6-2019

Size, Shape, and Sexual Dimorphism of Island and Mainland Melanerpes Woodpeckers of the Centurus Clade

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Recommended Citation

Silva Núñez, Lee Michelle, "Size, Shape, and Sexual Dimorphism of Island and Mainland Melanerpes Woodpeckers of the Centurus Clade" (2019). *Loma Linda University Electronic Theses, Dissertations & Projects*. 1876.
https://scholarsrepository.llu.edu/etd/1876

LOMA LINDA UNIVERSITY
School of Medicine
in conjunction with the
Faculty of Graduate Studies

Size, Shape, and Sexual Dimorphism of Island and Mainland *Melanerpes* Woodpeckers of the *Centurus* Clade

by

Lee Michelle Silva Núñez

A Thesis submitted in partial satisfaction of
the requirements for the degree
Master of Science in Biology

June 2019

Each person whose signature appears below certifies that this thesis in his/her opinion is adequate, in scope and quality, as a thesis for the degree Masters in Biology.

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ACKNOWLEDGMENTS

It is a pleasure to thank the many people who have helped and guided me through the process of finishing my thesis. To my mother, Dr. Maria A. Núñez, and to my sisters Sharon and Tania: your unconditional love and support made all the difference. Thank you for allowing me to grow as an individual and always encouraging me to do what I love.

To my thesis advisor, Dr. William Hayes: the completion of this thesis would not have been possible without your guidance. Your passion for research and nature is contagious and inspiring; it certainly made this process enjoyable. To the members of my committee, Dr. Kevin Nick, Dr. Anthony Metcalf, Dr. Melissa Price, and Dr. Michael Akresh: thank you for your advice, patience, and willingness to work with me. To my friends, colleagues, and other graduate students in the Department of Earth and Biological Sciences: thank you for your valuable input, questions, and help. I owe a special thank-you to Marsha Wright, for her friendship, generosity, and kindness.

Finally, and most importantly, I praise and thank God for opening the doors to this extraordinary opportunity. The study of His creation served as a daily reminder of His eternal love.

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ABBREVIATIONS

AK	Arturo Kirkconnell
DFA	Discriminant function analysis
LMS	Lee Michelle Silva
MEA	Michael E. Akresh
PC	Principal component
SBCD	Sexual body component dimorphism
SSD	Sexual size dimorphism
WKH	William K. Hayes

ABSTRACT OF THE THESIS

Size, Shape, and Sexual Dimorphism of Island and Mainland *Melanerpes* Woodpeckers of the *Centurus* Clade

by

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Master of Science, Graduate Program in Biology
Loma Linda University, June 2019
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Island ecosystems are widely studied as "natural laboratories” for biological change. Animals that colonize islands frequently exhibit differences from their mainland counterparts in morphology, physiology, and behavior. Some of the most striking features include changes in body size and shape, with extreme examples being dwarfism, gigantism, and flightlessness. These changes are generally driven by isolation and reduction in predators and competitors. The 10 woodpecker species belonging to the *Centurus* clade of genus *Melanerpes* are ideally suited to study evolutionary changes associated with island conditions because they include numerous populations restricted to islands, allowing comparisons among island and continent ecosystems.

To test specific hypotheses regarding overall body size, overall shape, and differences between the sexes in size (sexual size dimorphism, SSD) and shape (sexual body component dimorphism, SBCD), I analyzed six morphological measures in >1,500 museum specimens representing 43 taxa or populations, of which 20 were island forms. In contrast to prior studies of island birds, we computed overall body size as geometric mean of the six measurements to derive a reliable measure of body size. Although insular effects of body size and shape have been widely studied in birds, island effects on sexual dimorphism have been largely ignored, for which use of an unbiased reference character is essential.

For overall body size, I found no support at either the interspecific or intraspecific level for the island rule that small and large mainland taxa converge on an intermediate body size after colonizing islands. Sexual size dimorphism existed in all taxa and populations, with males being larger than females, but no consistent differences between island and mainland populations were detected at either taxonomic level. For overall body shape, island populations consistently exhibited relatively shorter wings, which followed the general trend for insular birds that places them on a trajectory toward flightlessness. For SBCD, males consistently possessed larger bill dimensions, whereas females had consistently longer wings, tails, and legs relative to overall size; however, no differences between island and mainland populations existed at either taxonomic level. Collectively, these findings augment our understanding of how island conditions influence the morphology of birds.

CHAPTER ONE

INTRODUCTION

“Islands, it seems, create birds that stay on islands.”
-Ed Yong

Island ecosystems are widely studied as “natural laboratories” for evolutionary change. Animals that live on islands frequently exhibit "island syndrome," which encompasses numerous differences in morphology, physiology, and behavior (Adler & Levins, 1994; McNab, 2002; Novosolov et al., 2013; Raia et al., 2010). The abiotic and biotic conditions of islands often differ sufficiently such that selection can favor dissimilar traits in organisms. Some of these traits can evolve over a relatively short period of time (Lister, 1989; Raia et al., 2010). Many island species have diverged from their mainland ancestors to the extent that it can be difficult to determine the mainland species they are most closely related to (e.g., Burns et al., 2002; Mathys & Lockwood, 2011). In terms of morphology, island influences can lead to differences in overall body size, body shape, and differences between the sexes (i.e., sexual dimorphism).

