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GEOGRAPHIC VARIATION IN THE FLIGHT CALL OF THE CUBAN PARROT (*AMAZONA LEUCOCEPHALA*) AND ITS TAXONOMIC RELEVANCE

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Abstract: Because bird vocalizations often reflect population differentiation and can create barriers to gene flow, ornithologists frequently rely on vocalizations for defining species limits. Our previous work on morphology and plumage variation within the Cuban Parrot (*Amazona leucocephala*) suggested greater diversity than previously recognized. Because some island populations are highly endangered, additional characters are needed to help define taxonomic units within this group. Here, we tested two hypotheses: that the flight call (a form of contact call) of parrots from each of the six extant island populations is diagnosably distinct, and that the structure of the call, as assessed by discriminant function analysis, corresponds to variation in molecular, morphological, and plumage characters (i.e., character concordance). To test these hypotheses, we spectrographically examined both qualitative and quantitative characters of the flight call of 23 individuals recorded from the six extant island populations on Abaco and Inagua (the Bahamas), Cuba, Isla de la Juventud, Cayman Brac, and Grand Cayman. As anticipated, we found the flight call of each population to be diagnosably distinct. However, when only quantitative characters were considered, flight call structure was not fully congruent with the molecular, morphological, and plumage differences that exist among island groups. Specifically, the flight calls from Grand Cayman were less distinct structurally than expected, and Cayman Brac calls were more distinct from those of Cuba and Isla de la Juventud than expected. Although diagnosability is important for examining taxonomic limits in birds, applying this principle to vocalizations may be problematic, particularly when a strong cultural component exists. This appears to be the case for psittacids, whose contact calls are subject to strong cultural influences (i.e., learning). Thus, the diagnosable differences we found among populations should not be interpreted as support for species-level differentiation. Although a more complete analysis of the cultural differences (vocal and other learned behaviors) among island populations is needed, we recommend that each population be managed not only as a separate conservation unit, but also as a culturally significant unit.

Key words: Amazona leucocephala, conservation taxonomy, Cuban Parrot, culturally significant unit, flight call, systematics, vocalization

Resumen: VARIACIÓN GEOGRÁFICA EN LA LLAMADA DURANTE EL VUELO DE LA COTORRA CUBANA (*AMAZONA LEUCOCEPHALA*) Y SU RELEVANCIA TAXONÓMICA. Como las vocalizaciones en las aves usualmente reflejan diferencias poblacionales y pueden crear barreras al flujo genético, los ornitólogos con frecuencia se apoyan en las vocalizaciones para definir los límites de las especies. Trabajos previos en morfología y variación del plumaje de la Cotorra Cubana (*Amazona leucocephala*) sugieren una mayor diversidad de la reconocida previamente. Debido a que las poblaciones en algunas islas estan fuertemente amenazadas, caracteres adicionales son necesarios para ayudar a definir las unidades taxonómicas dentro de este grupo. En este trabajo se someten a prueba dos hipótesis: que la llamada durante el vuelo (una forma de llamada de contacto) de cada una de las seis poblaciones isleñas remanentes son diferenciables con valor diagnóstico y que la estructura de la llamada, evaluada por un análisis de función discriminante, corresponde con las variaciones moleculares, morfológicas y caracteres del plumaje (ej. concordancia de caracteres). Para poner a prueba estas hipótesis, se examinaron desde el punto de vista espectrográfico caracteres cualitativos y cuantitativos de las llamadas de vuelo de 23 individuos grabados de poblaciones en Abaco e Inagua (Bahamas), Cuba, Isla de la Juventud, Cayman Brac y Grand Cayman. Como fue predicho, se encontró que las llamadas fueron diferentes. Sin embargo, cuando se consideraban solo caracteres cuantitativos, la estructura de la llamada de vuelo no fue totalmente congruente con las diferencias moleculares, morfológicas y diferencias de plumaje que existen entre estos grupos en las islas. Específicamente, los cantos durante el vuelo fueron menos diferentes que lo esperado, desde el punto de vista estructural, en Grand Cayman, mientras que en Cayman Brac fueron más diferentes que lo esperado, en relación con Cuba e Isla de la Juventud Aunque el valor diagnóstico es importante para examinar los límites entre especies en las aves, aplicar este principio a las vocalizaciones puede ser problemático, particularmente cuando existe un componente cultural fuerte. Este parece ser el caso de los psitácidos, cuyo canto está sujeto a fuertes influencias culturales (ej. aprendizaje). Por tanto, las diferencias diagnosticables encontradas entre poblaciones no deben interpretarse como apoyo para una diferenciación a nivel de especie. Aunque un análisis más completo de las diferencias culturales (vocales y otras conductas aprendidas) entre islas es necesario, se recomienda que cada población sea manejada no solo como unidades de conservación separadas sino también como unidades culturalmente significativas.

Palabras clave: Amazona leucocephala, Cotorra Cubana, llamadas de vuelo, sistemática, taxonomía para la conservación, unidad culturalmente significativa, vocalización

Résumé : VARIATION GEOGRAPHIQUE DU CRI AU VOL CHEZ L'AMAZONE DE CUBA (*AMAZONA LEUCOCEPHALA*) ET SA VALEUR TAXONOMIQUE. Les ornithologues utilisent les vocalisations des oiseaux pour séparer les espèces car ils reflètent souvent des différences populationnelles et peuvent être ainsi à l'origine de limitations aux échanges génétiques. Nos précédents travaux sur les variations morphologiques et de plumage de l'Amazone de Cuba (*Amazona leucocephala*) suggèrent une diversité plus forte que précédemment considérée. En raison des fortes menaces pesant sur certaines populations insulaires, il est important de pouvoir disposer de caractères supplémentaires d'identification taxonomique dans ce groupe. Nous avons testé deux hypothèses, d'une part que le cri au vol (une forme de cri de contact) des six populations insulaires pouvait être diagnostique, et d'autre part, que la structure de ce cri, tel que décrit par analyse discriminante correspondait à des variations de caractéristiques moléculaires, morphologiques et du plumage. Pour tester ces hypothèses, nous avons analysé de les spectrogrammes des cris au vol, qualitativement et quantitativement, pour 23 oiseaux issus des six populations de Abaco et Inagua (Bahamas), de Cuba, Isla de la Juventud, Cayman Brac, et Grand Cayman. Comme anticipé, les cris au vol de chaque sous population se sont avérés discriminants. Toutefois, la variabilité de la structure du cri au vol au niveau des seules caractéristiques quantitatives ne s'est pas avérée totalement corrélée avec les différences moléculaires, morphologiques et de plumage. En particulier, les cris au vol des oiseaux de Grand Cayman ont été moins structurellement distincts qu'attendu, alors que ceux de Cayman Brac l'ont été plus qu'attendu par rapport à ceux de Cuba et de l'ïle de la Juventud. L'utilisation de ce type de méthode bien qu'importante pour analyser les frontières taxonomiques chez les oiseaux, peut donc s'avérer problématique lorsqu'elle est appliquée aux vocalisations, en particulier lorsqu'il existe un fort facteur culturel. Cela semble être le cas chez les Psittacidés, pour lesquels existe une forte influence culturelle (comme l'apprentissage) sur les cris de contact. Ces différences diagnostiques trouvées entre les populations ne doivent donc pas être interprétées pour justifier une différence d'espèce. Bien qu'une analyse plus complète des différences culturelles (vocales ou pour d'autres comportements appris) soit nécessaire, nous recommandons que chaque unité de conservation soit gérée non seulement comme une unité de conservation particulière, mais aussi comme une unité culturelle unique.

Mots-clés : Amazona leucocephala, Amazone de Cuba, cri au vol, systématique, taxonomie de conservation, unité culturelle particulière, vocalisation

Birds frequently use vocalizations for decisions regarding mate choice and association with others (Marler and Slabbekoorn 2004). Many species learn to vocalize at an early age from their parents and neighbors, developing dialects and personal signatures (Nowicki and Searcy 2005). Upon reaching mating age, males have learned and females prefer vocalizations specific to their own species, subspecies, and local dialect (Slabbekoorn and Smith 2002, Nowicki and Searcy 2005, Grant and Grant 2006). The ability to learn songs can encourage the persistence of newly emerged alleles (both advantageous and disadvantageous) in allopatric populations, thereby increasing the rate of speciation (Lachlan and Servedio 2004). Song learning is one trait shared by the majority of the most species-rich families of birds, and has been hypothesized to account for at least part of their proliferation (Baker 2001).

