

CONSERVATION TAXONOMY OF THE CUBAN PARROT (*AMAZONA LEUCOCEPHALA*): VARIATION IN MORPHOLOGY AND PLUMAGE

M. BRYANT J. REYNOLDS^{1,2} AND WILLIAM K. HAYES^{1,3}

¹Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350 USA;

²Current address: 2751 Hennepin Ave S #135, Minneapolis, MN 55408 USA; email: mbryantjreynolds@gmail.com;

³email: whayes@llu.edu

Abstract: Conservation taxonomy, the study of organismal classification to clarify conservation priorities, seeks to define species and subspecies limits. Allopatric populations, such as those present on islands, pose special challenges to identifying taxonomic boundaries which can be practically addressed using diagnostic criteria. Because some of the island populations of Cuban Parrot (*Amazona leucocephala*) are highly endangered, the five recognized subspecies need careful re-evaluation. We measured 18 morphological and plumage characters from 188 museum specimens representing the six extant and one extirpated island populations. We relied largely on discriminant function analyses (DFA) to assess diagnosability and to examine patterns of similarity among the populations. Most morphological characters indicated sexual dimorphism, with males 1-4% larger than females. The plumage characters, in contrast, demonstrated complete absence of sexual dichromatism. Stepwise discriminant analyses including all specimens and 14 characters revealed substantial differentiation among island groups, with 81.4% of individuals classified correctly to island. Pairwise comparisons among islands showed reciprocal discrimination > 80%, with the exception of Cuba / Cayman Brac (67%). None of the populations possessed a single diagnostic character. Although currently lumped into a single subspecies (*A. l. bahamensis*), each of the three Bahamas populations, including an extirpated population on Acklins Island, was equally distinct as the four other currently-recognized subspecies. Collectively, the evidence supports the view that all seven island populations, including the extirpated population, warrant subspecies status. We apply the name *A. l. bahamensis* to the extirpated Acklins population and propose the new names *A. l. abacoensis* for the Abaco Parrot and *A. l. inaguaensis* for the Inagua Parrot. The small and vulnerable populations on Abaco, Inagua, Isla de la Juventud, Cayman Brac, and Grand Cayman deserve special conservation status and should be treated as independent conservation units. Exemplary programs using these threatened populations as "flagship" taxa illustrate why recognizing the subspecies rank can greatly benefit conservation efforts by island nations.

Key words: conservation taxonomy, systematics, Cuban Parrot, *Amazona leucocephala*, morphology, plumage, new subspecies

Resumen: TAXONOMÍA CONSERVACIONISTA DE LA COTORRA CUBANA (*AMAZONA LEUCOCEPHALA*): VARIACIÓN EN LA MORFOLOGÍA Y EL PLUMAJE. La taxonomía para la conservación, que es el estudio de la clasificación de los organismos para esclarecer las prioridades de conservación, busca definir los límites de las especies y subespecies. Las poblaciones alopatricas, como las presentes en las islas, plantean desafíos especiales para la identificación de los límites taxonómicos que pueden abordarse de forma práctica utilizando criterios de diagnóstico. Debido a que algunas de las poblaciones de Cotorra Cubana (*Amazona leucocephala*) están en grave peligro de extinción, las cinco subespecies reconocidas necesitan de una cuidadosa reevaluación. Se midieron 18 caracteres morfológicos y del plumaje de 188 especímenes de museo, que representan a las seis poblaciones existentes y a una población extirpada. Se basó en gran medida en análisis de función discriminante (DFA) para evaluar la capacidad de diagnóstico y examinar los patrones de similitud entre las poblaciones. La mayoría de los caracteres morfológicos indican dimorfismo sexual, siendo los machos 1-4% mayores que las hembras. Los caracteres del plumaje, en cambio, demostraron la ausencia completa de dicromatismo sexual. El análisis discriminante paso a paso, incluyendo todas las muestras y 14 caracteres, reveló diferencias sustanciales entre los grupos de las islas, con 81,4% de los individuos clasificados correctamente en relación con la isla. Las comparaciones por pares entre las islas mostraron la discriminación recíproca > 80%, con la excepción de Cuba / Cayman Brac (67%). Ninguna de las poblaciones tuvo un carácter de diagnóstico único. Aunque las tres poblaciones de Bahamas y la población extirpada de Acklins están incluidas en una sola subespecie (*A. l. bahamensis*), todas fueron igualmente diferentes, como ocurre con las restantes cuatro subespecies actualmente reconocidas. Colectivamente, las evidencias apoyan el punto de vista de que las siete poblaciones de diferentes islas, incluyendo la población extirpada, merecen el estado de subespecie. Le asignamos el nombre de *A. l. bahamensis* a la población extirpada de Acklins y proponemos los nuevos nombres de *A. l. abacoensis* para la cotorra de Abaco y *A. l. inaguaensis* para la cotorra de Inagua. Las poblaciones pequeñas y vulnerables de Abaco, Inagua, Isla de la Juventud, Caimán Brac y Gran Caimán, merecen un estatus especial de conservación y deben ser tratadas como unidades de conservación independientes. El uso de estos programas puede ser un ejemplo en el estudio de poblaciones amenazadas de especies banderas, ya que ilustra por qué el reconocimiento del rango de subespecies, puede beneficiar enormemente los esfuerzos conservacionistas en las naciones insulares.

Palabras clave: *Amazona leucocephala*, Cotorra Cubana, morfología, nuevas subespecies, plumaje, sistemática, taxonomía para la conservación

Résumé : TAXONOMIE ET CONSERVATION DE L'AMAZONE DE CUBA (*AMAZONA LEUCOCEPHALA*): VARIATION DE LA MORPHOLOGIE ET DU PLUMAGE. Taxonomie et conservation s'associent pour que l'étude de la classification des organismes permette de clarifier les priorités de conservation, en redéfinissant les limites séparant les espèces et les sous-espèces. Les populations allopatriques, telles que les populations insulaires, offrent des défis particuliers quant à l'identification de limites taxonomiques grâce à des critères de diagnostic. Certaines populations insulaires d'Amazona de Cuba (*Amazona leucocephala*) étant fortement menacées d'extinction, le statut des cinq sous-espèces actuellement reconnues doit être soigneusement ré-évalué. Nous avons mesuré 18 caractères morphologiques et de plumage, sur 188 spécimens de muséums, issus de 7 populations insulaires dont une éteinte localement. Nous nous sommes appuyés essentiellement sur des analyses discriminantes pour évaluer les possibilités de diagnostic et examiner des patrons de similitude entre populations. La plupart des caractères morphologiques présentaient un dimorphisme sexuel, les mâles étant de 1 à 4% plus grands que les femelles. Le plumage, en revanche, n'a montré aucun dichromatisme sexuel. Les analyses discriminantes pas à pas, concernant tous les spécimens et 14 caractères ont révélé des différences importantes entre les groupes d'îles, avec 81,4% des individus classés correctement par île. Les comparaisons par paires entre les îles ont montré une discrimination réciproque supérieure à 80%, à l'exception de Cuba / Cayman Brac (67%). Aucune des populations ne présentait un caractère de diagnostic unique. Bien qu'elles soient actuellement considérées comme appartenant à une seule sous-espèce (*A. l. bahamensis*), chacune des trois populations des Bahamas, y compris une population éteinte sur l'île Acklins, étaient toutes aussi distinctes que les quatre sous-espèces actuellement reconnues. Ainsi, ces résultats viennent soutenir l'hypothèse que les sept populations insulaires, y compris la population localement éteinte, justifient le statut de sous-espèce. Nous appliquons le nom de *A. l. bahamensis* à la population localement éteinte et nous proposons les nouveaux noms *A. l. abacoensis* pour l'Amazona Abaco et *A. l. inaguaensis* pour l'Amazona Inagua. Les populations d'Abaco, d'Inagua, de Isla de la Juventud, de Cayman Brac et de Grand Cayman sont petites et vulnérables. Elles méritent de ce fait un statut de conservation particulier et devraient être traitées comme des unités de conservation indépendantes. Des programmes exemplaires traitant ces populations menacées comme taxons «phares» démontrent en quoi la reconnaissance du rang de sous-espèce peut grandement bénéficier aux efforts de conservation des pays insulaires.

Mots clés : *Amazona leucocephala*, Amazone de Cuba, morphologie, nouvelle sous-espèce, plumage, systématique, taxonomie de la conservation

Ornithologists rely heavily on morphological and plumage variation to define taxonomic limits in birds (Johnson *et al.* 1999, Helbig *et al.* 2002). Diversity of morphology and plumage are often indicative of gene diversity (e.g., Avise 2000, Doucet *et al.* 2004). Differences in these characters generally reflect ecological segregation or reproductive isolation, and frequently form significant barriers to gene flow (e.g., Turner and Burrows 1995, Edwards *et al.* 2005). Sympatric species almost invariably differ in multiple characters; from this, we can infer that allopatric taxa having dissimilar characters are more likely to remain distinct should they ever come into contact (Helbig *et al.* 2002). Here, we examine geographic variation in morphology and plumage to help elucidate the taxonomic status of allopatric populations of *Amazona leucocephala*.