The influence of island conditions on bird size has been examined in numerous studies. The “island rule” predicts that smaller vertebrates on islands trend toward gigantism and larger vertebrates trend toward dwarfism (Clegg & Owens, 2002; Damuth, 1993; Lomolino, 1985; Mathys & Lockwood, 2011; Van Valen, 1965), but consensus on whether birds converge toward intermediate body size after island colonization remains elusive. Grant (1965) studied 69 insular populations of passerines from North America and Mexico, finding increased bill and tarsus lengths (shape differences) relative to mainland source populations, but no differences in wing or tail lengths, and therefore no consistent adherence to the island rule in overall size. Clegg & Owens (2002) subsequently used a larger and more comprehensive data set of 110 insular populations throughout the world, including a greater number of non-passerines and larger species than used by Grant, to show that island birds do follow the island rule, with smaller species having greater mass (overall size) and longer bills (shape), and larger species having smaller body size and shorter bills. In a comprehensive review of the island rule among several vertebrate groups, Lokatis & Jeschke (2018) found support for the rule in 50% of 16 studies of birds. Many of these studies nonetheless reveal idiosyncratic patterns of body size evolution on islands (e.g., Leisler & Winkler, 2015; Ruiz Ramos, 2014; Wright et al., 2016), with change often associated with taxon-specific resource use (e.g., Cook et al., 2013; Leisler & Winkler, 2015; but see Scott et al., 2003).

Island conditions also appear to influence bird shape. Of the major body components (bill, wings, tail, legs), larger bill size on islands has been widely reported. Although studies limited to specific bird groups or regions provide mixed evidence that wing length is often shorter and leg length longer on island forms (e.g., Blackburn et al., 2013; Danner et al., 2014; Grant, 1965; Leisler & Winkler, 2015; Mathys, 2010; Rodriguez et al., 2018), a study of the skeletal components of 366 populations of Caribbean and Pacific birds revealed a consistent evolutionary shift in investment from forelimbs to hindlimbs (Wright et al., 2016). In the latter study, the trend toward reduced flight muscles and larger legs was evident in separate analyses of nine avian families and four orders, representing a range of lifestyles, diets, foraging behaviors, flight styles, and body plans, and for birds on both continental and oceanic islands. Increasing insularity and especially reduced avian and mammalian predators best accounted for the trajectory toward flightlessness. Vegetation structure may also influence the shape of these morphologies (Cibois et al., 2007; Kaboli et al., 2007; Leisler & Winkler, 2015; Winkler & Leisler, 1985).

Insular conditions may likewise promote the evolution of sexual dimorphism (Butler et al., 2007; Dayan & Simberloff, 1994). Sexual differences can exist in overall body size (sexual size dimorphism, SSD) or between the size and/or shape of individual body components (sexual body component dimorphism, SBCD). Sexual dimorphism can be driven by natural selection, sexual selection, or non-adaptive processes such as body-size scaling, genetic correlations between female and male body size, and phylogenetic constraints or inertia (Fairbairn, 1997; Fairbairn & Preziosi, 1994). Sexual dimorphism has been linked to overall body size, with the well-studied Rensch's rule stating that SSD increases with size among species when males are larger, and decreases with size when females are larger (Rensch, 1950). Some bird groups adhere to this rule, whereas others do not (Dale et al., 2007; Nuñez-Rosas et al., 2017; Székely et al., 2007). Compared to island effects on overall body size and shape, few studies have examined insular effects on sexual dimorphism in birds. Selander & Giller (1963) described greater levels of male-biased bill size of island compared to mainland species of *Melanerpes* (and *Chryserpes*) woodpeckers. Greenberg & Danner (2013) and Danner et al. (2014) found greater male-biased bill size dimorphism but no differences in body mass dimorphism (SSD), wing length dimorphism, or tarsus length dimorphism of island populations of Song Sparrows (*Melospiza melodia*). Roulin & Salamin (2010) reported several differences in degree of sexual dichromatism in island populations of Barn Owls (genus *Tyto*). In the single comprehensive study of broader trends, Ruiz Ramos (2014) examined 242 island/mainland bird species pairs among four bird orders (Gruiformes, Passeriformes, Procellariiformes, Sphenisciformes), finding no general influence of island effects on SSD (body mass) or SBCD of bill length, wing length, or tarsus length, with the exception of mass in Sphenisciformes. Climate effects on SSD also appear to be weak (Friedman & Remeš, 2016). Thus, insular influences on sexual dimorphism in birds appear to be taxon- or even region-specific.