The study of vocalizations has become increasingly important in bird taxonomy. Because bird vocalizations often reflect population differentiation and can create barriers to gene flow, ornithologists frequently rely on vocalizations for defining species limits (Slabbekoorn and Smith 2002, Alstrom and Ranft 2003, Seddon 2005, Grant and Grant 2006, Brambilla *et al.* 2008). Defining species limits is especially important for island populations because their relatively small distribution and population size often render them more prone to extinction (Sekercioglu *et al.* 2004). Because of limited resources, conservation biologists rely on taxonomic relationships to prioritize which populations are most deserving of protection and management (Mace 2004, Winker *et al.* 2007). Here, we examine geographic variation in the flight call of the Cuban Parrot (*Amazona leucocephala*) to help elucidate the taxonomic status of its allopatric populations.

Although formerly more widespread (Wiley 1991, Williams and Steadman 2001), the five recognized subspecies of Cuban Parrot presently occur on six islands: Abaco and Inagua in the Bahamas (*A. l. bahamensis*), Cuba (*A. l. leucocephala*), Isla de la Juventud (formerly Isla de Pinos, *A. l. palmarum*), Cayman Brac (*A. l. hesterna*), and Grand Cayman (*A. l. caymanensis*). Collectively, the species is regarded by IUCN and Birdlife International as vulnerable, though individual subspecies and populations are endangered or critically endangered (Snyder *et al.* 2000, Wiley *et al.* 2004, Hayes 2006). Based on morphological and plumage differences among populations, Reynolds and Hayes (2009) split the Bahamas form into three subspecies, with *A. l. abacoensis* on Abaco, *A. l. inaguaensis* on Inagua, and *A. l. bahamensis* represented by the extinct population from Acklins. Studies of molecular divergence (Ottens-Wainright *et al.* 2004, Russello *et al.* 2010) offer support for several subspecies, including those from the Bahamas, being elevated to distinct species. This should not be surprising, as molecular studies indicate that many island subspecies are more likely to correspond to historical lineages, or "phylogroups," than temperate continental subspecies (Phillimore and Owens 2006).

Members of the parrot family (Psittacidae) are well known for their extensive acoustic repertoires and ability to learn new vocalizations throughout life (Farabaugh and Dooling 1996, Bradbury 2003). One prominent call type is the flight call, which is a form of contact call. In parrots, it is very loud, usually produced by both members of a pair in flight, and often exchanged by members of a pair or group when spatially separated but still within earshot (Bradbury *et al.* 2001). Parrots most often give this call during the beginning of a flight, and it is usually discontinued sometime before landing. Presumably encouraging pair or group cohesion while in flight and involving negotiations about group membership changes (fission, fusion) and leadership, flight calls are considered a learned vocalization that can be rapidly altered to converge upon (more closely match) or diverge from the calls of conspecifics (e.g., Saunders 1983, Hile *et al.* 2000, Wanker and Fisher 2001, Moravec *et al.* 2006, Balsby and Bradbury 2009, Scarl and Bradbury 2009). Flight calls of most species exhibit geographic variation (e.g., Wright 1996, Roberts 1997, Bradbury *et al.* 2001, Baker 2003, 2008, Chan and Mudie 2004, Bond and Diamond 2005, Kleeman and Gilardi 2005, Buhrman-Deever *et al.* 2007, Wright *et al.* 2005, 2008; see Guerra *et al.* 2008 for an exception) and, therefore, potentially contain phylogenetic signal (Baker 2008).

The purpose of this study was to examine geographic variation in the flight call of the Cuban Parrot. In the only quantitative study of the vocal repertoire of this species, González Alonso (2001) described 14 vocalization types from Cuba and Isla de la Juventud, including a flight call that he termed the "canto de localización" (location song). This call, within a range of 1–6 kHz, was used when flying in pairs, or when isolated and calling to announce a location. Although Snyder *et al.* (1987) provided spectrograms of parrot take-off and flight calls from the Bahamas, and Gnam and Burchsted (1991) mentioned vocalization differences between breeding pairs of two geographic regions on Great Abaco, no quantitative studies have been published for the Bahamas or Cayman races. In this study, we obtained and analyzed recordings from each major island of occurrence to evaluate two hypotheses: 1) that each population possesses diagnosably distinct flight call characteristics, which might be expected of well-differentiated taxa (Helbig *et al.* 2002); and 2) that spectrographic variation among populations, as assessed by discriminant function analysis, corresponds to previously described and strongly concordant variation in molecular (Russello *et al.* 2010) and combined morphological and plumage characters (Reynolds and Hayes 2009). Demonstrating character concordance among genetically independent characters can help to define taxonomic and conservation units (Avise and Ball 1990, Grady and Quattro 1999).

MATERIALS AND METHODS

STUDY AREAS AND METHODS

For the purposes of this study, we assumed that variation in flight call structure due to age, sex, and time of year was negligible relative to population differences. Although considered inconsequential in most studies of parrot contact calls, some variation from these sources exists. Age-related differences in contact calls were documented in the Kea (*Nestor notabilis*; Bond and Diamond 2005). Sexual differences in contact calls were demonstrated in the Puerto Rican Parrot (*Amazona vittata*; Roberts 1997), and behavioral responses to call playback suggested subtle sexual differences in the contact calls of the Orange-fronted Parakeet (*Aratinga canicularis*; Balsby and Scarl 2008). The Cuban Parrot is sexually monochromatic, but males average slightly larger than females (1–4% in most characters; Reynolds and Hayes 2009). González Alonso (2001) reported that Cuban Parrot group size varies seasonally, but made no mention of call structure varying.

We studied recordings of flight calls from 23 individuals representing all six extant populations. One of us (MBJR) recorded flight calls from Abaco and Inagua in the Bahamas from 4–20 January 2006, either in the morning (0700–1000) or late in the day (1600–1900). On Abaco, parrots were sighted and successfully recorded only at Bahama Palms Shores. On Inagua, parrots were recorded at Salt Pond Hill, Rocky Bank Salina, "The Backroad" (sea side of the airfield), Agro Cove, the northwestern point, and in Matthew's Town. Parrot vocalizations from Cuba, Isla de la Juventud, and Cayman Brac were recorded by JWW. These were obtained during morning hours (0700–0930) from La Belén, Camagüey, Cuba, on 12–19 July 1996; Los Indios, Isla de la Juventud, Cuba, 8 May to 1 June 1996 and 19–25 May 1997; and "The Bluff," Cayman Brac, 16–29 December 1992. Recordings from Grand Cayman were obtained by WKH during the mornings (0600-1200) of 9–14 April 2006 at three locations: Queen Elizabeth II Botanical Park, south end of the Mastic Trail, and Newlands Dyke. We limited our analyses to flight calls because we lacked adequate material to analyze other call types.

Recordings from the Bahamas and Grand Cayman were made with a Marantz PMD660 Portable Solid State Recorder (Marantz, Kanagawa, Japan), a Sennheiser ME62 microphone with K6 power supply (Sennheiser Electronic, Wedemark-Wennebostal, Germany), and a Telinga Pro Universal parabola (Telinga Microphones, Tobo, Sweden). Sounds were recorded on a compact flash card in PCM (.wav) audio format (48 kHz, 16 bit, mono). Recordings from Cuba, Isla de la Juventud, and Cayman Brac were made with either a Uher 4000 IC tape recorder (Uher Werke München, München, Germany) or Sony Walkman Professional WM D60 cassette recorder (Sony Corporation, Tokyo, Japan) on normal bias setting, with a Dan Gibson EPM parabolic reflector microphone. The latter recordings were digitized into PCM (.wav) audio format (44.1 kHz, 16 bit, mono) using Nero SoundTrax (Ahead Software AG, 2003, Karlsbad, Germany), and because there was no pre-amplification, we amplified these tracks by a factor of four when using software to analyze the sounds (see below).

