and downslurred terminal syllable song types); song types with upslurred terminal syllables had significantly fewer syllable types ($t_4 = 2.94$, $P < 0.05$), a higher maximum frequency ($t_4 = -4.41$, $P < 0.05$) and minimum frequency ($t_4 = -2.92$, $P < 0.05$), a lower FMA in the first syllable ($t_4 = 2.97$, $P < 0.05$), and a longer terminal syllable ($t_4 = -3.80$, $P < 0.05$) which was, not surprisingly, higher in pitch with respect to FMA ($t_4 = -4.12$, $P < 0.05$). These two groups of songs did not differ significantly in total number of syllables, repetition index (number of syllables/number of syllable types), FMA of the entire song, length

TABLE 1.   Key features of Mangrove Warbler song (n = 135 songs from seven males) based on recordings from 23–26 February 1999 in Celestun, Mexico. Similar measurements from four studies of Northern Yellow Warbler song are compared.

Feature	Mangrove Warbler Mean ± SD	Northern Yellow Warbler Mean ± SD	One-tailed *t*-test t	P
No. of syllables	8.30 ± 1.8	6.99 ± 1.71[a]	8.38	<0.0001
No. of different syllable types	5.34 ± 1.2	2.88 ± 0.92[a]	22.93	<0.0001
Repetition Index (no. syllables/no. different syllable types)	1.58 ± 0.2	2.42 ± 1.31[a]	−35.01	<0.0001
Maximum frequency (Hz)	6514 ± 104	8775 ± 389[b]	−25.26	<0.0001
Minimum frequency (Hz)	2376 ± 31	3299 ± 260[b]	−34.08	<0.0001
FMA song (Hz)	3629 ± 45	4833 ± 385[c]	−29.18	<0.0001
FMA first syllable, last rendition (Hz)	3797 ± 41	4740 ± 508[c]	−24.24	<0.0001
FMA last syllable (Hz)	3548 ± 60	5028 ± 829[b]	−26.46	<0.0001
Length of song (seconds)	1.41 ± 0.2	1.24 ± 0.2[b]	7.83	<0.0001
Length of last syllable (seconds)	0.22 ± 0.0	0.12 ± 0.04[b]	15.72	<0.0001
Timing of maximum amplitude of song (seconds from start)	1.056 ± 0.26	0.809 ± 0.201[d]	10.11	<0.0001

[a] Bankwitz and Thompson 1979; n = 745 songs from 45 males from Michigan; df = 878.
[b] Wittam 1995; n = 40 songs from 40 males from Ontario and Manitoba; df = 173.
[c] Spector 1991; n = 86 Type II songs from 8 males from Massachusetts; df = 219.
[d] Borror and Gunn 1985, Elliot et al. 1997; n = 25 songs from multiple males from northeastern USA, Manitoba, and Ontario; df = 158.
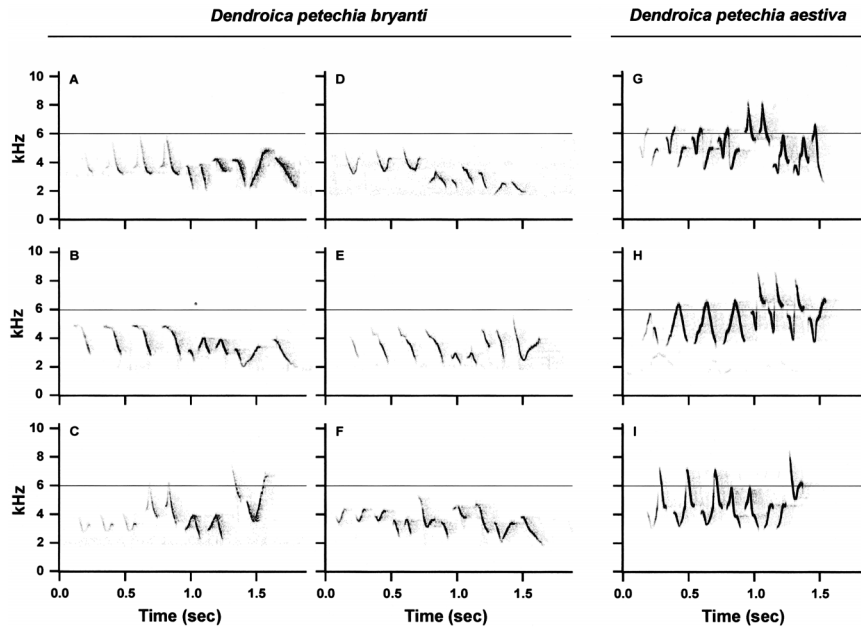
FIGURE 1.   Songs of the Mangrove Warbler and the Northern Yellow Warbler. Mangrove
            Warblers: (A–F) the six most common song types from Celestun, Mexico. Northern
            Yellow Warblers: (G–H) three common song types from Queen's University Biological
            Station, Ontario, Canada. Horizontal lines are added for reference.