Woodpeckers have become a useful model for exploring the evolution of overall body size, body shape, and sexual dimorphism in birds. Male-biased SSD and bill size SBCD are widespread among the nine families and >400 species (Short, 1982), including those belonging to the genus *Melanerpes* (Selander, 1966; Selander & Giller, 1963; Short, 1970; Wallace, 1974). Many of these taxa exhibit intersexual differences in foraging as well, which have been linked causally to dimorphism (e.g., Hogstad, 1991; Osiejuk, 1994; Pasinelli, 2000; Peters & Grubb 1983; Selander, 1966; Selander & Giller, 1963; Wallace, 1974). Reverse, or female-biased, SBCD for tail length has also been reported in many woodpecker taxa, though only in a few species within the genus *Melanerpes*, and female-biased wing dimorphism may exist as well in some taxa (Short, 1970).

Unfortunately, many studies of size and shape in woodpeckers, and birds in general, have a major shortcoming: they have been confounded by choice of an appropriate measure for overall body size. In *Melanerpes*, for example, Selander & Giller (1963) reported male-biased SBCD for bill, wing, tail, and tarsus length in virtually every species and subspecies examined. The problem with their analysis is that, because males average larger overall than females, they are likely to possess larger body components as well. A better approach to identify SBCD is to measure body components relative to an unbiased measure for body size. Selander et al. (1963) and Selander (1966) acknowledged this problem, and therefore expressed intersexual differences in bill length relative to wing length, tarsus length, and cubed root of body mass as alternative measures of overall body size.

Fortunately, a number of methods exist for finding a suitable measure of overall body size. The most direct approach uses a single character, such as body mass, that is closely associated with overall size; however, nutritional state and reproductive condition can influence this measure, and body mass is seldom available for museum study skins. In birds, wing length has been used, but is a poor measure of body size (Rising, 1988; Rising & Somers, 1989). Indeed, any single character, such as bill, wing, tail, or tarsus length, could potentially be dimorphic. A second approach features discriminant function analysis to identify the least dimorphic character (Fox et al., 2015; Olsson et al., 2002), but this method works best when a large number of characters are measured, and has gained little to no traction in studies of birds. The third and most widely applied approach is to use the first eigenvalue (principle component 1, PC1) of a principle component analysis, which often (but not always) encompasses overall size, with the additional orthogonal eigenvalues generally representing shape (e.g., Bookstein et al., 1985; Jolicoeur, 1963; Somers, 1986). A fourth approach computes the geometric mean of multiple measurements, which effectively removes shape to express overall size (Gallagher, 2015; Mosimann, 1970; Mosimann & James, 1979). Although this latter method was developed for study skins, ornithologists have largely overlooked it except for those who study skeletal material (e.g., Hughes, 2014; Kaboli et. al., 2007; Kudo et al., 2017; Leonard & Heath, 2010). Geometric mean is relatively straightforward to interpret and can be used to calculate a dimorphism index, whereas PC1 combines multiple variables that can be difficult to interpret, and generates both negative and positive values that are incompatible with a dimorphism index (unless used in an analysis of covariance model to generate estimated marginal means).

For this thesis, my goal was to characterize body size, body shape, and sexual dimorphism (SSD and SBCD) in select species of the woodpecker genus *Melanerpes*. The genus comprises a group of medium-sized woodpeckers found exclusively in the New World. Molecular analyses of the 24 currently recognized species yield multiple well-supported clades, including a monophyletic "*Centurus*" clade of 10 species (Navarro-Sigüenza et al., 2017; Table 1; Fig. 1). My study focused on this particular clade, which is especially useful for comparing insular influences because it includes a number of species with both island and mainland forms (Table 1).

Any prediction of how isolation might affect the evolution of body size in the *Centurus* clade depends, according to the island rule, on the relative body size of the source population, with smaller species becoming gigantic on islands and larger species becoming dwarfed. Different authors have used different size criteria, often ad hoc, to separate small versus large taxa. Grant (1965) assigned small and large groups relative to the mean of all birds he measured (mass 50 g, bill length 15 mm), as did Clegg and Owens (2002; mass 321 g, bill length 24 mm). Lomolino (2005) provided a scatterplot of the Clegg and Owens data, from which we assume Mathys & Lockward (2009) and others subsequently (Lokatis & Jeschke, 2018; Mathys 2010) inferred that birds below 70 g should be larger than mainland counterparts, whereas those above 120 g should be smaller. Curiously, the latter three publications gave credit for the intermediate range of 70–120 g to Clegg & Owens (2002), who made no such claim. Lakatis & Jeschke (2018) inexplicably used 30 g to divide small and large birds. Published values for woodpeckers in our study range from 35–52 g in *M. pygmaeus*/*rubricapillus* to 92–131 g in *M. radiolatus* (Short, 1982). Thus, the range in body size of birds in our study should be sufficient that smaller species might have larger forms on islands, and larger species might have smaller forms on islands.