We used Raven 1.2.1 for Windows™ (Cornell Lab of Ornithology, Ithaca, NY, USA) to produce the oscillograms and spectrograms of parrot syllables from which the measurements were obtained. For consistency, MBJR conducted all of the analyses. Spectrograms were produced with the default Hann analysis window and visually analyzed at 50% brightness and contrast with averaging. To standardize comparisons, all spectrograms were high-pass filtered (< 500 Hz) to remove low frequency background noise and viewed on a scale of 0–24 kHz (48 / 2 kHz) to avoid aliasing.

For comparative purposes, we focused on the repeated, monotypic syllables that followed the usually distinct two or three introductory syllables. Only one call was analyzed per individual bird to avoid pseudo-replication. Syllables were selected from the first call recorded that was identifiable as a single parrot, clear and distinct from other parrots. In several cases, noise from other parrots obscured some of the syllables in a given call. In these cases, we analyzed only the syllables that were clear.

We used standard terminology to describe the vocalizations (Brenowitz *et al.* 1997, Fernández-Juricic *et al.* 1998, Baker *et al*. 2000). A "syllable" is a unit of sound appearing as a single, continuous trace in the spectrogram and separable from other units by a distinct interval of silence visible in the spectrogram and oscillogram. A "call" is the entire collection of syllables separated by a variable amount of time. A "note" (sometimes called an "element") is any change in structure within a syllable that is visible on the spectrograph. Notes may vary by duration, amplitude, amplitude modulation, entropy, frequency (pitch), or frequency modulation. Examples of notes are frequency- or amplitude-modulation upwards or downwards, a trill or a buzz, a pure tone of a specific frequency, or occurrence of subharmonics partway through a syllable. A "harmonic" is a multiple of the fundamental frequency, whereas a "subharmonic" is a fraction of the fundamental frequency (Wilden *et al.* 1998).

To illustrate our classification of notes, a syllable from an Inagua parrot (Fig. 1, first syllable) typically began with a modulation in fundamental frequency from 400 to 3000 Hz in 0.005 seconds, leveled off at 3000 Hz for 0.01 seconds, abruptly lowered to 1200 Hz, modulated down to about 400Hz, and finally dropped off at the end; we considered this to be five separate notes. On Abaco (Fig. 2, but notes not labeled), each syllable typically started with a short and small modulation upward, leveled off for most of the call, and ended with a similarly short, small modulation downward; we considered this to be three notes.

For each syllable within a call, we measured up to 11 spectrographic characters (Fig. 1). These included syllable duration (sec), frequency of maximum power (Hz, measured automatically by Raven), time to maximum power (sec, measured by Raven), time to maximum amplitude (sec, measured by Raven), interval between syllables or paired syllables (sec), interval between paired syllables (sec), number of frequency-jumps, number of notes per syllable, and highest fundamental frequency (Hz). We also recorded for each call the percent of syllables that were

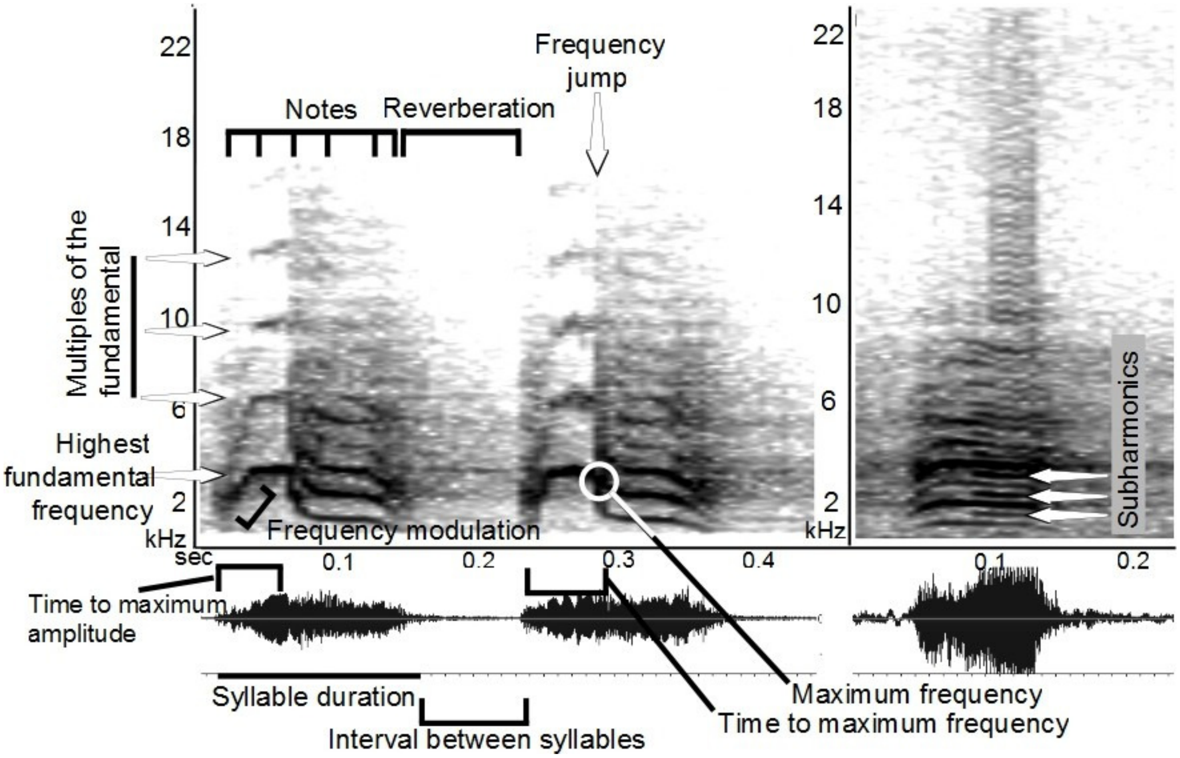

Fig. 1. Syllabic measurements obtained in this study from spectrograms of the flight calls of Cuban Parrots

paired and the percent of syllables containing subharmonics. Accuracy for highest fundamental frequency was dependent on the window scale and the size of the cursor on the computer screen; we deemed this to be ± 50Hz. For each call, the measurements from all syllables (2–15 per call; $\bar{x} = 6.8$) were averaged to produce a single value for each measurement from each parrot. Absolute amplitude and high frequency measurements could not be used due to attenuation and a variable distance to the microphone from the sound source. Due to heavy vegetation, there was considerable reverberation in most recordings, which made measurements more difficult. Reverberation was not measured.

STATISTICAL ANALYSES

All statistical analyses were conducted using SPSS 12.0 for Windows™ (SPSS Inc. 2003). We examined population differences using two nonparametric tests (Conover 1999): Kruskal-Wallis one-way ANOVAs for quantitative characters and Cramer's *V* tests of asymmetry for qualitative characters (presence/absence of paired syllables, frequency jumps, and subharmonics). We set alpha at 0.05; because of low statistical power, we did not employ Bonferroni adjustments to control experimentwise error (Nakagawa 2004). Although the data failed to meet parametric assumptions, a stepwise discriminant function analysis (DFA; Mertler and Vannatta 2002) was used to evaluate population differentiation among six of the quantitative characters recorded in all samples (syllable duration, frequency of maximum power, time to maximum power, time to maximum amplitude, number of notes per syllable, and highest fundamental frequency). The interval between syllables/pairs was excluded because two calls (from Abaco) had missing values for this character. The DFA used SPSS defaults with prior probabilities computed from group sizes. We also used leave-one-out classification for cross-validating accuracy of group assignments. This procedure is essential for small sample sizes to reduce bias toward intertaxon distinctiveness (Lance *et al.* 2000). Because of uneven sample sizes, we report standard errors (1 SE) rather than standard deviations.