Conservation taxonomy, the study of organismal classification to clarify conservation priorities, seeks to define species and subspecies limits (Hayes 2006). Our understanding of taxonomic relationships has profound, often-unappreciated implications for conservation priorities (e.g., McNeely 2002, Dubois 2003, Mace 2004). Biodiversity can

be recognized at many levels, with species generally accepted as the fundamental unit of biodiversity (e.g., Agapow *et al.* 2004, Agapow 2005, Haig *et al.* 2006). Although subspecies typically merit less priority, they often enjoy protection as well, most notably from the U. S. Endangered Species Act of 1973 (sec. 3 (15)). Taxonomists heatedly debate the distinction between species and subspecies, and the relevance of the latter to evolutionary and conservation biology (e.g., Zink 2004, 2006, Remsen 2005, Phillimore and Owens 2006). Indeed, subspecies definitions can have significant management implications, with billions of dollars potentially at stake (Rojas 1992, Zink *et al.* 2000, Zink 2004).

Because of their isolation and limited geographic extent, island ecosystems are ideally suited for conservation taxonomy (Hayes 2006). Numerous overlooked, geographically-distinct forms, some at the brink of extinction, await formal recognition. For some of these, particularly the more charismatic vertebrates, recognition of and elevation to species status could dramatically alter conservation priorities and generate considerable publicity and support. Although taxonomy should inform conservation,

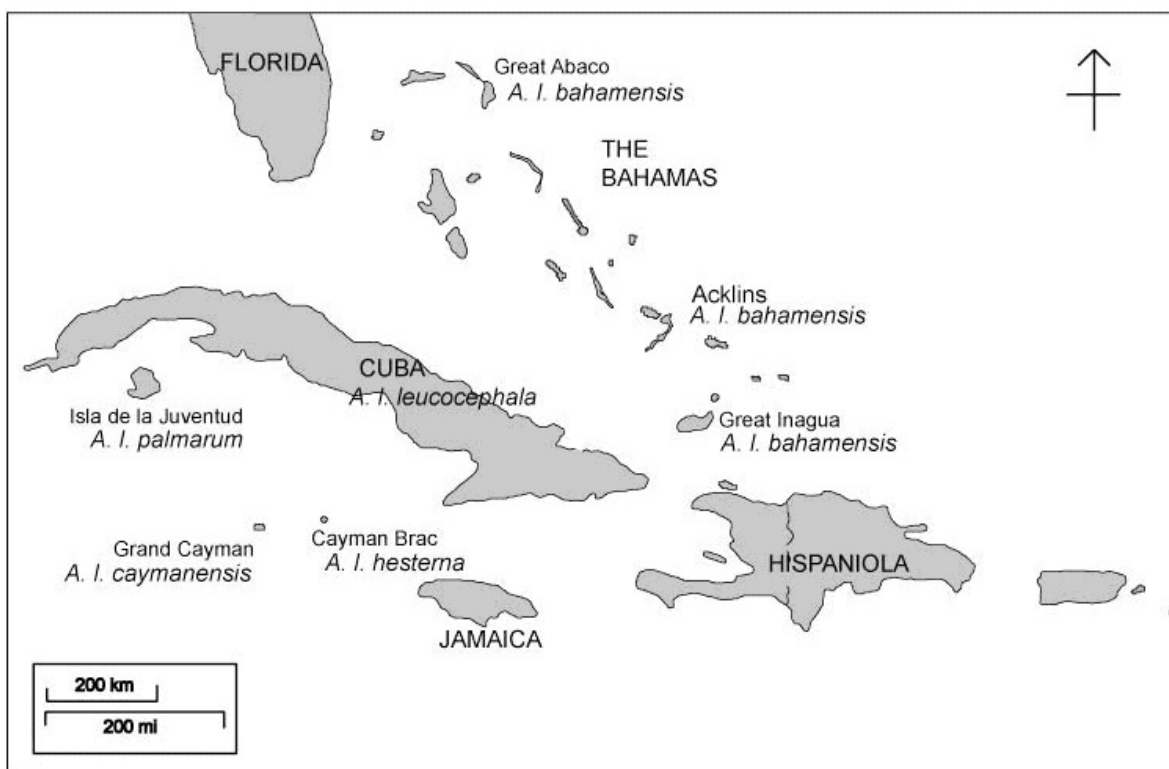


Fig. 1. Distribution of seven island populations used in this study. The five recognized subspecies of *Amazona leucocephala* are extant on six islands and extirpated on one island (Acklins) in the West Indies. Map adapted from Williams and Steadman (2001).

conservation priorities should never influence taxonomic decisions (Bowen and Karl 1999).

Five subspecies of *A. leucocephala* occur on six major islands in the West Indies (Fig. 1): Great Abaco and Great 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*). Historically, substantial populations presumably existed on all major islands in the Bahamas, Cuba, and the Cayman Islands (Williams and Steadman 2001, Ottens-Wainright *et al.* 2004). In the Bahamas, Christopher Columbus wrote of “flocks of parrots that darkened the sun” on what some believe was Acklins Island (Hale 1891, Keegan 1992). Two populations, on Crooked and Acklins Islands and on Little Cayman, became extirpated in the 1940s (Wiley 1991). Records indicate that parrots were also on New Providence, San Salvador, Long, Crooked, and Long Cay islands in the Bahamas (Wiley *et al.* 2004).

Collectively, *A. leucocephala* is regarded by

IUCN and BirdLife International as near-threatened, though individual subspecies and populations are endangered or critically endangered (Snyder *et al.* 2000, Wiley *et al.* 2004, Hayes 2006). Now recognized as an important symbol for conservation, this species is an economic resource, drawing tourists and birdwatchers to the Caribbean. In recognition of this, the Bahamas Government created Abaco National Park in 1994 primarily to protect the northernmost population (Wiley *et al.* 2004). Management plans, including captive breeding and attempts to reintroduce parrots into their former range (Wiley 1991, Wiley *et al.* 1992, 2004, Snyder *et al.* 2000), must take into consideration existing variation in its many forms.

Early methods for designating subspecies, ranging from qualitatively-assessed mean differences to separation by political boundaries, have been plagued by subjectivity and have been inconsistently applied (Patten and Unitt 2002, Cicero and Johnson 2006). Previous designations of *A. leucocephala* taxonomy were no exception, resulting in

confusion over the taxonomic status of this species. Geographic variation in *A. leucocephala* has been described qualitatively for morphology and plumage several times in the past 150 years, but never quantitatively. In the late 1800s, the Cayman populations were considered full species separate from the Cuban populations (Cory 1886, Clark 1905). After examining specimens from the Museum of Comparative Zoology, Peters (1928) placed all populations within four subspecies of a single species. He declared *A. l. leucocephala* and *A. l. palmarum* indistinguishable and synonymous. However, some still recognize the two Cuban races (Raffaele *et al.* 1998, Snyder *et al.* 2000, Ottens-Wainright *et al.* 2004).

Using mitochondrial cytochrome b sequence data, Ottens-Wainright *et al.* (2004) demonstrated modest differentiation among the five populations examined (no data were available from Cayman Brac). The Bahamas and Grand Cayman subspecies were particularly distinct, with both forms being monophyletic with the “short” and “long” data sets, respectively. The two Bahamas populations were less resolved by the sequence data, but their genetic divergence of 0.9% was congruent with cited behavioral, ecological, and plumage differences. These results were similar to more recent analyses of mitochondrial DNA control region sequences by Stahala (2007). The Bahamas and Grand Cayman subspecies formed well-supported reciprocally monophyletic lineages (again, no data were available from Cayman Brac), but the two Bahamas populations were also reciprocally monophyletic and possessed a high proportion of private alleles among six microsatellite loci sampled within *A. l. bahamensis*. Both studies indicated little genetic differentiation between *A. l. leucocephala* and *A. l. palmarum*. Although systematists now rely heavily on molecular analyses, morphological and molecular data sometimes conflict, such that combined approaches give us added clarity (Wiens 2004).

The purpose of this study was to examine morphological and plumage variation to help clarify the taxonomic status of and appropriate conservation units for *A. leucocephala*. In the 81 yr since the most recent morphological and plumage evaluation (Peters 1928), advances in statistical methods have been developed, providing a degree of objectivity. Here, we rely on multivariate analyses to evaluate the distinctiveness of each of the six extant and one extirpated island populations. A companion paper will address variation in flight calls.