Objectives

By taking six measurements of study skins for all available species and subspecies within the clade, as well as some distinct populations, I tested six hypotheses consistent with current evidence from birds in general and *Melanerpes* woodpeckers in particular, as summarized above. (1) Smaller mainland taxa become larger on islands and larger mainland taxa become smaller, as predicted by the island rule. If an island effect exists, it should also be more accentuated on smaller islands than larger islands. (2) Island forms exhibit greater levels of male-biased SSD compared to mainland forms, and to a greater extent on smaller islands than larger islands (as shown in at least some *Melanerpes* woodpeckers). (3) Extent of SSD corresponds to overall body size, as predicted by Rensch's Rule and demonstrated in many groups of birds. (4) Island forms exhibit distinctive body shapes relative to mainland forms, especially with reduced wing length and increased tarsus length (as documented in many bird species globally). The island effect should also be more evident on smaller islands than larger islands (5) Male-biased SBCD in bill size will be greater in island than mainland forms (as shown in many

Melanerpes woodpeckers), and greater on smaller than larger islands. And finally, (6) sexual differences in wings, tail, and legs will either be neutral or female-biased SBCD, and independent of insular effects (as hinted by prior studies). This investigation builds on prior studies by focusing on a large group of taxa and populations within a single clade, by using a proper correction for overall body size, and by providing what may be the most detailed analyses to date for SBCD in birds.

CHAPTER TWO

METHODS

Specimens

My collaborators and I obtained measurements from more than 1,500 study skins at various North American museums (Appendix 1). The taxa included all 10 species in the *Centurus* clade of *Melanerpes* woodpeckers delineated by Navarro-Sigüenza et al. (2017), and 43 of the 44 recognized subspecies and isolated populations (Table 1; Fig. 2); we were unable to sample any *M. santacruzi hughlandi*. Following Navarro-Sigüenza (2017), we treated *M. aurifrons* and *M. santacruzi* as distinct species, which additional molecular analyses have supported as well (Dufort, 2016; García-Trejo et al., 2009; Shakya et al., 2017). We included one additional species, the only member of the *Zebrapicus* clade, *M. hypopolius* (Navarro-Sigüenza et al., 2017), which shares similar plumage features (barred back, pale chest and cheeks) and overlaps in range with at least one *Centurus* species. We justified inclusion of *M. hypopolius* because size and shape differences between closely-related sympatric species may offer insight on phylogenetic and/or environmental causes of variation. Of the 43 taxa or populations sampled, two species are island endemics (*M. radiolatus*, *M. superciliaris*) and 20 subspecies or populations are restricted to islands (Table 1). The islands vary substantially in size (listed in Table 1) and distance from mainland or other islands; however, all are relatively small (<2,500 km^2) except Jamaica (10,991 km^2) and Cuba (105,007 km^2), with the latter likely having mainland-like attributes by virtue of its size (c.f. Lomolino, 2005). To avoid confounding phylogenetic effects, we analyzed morphology primarily at the population level, with the number of populations in any statistical model too few to include island attributes as predictors.

For the seven polytypic species (*M. carolinus*, *M. chrysogenys*j, *M. pygmaeus*, *M. rubricapillus*, *M. santacruzi*, *M. superciliaris*; and *M. uropygialis*), we assigned subspecies membership to individual specimens based on published descriptions of distribution (Table 1). Because distribution boundaries remain poorly defined for many subspecies, especially those of *M. carolinus*, *M. santacruzi*, and *M. uropygialis*, we applied conservative criteria, leaving unassigned some specimens of questionable membership. For *M. chrysogenys*, we assigned specimens to three groups: the two recognized subspecies, and intergrades collected from Nayarit, Mexico (Sieburth et al., 2018). We also had access to *M. superciliaris* specimens from several archipelagos in Cuba, including Cayo Avalos (presumably *M. s. murceus* by proximity, though treated by others as *M. s. superciliaris*), Cayos Los Indios (presumably *M. s. murceus*), Cayo Largo (sensu stricto *M. s. florentinoi*), and Cayos de San Felipe (sensu stricto *M. s. sanfelipensis*; see Buden and Storrs, 1989, and Garrido, 1992, for descriptions of cays and taxonomy).

Our working hypothesis for body size—the island rule—makes explicit predictions based on the relative body size of source populations for the island populations. From measures provided by Short (1982), we contrived three size groups: (1) three small species, *M. pygmaeus* (35–42 g), *M. rubricapillus* (35–42 g; mass lumped with *M. pygmaeus* by Short), and *Melanerpes hypopolius* (46–54 g) of the *Zebrapicus* clade; (2) six species of intermediate size: *M. uropygialis* (51–79 g), *M. chrysogenys* (55–85 g), *M. hoffmannii* (62–84 g), *M. carolinus* (67–91 g), *M. aurifrons* (67–100 g), and *M.*

santacruzi (67–100 g; mass lumped with *M. aurifrons* by Short); and (3) two large species: *M. radiolatus* (92–131 g) and *M. superciliaris* (70–126 g), which happen to be sister species (Fig. 1). We did not apply these body size groupings to other hypotheses involving shape and dimorphism.