RESULTS

DESCRIPTIONS BY ISLAND

Flight calls of Cuban Parrots typically began with

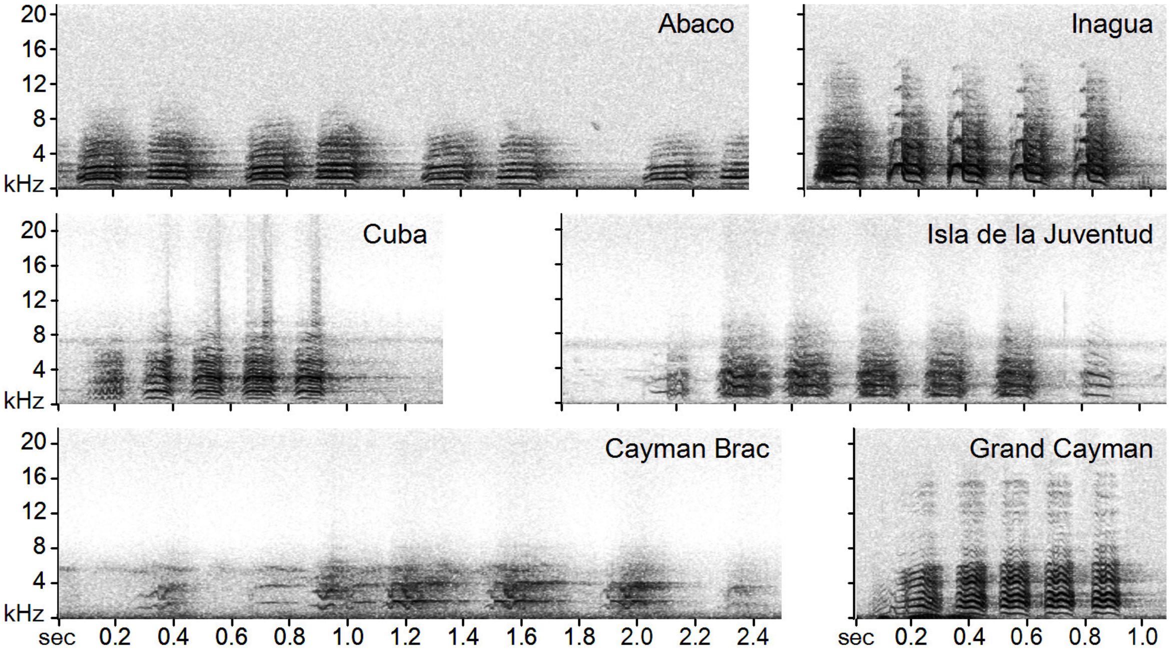

Fig. 2. Representative spectrograms of the flight call of Cuban Parrots (*Amazona leucocephala*), illustrating differences among the extant island populations. Note the paired syllables in Abaco calls (introductory notes not shown), syllables divided by a frequency jump in Inagua, subharmonics in Cuba and Isla de la Juventud, lengthy syllables lacking subharmonics in Cayman Brac, and brief syllables lacking subharmonics in Grand Cayman.

up to three syllables that were distinct from the single, monotypic syllable repeated thereafter for a variable amount of time during flight. In this section, we describe the distinctive characteristics of flight calls within each population. Representative flight call syllables from each island population are illustrated in Fig. 2, where the calls are scaled similarly for ease of comparison. Spectral differences among the six populations are summarized in Table 1. Within-population variation was substantially less than between-population variation, as revealed by statistical analyses (in the next section).

Abaco (*n* = 4 individuals). Flight calls on Abaco began with an introduction (introductory syllables not shown in Fig. 2) that tended to ramp up, increasing in amplitude and frequency from syllable to syllable, for two to three syllables. After the introductory syllables, spaced 0.059–0.089 sec apart, repeated monotypic syllables were paired, with the first syllable of a pair slightly lower in frequency ($\bar{x}$ = 786 Hz) than the second ($\bar{x}$ = 853 Hz). Each syllable of the pair usually modulated up slightly in frequency at the beginning, leveled off for most of the syllable, and then modulated down slightly at the end, producing three notes. Frequency modulation was minimal compared to other populations and without frequency jumps. The mean interval between syllables within a pair ($\bar{x}$ = 0.085 sec) was about half that between the syllable pairs ($\bar{x}$ = 0.199 sec), and these intervals were consistent throughout the duration of the call. To the ear, the call sounded like "chek-chek, chek-chek, chek-chek…" Each flight call recorded had paired syllables, and paired syllables were not recorded on other islands. However, one individual on a track not suitable for analysis, and therefore not included in our sample, appeared to use non-paired syllables.

Inagua (*n* = 6 individuals). Flight calls of Inagua parrots exhibited distinct frequency changes and modulation. Half of the individuals had introductory syllables (variable in form) that differed from the repeated, monotypic syllables. Most of the repeated syllables were partitioned into two parts with a severe frequency jump. Each syllable typically started by quickly modulating up to a relatively high fundamental frequency (~ 3500 Hz), resulting in comparatively few visible harmonics (4–5). After the frequency jump, the fundamental frequency shifted

Table 1. Spectral characters ($\bar{x}$ ± 1 SE, range in parentheses) of the repeated, monotypic Cuban Parrot (*Amazona leucocephala*) flight calls from the six extant island populations. The number of individual calling birds (*n*) is shown for each island. See text for explanation of characters.

Character	Abaco ($n = 4$)	Inagua ($n = 6$)	Cuba ($n = 1$)	Isla de la Juventud ($n = 5$)	Cayman Brac ($n = 2$)	Grand Cayman ($n = 5$)	*P*
Syllable duration (sec)	0.165±0.005 (0.160-0.170)	0.158±0.008 (0.130-0.185)	0.115	0.146±0.006 (0.125-0.159)	0.274±0.035 (0.239-0.309)	0.119±0.002 (0.112-0.125)	0.003^{b}
Frequency of maximum power (Hz)	2089.1±10.9 (2078-2100)	2805.3±70.3 (2571-3010)	3165.4	2235.6±174.0 (1938-2857)	3445.3±775.2 (2670-4221)	2309.1±181.6 (1688-2813)	0.056^{b}
Time to maximum power (sec)	0.084±0.002 (0.082-0.085)	0.080±0.010 (0.043-0.113)	0.085	0.086±0.010 (0.054-0.115)	0.145±0.009 (0.136-0.154)	0.064±0.006 (0.044-0.077)	0.061^{b}
Time to maximum amplitude (sec)	0.088±0.008 (0.080-0.095)	0.085±0.009 (0.049-0.109)	0.089	0.103±0.012 (0.066-0.137)	0.143±0.009 (0.133-0.152)	0.076±0.011 (0.039-0.106)	0.132^{b}
Interval between syllables/pairs (sec)	0.199±0.033^{a} (0.166-0.232)	0.086±0.011 (0.056-0.131)	0.061	0.072±0.004 (0.061-0.084)	0.187±0.126 (0.061-0.312)	0.066±0.008 (0.043-0.089)	0.276^{b}
Interval between paired syllables (sec)	0.086±0.003 (0.083-0.089)	---	---	---	---	---	---
Paired syllables (% of calls)	100	0	0	0	0	0	<0.001^{c}
Number of frequency jumps	0	1-2	0	0	0	0	<0.001^{c}
Sub-harmonics (% of syllables)	0	0	100	64.8±5.7 (50-82)	0	0	<0.001^{c}
Number of notes	2.6±0.0 (2.60-2.67)	4.8±0.5 (3.0-6.4)	4.8	4.7±0.4 (4.0-5.6)	5.4±0.6 (4.8-6.0)	4.2±0.4 (3.43-5.5)	0.040^{b}
Highest fundamental frequency (Hz)	815±3 (812-818)	2987±65 (2772-3220)	843	1088±65 (929-1243)	2025±5 (2020-2030)	1387±223 (840-1931)	0.002^{b}

[a] $n = 2$
[b] Kruskal-Wallis asymptotic *P*
[c] Cramer's *V* test (for presence/absence of character; all $V = 1.0$)

downward (to ~ 1500–2000 Hz), increasing the number of harmonics (7+), and then modulated downward at the end of the syllable. There was some variation between individuals in the duration preceding (0.047–0.117 sec) and following (0.038–0.103 sec) the frequency jump. Some individuals appeared to lack the initial upward modulation and one individual had two frequency jumps (Fig. 3), with both an upward jump and a downward jump. In spite of individual variation, repeated syllables within a single individual's call were similar (Fig. 3). Overall, there was a higher fundamental frequency than for parrots from other populations, giving a squeaky quality to the call.