MATERIALS AND METHODS

MEASUREMENTS

We measured up to 18 characters from 188 specimens examined at or borrowed from six museums. For consistency, one of us (MBJR) made all measurements. With digital calipers (to nearest 0.1 mm), we measured culmen width and depth at the anterior nares, longest toe (“straight longest toe,” knuckle to base of nail), metatarsus (flexor side of ankle joint to extensor side of longest toe), rose patch on throat (base of culmen to caudal-most red feather), extent of continuous white on head (“white head length” along midline from posterior nares caudally), and tail length. We measured culmen curvature (curved culmen; nearest 1 mm) from the ceres to the tip with a flexible plastic ruler. The wing chord (non-flattened; nearest 1 mm) was measured using a wooden ruler with an L bracket attached to the end. We also measured the longest toe along its curve (“curved longest toe,” nearest 1 mm) using a fabric tape. Total white area on the head (“white head area” in mm²) was measured with a transparent 2 × 2 mm acetate grid placed over the head and wrapped around the throat to count squares (when viewed at a right angle) having > 50% white plumage (Fig. 2A,B). Presence of red on belly was a relative measurement scored from 0 (complete absence) to 5 (maximum red, sometimes contacting the different shade of red from the throat) by comparison to a photograph of a standard set of parrots from USNM (specimens used: 1 = 453655; 2 = 172763; 3 = 172764; 4 = 453657; 5 = 172768; Fig. 2C).

The proportion of three color groups (white, rose/white, black/green) around the eye was estimated using a transparent acetate grid with a 1 cm diameter circle divided into ten equal pie pieces drawn onto it (Fig. 2D). The center of the circle was positioned over the center of the eye, the number of pie pieces containing each color was counted, and the proportion of each color was estimated to within 5%. This was done for feathers closest to (at orbit of) the eye to measure the characters “inner white,” “inner red,” and “inner green,” and at the 1 cm diameter of the circle to measure the characters “outer white,” “outer red,” and “outer green.” In some specimens, “inner” and “outer” colors overlapped in the loreal region (Fig. 2D).

Several characters (curved long toe and outer eye colors) were not measured initially and, therefore, were obtained from only 61% of the specimens. Three outlier measurements among the entire data set (data entry error and/or obviously anomalous

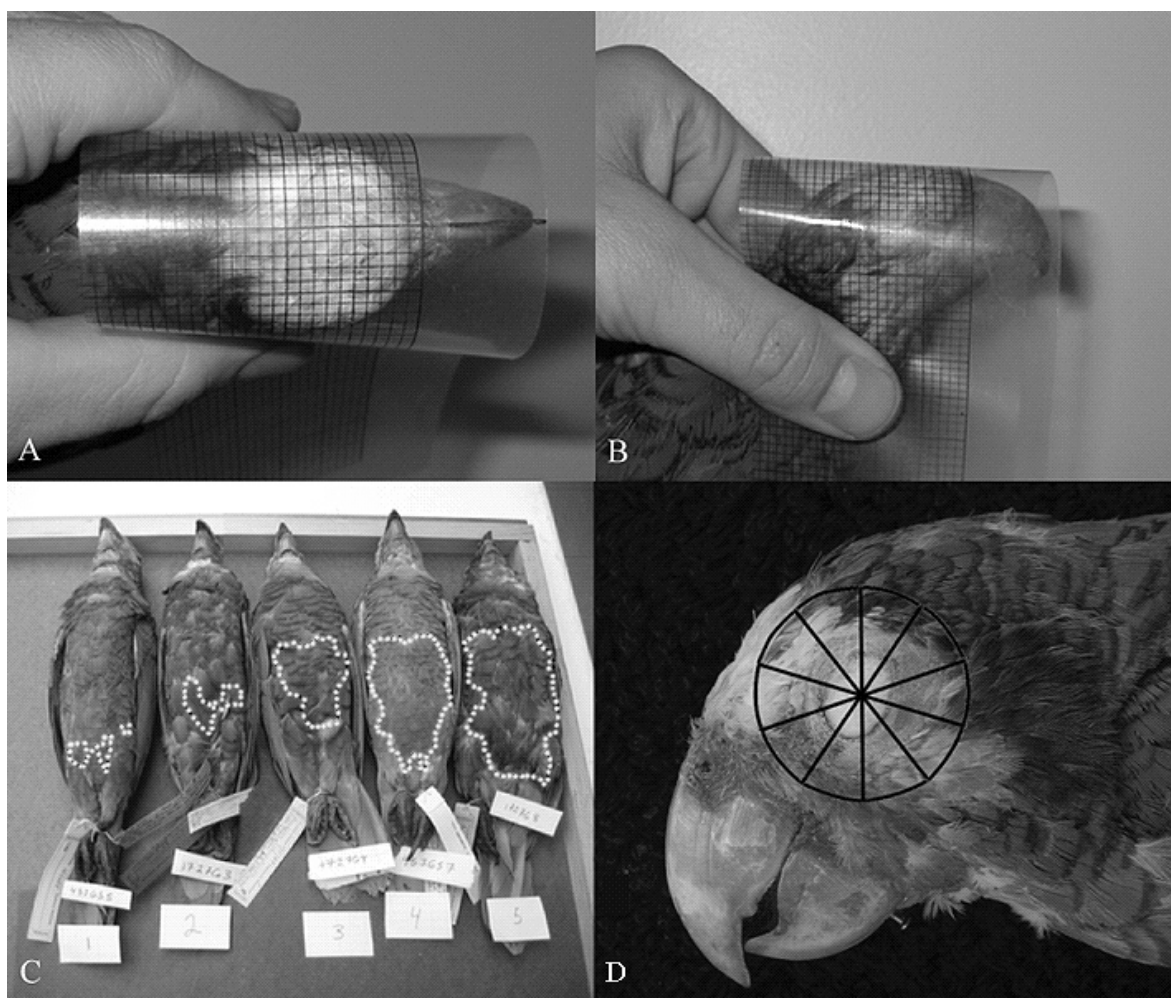


Fig. 2. Plumage measurements of *Amazona leucocephala* specimens. (A and B) Use of a 2x2 mm acetate grid to quantify extent of white on the head. (C) Photo of voucher specimens from the National Museum of Natural History to score extent of red (area within white dots) on the belly using a scale (left to right) of 0 (not shown) to 5. (D) Use of an acetate circle to quantify “outer eye” feather coloration 1 cm from center from eye.

characters) were identified and removed prior to analysis.

ANALYSES

All statistics were performed with SPSS 12.0 for Windows™ (SPSS Inc. 2003) with $\alpha = 0.05$. To test for sexual dimorphism and population differences, we subjected each character to a 2×7 (sex \times island population) analysis of variance (ANOVA; Mertler and Vannatta 2002), treating sex and island population as between-subjects factors. The island populations included Abaco, Acklins, Inagua, Cuba, Isla de la Juventud (Isla de Pinos), Cayman Brac (in-

cluding one specimen from Little Cayman, where the subspecies formerly occurred; Wiley *et al.* 2004), and Grand Cayman. Although *A. l. palmarum* occurs on both Cuba and Isla de la Juventud, we chose to treat each island as a separate biogeographic unit. The data were prescreened and found suitable for parametric analyses. To confirm presence or absence of sexual dichromatism in plumage characters, we also tested each plumage character using analysis of covariance (ANCOVA; Mertler and Vannatta 2002), adding body size as a covariate to control for dimorphism in body size. Each character was tested three times using a differ-

ent covariate: chord, curved culmen, or culmen depth. Because culmen depth consistently explained the most variance in plumage characters, we report only those tests including this covariate. For ANOVA and ANCOVA models, effect sizes (proportion of variance explained by an independent variable or interaction) were computed as partial η^2 values (Mertler and Vannatta 2002).

To test the hypothesis that body size (mean wing chord for males) is associated with island size, we used a Spearman rank correlation (Conover 1999). Island sizes were obtained from multiple internet sources for Great + Little Abaco (1,681 km²), Crooked + Acklins Islands (586 km²), Great + Little Inagua (1,544 km²), Cuba (105,806 km²), Isla de la Juventud (2,419 km²), Cayman Brac + Little Cayman (62 km²), and Grand Cayman (196 km²).

We used stepwise discriminant function analysis (DFA; Mertler and Vannatta 2002) to evaluate distinctiveness among the seven island populations. The DFA included 14 characters (curved long toe, outer white, outer red, and outer green were excluded) using SPSS defaults with prior probabilities computed from group sizes. We also used leave-one-out classification to assess classification bias arising from small samples (Lance *et al.* 2000) and cross-validate accuracy of group assignments. Because some specimens were worn or damaged, we were sometimes unable to measure every character on a specimen. Thus, for classification purposes, we replaced missing values with the mean for those variables using SPSS. Missing data accounted for no more than 3.2% of the cases within any given variable, and 17% of the individuals in the DFA had at least one missing value. Males and females were analyzed together and separately, but because results were similar, we report only analyses from the pooled data. We also used additional DFAs for pairwise comparisons among select populations to further examine reciprocal diagnosability (*sensu* Helbig *et al.* 2002, Patten and Unitt 2002).