of song, or the timing of maximum amplitude (seconds from start of song
to point of maximum amplitude; $P > 0.05$).

  Song Playback Experiment.—All territorial males responded to playback
by approaching to within 1 m of the speaker after playback of only 7.0 ±
3.9 songs (1.4 ± 0.8 min. after start of playback). Males gave chip notes
rapidly and regularly after initial approach (i.e., as frequently as two calls
per second) while circling and repeatedly approaching the speaker at a
distance of 0.5–5.0 m. Subjects did not begin singing until 2.43 ± 1.51
min after playback had ceased (5.43 ± 1.51 min after start of playback),
after which they sang at a low rate of 1.01 ± 0.52 songs per minute. In
four of six trials males continued to call and sing for >15 min after the
last playback stimulus, while in two cases males left the speaker location
within 5 min of playback to forage silently with females. In one trial the
focal male did not sing, but his behavior was similar to the other subjects
in all other respects. Females approached the playback speaker with males
in two of six trials, and their chipping and circling behavior was much
the same as the males' behavior.

  Songs given by Mangrove Warblers in response to playback were sig-
nificantly different from songs given in apparently non-aggressive contexts
with respect to any of the variables examined (two-tailed paired *t*-tests for

TABLE 2. Eigenvalues from principal components analysis of nontransformed song measures for Mangrove Warblers and Northern Yellow Warblers ($n = 135$ Mangrove Warbler songs and 25 Northern Yellow Warbler songs). Principal components with eigenvalues greater than 1.0 are reported.

Variable	Principal component		
	1	2	3
Number of syllables	−0.387	0.855	−0.032
Number of different syllable types	−0.765	0.329	−0.225
Maximum frequency	0.702	0.166	0.467
Minimum frequency	0.792	0.094	0.109
FMA of song	0.819	0.344	−0.061
FMA of first syllable	0.751	0.329	−0.268
FMA of last syllable	0.780	0.321	0.227
Length of song	−0.428	0.715	0.416
Length of last syllable	−0.213	−0.585	0.638
Timing of maximum amplitude of song	−0.587	0.349	0.361
Eigenvalue	4.269	2.180	1.119
Cumulative variance explained (%)	42.69	64.49	75.68

the four males for whom I had both playback response songs and non-playback songs, $P > 0.05$; two-tailed independent t-test for all songs recorded from all males in either context, $P > 0.05$). Furthermore, the proportion of songs with upslurred terminal syllables among all songs did not differ between all playback response songs versus all songs in non-aggressive contexts (two-tailed independent t-test, $t_3 = 1.21$, $P > 0.3$).

Comparison Between Subspecies.—Multivariate analysis generated three principal components that explain 75.7% of the total variance in measured structural characteristics of Mangrove and Northern Yellow Warbler songs (Table 2). The 95% confidence ellipses for the principal component scores of Mangrove and Northern Yellow Warblers clearly reveal that PC1 and PC2 separate the songs of these two subspecies entirely (Fig. 2). PC1 explains 42.7% of the variance with strong positive loadings for all frequency measurements and strong negative loadings for both syllabic measurements and length measurements. Thus, positive values for PC1 reflect shorter songs of higher pitch with fewer total syllables and types of syllables per song. PC2 explains 21.8% of the variance with strong positive contributions from all variables except frequency range measures and a strong negative contribution from the length of the terminal syllable. Thus, positive values for PC2 distinguish longer songs with a short terminal syllable but a larger total number of syllables and a slightly higher FMA.