Cuba ($n = 1$ individual). Unfortunately, only one flight call was available from Cuba. The single introductory syllable was clearly trilled, increasing in amplitude. Repeated syllables were similar to Abaco in having little modulation in frequency and amplitude, but they were not paired. Subharmonics (half the fundamental frequency) appeared partway through each syllable.

Isla de la Juventud ($n = 5$ individuals). In this population, one or two introductory syllables preceded the flight call, and these appeared to be lower in overall frequency and amplitude than the repeated syllables. Among the repeated syllables, there was some upward modulation at the beginning of each syllable, followed by a leveling-off and downward modulation at the end. Subharmonics also appeared partway through most syllables and were present in all calls. The presence of subharmonics was unique to calls from Cuba and Isla de la Juventud.

Cayman Brac ($n = 2$ individuals). The single introductory syllable in both calls was similar to the repeated syllable, but gently increased in frequency

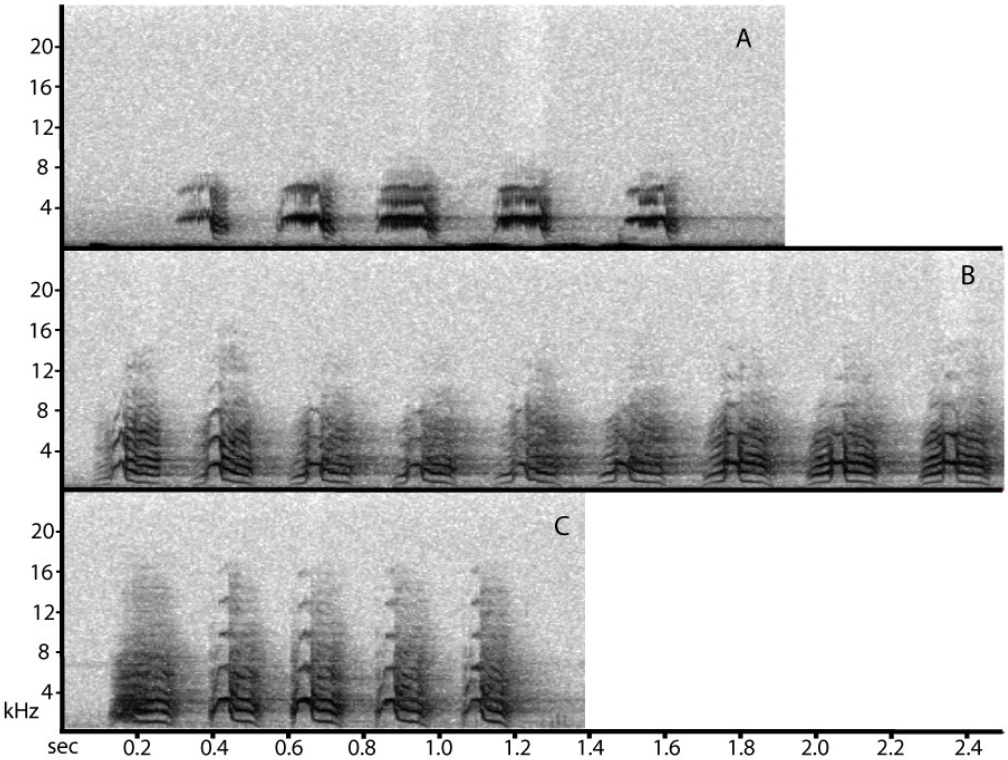

Fig. 3. Representative spectrograms of Cuban Parrots (*Amazona leucocephala*) on Inagua, the Bahamas, showing consistent division of syllable into two or three parts and variation between individuals in placement of division. For A, there is no introductory syllable and no upward modulation at the beginning of the syllable. The frequency jump is late in each syllable. In B, there is a prolonged modulation upward followed by a frequency jump upward, a brief time of little modulation, and then a jump downward followed by prolonged modulation downward. In C, a noisy introductory syllable is followed by the repeated, monotypic syllable with abrupt modulation from low (ca. 600 Hz) to high frequency (ca. 3000 Hz), a period of little modulation, and then a frequency jump downward and further modulation downward.

and was much softer in amplitude. Repeated syllables had a high fundamental frequency (~ 2025 Hz) that remained fairly constant throughout the syllable. There was rising and falling frequency modulation at the beginning of each syllable, resulting in more notes on average than in other populations ($\bar{x}$ = 5.4). The mean duration of each syllable (0.24 and 0.31 sec for two individuals) averaged approximately twice as long as, and never overlapped with, that of other populations (Table 1). The interval between syllables increased during the duration of the call ($\bar{x}$ = 0.206 and 0.355 sec).

Grand Cayman (*n* = 5 individuals). Only one call observed from Grand Cayman parrots had an introductory syllable. In that case, the introductory syllable was about twice as long (0.251) as the repeated syllable ($\bar{x}$ = 0.119 sec), with three-quarters of the syllable increasing in frequency before dropping off in the final one-quarter of the syllable. Repeated syllables contained fewer notes ($\bar{x}$ = 4.2) than those from Cayman Brac, with frequency modulation rising and falling several times within each syllable. There were no subharmonics like those present in the calls from Cuba and Isla de la Juventud. The interval between syllables remained constant and short for the duration of the call, unlike recordings from Cayman Brac.

STATISTICAL ANALYSES

Three of the seven quantitative characters measured for all populations differed significantly among the populations (Table 1). Syllable duration was greatest in flight calls from Cayman Brac ($\bar{x}$ = 0.274 sec), which, along with Abaco, also had the longest interval between syllables ($\bar{x}$ = 0.199 and 0.187 sec, respectively). The briefest syllables were from Cuba and Grand Cayman ($\bar{x}$ = 0.115 and 0.119 sec, respectively), and these also had the shortest interval between syllables ($\bar{x}$ = 0.061 and 0.066 sec, respectively). The number of notes was greatest for Cayman Brac ($\bar{x}$ = 5.4) and least for Abaco ($\bar{x}$ = 2.6), with no overlap between Abaco and other populations. Other populations each had a similar number of notes ($\bar{x}$ = 4.2–4.8). Abaco had the lowest fundamental frequency ($\bar{x}$ = 815 Hz) followed by Cuba (843 Hz), but the populations did not overlap (though this may have been due to measurement error and small sample size). Grand Cayman ($\bar{x}$ = 1088 Hz) and Isla de la Juventud ($\bar{x}$ = 1387 Hz) were in the mid range and overlapped. Cayman Brac ($\bar{x}$ = 2025 Hz) and Inagua ($\bar{x}$ = 2987 Hz) had the highest fundamental frequencies and did not overlap with each other or other populations. Two additional quantitative characters were nearly significant (Table 1): frequency of maximum power and time to maximum power. The values for these were greatest for Cuba and Cayman Brac ($\bar{x}$ = 3165 Hz in 0.085 sec and 3445 Hz in 0.086 sec, respectively) and lowest for Abaco and Grand Cayman ($\bar{x}$ = 2089 Hz in 0.084 sec and 2309 Hz in 0.064 sec, respectively).

The three qualitative characters (treated as present/absent) also differed significantly among populations (paired syllables: $P < 0.001$; frequency jumps: $P < 0.001$; subharmonics: $P < 0.001$; Table 1). Paired syllables were present only in flight calls from Abaco, frequency jumps occurred only on Inagua, and the presence of subharmonics was confined to Cuba and Isla de la Juventud. All four syllables in the single call from Cuba contained subharmonics, whereas they were found in 50–82% of the 6-11 syllables recorded in each of the five calls from Isla de la Juventud (i.e., each call had some syllables with harmonics).