RESULTS

SEXUAL DIMORPHISM AND ISLAND COMPARISONS

The ANOVA results revealed sexual dimorphism for most morphological characters (all $P < 0.031$; partial $\eta^2 = 0.03$ -0.15; Table 1). Males averaged 1-4% larger for most morphological characters, with the one exception being tail length, which was similar for the two sexes. The ANOVAs identified only one dimorphic plumage character: white head length ($P = 0.020$; partial $\eta^2 = 0.03$), with the mid-

line extent of white greater for males. Compared to body size, sexual differences in plumage explained very little variation (partial $\eta^2 = 0.00$ -0.03). From ANCOVA models considering island, sex, and body size (culmen depth) simultaneously, four plumage characters were found to be weakly associated with body size: white head length, white head area, and throat were positively associated (all $P \leq 0.002$, partial $\eta^2 = 0.06$ -0.10), and inner green was negatively associated ($P = 0.034$, partial $\eta^2 = 0.03$). Sex was not significant in any of these models (all $P > 0.17$, partial $\eta^2 \leq 0.01$), confirming the absence of sexual dichromatism among all characters, including white head length, which was confounded with body size in the aforementioned ANOVA result.

The ANOVA results also indicated highly significant differences among islands, with population differences explaining substantial variation in all morphological and plumage characters (all $P < 0.001$; partial $\eta^2 = 0.20$ -0.69; Table 1). For most morphological characters, parrots from the Bahamas were largest and those from Cuba and Cayman Brac were smallest (Fig. 3A, B). Parrots from Isla de la Juventud were also slightly larger than the Cuban or Cayman populations. The extent of white on the head was greatest in the northern (Bahamas) populations and least in the southern (Cayman) populations (Fig. 3C). The red throat plumage was most extensive in the northern populations, least extensive in Cuba, and declined from Isla de la Juventud southward (Fig. 3D). The red belly was most extensive in Cuba and Isla de la Juventud, least extensive in the northern populations, and intermediate in the southern populations. The red on the belly was consistently a darker shade of red than that of the throat, and this was evident even in birds from Isla de la Juventud, where both colors met in some specimens. A north-to-south decrease in values was observed for the characters inner white eye and outer white eye, and the opposite for the green and red eye measurements.

We found one weak but significant interaction among the characters (curved culmen, $P = 0.03$; partial $\eta^2 = 0.09$; Table 1), with dimorphism particularly strong in the Acklins population (males having much larger bills). Considering the high experimentwise error arising from so many characters under consideration, we suspect this interaction to be spurious, as supported by the small proportion of variance explained relative to the main effects of island population and sex.

Considering the four measurements not taken from all birds (curved longest toe and the three

Table 1. Morphological and plumage measurements (mean \pm 1 S.E.) for seven island populations of *Amazona leucocephala*. Analysis of variance results (including partial η^2 effect sizes) are included.

Character (units)	Sex	Island						ANOVA Effects			
		Abaco	Acklins	Inagua	Cuba	Isla de la Juventud	Cayman Brac	Grand Cayman	Island	Sex	Interac- tion
		♂ $n=2$ ♀ $n=7$	♂ $n=5$ ♀ $n=3$	♂ $n=6$ ♀ $n=6$	♂ $n=20$ ♀ $n=26$	♂ $n=20$ ♀ $n=16$	♂ $n=7$ ♀ $n=8$	♂ $n=25$ ♀ $n=18$	P η^2	P η^2	P η^2
chord (mm)	♂ ♀	205 \pm 4 200 \pm 3	213 \pm 2 203 \pm 1	202 \pm 1 195 \pm 2	183 \pm 1 182 \pm 1	194 \pm 1 188 \pm 1	184 \pm 2 180 \pm 2	197 \pm 1 196 \pm 2	<0.001 0.66	<0.001 0.10	0.174 0.05
curved culmen (mm)	♂ ♀	33 \pm 2 33 \pm 1	39 \pm 2 34 \pm 1	33 \pm 1 33 \pm 0	29 \pm 0 27 \pm 0	30 \pm 0 30 \pm 0	30 \pm 0 28 \pm 1	30 \pm 0 29 \pm 0	<0.001 0.61	<0.001 0.11	0.025 0.09
culmen width (mm)	♂ ♀	16.0 \pm 0.3 15.6 \pm 0.3	16.5 \pm 0.6 15.8 \pm 0.3	16.8 \pm 0.7 15.8 \pm 0.3	13.9 \pm 0.2 14.0 \pm 0.2	14.4 \pm 0.2 14.2 \pm 0.2	15.4 \pm 0.4 14.4 \pm 0.3	14.6 \pm 0.2 14.3 \pm 0.2	<0.001 0.40	0.009 0.04	0.270 0.05
culmen depth (mm)	♂ ♀	28.3 \pm 0.8 28.8 \pm 0.6	32.0 \pm 0.37 30.2 \pm 0.83	30.2 \pm 0.41 29.4 \pm 0.61	27.1 \pm 0.36 26.1 \pm 0.24	28.3 \pm 0.24 27.6 \pm 0.25	26.1 \pm 0.59 24.6 \pm 0.25	27.5 \pm 0.20 26.9 \pm 0.30	<0.001 0.54	0.001 0.06	0.603 0.03
tail length (mm)	♂ ♀	122 \pm 3 115 \pm 2	123 \pm 1.7 121 \pm 2	114 \pm 2.3 114 \pm 2	101 \pm 1.7 101 \pm 0.8	109 \pm 1.5 108 \pm 1.2	106 \pm 2.5 106 \pm 1.8	115 \pm 1.3 115 \pm 1.4	<0.001 0.55	0.222 0.01	0.928 0.01
metatarsus (mm)	♂ ♀	22.7 \pm 0.70 22.5 \pm 0.35	24.1 \pm 0.67 23.3 \pm 0.91	22.8 \pm 0.24 22.2 \pm 0.75	21.5 \pm 0.26 20.9 \pm 0.35	21.9 \pm 0.21 22.1 \pm 0.24	21.4 \pm 0.53 20.1 \pm 0.28	22.3 \pm 0.35 21.3 \pm 0.25	<0.001 0.20	0.031 0.03	0.572 0.03
straight longest toe (mm)	♂ ♀	30.1 \pm 2.85 31.9 \pm 1.00	31.9 \pm 0.80 31.6 \pm 1.67	32.6 \pm 0.40 31.1 \pm 1.28	29.4 \pm 0.21 28.5 \pm 0.29	30.4 \pm 0.23 29.6 \pm 0.27	28.9 \pm 0.81 26.2 \pm 0.54	28.4 \pm 0.26 28.0 \pm 0.34	<0.001 0.41	0.032 0.03	0.088 0.07
curved long toe ^a (mm)	♂ ♀	35 \pm 0.0 32 \pm 0.8	36 \pm 1.0 35 \pm 0.9	34 \pm 1.5 31 \pm 1.4	31 \pm 0.7 30 \pm 0.3	32 \pm 0.4 31 \pm 0.5	31 \pm 0.4 29 \pm 0.3	30 \pm 0.4 29 \pm 0.4	<0.001 0.57	0.000 0.15	0.687 0.04
white head length (mm)	♂ ♀	36.4 \pm 3.30 33.3 \pm 1.26	37.0 \pm 1.70 35.4 \pm 1.40	30.4 \pm 1.13 28.6 \pm 1.95	25.0 \pm 0.51 26.4 \pm 0.70	27.8 \pm 0.64 27.0 \pm 0.63	26.1 \pm 1.04 23.1 \pm 0.83	20.2 \pm 0.88 17.8 \pm 0.98	<0.001 0.66	0.020 0.03	0.137 0.06
white head area (mm ²)	♂ ♀	1084 \pm 42.0 1184 \pm 78.6	1256 \pm 81.2 1240 \pm 101.8	776 \pm 84.0 852 \pm 90.2	624 \pm 25.6 664 \pm 33.6	672 \pm 29.4 680 \pm 31.6	688 \pm 70.1 504 \pm 55.3	384 \pm 35.0 264 \pm 29.0	<0.001 0.69	0.672 0.00	0.065 0.07
rose throat (mm)	♂ ♀	77.0 \pm 0.00 81.7 \pm 2.17	86.8 \pm 2.65 78.7 \pm 5.33	64.5 \pm 7.98 63.0 \pm 3.60	51.3 \pm 2.28 49.5 \pm 2.08	59.8 \pm 3.22 62.4 \pm 2.78	55.7 \pm 4.54 50.9 \pm 2.93	50.9 \pm 1.95 55.5 \pm 3.20	<0.001 0.34	0.814 0.00	0.660 0.03
red belly (scale)	♂ ♀	2 \pm 0.5 1 \pm 0.2	1 \pm 0.2 1 \pm 0.3	2 \pm 0.2 2 \pm 0.3	3 \pm 0.2 3 \pm 0.2	3 \pm 0.2 4 \pm 0.2	3 \pm 0.1 3 \pm 0.1	3 \pm 0.2 3 \pm 0.3	<0.001 0.45	0.558 0.00	0.531 0.03
inner white eye (%)	♂ ♀	100 \pm 0.0 86 \pm 6.5	62 \pm 8.0 87 \pm 13.3	35 \pm 7.5 55 \pm 5.6	35 \pm 4.5 40 \pm 3.9	44 \pm 5.1 42 \pm 5.0	37 \pm 6.1 31 \pm 8.3	12 \pm 2.3 8 \pm 3.2	<0.001 0.53	0.369 0.01	0.170 0.06
inner red eye (%)	♂ ♀	0 \pm 0.0 6 \pm 3.0	34 \pm 6.0 13 \pm 13.3	35 \pm 3.7 37 \pm 3.3	32 \pm 2.3 30 \pm 2.6	37 \pm 3.2 35 \pm 2.8	4 \pm 6.2 39 \pm 6.6	43 \pm 2.5 39 \pm 4.7	<0.001 0.25	0.191 0.01	0.664 0.03
inner green eye (%)	♂ ♀	0 \pm 0.0 9 \pm 4.0	4 \pm 4.0 0 \pm 0.0	30 \pm 7.3 8 \pm 4.8	35 \pm 3.9 31 \pm 4.2	19 \pm 4.4 23 \pm 4.0	19 \pm 8.6 29 \pm 5.7	45 \pm 2.6 53 \pm 4.9	<0.001 0.38	0.976 0.00	0.180 0.05