The total difference in the song features of Mangrove Warblers and Northern Yellow Warblers suggested by PCA finds robust support through comparison of individual song features to published studies of Northern Yellow Warbler song or measures taken from my sample of Northern Yellow Warblers where no similar measures have been published (Table 1). Thus both univariate and multivariate analyses show that Mangrove
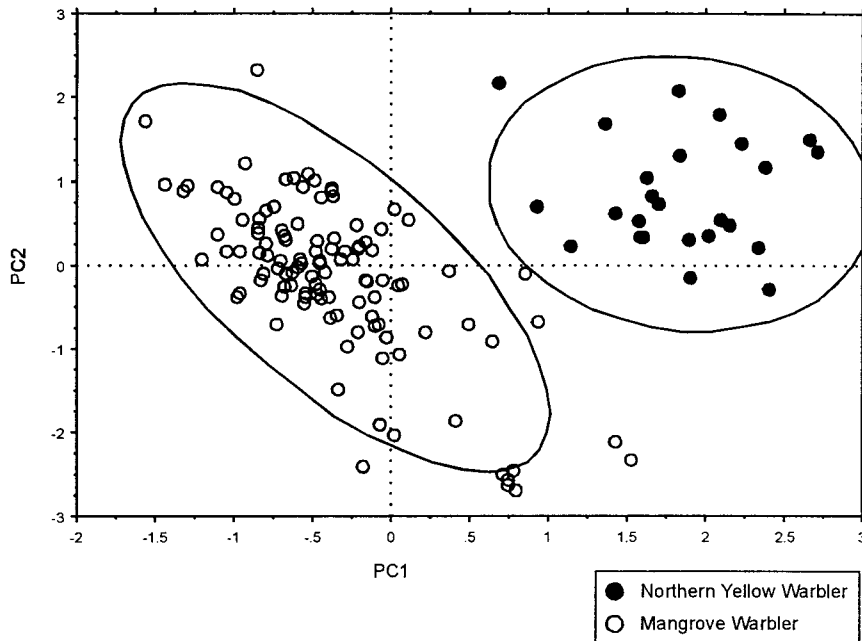
FIGURE 2.   Plot of PC1 vs. PC2 scores for song characteristics of the Mangrove Warbler (open
circles) and the Northern Yellow Warbler (closed circles) generated from eigenvectors
of PCA. Ellipses represent 95% confidence spaces for each subspecies. See Table 2 for
contributions of each song measure to each axis.

Warbler songs have significantly more syllables and more types of syllables
and hence a lower repetition index compared to Northern Yellow Warbler
songs. These analyses also show that Mangrove Warbler songs are 1000 to
2000 Hz lower than Northern Yellow Warbler songs depending on which
frequency measure is compared, and Mangrove Warbler songs are signif-
icantly longer, have a longer terminal syllable and the point of maximum
amplitude comes significantly later in the song.

DISCUSSION

Of 20 song types found in a sample of 135 songs from seven Mangrove
Warblers, all were recorded from song bouts with a high level of imme-
diate variety and all songs were interspersed with chip notes. Subjects
responded to playback by using these song types in an intrasexual, terri-
tory defense context. Like breeding Northern Yellow Warblers, each Man-
grove Warbler possesses a repertoire of song types, and most song types
are shared between at least two neighbours, suggesting that Mangrove
Warblers learn song types from local conspecific males or preferentially
use shared song types. The pattern of juvenile dispersal and period of
song learning remains to be studied.

