MORPHOMETRIC-BASED SEXUAL DETERMINATION OF BANANAQUITS (COEREBA FLAVEOLA)

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INTRODUCTION

Bananaquits (Coereba flaveola) are an abundant passerine found throughout much of the new world tropics. Generally, they have small territories and occur at high densities on many Caribbean islands (Wunderle 1984). The diet of Bananaquits has made them an interesting species for studies of sugar preferences and physiological aspects of nectarivory (Mata & Bosque 2004) and competition with other nectarivorous birds (Askins et al. 1987). The
species exhibits plumage polymorphism in parts of its range, such as Grenada, and has been closely studied in context of temporal shifts in the morph ratio cline (Wunderle 1981a, 1981b, 1983; MacColl & Stevenson 2003). The extensive variation in plumage and other features, including size, have prompted several studies to document and explain the variation (e.g., Diamond 1973, Prys-Jones 1982), and infer evolutionary history (Seutin et al. 1994, Bellemain et al. 2008). Despite its abundance and widespread distribution, relatively few studies have examined the basic biology (Biaggi 1955, Gross 1958, Wunderle et al. 1987, Wunderle et al. 1992) and breeding ecology (Wunderle 1982, 1984) of Bananaquits.

Because they have sexually monomorphic plumage, Bananaquits cannot be reliably sexed unless in breeding condition (i.e., presence of brood patch or cloacal protuberance). However, this is contingent upon banding studies being conducted during the breeding season. Many studies in the tropics are conducted during the migration or wintering season when most resident tropical birds are not in a breeding state (Faaborg et al. 1984, Murphy et al. 2004, Boal et al. 2006). Sophisticated modeling of survival and demography are contingent upon accurately aging and sexing individuals in the marked sample. Failure to account for sex ratio, or removing unsexed individuals from samples, can lead to introduction of bias, weak inference, and erroneous conclusions. Wolfe et al. (2009) recently emphasized this need for better quantitative data on gender determination and other characteristics. Here we address these needs for one of the most common Caribbean passerines by analyzing measurements for Bananaquits captured on Guana Island, British Virgin Islands, to determine if the sexes of adult individuals can be differentiated using some standard morphological measurements.

METHODS

We conducted bird surveys on Guana Island (18°30’N, 64°30’W), a small (3 km²) island located approximately 0.5 km north of Tortola, British Virgin Islands. The British Virgin Islands, along with the U. S. Virgin Islands, are a chain of approximately 76 islands and cays located roughly 150 km east of Puerto Rico that, combined with Puerto Rico, constitute the Puerto Rican Bank (Lazell 2005). Temperature in the British Virgin Islands normally ranges from 28–33°C, with annual mean rainfall for Guana Island estimated at 92 cm (Lazell 2005).

Guana Island is topographically rugged with elevations ranging from sea level to 246 m. It is privately owned and has undergone little development or fragmentation. A resort area occupies approximately 3% of the island; the remainder of the island is a de facto nature preserve. The majority of the island is vegetated with subtropical dry forest (90%) and mesic ghaut forest (5%) (Lazell 2005). The primary native vegetation on Guana Island includes Tabebuia heterophylla, Bursera simaruba, Pinonia subordata, Conocarpus erectus, Plumeria alba, Acacia maritica, and Cocosobola uinifera. Leucaena leucocephela is common in disturbed areas. Other introduced species include Cocos nucifera, Tamarinda indica, and Delonix regia (Lazell 2005).

We operated a banding station on Guana Island during each October of 2003–2010. Altogether 12 32-mm mist nets were opened for an average of 422 (± 57 SE) h each year. All nets were placed in subtropical dry forest and in human-altered areas near the island hotel. Nets were located in the same locations along a northeast–southwest ridge on the west side of the island at ca. 70 m a.s.l. each year.

Captured Bananaquits were placed in temporary holding bags and transported to a banding station for processing. We recorded
unflattened wing chord with a stopped wing ruler. We measured mass with an electronic scale accurate to 0.1 g (Ohaus Model CS200). We aged each Bananaquit as adult or juvenile based on plumage (Raffaele et al. 1998), and examined adults for evidence of breeding status (i.e., brood patch, cloacal protuberance). To ensure consistency, one person performed all measurements and classifications. We attached an aluminum leg band provided by the U. S. Geological Survey Bird Banding Laboratory and, beginning in 2005, we attached unique combinations of two plastic colored bands to adults.

Preliminary examination of wing chord and mass of known sex Bananaquits led us to suspect we could use these metrics to determine sex of individuals with a high level of confidence. We compared mass and wing chord of all adult Bananaquits, male only, and females only using linear regression. We used these individuals to calculate 95% confidence intervals on mass and wing chord for male and female Bananaquits. We used logistic regression to develop a predictive model for classification of individuals of unknown sex. The logistic model was developed using individuals captured from 2003–2010 for which sex was verified by presence of brood patch or cloacal protuberance. Adult individuals classified as unknown sex were included if they were sexed at a later capture, with the measurements from the initial capture utilized for the analysis. Only one set of measurements was included for each individual to avoid lack of independence of data. We randomly selected 50 known-sex adults, 25 of each sex, for removal from the dataset to use for model validation. Four logistic regression models were run: 1) wing chord only, 2) mass only, 3) wing chord-mass additive model, and 4) wing chord-mass interaction model. The model best fitting the data was chosen using AIC (Burnham & Anderson 2002). Sex of validation individuals was predicted using the best model with a predicted probability of being female = 0.5 indicating females. We then compared the assigned values with the known sex. The model was then applied to all unknown sex individuals for whom we had wing chord and mass measurements.