Measurements

We used calipers to take all six morphological measurements: bill length (culmen from nares to distal tip), bill width (width of both mandibles at nares), bill depth (height of both mandibles at nares), wing chord length (unflattened, from bend of wing to tip of longest primary feathers), tail length (from base of tail to tip of longest feather), and tarsus length (from notch at ankle joint to palmar base of first metatarsus [hallux]). We chose these morphological measurements because of their common use among ornithologists and because differences between the sexes would most likely be evident in these features (Pyle 1997; Short, 1982). We sexed specimens based on well-described head patterns for each taxon (e.g., Short, 1982), and excluded juveniles, which were generally recognized by indistinct head markings and often smaller body size.

We obtained two data sets. For the larger data set derived from U.S. museum specimens, three investigators (LMS, MEA, WKH) took measurements of birds based on the above agreed-upon methods, although LMS was responsible for the large majority. Visual inspection of bivariate scatterplots for those taxa measured by two or three investigators indicated absence of bias with the exception of one character: bill width averaged slightly narrower in LMS measurements compared to those of MEA and WKH (which we address in the Discussion). The fourth investigator (AK) had access to *M.*

superciliaris specimens collected from several Cuban archipelagos, and available only from Cuba museums. Because his methods differed (exposed culmen for bill length, flat wing length, and slightly different tarsus length), we used his data, which also included additional Cuban specimens from North American collections, only for a separate analysis of *M. superciliaris* populations representing Cuba, Isla de la Juventud, and associated Cuban archipelagos.

Analyses

We obtained relatively unbiased measures of overall body size via two approaches. First, using the Mosimann method, we computed the geometric mean (*n*th root of the product of *n* variables) of the six body measures, which effectively isolates size from shape (Gallagher, 2015; Mosimann, 1970; Mosimann & James, 1979). Second, we used principal components analysis (PCA) to derive the first principal component (PC1), which likewise is recognized as a measure of overall body size, with other components extracted incorporating shape (Gallagher, 2015; Mosimann, 1970; Mosimann & James, 1979). Because results were similar when using the Mosimann method and PCA (though with some minor differences in two species), we present results based only on use of geometric means.

We conducted all statistical analyses using SPSS 20.0 for Mac or Windows (Statistical Package for the Social Sciences, Inc., Chicago, 2011), with alpha set to 0.05. Prior to analyses, we subjected data from each sex of each taxon to standard tests for univariate normality (Kolmogorov-Smirnov test) and homoscedasticity (Levene’s test), and used bivariate scatterplots to screen for outliers (Field, 2005). We removed 13 birds with one or more outlier measurements from the larger data set and none from the Cuba-specific data set. The remaining data largely met these assumptions, with exceptions being mild and judged non-problematic. Further inspection of bivariate scatterplots across all variables, including geometric mean, indicated the original measurements met the assumption of linearity. Log-transformed measurements created mild curvilinearity in some bivariate relationships, so we used only untransformed data for all analyses.

We conducted three major sets of analyses to examine (1) variation in overall body size and SSD, (2) variation in overall body shape, and (3) the presence of SBCD in each of the six body components measured. For each of these three sets of analyses, we first analyzed all 11 species, and then analyzed subspecies within each of the seven polymorphic taxa.

Our first set of analyses considered geographic and sexual variation in overall body size. We conducted two-way analyses of variance (ANOVAs; Tabachnick & Fidell, 2013) with geometric mean as the measure of body size, and sex and group (species or subspecies/population) treated as between-subjects variables. We included only those taxa with at least one male and one female (i.e., no empty cells in model). We used Tukey’s honestly significant difference (HSD) for post-hoc multiple comparisons. To evaluate SSD for each taxon or population, we calculated the Lovich-Gibbons (1992) index using one of two equations: (1) if females were larger, then SSD = ((mean female geometric mean) / (mean male geometric mean)) - 1; (2) if males were larger, then SSD = - ((mean male geometric mean) / (mean female geometric mean)) + 1. With this index, SSD = 0 means absence of sex differences; positive values indicate female-biased dimorphism; and negative values indicate male-biased dimorphism. We multiplied values by 100 to obtain the percent difference relative to the smaller sex, which we report because doing so is more intuitive and avoids values with excessive decimal places. We subjected the SSD values to similar two-way (sex × group) ANOVAs. We computed Spearman's rank correlation (ρ; Field, 2005) to evaluate the relationship between mean male body size and SSD (Rensch's rule). For the larger *M. superciliaris* data set including six populations, we also used ρ to evaluate the association of mean male body size with island size. We chose not to test correlations for the data set from Cuba because of the smaller sample sizes and closer geographic proximity of populations, with the latter likely to mitigate any effects of island size.