Table 1 continued.

Character (units)	Sex	Island								ANOVA Effects											
		Abaco		Acklins		Inagua		Cuba		Isla de la Juventud		Cayman Brac		Grand Cayman		Island		Sex		Inter- action	
		♂ n=2	♀ n=7	♂ n=5	♀ n=3	♂ n=6	♀ n=6	♂ n=20	♀ n=26	♂ n=20	♀ n=16	♂ n=7	♀ n=8	♂ n=25	♀ n=18	P	η ²	P	η ²	P	η ²
outer white eye ^a (%)	♂	70±5.0		43±2.5		45±7.6		31±3.5		30±1.9		31±2.0		19±2.7		<0.001	0.113			0.348	
	♀	54±6.5		42±4.4		36±5.5		32±1.5		32±1.8		33±1.7		15±3.5		0.62	0.03			0.07	
outer red eye ^a (%)	♂	13±2.5		34±2.4		28±1.7		32±2.1		34±1.8		33±1.7		40±3.4		<0.001	0.212			0.620	
	♀	23±5.2		37±1.7		34±2.4		32±1.1		34±1.2		29±0.8		42±2.7		0.36	0.02			0.05	
outer green eye ^a (%)	♂	13±2.5		24±2.4		27±8.8		39±3.7		36±2.2		36±2.4		42±2.4		<0.001	0.372			0.572	
	♀	24±3.0		22±4.4		30±3.5		36±2.1		35±2.0		38±2.1		43±2.2		0.47	0.01			0.05	

^aReduced sample size; see text

outer eye colors), the higher partial η^2 values for population differences (Table 1) compared to their analogous measures (straight longest toe and the three inner eye colors) suggest that the former might be better discriminators.

There was no significant association between island size and mean wing chord length of males ($r_s = -0.21$, $P = 0.65$). The two populations having the smallest birds—Cuba and Cayman Brac + Little Cayman—were from the largest island and the smallest island group, respectively.

DISCRIMINANT ANALYSES

The stepwise DFA for all populations generated a final model with six functions that included eight of the 14 characters. The overall Wilks' lambda was significant ($\lambda = 0.023$, $\chi^2_{48} = 556.02$, $n = 156$, $P < 0.001$), indicating that the predictors were sufficient to differentiate between the seven island populations. Separation of the populations on the first two functions is depicted in Fig. 4. The first function (48.6% of variance) was positively associated with white head area (standardized coefficient = 0.548), curved culmen (0.308), and throat (0.303), and negatively associated with belly (-0.525), leading to good separation of the Bahamas populations. The second function (35.3% of variance) was comprised positively of chord (0.825) and negatively of white head area (-0.791), and best separated the Grand Cayman population. The Cuba, Isla de la Juventud, and Cayman Brac populations were least differentiated.

Classification results (Table 2) indicated that 81.4% of parrots overall were classified correctly and somewhat fewer (73.4%) were cross-validated using leave-one-out. Accuracy for each island group was Abaco 89%, Acklins 60%, Inagua 73%, Cuba 80%, Isla de la Juventud 80%, Cayman Brac 67%, and Grand Cayman 95%. These results far exceeded those expected from random; based on sample sizes, prior probabilities for each island were, respectively, 5%, 4%, 8%, 28%, 21%, 8%, and 26%.

Stepwise DFAs were also conducted pairwise between geographically close island populations. Each model was significant (all $P \leq 0.013$) and included 2-8 characters for discrimination (Table 3). Leave-one-out cross-validation gave either identical results or reduced classification success by only a few percentage points. Among the pairwise comparisons, the extant Bahamas populations (Abaco and Inagua) appeared to be most distinct, with 100% reciprocal diagnosis (also with cross-validation) based on just two characters (inner red

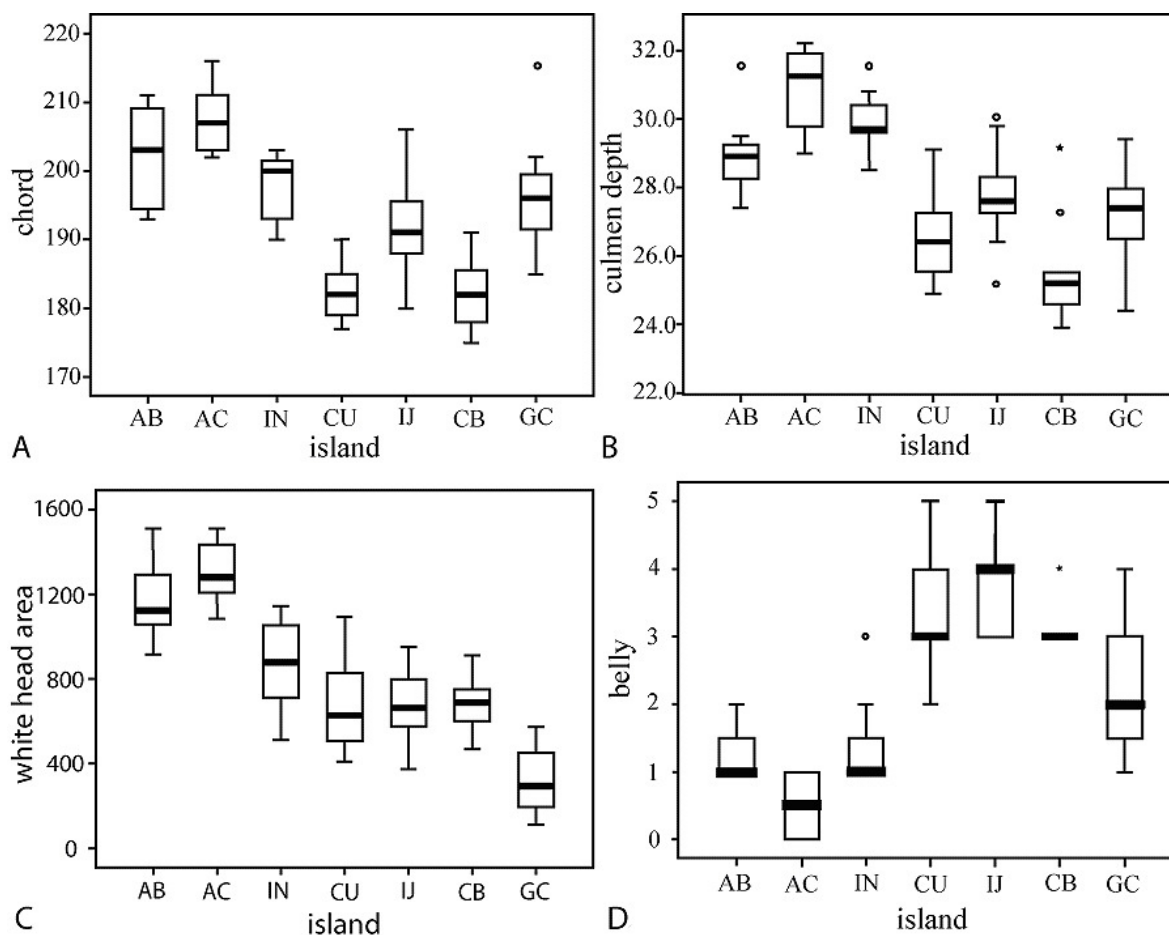


Fig. 3. Boxplots comparing four representative characters (A = wing chord, mm; B = culmen depth, mm; C = area of white on head, mm²; D = extent of red on belly, based on scale; see text for explanation of characters) among the seven island populations of *Amazona leucocephala* (AB = Abaco; AC = Acklins; IN = Inagua; CU = Cuba; IJ = Isla de la Juventud; CB = Cayman Brac; GC = Grand Cayman). The box contains 50% of the values, the horizontal line represents the median, the vertical whiskers show the highest and lowest values excluding extreme values, and the circles and asterisks indicate extreme values.

eye feathers, and white head length). All pairwise comparisons showed reciprocal discrimination > 80%, except for Cuba / Cayman Brac, for which only 67% of Cayman Brac individuals were correctly predicted (also with cross-validation).