RESULTS

A total of 519 captures of adult Bananaquits from 2003–2010 represented 304 individuals, of which 285 had both wing chord and mass measured. Of these, 222 birds were field-sexed (131 male, 91 female). Wing chord for all individuals was 57.0 mm (SE = 0.155 mm, range 51–62 mm). Males had larger wing chords (mean = 59.1 mm, SE = 0.114 mm, range 55–62 mm) than females (mean = 54.6 mm, SE = 0.133 mm, range 51–58 mm) ($t_{220} = -25.523$, $P < 0.0001$). Males also were heavier (mean = 10.2 g, SE = 0.063 g, range 8.0–12.5 g) than females (mean = 9.4 g, SE = 0.086 g, range 6.4–11.8 g) ($t_{220} = -8.151$, $P < 0.0001$). Wing chord exhibited substantially less variation (male CV = 2.2; female CV = 2.3) than mass (male CV = 7.1; female CV = 8.7). Unknowns generally exhibited the full range of observed wing chords (mean = 56.0 mm, SE = 0.324 mm, range 51–62 mm) and mass (mean = 9.3 g, SE = 0.086 g, range 6.4–11.8). Overlap of sexes was observed with both metrics, with extensive overlap in mass and overlap in the 55–58 mm wing chord range (Fig. 1). In addition, average mass varied considerably between years, ranging from 9.8 g in 2009 to 10.9 g in 2008 for males, and from 8.8 g in 2009 and 9.8 g in 2007 for females. Mass and wing chord exhibited a positive relationship for both sexes (linear regression: male $P = 0.0010$; female $P = 0.0064$), although the relationship was noisy and mass provided little explanation for variation in wing chord (male $R^2 = 0.0815$; female $R^2 = 0.0805$). The relationship appeared to be additive, with no difference in slope of the
relationship between sexes (male slope = 0.516, 95% CI [0.214, 0.817]; female slope = 0.439, 95% CI [0.127, 0.751]), but males had a somewhat higher intercept (male intercept = 53.83, 95% CI [50.74, 56.927]; female intercept = 50.49, 95% CI [47.55, 53.42]).

Measurements from 172 birds in Definitive plumage (106 male, 66 female) were used to perform the logistic regressions. The best model was the Wing Chord + Mass additive model (AIC = 46.715), followed by Wing Chord only (ΔAIC = 1.47), and the Wing Chord * Mass interaction (ΔAIC = 1.955) models (Table 1). The Mass only model performed poorly compared to the other models (ΔAIC = 149.082). The best model provides the probability of the bird being female given the measurements by the equation:

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Pr\{\text{Female} \mid \text{Mass, Wing Chord}\} = \frac{1}{1 + e^{136.8 + 0.8947(\text{Mass}) - 2.5749(\text{Wing Chord})}}
\]

The 95% profile likelihood confidence interval on the slope parameter for wing chord (≈ –2.5749) did not encompass zero (≈ –3.8901, –1.7311), but the confidence interval for mass did include zero (≈ –0.0450, 1.9341), suggesting that wing chord has significant explanatory power in classifying sex. When applied to the validation samples, the model correctly classified 100% of males and 92% of females. The 95% confidence intervals on the probability included 0.5 for six (12%) of the classifications, including one of the two misclassifications. Censoring of individuals for which the 95% confidence interval included any value between 0.4 and 0.6 resulted in 100%
classification success, but required removal of nine (18%) of the validation individuals. In both failed classifications, the females had larger than average wing chords (both 57.0 mm) and larger than average mass (9.6 and 10.2 g, respectively). Based on this model, adult Bananaquits with wing chords < 55.0 mm can be assumed female, and those with wing chords > 57.5 mm can be assumed males. Within the 55.5–57.5 mm wing chord, mass becomes important with, counter-intuitively, larger mass individuals being females (Fig. 2). The model classified the 63 unknown sex individuals as 29 males and 34 females. Certainty of classification was similar to that for the validation test. Ninety-five percent confidence intervals on the probability of being female included 0.5 for eight (13%) individuals, and included a value between 0.4 and 0.6 for 13 (21%) individuals.

**DISCUSSION**

Bananaquits exhibit sexual dimorphism in wing chord although some overlap exists. Based on presence of breeding criteria, we observed adult males with wing chords as short as 55 mm, and adult females with wing chords as long as 58 mm. This range of overlap was supported by the results of our predictive model. In a well-developed guide for aging and sexing Bananaquits in Jamaica, Susan Koenig (unpub. data) found individuals with wing chord < 52 mm can be reliably sexed as female, and those > 57 mm can be reliably sexed as males. On Dominica, 89% of individuals with wing lengths less than a median of 62 mm showed evidence of brood patches (Prys-Jones 1982). These data suggest that sexing individuals based only on wing chord is questionable, and requires classifying individuals within the zone of overlap as unknowns, which may compromise results of subsequent demographic analyses. Other measurements likely present the same problem. We found substantial overlap (62% of the observed range) in mass of males and females.