Our second set of analyses relied on discriminant function analyses (DFAs; (Tabachnick & Fidell, 2013) to characterize shape variation among the 11 species (including all island and mainland forms) and among subspecies/populations for each of the seven polytypic species. This approach allowed us to identify which among the six body components (bill length, width, and height; wing, tail, and tarsus length) were best at discriminating among groups. We included all taxa, even if $N = 1$. To be conservative, we set all groups equal for prior probabilities, and used leave-one-out classification, a jackknife procedure, which is essential for smaller sample sizes (Lance et al., 2000). For each of these comparisons, we ran separate analyses for males, females, and both sexes combined. Because sexual dimorphism existed, which increased within-taxon variation and decreased between-taxon variation, discrimination success proved better when analyzing a single sex. Because sample sizes were always larger for males, we report details only for males for these DFA models, with the exceptions of *M. chrysogenys* groups, for which sample sizes were small, and Cuba *superciliaris*, for which inclusion of both sexes allowed us to keep all populations of interest in a single analysis. For the two exceptions, results were similar to those obtained from individual sexes. For the larger data set of six *M. superciliaris* populations, we used Spearman's rank correlation to evaluate associations between centroid values of discriminant functions reflecting body proportions and island size.

To characterize SBCD in our third set of analyses, we divided the measurement for each of the six body components by the geometric mean to get size-corrected measures, and then ran two-way ANOVAs on these values for each body component, treating sex and group (species or subspecies/population) as between-subjects factors. We used the mean value of each sex to derive the aforementioned Lovich-Gibbons index value for each body component of each species and subspecies/population. Again, values greater than zero indicated females had a relatively larger body component, and values less than zero indicated males had a relatively larger body component.

Because null-hypothesis tests (*P*-values) are severely constrained by sample sizes and index values do not take into consideration variance, we relied on effect sizes to interpret the relative importance of group differences. We computed partial eta-squared (η^2) as a measure of effect size for each variable and interaction in the ANOVA models (Cohen, 1988). We also calculated η^2 (as $1 - \Lambda$) for each DFA model. These effect size estimators indicate the approximate proportion of variance explained in the dependent variable, with values of ~0.01, ~0.06, and ≥ 0.14 loosely deemed as small, medium, and large effects, respectively (Cohen, 1988). Because η^2 is upward-biased when multiple variables are included (Pierce, 2004), we adjusted these when values for main effects (and interaction if present) summed to >1.0 by dividing each value by the sum of all values (Revell & Hayes, 2009). For correlations, we considered ρ values of ~0.1, ~0.3, and ≥0.5 to be relatively small, medium, and large effects, respectively (Cohen, 1988). Index values computed for SSD and SBCD are based on mean values, and do not consider variance; we therefore computed Cohen's *d* to assess the relative size or importance of sex differences, with values of ~0.2, ~0.5, and ≥0.8 corresponding to small, medium, and large effects, respectively (Cohen, 1988). Following Nakagawa (2004), we chose not to adjust alpha for multiple tests because doing so overemphasizes the importance of null hypothesis testing when effect size is more meaningful, and unacceptably increases the probability of making type II errors (i.e., the hyper-Red Queen phenomenon: the more research one does, the lower the probability that a significant result will be found; Moran, 2003).

CHAPTER THREE

RESULTS

Body Size

Among the 11 woodpecker species examined, overall body size measured by geometric mean varied dramatically (taxon effect: $P < 0.001$; Table 2, Fig. 3A; sex differences, including the significant interaction, are addressed in the next section). Size differences based on geometric mean matched expectations from the reported body mass for each species (Short, 1982), supporting our distinctions between small, intermediate, and large species. The two island forms, *M. radiolatus* and *M. superciliaris* of the West Indies, were the largest species within the clade; however, some *M. superciliaris* subspecies were similar in size to the larger group of intermediate-sized species (Fig. 3).

Intraspecific variation in overall body size also existed within each polytypic species (Table 2; Fig. 3B–2I), but there was no relationship between body size and geography consistent with the island rule. We predicted that the two smallest species, *M. pygmaeus* and *M. rubricapillus*, would become larger on islands compared to the mainland. For *M. pygmaeus*, one of the two island subspecies (*tysoni*) was significantly larger (Tukey's HSD: $P < 0.001$) than the mainland subspecies (*rubricomus*), but the other (*pygmaeus*) was significantly smaller ($P < 0.001$; Fig. 3D). For *M. rubricapillus*, one island form (*seductus*) was significantly larger (Tukey's HSD: $P = 0.027$) than the one mainland form (*rubricapillus*) with adequate data, but the other island form (*subfusculus*) was of similar size ($P = 0.35$; Fig. 3E). For species of intermediate size, island forms averaged significantly larger than all mainland forms (Tukey's HSD: all $P < 0.001$) in two of the nine *M. santacruzi* subspecies (*canescens* and *leei*), but the third island form (*insulanus*) with adequate data was similar in size to all mainland forms (all $P \geq 0.08$) except the smaller *veraecrucis* ($P = 0.010$; Fig. 3F). The single island form of seven *M. uropygialis* subspecies (*tiburonensis*) was relatively small but statistically similar in size (Tukey's HSD: all $P \geq 0.45$) to the six mainland forms (Fig. 3I).