DISCUSSION

This study represents the first quantitative analysis of morphological and plumage character variation within *A. leucocephala*. The most important outcome concerns the taxonomic distinctiveness of each island group. However, the results also shed light on sexual differences and clinal variation, which must be taken into consideration when using

morphological and plumage characters for taxonomic purposes.

SEXUAL DIMORPHISM AND POPULATION VARIATION

The analyses of variance revealed significant dimorphism in body size. Males averaged 1-4% larger than females in most body size measurements (c.f. Snyder *et al.* 1987:48). The one exception was tail length, being equal for both sexes. Sexual dimorphism has not been described for *A. leucocephala* and is rare in most parrots (de Mattos *et al.* 1998). A practical application would be the cautious use for sex determination without the cost of DNA testing. In contrast to body size dimorphism, the same

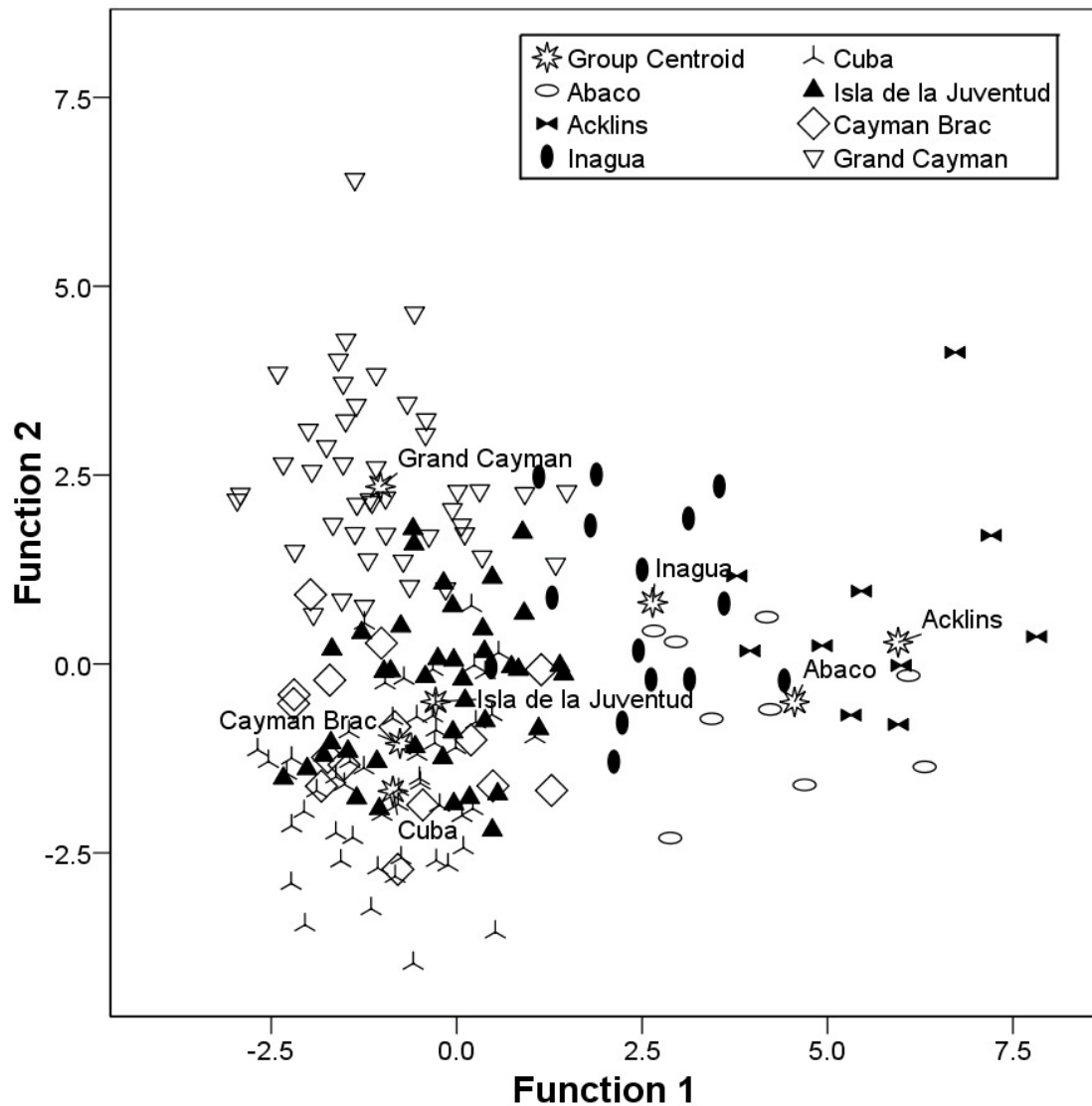


Fig. 4. Canonical plot of discriminant scores for each specimen from the seven island populations of *Amazona leucocephala*. Group centroids are also shown. Function 1 (48.6% of variance) was positively associated with extent of white on head, curved culmen length, and extent of rose on throat, and negatively associated with extent of red on belly. Function 2 (35.3% of variance) was positively associated with wing chord length and negatively associated with extent of white on head.

analyses confirmed complete absence of sexual dichromatism. Although some parrots exhibit sexually distinct coloration patterns, most do not (de Mattos *et al.* 1998) and sexual dichromatism tends to be reduced among island species (Doucet *et al.* 2004).

Both body size and plumage varied considerably among the island populations. Importantly, clinal variation among populations was minimal or non-existent. Body size was independent of island size

(ecological diversity) and the range of variation was similar among each of the populations (Fig. 3). Several plumage characters tended toward a north-south trend, most notably extent of white on the head and face, but other characters, such as red on the belly, showed no latitudinal cline. The possible cline in white plumage could conceivably result from climatic and seasonal food variation. *Amazona leucocephala* flocks more so during the winter (González

Table 2. Results of the stepwise discriminant function analysis for classifying voucher specimens into seven island populations of *Amazona leucocephala* (sexes pooled) based on eight morphological and plumage characters. Individuals were correctly assigned 81.4% of the time. Bold fonts indicate correctly assigned specimens by count and percentage.

		Predicted Group Membership						
	Island	Abaco	Acklins	Inagua	Cuba	Isla de la Juventud	Cayman Brac	Grand Cayman
Count	Abaco	8	1	0	0	0	0	0
	Acklins	3	6	1	0	0	0	0
	Inagua	0	1	11	0	2	0	1
	Cuba	0	0	1	43	7	3	0
	Isla de la Juventud	0	0	0	5	32	0	3
	Cayman Brac	0	0	0	3	1	10	1
	Grand Cayman	0	0	0	0	2	0	43
%	Abaco	88.9	11.1	0.0	0.0	0.0	0.0	0.0
	Acklins	30.0	60.0	10.0	0.0	0.0	0.0	0.0
	Inagua	0.0	6.7	73.3	0.0	13.3	0.0	6.7
	Cuba	0.0	0.0	1.9	79.6	13.0	5.6	0.0
	Isla de la Juventud	0.0	0.0	0.0	12.5	80.0	0.0	7.5
	Cayman Brac	0.0	0.0	0.0	20.0	6.7	66.7	6.7
	Grand Cayman	0.0	0.0	0.0	0.0	4.4	0.0	95.6

Table 3. Pairwise classification results for stepwise discriminant function analyses between geographically close island populations of *Amazona leucocephala*.

