ORNITOLOGIA NEOTROPICAL 23: 507–515, 2012

MORPHOMETRIC-BASED SEXUAL DETERMINATION OF BANANAQUITS (*COEREBA FLAVEOLA*)

Brent D. Bibles[1] **& Clint W. Boal**[2]

[1]Unity College, Unity, ME 04988, USA.
[2]U. S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, TX 79409, USA. *E-mail*: clint.boal@ttu.edu

Resumen. – Morfometría basada en la determinación sexual de la reinita común (*Coereba flaveola*). – La Reinita Común (*Coereba flaveola*) es un passerino común en los trópicos y ha sido una especie conveniente para estudios ecológicos. Esta especie tiene un plumaje sexualmente monomórfico, y no se puede ser sexada, a menos que los individuos esten en condición reproductiva. Esto es problemático para estudios demográficos y comparativos que requieren una determinación precisa de la edad y sexo de los individuos. Aunque los machos son mas grandes que las hembras, existe traslape tanto en cuerda alar como en masa corporal. Usamos datos morfométricos colectados durante mas de ocho años para desarrollar modelos predictivos, basados en una regresión logística para asignar reinitas comunes adultas a sexo. Nuestra modelo ha clasificado 96% de individuos de validación al sexo correcto. Sugerimos que este enfoque puede mejorar los estudios ecológicos de la especie, facilitando la determinación correcta del sexo, independientemente de su estatus reproductivo. Creemos que nuestra modelación es aplicable en otras localidades, pero debido a que existen variaciones a través de la distribución de la especie, los modelos necesitan ser ajustado a las poblaciones locales.

Abstract. – The Bananaquit (*Coereba flaveola*) is a common passerine throughout the tropics and has been a convenient species for ecological studies. This species has sexually monomorphic plumage and cannot be reliably sexed unless in breeding condition. This is problematic for demographic and comparative studies, which are contingent upon accurately aging and sexing individuals. Although male Bananaquits are larger than females, there is overlap in both wing chord and mass. We used morphometric data collected over eight years to develop a predictive model based on logistic regression to assign adult Bananaquits to sex. Our model classified 96% of validation individuals to the correct sex. We suggest that this approach may enhance ecological studies of the species by facilitating correct sex determination independent of breeding status. We believe our modeling approach is applicable elsewhere but, because there may be geographical variation across the species distribution, models will need to be customized to local populations. *Accepted 8 December 2012.*

Key words: Bananaquit, *Coereba flaveola*, monomorphic plumage, morphometry, sex determination, size dimorphism.

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 km^2) 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*, *Pisonia subcordata*, *Conocarpus erectus*, *Plumeria alba*, *Acacia muricata*, and *Coccoloba uvifera*. *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