The final model of the stepwise DFA was highly significant ($\Lambda = 0.002$, $\chi^2_{15} = 105.64$, $n = 23$, $P < 0.001$), yielding three functions derived from three characters (see below). Discriminant scores of individual calls, plotted on the first two functions in Fig. 4 (bottom panel), showed strong differentiation among the populations. Function 1 (77.3% of variance) was comprised primarily of and positively associated with highest fundamental frequency and number of notes (standardized coefficients = 1.255 and 0.943, respectively). Function 2 (20.5% of variance) was positively associated with syllable duration (1.029). Not surprisingly, the three characters selected were those that varied significantly among populations (Table 1), giving added confidence in the DFA. The Cayman Brac population was readily separated from other populations by its lengthy syllable duration (Function 2). The two Bahamas populations were clearly separated from each other and from the other populations by Function 1. Quantitative qualities of flight calls from Cuba, Isla de la Juventud, and Grand Cayman were the most similar. These results can be compared to discriminant scores from combined morphological and plumage characters (Fig. 4, upper panel) analyzed by Reynolds and Hayes (2009), demonstrating lack of concordance between the character sets.

The DFA predicted overall group membership successfully for 91.3% of the calls. Flight calls from Abaco, Inagua, Cuba, and Cayman Brac were classified correctly 100% of the time. However, two of the five calls from Grand Cayman were misclassified, one as Cuba and the other as Isla de la Juventud. For the cross-validated classification, 82.6% of the calls were classified correctly. The same two Grand Cayman calls were misclassified, the single Cuba call was misclassified as Isla de la Juventud, and one Isla de la Juventud call was misclassified as Grand Cayman.

DISCUSSION

We identified distinct differences among island populations in the flight call structure of Cuban Parrots. As hypothesized, each population was diagnosable from other populations, with the possible exception of Cuba compared to Isla de la Juventud. Populations on these two islands had non-overlapping characters, but the sample size for Cuba was one. The flight calls of Abaco parrots were uniquely paired and exhibited a low fundamental frequency and relatively few notes. There was some variation among Inagua parrots, but they were consistent in having the highest fundamental frequency and a frequency jump bifurcation wherein the highest fundamental frequency dropped part way through. On Cayman Brac, long syllable duration and increasing length of the interval between syllables set that population apart. Grand Cayman was distinct from Cayman Brac in having shorter syllables, and both Cayman populations lacked the subharmonics present in Cuba and Isla de la Juventud. Although local dialects exist within Cuba, with greatest distinction from the western peninsula of Guanahacabibes (J. W. Wiley, pers. obs.), the presence of subharmonics on both Cuba and Isla de la Juventud suggests structural similarity across a

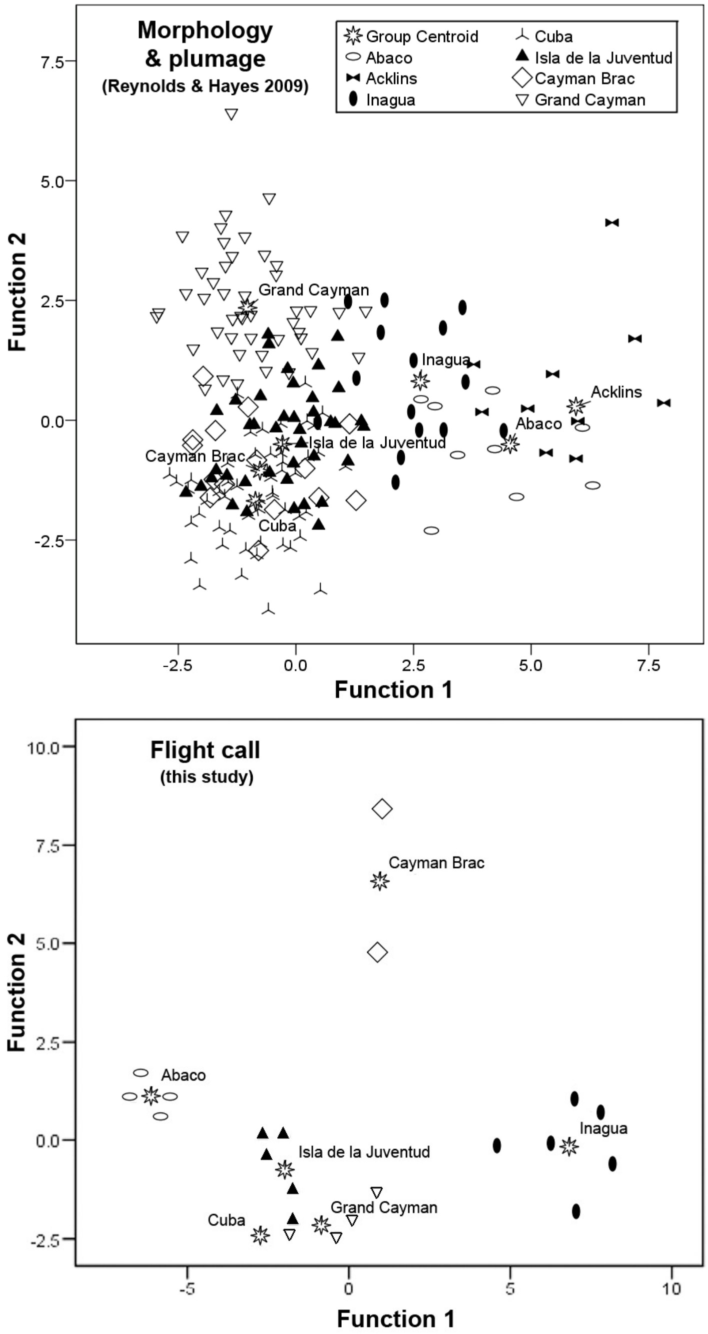

Fig. 4. Canonical plots of discriminant scores for morphology and plumage characters (top panel; see Reynolds and Hayes 2009) and flight call characters (bottom panel; this study) from the six extant and one extirpated (Acklins) island populations of Cuban Parrot (*Amazona leucocephala*). Group centroids are also shown. Note the lack of character concordance: for morphology and plumage characters, Abaco, Inagua, and Grand Cayman are well separated from the cluster of Cayman Brac, Cuba, and Isla de la Juventud; for flight call characters, Abaco, Cayman Brac, and Inagua are well separated from the cluster of Cuba, Isla de la Juventud, and Grand Cayman. For flight calls, function 1 (77.3% of variance) is comprised primarily of and positively associated with highest fundamental frequency and number of notes. Function 2 (20.5% of variance) is positively associated with syllable duration.

broad geographic area. Sample sizes were small, but variation within and among individuals of a population for most measurements was very low relative to between-island variation, as confirmed by statistical tests despite limited statistical power.

Although each population could be diagnosed by the flight calls, the quantitative characters analyzed in multivariate space (i.e., stepwise DFA; Fig. 4) were largely but not entirely congruent with the previously described and strongly concordant variation in molecular (Russello *et al.* 2010; haplotype tree not shown here) and combined morphological and plumage (Reynolds and Hayes 2009; Fig. 4) characters. Based on molecular, morphological, and plumage characters, we expected flight calls to be most distinct from the Bahamas and Grand Cayman, and to be most similar for Cuba, Isla de la Juventud, and Cayman Brac. Flight calls from the two Bahamas populations were indeed distinct from other populations and from each other, but the calls from Cayman Brac were surprisingly distinct and those from Grand Cayman clustered closely with Cuba and Isla de la Juventud (Fig. 4). Differences in the quantitative characters of flight calls may be genetic or learned (or both), and could arise through natural selection (e.g., via habitat structure or as a byproduct of morphological adaptation; Morton 1975, Ryan and Brenowitz 1985, Slabbekoorn and Smith 2002, Seddon 2005) or by founder effects and drift (e.g., via culture; Podos and Warren 2007). The similarity of Grand Cayman to Cuba/Isla de la Juventud calls, although separable by a qualitative character (presence of subharmonics), may have resulted from convergent evolution (independent of vocal mimicry).

In social animals such as parrots, adaptive behaviors may be horizontally transmitted between neighbors not necessarily related. The collection of behaviors and language that exist in a population and are not inherited genetically is termed “culture,” and a “meme” is an arbitrary unit of culture that is behaviorally transmitted and subject to natural selection or drift (Dawkins 1976). The ability to learn a meme, such as a specific nesting or foraging behavior, can increase fitness and may even be essential for reproductive success. Studies of bird vocalizations have contributed much to our understanding of cultural transmission (Baker and Gammon 2008). Designating a population as a culturally significant unit has been suggested as a way to protect cultural diversity in non-human species (Whitehead *et al.* 2004, Ryan 2006). Although we do not know the extent to which the flight call differences we documented correspond to genetic or cultural causes, many parrot vocalizations are undoubtedly acquired or modified socially, and contact calls in particular show strong cultural influences (Bradbury 2003; see examples below).