The observed variation in size due to sex suggests that averaging morphometrics in ecological studies of Bananaquits without accounting for sex may be problematic. Diamond (1973) found positive correlations between elevation and several morphometrics (i.e., mass, wing length, and bill length) of unsexed Bananaquits in Jamaica. However, when museum specimens of known sex from Central and South America were measured, the relationship was only significant for wing length and elevation in males (Diamond 1973). Prys-Jones (1982) found a strong positive correlation between wing length and mass of Bananaquits in Dominica without accounting for differences in sex. We observed a similar relationship although mass had little explanatory power for wing chord for either sex (male $R^2 = 0.0815$, female $R^2 = 0.0805$).
This weak relationship is probably due to high yearly variation in mass.

Determining sex based on morphometrics may be confounded by not only altitudinal variation in size (Diamond 1973) but also variance in sizes across the species distribution. For example, examining data from disparate locations within the range of the Bananaquit reveals the potential for substantial spatial variation in body size, even though direct comparison is difficult due to differences in measurement technique. In the South and Central America, flattened wing chord of male and female Bananaquits averaged 57.0 mm (N = 64, SE = 0.378, 5.30 CV) and 54.1 mm (N = 25, SE = 0.011, 5.44 CV), respectively (Diamond 1973). In the northeast region of the Caribbean within the BVI, we found males had a much longer average unflattened wing chord of 59.1 mm whereas females only had a slightly larger average wing chord of 54.6 mm than that of mainland females. Southward at the center of the Lesser Antilles, Prys-Jones (1982) reported an overall average wing chord for Bananaquits on Dominica as 60.6 mm (± 3.2 mm). However, Prys-Jones (1982) used maximum chord rather than unflattened chord. Converting unflattened wing chord to maximum chord (Pyle 1997) suggests that average wing chord in the BVI is similar to that on Dominica. Unflattened wing chord measurements used for sexing on Jamaica (male > 57 mm, female < 52 mm; Susan Koenig, unpub. data) sug-
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gests that Bananaquits on Jamaica are similar in size to mainland birds.

Ecological studies involving size should either avoid using unsexed individuals or censor individuals of unknown sex. First, averaging morphometrics using unsexed individuals requires the assumption that comparison samples have equivalent sex ratios. For example, when removing unknown sex individuals (22% of 285 individuals), we observed a sex ratio of 0.59 (males vs females) and obtained an average wing chord of 57.3 mm. Using the averages for each sex and assuming a 50:50 sex ratio results in a drop of 0.5 mm (56.8 mm) in the estimated average, which is 5% of the overall range in observed measurements.

Second, use of threshold criteria that create a zone of “unknown” create a bias by tending to censor larger individuals of the smaller sex, and vice versa, leading to an apparent larger difference between sexes than exists. In addition, this censoring leads to smaller variance estimates than appropriate, increasing the probability of finding a non-existent difference (i.e., committing Type I error). For example, we found that coefficients of variation on wing chord for males and females were 2.2 and 2.3%, respectively, when Bananaquits were sexed based on breeding characters. Had we used a wing chord criteria classifying individuals from 55.0–57.5 mm as unknown sex, the coefficients of variation for males and females would have been 1.7 and 1.4%, respectively.

Errors in classifying sex using our model could have deleterious effects on an analysis. However, we believe that the level of error is very low and unlikely to have significant influence, especially in comparison to the impact of censoring unknown sex individuals from the analysis. In our classification of the 63 individuals of unknown sex, classifying using the 55–57.5 wing chord criteria would have resulted in censoring 28 (44%) individuals from further analysis. Using the conservative approach of censoring individuals in which the probability of being female was approaching 0.5 (e.g., 0.4–0.6) would have only removed 13 individuals (21%) from further consideration, resulting in substantially less bias. We believe the model we have developed is a valid, field-applicable approach for determining sex of non-breeding adult Bananaquits. We suggest adult Bananaquits (i.e., those individuals in Definitive plumage) should be sexed using breeding criteria, if possible, and then classifying the remaining unknown sex individuals using our approach.

This approach had a high success rate (96%) in classifying adult individuals that did not exhibit breeding characteristics, and has the potential to significantly reduce the analysis problems associated with having unknown sex individuals within a dataset. We believe our current model is applicable to adult Bananaquits in the British and U. S. Virgin Islands, but have not yet tested it beyond our study island. However, we also suspect it will need to be modified to account for regional variance across the Bananaquit distribution, but see no reason the approach we took to developing morphometric-based sexing criteria could not be applied elsewhere. Development of localized models using this approach and existing morphometric data is currently possible for many portions of the species’ range. In addition, incorporation of other metrics, such as tail chord or exposed culmen, may benefit the model and should be explored.

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