The only large polytypic species, *Melanerpes superciliaris*, exhibited the most profound intraspecific variation in body size. Males of the largest subspecies averaged 16.3% larger than those of the smallest subspecies (for the larger data set), which far exceeded size differentiation in subspecies of *M. pygmaeus* (9.1%), *M. santacruzi* (8.3%), *M. carolinus* (5.5%), *M. rubricapillus* (4.9%), *M. uropygialis* (2.9%), and *M. chrysogenys* (1.4%). Considering the six subspecies of *M. superciliaris* in the larger data set, body size was positively associated with island size (Spearman's $\rho = 0.83$, $P = 0.042$), with the largest taxa being *superciliaris* on Cuba (the largest island) followed by *murceus* on Isla de la Juventud (the second largest island), and the smaller taxa occurring on the smaller islands to the north (*bahamensis*, *blakei*, *nyeanus*) and south (*caymanensis*; Fig. 3G). Because different methods were used to measure bill and wing length, obvious differences existed for *M. superciliaris* specimens in the larger and smaller (Cuba only) data sets (compare Fig. 3G and 3H). For populations of the Cuba archipelago, island size appeared to be unimportant because birds on small, well-isolated cays (Cayo Avaco [*murceus*-CA], Cayos Los Indios [*murceus*-LI], Cayo Largo [*florentinoi*], Cayos de San Felipe [*sanfelipensis*]) were not appreciably smaller than those on the much larger Isla de la Juventud (*murceus*) and Cuba (*superciliaris*; Fig. 3H). Several Cuban population/sex groups were represented by a single individual, but the sample for *florentinoi* was sufficient to demonstrate a body size more similar to *superciliaris* than *murceus*.

Sexual Size Dimorphism (SSD)

At the species level, the significant interaction between species and sex (*P* < 0.001; Table 2) suggests that SSD differed substantially among the 11 taxa. Sexual size dimorphism was greatest for *M. uropygialis* (males 8.38% larger than females; see SSD index values in Table 3), and least for *M. hypopolius* of the *Zebrapicus* clade (males 1.73% larger), with SSD for the latter clearly smaller than any of the 10 *Centurus* clade members (Table 3; Fig. 3A). No trend was evident for differences in SSD values between island and mainland taxa, with *M. superciliaris* exhibiting moderate SSD relative to others in the *Centurus* clade, and *M. radiolatus* having the least SSD within the clade. Contrary to Rensch's rule, no relationship existed between magnitude of SSD and mean male body size of the 11 species (ρ = -0.145; *P* = 0.670).

Among the polytypic species, the extent of SSD varied (significant taxon effect or interaction in Table 2; see also Fig. 3A) for all except *M. chrysogenys*. Males were larger than females in all taxa and populations (Table 3; Fig. 3A). No consistent trend existed for differences in SSD values between island and mainland populations, but island populations tended to be at the high or low extreme. For both *M. pygmaeus* and *M. rubricapillus*, the two island forms exhibited markedly greater SSD (males 5.5–8.2% larger than females) than the single mainland subspecies (males 0.7–1.5% larger; Table 3; Fig. 3D-E). For *M. santacruzi*, in contrast, the three island forms with adequate data (*canescens*, *insulanus*, *leei*) had less SSD (males 4.1–4.7% larger) than any of the six mainland subspecies (males 5.3–9.6% larger; Table 3; Fig. 3F). For *M. uropygialis*, the single island form had the second greatest SSD of the seven subspecies (Table 3; Fig. 3I). For *M. superciliaris*, there was no association of SSD with island size (ρ = -0.13, *P* =

0.81), with some forms on smaller islands having less and others having greater SSD than *superciliaris* on Cuba, the largest island (Table 3, Fig. 3G-H).

Body Shape

Among the 11 woodpecker species examined together, the highly significant DFA model revealed considerable interspecific variation of body shape in canonical space (Table 4; Fig. 4A). Discrimination success (74.6% for cross-validated data) far exceeded that expected of chance (9.1% for the 11 taxa in the model). The island forms *M. radiolatus* and *M. superciliaris* were well separated from the other species on function 1 (Fig. 4A), having longer tails and tarsi (see coefficients in Table 4; DFA does not provide pairwise comparisons). The two smallest species (*M. pygmaeus* and *M. rubricapillus*), along with *M. hoffmannii*, had relatively short tails and tarsi (Fig. 4A).

Intraspecific variation in body shape also existed within each polytypic species, with discrimination success always exceeding that expected by chance (Table 4; Fig. 4B–I). Shape differentiation was relatively large within *M. chrysogenys*, *M. pygmaeus*, and *M. rubricapillus* (η^2 effect sizes = 0.76, 0.87, and 0.89, respectively), and among at least some subspecies of *M. santacruzi* and *M. superciliaris* (0.87 and 0.94, respectively), but was comparatively weak in *M. carolinus* and *M. uropygialis* (η^2 = 0.56 and 0.51, respectively; Table 4). For *M. chrysogenys*, intergrades had intermediate bill and tail lengths, as expected, but their wing lengths were shorter than either of the two subspecies (Fig. 4C). Island forms usually exhibited shorter wings compared to mainland forms. This was true for the two island forms of *M. pygmaeus* (*pygmaeus* and *tysoni*) compared to the mainland subspecies (*rubricomus*; Fig. 4D); the two island forms of *M.*