Diagnosability is important for identifying species limits in birds (Helbig *et al.* 2002), but applying this principle to vocalizations may be problematic, particularly when a strong cultural component exists (Seddon 2005), as is the case for psittacids. At present, we do not know how far or rapidly culturally-driven differences can evolve, and whether such differences can lead to reproductive barriers, but numerous studies of psittacids over the past two decades offer insight. Most species studied to date exhibit geographic variation in their contact calls, sometimes with well-demarcated regional (cultural) dialects (e.g., Wright 1996, Roberts 1997, Bradbury *et al.* 2001, Baker 2003, 2008, Chan and Mudie 2004, Bond and Diamond 2005, Kleeman and Gilardi 2005, Buhrman-Deever *et al.* 2007, Wright *et al.* 2005, 2008; see Guerra *et al.* 2008 for an exception). Many species can rapidly alter their contact calls to converge upon or diverge from the calls of others, often doing so within minutes (e.g., Saunders 1983, Hile *et al.* 2000, Wanker and Fisher 2001, Moravec *et al.* 2006, Balsby and Bradbury 2009, Scarl and Bradbury 2009). Although Budgerigars (*Melopsittacus undulatus*) pair assortatively based on contact call similarity (Moravec *et al.* 2006) and Yellow-naped Parrots (*Amazona auropalliata*) discriminate between regional dialects and exhibit apparent roost site fidelity corresponding to dialect (Wright and Dorin 2001), the lack of concordance between genetic variation (in the neutral alleles examined) and vocal dialects in Yellow-naped Parrots suggests dispersal of individuals that subsequently learn the local dialect (Wright *et al.* 2005). Dialects may be maintained by a combination of biased transmission of local call types and purifying selection against foreign call types, with migration, copying errors, and cultural drift contributing to change (Wright *et al.* 2008). In terms of phylogenetic signal, diagnosably distinct flight calls exist within populations of several polytypic species, including the Monk Parakeet (*Myiopsitta monachus*; Buhrman-Dever *et al.* 2007) and the Australian Ringneck (*Barnardius zonarius*; Baker 2008). Collectively, these findings suggest that the diagnosable differences we found among populations of Cuban Parrots should not be interpreted as support for species-level differentiation, though substantial divergence exists in plumage, morphology, behavior, ecology, and genetics (Ottens-Wainright *et al.* 2004, Reynolds and Hayes 2009, Russello *et al.* 2010).

Future research should broaden the comparisons into other aspects of the Cuban Parrot's vocal repertoire and social behaviors. Although we examined only one type of vocalization, we expect that much more population variation exists among the other vocalization types. Vocal playback experiments would be ideal to examine how individuals respond to calls from other populations and the extent to which rapid vocal convergence or divergence occurs. The findings could potentially reinforce inferences about taxonomic boundaries. Cross-breeding or cross-fostering in captivity would present an opportunity to determine whether there is any genetic component to the flight call and other vocalizations (e.g., Rowley and Chapman 1986). In addition to vocalizations, behaviors such as nesting and foraging may also be socially learned. To determine their importance, future research should investigate to what extent non-language behaviors are cultural and to what extent they increase fitness. As an example, the unique ground-nesting behavior of the Abaco population of Cuban Parrot may be a learned behavior advantageous for surviving frequent forest fires (O'Brien *et al.* 2006). Although a more complete analysis of the cultural differences among island populations is needed, we recommend that the island populations studied here, and perhaps even local populations on Abaco, Cuba, and Isla de la Juventud (c.f., Kleeman and Gilardi 2005), be managed as separate culturally significant units. Each of the island populations currently warrants management as a separate conservation unit (Reynolds and Hayes 2009, Russello *et al.* 2010).

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LITERATURE CITED

ALSTROM, P., AND R. RANFT. 2003. The use of sounds in avian systematics and the importance of bird sound archives. Bulletin of the British Ornithologists' Club 123A:114–135.

AVISE, J. C., AND R. M. BALL, JR. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surveys in Evolutionary Biology 7:45–67.

BAKER, M. C. 2001. Bird song research: the past 100 years. Bird Behavior 14:3–50.

BAKER, M. C. 2003. Local similarity and geographic differences in a contact call of the Galah (*Cacatua roseicapilla assimilis*) in Western Australia. Emu 103:233–237.

BAKER, M. C. 2008. Analysis of a cultural trait across an avian hybrid zone: geographic variation in plumage morphology and vocal traits in the Australian Ringneck Parrot (*Platycercus zonarius*). Auk 125:651–662.

BAKER, M. C., AND D. E. GAMMON. 2008. Vocal memes in natural populations of chickadees: why do some memes persist and others go extinct? Animal Behavior 75:279–289.

BAKER, M. C., T. M. HOWARD, AND P. W. SWEET. 2000. Microgeographic variation and sharing of the gargle vocalization and its component syllables in Black-capped Chickadee (Aves, Paridae, *Poecile atricapillus*) populations. Ethology 106: 819–838.

BALSBY, T. J. S., AND J. W. BRADBURY. 2009. Vocal matching by Orange-fronted Conures (*Aratinga canicularis*). Behavioural Processes 82: 133–139.

BALSBY, T. J. S., AND J. C. SCARL. 2008. Sex-specific responses to vocal convergence and divergence of contact calls in Orange-fronted Conures (*Aratinga canicularis*). Proceedings of the Royal Society of London, Series B, 275:2147–2154.

BOND, A. B., AND J. DIAMOND. 2005. Geographic and ontogenetic variation in the contact calls of the Kea (*Nestor notabilis*). Behaviour 142:1–20.

BRADBURY, J. W. 2003. Vocal communication in wild parrots. Pp. 293–316 *in* Animal social complexity: intelligence, culture, and individualized societies (F. B. M. de Waal and P. L. Tyack, eds.). Harvard University Press, Cambridge, MA.

BRADBURY, J. W., K. A. CORTOPASSI, AND J. R. CLEMMONS. 2001. Geographical variation in the contact calls of Orange-fronted Parakeets. Auk 118:958–972.

BRAMBILLA, M., O. JANNI, F. GUIDALI, AND A. SORACE. 2008. Song perception among incipient species as a mechanism for reproductive isolation. Journal of Evolutionary Biology 21:651–657.

BRENOWITZ, E. A., D. MARGOLIASH, AND K. W. NORDEEN. 1997. An introduction to birdsong and the avian song system. Journal of Neurobiology 33:495–500.

BUHRMAN-DEEVER, S. C., A. R. RAPPAPORT, AND J. W. BRADBURY. 2007. Geographic variation in contact calls of feral North American populations of the Monk Parakeet. Condor 109:389–398.

CHAN, K., AND D. MUDIE. 2004. Variation in vocalisations of the Ground Parrot at its northern range. Australian Journal of Zoology 52:147–158.

CONOVER, W. 1999. Practical nonparametric statistics. 3rd edn. John Wiley & Sons, Inc. New York, NY.

DAWKINS, R. 1976. The selfish gene. Oxford University Press, Oxford, UK.

FARABAUGH, S. M., AND R. J. DOOLING. 1996. Vocal communication in parrots: laboratory and field studies of Budgerigars, *Melopsittacus undulatus*. Pp. 97–117 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, eds.). Cornell University Press, Ithaca, NY.

FERNÁNDEZ-JURICIC, E., M. B. MARTELLA, AND E. V. ALVAREZ. 1998. Vocalizations of the Blue-fronted Amazon (*Amazona aestiva*) in the Chancani Reserve, Cordoba, Argentina. Wilson Bulletin 110:352–361.

GNAM, R., AND A. BURCHSTED. 1991. Population estimates for the Bahama Parrot on Abaco Island, Bahamas. Journal of Field Ornithology 62:139–146.