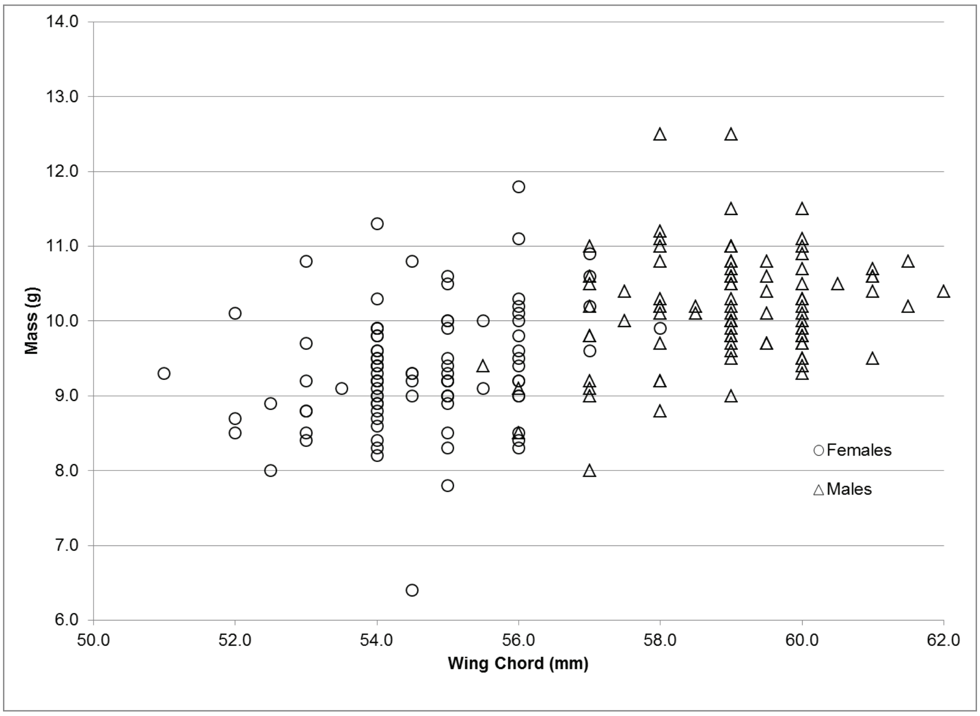

FIG. 1. Scatterplot illustrating mass (g) and wing chord (mm) of adult Bananaquits, by sex, on Guana Island, BVI, 2003-2010. Data from 222 individuals (131 M, 91 F).

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:

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

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%

TABLE 1. Ranking of logistic models for determining sex of adult Bananaquits based on measurements of mass (g) and wing chord (mm). Number of parameters (K), Akaike Information Criterion (AIC), difference in AIC (ΔAIC), -2 * ln likelihood (-2 ln), and model (Akaike) weights (w_i) are provided.

Model	K	AIC	ΔAIC	-2 ln	w_i
Wing Chord + Mass	3	46.715	0.000	40.715	0.539
Wing Chord	2	48.185	1.470	44.185	0.258
Wing Chord * Mass	4	48.670	1.955	40.670	0.203
Mass	2	195.797	149.082	191.797	0.000

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).

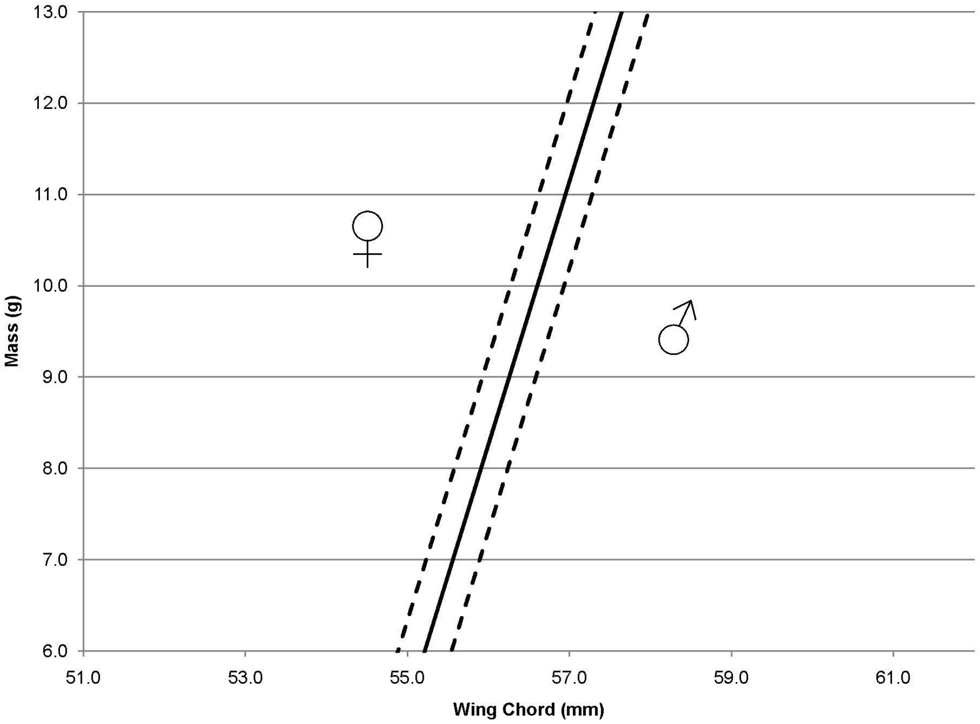

FIG. 2. Assignment of sex of adult Bananaquits based on logistic model using wing chord (mm) and mass (g). Solid line indicates predicted probability of being female = 0.5. Dashed lines indicate predicted probabilities of being female = 0.7 (left) and 0.3 (right).

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) suggests 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 analyss 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.