Islands Compared	Accuracy	<i>n/n</i>	Characters	Best Discriminating Characters
	by Group %/%		Entered in Model	
Abaco/Acklins	100/90	9/10	2	belly, inner red eye
Acklins/Inagua	100/93	10/15	5	white head area, culmen width
Abaco/Inagua	100/100	9/15	2	inner red eye, white head length
Abaco/Cuba	89/98	9/54	6	inner red eye, curved culmen
Acklins/Cuba	100/100	10/54	5	belly, white head length = throat
Inagua/Cuba	93/100	15/54	6	belly, straight longest toe
Cuba/Isla de la Juventud	80/85	54/40	5	chord, metatarsus
Cuba/Cayman Brac	93/67	54/15	9	culmen depth, tail
Cuba/Grand Cayman	98/100	54/45	4	white head area, chord
Isla de la Juventud/Cayman Brac	93/87	40/15	4	culmen width, straight longest toe
Isla de la Juventud/Grand Cayman	98/100	40/45	6	white head length, tail
Cayman Brac/Grand Cayman	87/100	15/45	5	chord, inner green

2001, Rivera-Milán *et al.* 2005, Stahala 2005), and winters are harsher in northern latitudes. White coloration in birds may become adapted as a signal to recruit conspecifics to a foraging flock, thus increasing vigilance and decreasing risk of predation (Beauchamp and Heeb 2001). However, no clinal variation in flocking seems evident among Cuban Parrots. In fact, *A. l. caymanensis* on Grand Cayman, which sometimes travels in large flocks simi-

lar to those of other Greater Antilles parrots, actually has less white than *A. l. hesternus* on nearby Cayman Brac, which is comparatively secretive and travels in small groups similar to those of Lesser Antilles parrots (Wiley *et al.* 2004, Enkerlin-Hoeflich *et al.* 2006). The contrast between populations of these two Cayman islands, and between the Greater and Lesser Antilles, more likely results from differences in avian predation risk, with Grand

Cayman and other Greater Antilles islands supporting significant raptor populations that Cayman Brac and the Lesser Antilles lack (Enkerlin-Hoeflich *et al.* 2006). Snyder *et al.* (1987) found that plumage characters were better than morphological characters for diagnosing currently-accepted parrot species of the Greater Antilles and Central America. Within *A. leucocephala*, however, we found that morphological and plumage characters were equally discriminating, with similar effect sizes for population differences.

TAXONOMY

Considering the relatively small effect sizes of sexual dimorphism and negligible clinal variation, we assume that the character differences between populations have resulted from evolution in isolation and are good predictors for taxonomy. Our analyses indicated that island populations were discriminated fairly accurately, with 81% success in the omnibus model comprised of eight characters (Table 2). Although size and plumage variation fit the general descriptions given by Peters (1928), notable differences emerged. First, the three Bahamas populations, including the extirpated Acklins population, were each as distinct as any other currently-recognized subspecies. This was apparent not only in discrimination, but also in the number of characters selected to achieve the final model in pairwise comparisons (Table 3). The extant Abaco and Inagua populations, for example, were 100% reciprocally diagnosable based on only two discriminators, inner red (feathers surrounding the eye) and white head length (feathers along the crown). Other currently-recognized subspecies pairs required four or more characters in combination to achieve weaker discrimination. Moreover, whereas Peters synonymized the Cuban and Isla de la Juventud populations, which would be consistent with genetic analyses (Ottens-Wainright *et al.* 2004, Stahala 2007), our results suggest the two island populations can be discriminated with 90% success, primarily by wing chord length and extent of red on the throat.

With the present data set, none of the populations could be diagnosed by a single character. Although the Abaco and Inagua populations were fully diagnosed by the combination of two characters, neither Bahamas population was 100% separable from the Cuba population. To elevate candidate taxa to species status, the taxonomic subcommittee of the British Ornithologists' Union recommended 100% diagnosability based on a single character or the combi-

nation of two or three functionally independent characters (Helbig *et al.* 2002). Although most populations met the 75% reciprocal diagnosis criterion for delineating subspecies (Patton and Unitt 2002), the majority of discriminations required more than four characters in combination. Helbig *et al.* (2002) recommended that no more than two to three characters be combined for use in diagnosing full species.

The ability of the DFAs to discriminate more accurately between more geographically distant populations supports the suggestion of a late Pleistocene radiation away from Cuba to the Caymans, followed by a more recent separation between Cuba and Isla de la Juventud (Ottens-Wainright *et al.* 2004). To underscore the genetic independence of these populations, there is no evidence of continued movement over large distances of sea, except perhaps by human influence (Hale 1891, Fernández de Oviedo y Valdés 1959, Wilson 1990, Wiley *et al.* 2004, Stahala 2007). At present, the Convention on the International Trade of Endangered Species (CITES) Appendix 1 protection is awarded to *A. leucocephala*, making it illegal to transport birds between islands without special permits. Consequently, there is little to suggest the populations will interbreed naturally.

Our results show that the Abaco parrots are as distinct from Inagua as any of the currently-recognized subspecies are from each other. The morphological and plumage distinctiveness complements other unique qualities of the Abaco parrot. Molecular divergence of 0.9% between the two populations is close to the maximum (0.94%) between that of any *A. leucocephala* population (Ottens-Wainright *et al.* 2004). Behaviorally, the Abaco parrot differs from other *A. leucocephala* populations by nesting in limestone cavities in the ground rather than in tree cavities (Snyder *et al.* 1982, Gnam and Rockwell 1991, Wiley 1991, Stahala 2005), which may give them special advantages on an island frequently afflicted with hurricanes and wildfires (e.g., Stahala 2005, O'Brien *et al.* 2006). The flight calls also appear to be 100% diagnosable from all other *A. leucocephala* (Reynolds 2006). One might ask whether the Abaco parrot, and possibly other *A. leucocephala* populations, should be considered distinct species.

At a minimum, each extant island population should be treated as a distinct subspecies and a separate conservation unit (*sensu* Fraser and Bernatchez 2001, Green 2005). Our analyses suggest that the extirpated Acklins population also warrants

subspecies status. Accordingly, we split *A. l. bahamensis* into three subspecies. The subspecies name *bahamensis* was bestowed by Bryant (1867:65) on populations he found abundant on Acklins Island, nearby Fortune Island (currently Long Cay), and Inagua. His description apparently was based only on visual observations, as no mention was made of specimens examined. After correspondence with museum curators (major North American collections, British Museum of Natural History) and J. W. Wiley (who examined material at Museum National d'Histoire Naturelle, in France, and at most museums in Cuba), and after reviewing all papers cited in Ridgway's (1916) synonymy and Peters's (1928) assessment of the species, we conclude that no holotype of *A. l. bahamensis* has been designated. Because Bryant (1867:63) clearly visited and mentioned Acklins Island and Long Cay prior to Inagua, we hereby restrict the type locality of *A. l. bahamensis* to Acklins Island and its distribution to the Acklins, Crooked, and Long Cay island group (these three adjacent islands occupy a single bank). We propose the new names *A. l. abacoensis* for the Abaco Parrot and *A. l. inaguaensis* for the Inagua Parrot.

Amazona leucocephala bahamensis (Bryant, 1867)

Neotype.—We designate Carnegie Museum of Natural History (CMNH) specimen #30888 as the neotype, a female specimen collected by Willis W. Worthington on 4 March 1909 at Pompey Bay, Acklins, the Bahamas. Worthington provided a first-hand account of this bird's acquisition (Todd and Worthington 1911:452).

Paratypes.—We assign two additional specimens, CMNH #30890 (male) and #30892 (female), as paratypes. These were collected for Worthington by an unnamed guide on 5 March and 8 March 1909, respectively, at Pompey Bay, Acklins, the Bahamas (Todd and Worthington 1911:452-453).

Diagnosis.—Compared to all other *A. leucocephala* populations, specimens exhibit the largest average body size, greatest extent of white on head and face, greatest extent of rose on throat, and least extent of red on belly.

Etymology and range.—Named and described as a Bahaman variety of *A. leucocephala* by Bryant (1867:65), this now extinct subspecies was presumably confined to the Acklins, Crooked, and Long Cay island group. Historic reports and remains of *A. leucocephala* from other islands in the Bahamas have been referred to *A. l. bahamensis* (Williams and Steadman 2001, Wiley *et al.* 2004),

but some such populations may have represented other extinct subspecies.

Amazona leucocephala abacoensis New subspecies

Holotype.—Academy of Natural Sciences of Philadelphia (ANSP) specimen #111884, a female collected by James Bond on 4 March 1933 at Eight Mile Bay, Abaco, the Bahamas.

Paratypes.—We assign ANSP specimens #111886 (male) and #111887 (female) as paratypes. These were collected by Bond on the same date and at the same location as the holotype.

Diagnosis.—Distinguished from Cuba, Isla de la Juventud, and Cayman populations by larger size, greater extent of white on head and face, greater extent of rose on throat, and less red on the belly. Averages more red on belly and less red at orbit of eye than *bahamensis*. Averages more white on head and face and less red at orbit of eye than *inaguaensis*. Flight call typically consists of diagnostic paired syllables, unlike those of any other extant *A. leucocephala* population (Reynolds 2006).

Etymology and range.—This taxon is named on the basis of its documented historic and current distribution on Abaco, the Bahamas (Wiley *et al.* 2004). Most of the population resides on the southern portion of Great Abaco (Rivera-Milán *et al.* 2005). At one time, populations probably occurred elsewhere on the Little Bahama Bank, including present-day Little Abaco and Grand Bahama.

Amazona leucocephala inaguaensis New subspecies

Holotype.—Field Museum of Natural History specimen (FMNH) #40392, a female apparently collected by Charles B. Cory on 19 June 1891 at Willow Pond, Great Inagua, the Bahamas (Cory 1891).

Paratypes.—We assign four additional specimens from Cory's collection as paratypes. These include FMNH #40398 (female) and #40399 (male), collected 19 June 1891 at Northeastern Point, and FMNH #40394 and #40395 (males), collected 14 July 1891 at Marc Pond, Great Inagua, the Bahamas.