GONZÁLEZ ALONSO, H. 2001. Conductas de gregarismo y vocalización de la Cotorra Cubana (*Amazona leucocephala*). Ornitología Neotropical 12:141–152.

GRADY, J. M., AND J. M. QUATTRO. 1999. Using character concordance to define taxonomic and conservation units. Conservation Biology 13: 1004–1007.

GRANT, P. R., AND B. R. GRANT. 2006. Species before speciation is complete. Annals of the Missouri Botanical Garden 93:94–102.

GUERRA, J. E., J. CRUZ-NIETO, S. G. ORTIZ-MACIEL, AND T. F. WRIGHT. 2008. Limited geographic variation in the vocalizations of the endangered Thick-billed Parrot: implications for conservation strategies. Condor 110:639–647.

HAYES, W. K. 2006. The urgent need for conservation taxonomy in the Bahamas: new bird species as an example. Bahamas Naturalist and Journal of Science 1:12–24.

HELBIG, A. J., A. G. KNOX, D. T. PARKIN, G. SANGSTER, AND M. COLLINSON. 2002. Guidelines for assigning species rank. Ibis 144:518–525.

HILE, A. G., T. K. PLUMMER, AND G. F. STREIDTER. 2000. Male vocal imitation produces call convergence during pair bonding in Budgerigars. Animal Behavior 59:1209–1218.

KLEEMAN, P. M., AND J. D. GILARDI. 2005. Geographical variation of St. Lucia Parrot flight vocalizations. Condor 107:62–68.

LACHLAN, R. F., AND M. R. SERVEDIO. 2004. Song learning accelerates allopatric speciation. Evolution 58:2049–2063.

LANCE, R. F., M. L. KENNEDY, AND P. L. LEBERG. 2000. Classification bias in discriminant function analyses used to evaluate putatively different taxa. Journal of Mammalogy 81:245–249.

MACE, G. M. 2004. The role of taxonomy in species conservation. Philosophical Transactions of the Royal Society of London B 359:711–319.

MARLER, P., AND H. SLABBEKOORN (EDS.). 2004. Nature's music: the science of birdsong. Elsevier Academic Press, San Francisco, CA.

MERTLER, C. A., AND R. A. VANNATTA. 2002. Advanced and multivariate statistical methods. 2nd edn. Pyrczak Publishing, Los Angeles, CA.

MORAVEC, M. L., G. F. STRIEDTER, AND N. T. BURLEY. 2006. Assortative pairing based on contact call similarity in Budgerigars *Melopsittacus undulatus*. Ethology 112:1108–1116.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. American Naturalist 109: 17–34.

NAKAGAWA, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behavioral Ecology 15:1044–1045.

NOWICKI, S., AND W. A. SEARCY. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. Auk 122: 1–14.

O'BRIEN, J. J., C. STAHALA, G. P. MORI, M. A. CALLAHAM, JR., AND C. M. BERGH. 2006. Effects of prescribed fire on conditions inside a Cuban Parrot (*Amazona leucocephala*) surrogate nesting cavity on Great Abaco, Bahamas. Wilson Journal of Ornithology 118:508–512.

OTTENS-WAINRIGHT, P., K. M. HALANYCH, J. R. EBERHARD, R. I. BURKE, J. W. WILEY, R. S. GNAM, AND X. G. AQUILERA. 2004. Independent geographic origin of the genus *Amazona* in the West Indies. Journal of Caribbean Ornithology 17:23–49.

PHILLIMORE, A. B., AND I. P. F. OWENS. 2006. Are subspecies useful in evolutionary and conservation biology? Proceedings of the Royal Society of London B 273:1049–1053.

PODOS, J., AND P. S. WARREN. 2007. The evolution of geographic variation in birdsong. Advances in the Study of Behavior 37:403–458.

REYNOLDS, M. B. J., AND W. K. HAYES. 2009. Conservation taxonomy of the Cuban Parrot (*Amazona leucocephala*): variation in morphology and plumage. Caribbean Journal of Ornithology 22:1–18.

ROBERTS, B. Z., JR. 1997. Dialects, sex-specificity, and individual recognition in the vocal repertoire of the Puerto Rican Parrot (*Amazona vittata*). Unpublished M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.

ROWLEY, I., AND G. CHAPMAN. 1986. Cross-fostering, imprinting, and learning in two sympatric species of cockatoos. Behaviour 96:1–16.

RUSSELLO, M. A., C. STAHALA, D. LALONDE, K. SCHMIDT, AND G. AMATO. 2010. Cryptic diversity and conservation units in the Bahama Parrot. Conservation Genetics 11:1809–1821.

RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126: 87–100.

RYAN, S. J. 2006. The role of culture in conservation planning for small or endangered populations. Conservation Biology 20:1321–1324.

SAUNDERS, D. A. 1983. Vocal repertoire and individual vocal recognition in the Short-billed White-tailed Black Cockatoo, *Calyptorhynchus funereus latirostris* Carnaby. Australian Wildlife Research 10:527–536.

SCARL, J. C., AND J. W. BRADBURY. 2009. Rapid vocal convergence in an Australian cockatoo, the Galah *Eolophus roseicapillus*. Animal Behavior 77:1019–1026.

SEDDON, N. 2005. Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. Evolution 59:200–215.

SEKERCIOGLU, C. H., G. C. DAILY, AND P. R. EHRLICH. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Science 101:18042–18047.

SLABBEKOORN, H., AND T. B. SMITH. 2002. Bird song, ecology and speciation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 357:493–503.

SNYDER, N. F. R., P. MCGOWAN, J. GILARDI, AND A. GRAJAL (EDS.). 2000. Parrots: status, survey, and conservation action plan 2000–2004. International Union for Conservation of Nature. Gland, Switzerland.

SNYDER, N. F. R., J. W. WILEY, AND C. B. KEPLER. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles.

SPSS INC. 2003. SPSS for Windows. Version 12.0. SPSS Inc., Chicago.

WANKER, R., AND J. FISHER. 2001. Intra- and interindividual variation in the contact calls of Spectacled Parrotlets *Forpus conspicillatus*. Behaviour 138:709–726.

WHITEHEAD, H., L. RENDELL, R. W. OSBORNE, AND B. WUERSIG. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biological Conservation 120:431–441.

WILDEN, I., H. HERZEL, G. PETERS, AND G. TEMBROCK. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. Bioacoustics 9:171–196.

WILEY, J. W. 1991. Status and conservation of parrots and parakeets in the Greater Antilles, Bahama Islands, and Cayman Islands. Bird Conservation International 1:187–214.

WILEY, J. W., R. S. GNAM, S. E. KOENIG, A. DORNELLY, X. GÁLVEZ, P. E. BRADLEY, T. WHITE, M. ZAMORE, P. R. REILLO, AND D. ANTHONY. 2004. Status and conservation of the family Psittacidae in the West Indies. Journal of Caribbean Ornithology 17:94–154.

WILLIAMS, M. I., AND D. W. STEADMAN. 2001. The historic and prehistoric distribution of parrots (Psittacidae) in the West Indies. Pp. 175-189 *in* Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). 2nd edn. CRC Press, Boca Raton, FL.

WINKER, K., D. A. ROCQUE, T. M. BRAILE, AND C.

L. PRUETT. 2007. Vainly beating the air: species-concept debates need not impede progress in science or conservation. Ornithological Monographs 63:30–44.

WRIGHT, T. F. 1996. Regional dialects in the contact call of a parrot. Proceedings of the Royal Society of London Series B Biological Sciences 263:867–872.

WRIGHT, T. F., C. R. DAHLIN, AND A. SALINA-MELGOZA. 2008. Stability and change in vocal dialects of the Yellow-naped Amazon. Animal Behavior 76:1017–1027.

WRIGHT, T. F., AND M. DORIN. 2001. Pair duets in the Yellow-naped Amazon (Psittaciformes: *Amazona auropalliata*): responses to playbacks of different dialects. Ethology 107:111–124.

WRIGHT, T. F., A. M. RODRIGUEZ, AND R. C. FLEISCHER. 2005. Vocal dialects, sex-biased dispersal, and microsatellite population structure in the parrot *Amazona auropalliata*. Molecular Ecology 14:1197–1205.