ACKNOWLEDGMENTS

Our thanks to the Jarecki family, the Falconwood Foundation, and The Conservation Agency for their continued access to Guana Island and support for this research, and to the USGS Cooperative Research Units and Utah State University for facilitating this research. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U. S. Government. Special thanks to J. D. Lazell and G. Perry for coordinating research opportunities on Guana Island. We thank T. S. Estabrook, T. Willard, S. Cooper, E. P. Estabrook, and several other volunteers that have assisted in the ornithological research program on the island. This manuscript benefitted from the thoughtful reviews and suggestions of J. M. Wunderle and S. Koenig. We thank J. W. Beltran S. for kindly providing the Spanish language abstract.

REFERENCES

Askins, R. A., K. M. Ercolino , & J. D. Waller. 1987. Flower destruction and nectar depletion by avian nectar robbers on a tropical tree, *Cordia sebestena*. J. Field Ornithol. 58: 345–349.

Bellemain, E., E. Bermingham, & R. E. Ricklefs. 2008. The dynamic evolutionary history of the Bananaquit (*Coereba flaveola*) in the Caribbean revealed by a multigene analysis. Evol. Biol. 8: 240

Biaggi, V. 1955. The Puerto Rican honeycreeper (Reinita) *Coereba flaveola* (Bryant). Univ. of Puerto Rico Agricultural Experiment Station, Mayaguez, Puerto Rico, USA. Special Publication, 61 pp.

Boal, C. W., F. C. Sibley, T. S. Estabrook, & J. Lazell. 2006. Insular and migrant species, longevity records, and new species records on Guana Island, British Virgin Islands. Wilson J. Ornithol. 118: 218–224.

Burnham, K. P., & D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York, New York, USA.

Diamond, A. W. 1973. Altitudinal variation in a resident and a migrant passerine on Jamaica. Auk 90: 610–618.

Faaborg, J., W. J. Arendt, & M. S. Kaiser. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. Wilson Bull. 96: 575–593.

Gross, A. O. 1958. Life history of the Bananaquit of Tobago Island. Wilson Bull. 70: 257–279.

Lazell, J. 2005. Island: fact and theory in nature. Univ. of California Press, Berkeley, California, USA.

MacColl, A. D. C., & I. R. Stevenson. 2003. Stasis in the morph ratio cline in the Bananaquit on Grenada, West Indies. Condor 105: 821–825.

Mata, A., & C. Bosque. 2004. Sugar preferences, absorption efficiency and water influx in a Neotropical nectarivorous passerine, the Bananaquit (*Coereba flaveola*). Comp. Biochem. Phys. A 139: 395–404.

Murphy, M. T., J. Zysik, & A. Pierce. 2004. Biogeography of the birds of the Bahamas with special reference to the island of San Salvador. J. Field Ornithol. 75: 18–30.

Prys-Jones, R. P. 1982. Molt and weight of some land-birds on Dominica, West Indies. J. Field Ornithol. 53: 352–362.

Pyle, P. 1997. Identification guide to North American birds-Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

Raffaele, H., J. Wiley, O. H. Garrido, A. Keith, & J. I. Raffaele. 1998. A guide to the birds of the West Indies. Princeton Univ. Press, Princeton, New Jersey, USA.

Seutin, G., N. K. Klein, R. E. Ricklefs, & E. Bermingham. 1994. Historical biogeography of the Bananaquit (*Coereba flaveola*) in the Caribbean region: a mitochondrial DNA assessment. Evolution 48: 1041–1061.

Wolfe, J. D., P. Pyle, & C. J. Ralph. 2009. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. Wilson J. Ornithol. 121: 556–567.

Wunderle, J. M. 1981a. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. Evolution 35: 333–344.

Wunderle, J. M. 1981b. Movements of adult and juvenile Bananaquits within a morph-ratio cline. Auk 98: 571–577.

Wunderle, J. M. 1982. The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on the island of Granada, WI. Biotropica 14: 124–131.

Wunderle, J. M. 1983. A shift in the morph ratio cline in the Bananaquit on Grenada, West Indies. Condor 85: 365–367.

Wunderle, J. M. 1984. Mate switching and a seasonal increase in polygyny in the Bananaquit. Behaviour 88: 123–144.

Wunderle, J. M., M. S. Castro, & N. Fletcher. 1987. Risk-averse foraging by Bananaquits on negative energy budgets. Behav. Ecol. Sociobiol. 21: 249–255.

Wunderle, J. M., R. A. Cortes, & W. Carromero. 1992. Song characteristics and variation in a population of Bananaquits on Puerto Rico. Condor 94: 680–691.