Diagnosis.—Distinguished from Cuba, Isla de la Juventud, and Cayman populations by larger size, greater extent of white on head and face, greater extent of rose on throat, and less red on the belly. Averages much less white in the head and face than *A. l. bahamensis*. Averages less white on head and face and more red at orbit of eye than *A. l. abacoensis*. Diagnostic flight call syllables have a high fundamental frequency and a severe frequency jump

that, together, create a squeaky quality (Reynolds 2006).

Etymology and range.—This taxon is named on the basis of its historic and current distribution on the Inaguas, the Bahamas. Although largely confined to Great Inagua (Rivera-Milán *et al.* 2005), birds have been recorded on Little Inagua (Wiley *et al.* 2004).

Clearly, additional studies need to address species limits within this group. Molecular analyses would benefit from larger samples that also include material from both Cayman Brac (*A. l. hesternus*) and from museum specimens of the Acklins Island population. Experimental tests should evaluate the genetic and cultural components of nest site choice, as other New World parrots nest in cliff cavities (e.g., Forshaw 1989, Masello *et al.* 2006) and cliff-nesting sometimes occurs in the Puerto Rican Parrot (*A. vittata*; Snyder *et al.* 1987), suggesting a degree of plasticity in this trait. Further analyses of vocalizations are needed, including playback experiments to examine behavioral responses to conspecific and heterospecific calls. Carefully planned mate choice experiments in captivity would also be informative, as would monitoring of reported *A. l. caymanensis* introduction on Cayman Brac (Wiley *et al.* 2004).

CONSERVATION

The conservation status of five *A. leucocephala* populations warrants special consideration. Those on Abaco, Inagua, Isla de la Juventud, Cayman Brac, and Grand Cayman number in the hundreds or low thousands and remain highly vulnerable to exotic mammal predation, hurricanes, habitat loss to development, illegal hunting and trapping, competition from introduced psittacines, and exotic disease risks (Snyder *et al.* 2000, Wiley *et al.* 2004, Rivera-Milán *et al.* 2005). Efforts to control non-native mammal predators and to set aside protected habitat should be continued. Captive breeding and translocation proposals should also move ahead (Wiley 1991, Wiley *et al.* 1992, 2004, Snyder *et al.* 2000), the latter only after habitat suitability analyses have been completed for candidate islands (e.g., northern Abaco, Grand Bahama, and Andros for the Abaco population; Crooked and Acklins Islands for the Inagua population; Little Cayman for the Cayman Brac population). For any such programs, the unique identity of each population must be maintained.

Formal recognition of subspecies status for each population, including the two heretofore subsumed

under *A. l. bahamensis*, may also have far-reaching conservation implications. Although Zink (2004) proposed that the subspecies rank hinders conservation because most continental subspecies lack genetic distinctiveness, Phillimore and Owens (2006) showed that the majority of insular subspecies are monophyletic (i.e., phylogenetic species), suggesting that subspecies serve as useful proxies for species substructure and conservation units. Regardless of monophyletic status, the subspecies rank can galvanize conservation efforts by island nations, which often rely on endemic “flagship” taxa (*sensu* Caro *et al.* 2004) to promote environmental goodwill. The Bahamas government, Bahamas National Trust, and other non-government organizations have made remarkably effective use of the “Bahama” parrot for such purposes (Wiley *et al.* 2004). Having two endemic taxa (the Abaco Parrot and Inagua Parrot), which our data provide strong support for, would enhance a sense of pride and awareness of ownership for a nation seeking a stronger conservation ethic (Hayes 2006), and potentially boost tourist traffic to the relatively ignored Inaguas. Wiley *et al.* (2004) describe similarly effective programs for parrots of Isla de la Juventud and the Cayman Islands. Moreover, endangered subspecies are frequently given the same protection as full species (e.g., Haig *et al.* 2006), and their recognition can be used by governments and local groups to forestall development in sensitive habitats.

The case of *A. leucocephala* clearly illustrates the conservation value of recognizing the subspecies rank, particularly for island nations. If conservation priorities were based solely at the species level, ongoing conservation efforts and attendant benefits would be viewed as wasteful, or misdirected from more critically endangered species, since the collective status of the Cuban Parrot is only “near-threatened” (BirdLife International 2009). We strongly disagree with the view that efforts on behalf of this parrot might have been wasteful or misdirected.

ACKNOWLEDGMENTS

We thank the curators of and the following museums for arranging visits or loaning specimens for this study: American Museum of Natural History; Academy of Natural Sciences of Philadelphia; Carnegie Museum of Natural History; Field Museum of Natural History; Museum of Comparative Zoology, Harvard University; and United States National Museum of Natural History, Smithsonian Institution. Nate Rice (ANSP), Steve Rogers (CMNH), and David Willard (FMNH) kindly examined speci-

mens to confirm details of type designations. We thank Carolyn Stahala for sharing the results of her studies and informative discussion. John B. Iverson generously offered input on taxonomic procedures. We appreciated comments on the manuscript from Jim Wiley and two anonymous reviewers. Research was supported by the Department of Earth and Biological Sciences at Loma Linda University and by the Grand Bahama Power Company.

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APPENDICES

Appendix 1. Summary of specimens examined.

Amazona leucocephala bahamensis.—34: Abaco 9 (2♂, 7♀); Aklins 10 (5♂, 3♀, 2 unknown); Inagua 15 (6♂, 6♀, 3 unknown).

A. l. leucocephala.—54: Guantánamo 23 (10♂, 13♀); Pinar del Rio 3 (3 unknown); Oriente 3 (1♂, 2♀); Santa Clara 2 (1♂, 1♀); Unknown 13 (9♂, 3♀, 1 unknown); Camaguey 5 (5♀); Cienega de Zapata 1 (1♀); Matanzas 3 (2♂, 1 unknown); Holguín 1 (1♀).

A. l. palmarum.—40: Isla de la Juventud (Isla of Pinos, 21♂, 17♀, 2 unknown).

A. l. caymanensis.—45: Grand Cayman (25♂, 18♀, 2 unknown).

A. l. hesterna.—15: Cayman Brac 14 (7♂, 7♀); Little Cayman 1 (1♀).

Total: 188 from eight islands (89♂, 85♀, 14 unknown).

Appendix 2. List of specimens examined from the following museums: American Museum of Natural History (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Museum of Comparative Zoology, Harvard University (MCZ); United States National Museum of Natural History, Smithsonian Institution (USNM).

Amazona leucocephala bahamensis.—Abaco: ANSP 111880, 111881, 111882, 111883, 111884, 111885, 111886, 111887, MCZ 170418. Aklins: AMNH 95479, CMNH 30888, 30889, 30890, 30892, 30893, MCZ 41021, 47505, 58508, 68615. Inagua: AMNH 174667, 174668, 174669, 88792, ANSP 88793, FMNH 40390, 40392, 40394, 40395, 40397, 40398, 40399, USNM 323465, 323466, 323467.

A. l. leucocephala.—Cuba: CMNH 138854, 138855, FMNH 40379, 40380, 40381, 40382, 40384, 40385, 40386, MCZ 61056, 61057, 61058, 67531, 67537, 104704, 114920, 115752, 115753, 115754, 235101, 235104, 235106, 235108, USNM 65352, 172573, 172574, 177451, 177562, 316225, 316226, 316227, 354346, 395906, 396597, 453638, 453639, 453640, 453641, 453642, 453643, 453644, 453645, 453646, 453647, 453648, 453649, 453650,

453651, 453652, 453653, 453654, 453655, 453656, 453657.

A. l. palmarum.—Isla de la Juventud (Isla de Pinos): AMNH 175001, 175002, 175003, 175004, 475328, CMNH 39496, 39533, 39536, 39539, 39540, 39541, 39563, 39564, 39673, 39710, 39729, 39912, 39913, 39915, 39916, 39974, 39983, 39985, 39990, FMNH 371905, MCZ 67527, 67528, 67529, 67530, 113442, USNM 172763, 172764, 172765, 172766, 172767, 172768, 172769, 172770, 323471, 323472.

A. l. hesterna.—Cayman Brac: ANSP 67609, FMNH 40383, 40401, MCZ 68310, 68311, 68312,

68313, 68314, 68315, 68316, 68317, USNM 323468, 323469, 323470. Little Cayman: MCZ 68308.

A. l. caymanensis.—Grand Cayman: AMNH 154344, 174670, 174671, 174673, 174674, 174675, 475331, 475332, 475333, 475334, 475335, 475336, 475337, ANSP 89627, 89628, FMNH 20906, 40402, 40403, 40406, 40408, 40409, 40410, 40411, 40413, 40414, 40416, 40417, 40418, 40419, 40420, 40422, 40423, 40430, MCZ 68298, 68299, 68300, 68301, 68302, 68304, 68305, 68306, 68307, USNM 316753, 316754, 316755.