I found that Mangrove Warbler songs can be arbitrarily categorized into

two groups based on characteristics of the terminal syllable: those with upslurred terminal syllables and those with downslurred terminal syllables. Although structurally distinct, results from playback responses suggest these two song groups are functionally similar. Consequently, grouping songs by upslurred versus downslurred terminal syllables is not a useful distinction, although it corresponds with the distinction between accented ending (AE) and unaccented ending (UE) songs in Northern Yellow Warblers. Although AE and UE songs appear to be functionally equivalent to Type I and II song categories (respectively) in one study of Northern Yellow Warblers (Morse 1966), other studies find no relationship between terminal syllable structure and song type function in both Northern Yellow Warblers (Spector 1991) and Mangrove Warblers (this study). Because Northern Yellow Warbler Type I and II song categories are not structurally distinct, my sampling from songs of unknown category could not be responsible for the observed differences between Mangrove and Northern Yellow Warbler song. To group Mangrove Warbler songs into Type I or II categories would require comparison of songs given during the dawn chorus with those given throughout the day during the breeding season (Spector 1992) or comparison of songs between mated and unmated males and is an avenue for future research in this subspecies.

Between-subspecies comparison of winter song behavior reveals substantial behavioral differences between the vocalizations and territorial behavior of migratory versus resident Yellow Warblers. Northern Yellow Warblers do not sing on their wintering grounds, but both sexes use chip note calls to defend exclusive winter feeding territories both intersexually and intrasexually (Neudorf and Tarof 1998). Mangrove Warblers, on the other hand, appear to defend territories year-round using both calls and songs. Furthermore, male and female Mangrove Warblers jointly defend shared territories outside of the breeding season, whereas male and female Northern Yellow Warblers are segregated at the same time of year (Rappole and Warner 1980; Neudorf and Tarof 1998).

While superficially similar in timbre and basic form, the songs of the Mangrove Warbler and the Northern Yellow Warbler exhibit significant differences in many fine structural characteristics. Mangrove Warbler songs are significantly lower in pitch, contain more syllables and syllable types, and have slightly longer features than the songs of the Northern Yellow Warbler. Many authors treat the major groups of Yellow Warbler subspecies differently based on ecological and morphological characteristics (Stiles and Skutch 1989; Curson et al. 1994; Howell and Webb 1995; Dunn and Garrett 1997). The differences presented here between the songs of one Mangrove Warbler subspecies (*D. p. bryanti*) and the songs of a Northern Yellow Warbler subspecies (*D. p. aestiva*) parallel the differences in plumage and geographical range between subspecies found by Browning (1994). However, unequivocal evidence that these distinct groups might be better understood as separate species will depend on

forthcoming molecular taxonomy (N. Klein, pers. comm.) and behavioral tests.

Several interpretations may explain the observed differences in song features of Mangrove Warblers and Northern Yellow Warblers. Structural differences between these subspecies may simply result from memetic or genetic drift (Lynch 1996). Song variation across subspecies may also reflect physiological differences between groups. Bowman (1983) demonstrated that FMA of song varies inversely with body weight across 14 species of Darwin's finches. A similar trend might explain the low frequency characteristics of Mangrove Warblers, which are slightly larger than Northern Yellow Warblers (Browning 1994; Dunn and Garrett 1997). Variation in structural characteristics of Yellow Warbler subspecies songs may reflect acoustic adaptation; given that high frequencies attenuate faster in forests than open spaces (Wiley and Richards 1982), perhaps the Central American mangrove habitat favors transmission of lower frequencies of Yellow Warbler song than the thickets of North America. Sound transmission experiments across these different habitat types are required to substantiate this hypothesis. In addition, subspecies song differences may be associated with mate recognition. Although group-specific song characteristics may not be important for subspecies with breeding ranges as geographically separate as those of *D. p. bryanti* and *D. p. aestiva,* such characteristics may have been an isolating mechanism in the ancestral environment (Martens 1996). It would be particularly revealing to conduct a between-subspecies song recognition playback experiment to test the validity of this interpretation.

Whether we consider Mangrove Warblers and Northern Yellow Warblers distinct species or groups of subspecies within a larger Yellow Warbler complex, this system presents a remarkable opportunity for understanding paruline singing behavior and bird song at large. In particular, the tremendous diversity and geographical range among and between these groups may provide revealing answers about differences between tropical and temperate song systems (Morton 1996), the spread of song dialects and the nature of song type sharing, and the relationship between song diversity and genetic diversity. Future investigations should focus on a large scale comparison of song characteristics and singing behavior of multiple subspecies of Mangrove, Golden and Northern Yellow Warblers and should include within- and between-group comparisons, behavioral tests, and molecular taxonomy.

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