rubricapillus (*seductus* and *subfusculus*) compared to the mainland subspecies with adequate data (*rubricapillus*; Fig. 4E); several island forms of the nine *M. santacruzi* subspecies with adequate data (*canescens* and *leei*; *insulanus* was an exception, but the single specimen of *turneffensis* had short wings; Fig. 4F); and the single island form of the seven *M. uropygialis* subspecies (*tiburonensis*; Fig. 4I). Within *M. superciliaris,* relative wing length assessed as centroid values at discriminant function 1 (F1) corresponded to island size ($\rho = 0.94$, $P = 0.005$), being larger for subspecies on the largest islands (*murceus*, *superciliaris*) and smaller for subspecies on the smallest, most isolated islands (*bahamensis*, *blakei*, *caymanensis*, *nyeanus*; Fig. 4G). This relationship appeared to hold even for *M. superciliaris* within the Cuba archipelago (Fig. 4H). Relative bill size (length, width, and/or depth) also averaged larger in island forms of several species (*M. pygmaeus*, *M. rubricapillus*, *M. santacruzi*; Figs. 4D–F), but not in the single island form of *M. uropygialis* (*tiburonensis*; Fig. 4I). Within *M. superciliaris*, relative bill length (F1, as tested above, but not bill depth, F2) corresponded to island size (Fig. 4G), though not within the Cuban archipelago (Fig. 4H).

Sexual Body Component Dimorphism (SBCD)

Relative size of the six body components (bill length, width, and depth; wing, tail, and tarsus length) almost always differed among the groups (species and subspecies/populations) and between the sexes, as indicated by significant ANOVA effects in Table 3. The consistent trend across virtually all taxa and populations was male-biased bill size (bill length being most dimorphic) and female-biased wing, tail, and tarsus lengths, though some reversals were evident, usually in groups with comparatively small sample sizes. Colors in Table 3 make this interpretation easier: blue colors indicate male-biased index values of medium or greater effect size (Cohen's d ≥ 0.5), and yellow colors indicate female-biased index values of comparable size. Relatively large SBCD index values were sometimes small effects because of high levels of variance among the groups. Moreover, index values derived from small samples should be considered judiciously (e.g., *M. s. murceus*-CLI).

Numerous significant interactions between groups (species or subspecies/populations) and sex for the six body components (Table 3) suggest that degree of SBCD often varied at both specific and intraspecific levels. This was evident at the species level, where the extent of SSD corresponded loosely with SBCD. As an example, the species with the largest SSD, *M. uropygialis*, also exhibited the largest SBCD for bill length (male-biased) and the largest SBCD for wing and tarsus lengths (female-biased; Table 3). However, the species with the least SSD, *M. hypopolius* of the *Zebrapicus* clade, had negligible SBCD of bill length as might be anticipated, but bill depth was the most dimorphic (male-biased) of any species, suggesting a bill shape difference compared to the *Centurus* clade members. For *M. hypopolius*, SBCD of wing length and tail length also approached the average for all species.

No consistent differences in SBCD existed between island and mainland groups (Table 3). For *M. pygmaeus*, the two island forms (*pygmaeus* and *tysoni*) exhibited greater male-biased SBCD of bill size (length, width, and depth), and greater female-biased SBCD for wing, tail, and tarsus lengths compared to the mainland subspecies (*rubricomus*). For *M. rubricapillus*, the two island forms (*seductus* and *subfusculus*) likewise had greater male-biased SBCD for bill size (length and width, but not depth) and greater female-biased SBCD for wing and tail length compared to the mainland subspecies (*rubricapillus*). In *M. santacruzi*, however, island forms were similar to mainland subspecies in SBCD for bill length and width, and wing, tail, and tarsus lengths. In *M. uropygialis*, the single island form, *tiburonensis*, exhibited relatively large male-biased SBCD for bill length compared to the mainland subspecies, but female-biased SBCD of wing and tarsus length was least compared to the six mainland taxa. For *M. superciliaris*, associations of island size with degree of SBCD were relatively small for bill length, width, and depth ($\rho = 0.09$, 0.20, and -0.26, respectively), moderate-to-large and negative for female-biased wing and tail lengths ($\rho = -0.43$ and -0.49, respectively; least for *superciliaris* on Cuba, the largest island), and substantial and positive for female-biased tarsus length ($\rho = 0.66$; greatest for *superciliaris* on Cuba), though no correlations were significant because of the small sample sizes. For the Cuba archipelago, SBCD for *superciliaris* on Cuba appeared to be comparable to other taxa/populations on smaller islands, though sample sizes for *florentinoi* and especially *murceus* on Cayo Los Indios (effect sizes not available) were very small.

CHAPTER FOUR

DISCUSSION

This study examined size and shape variation and extent of sexual dimorphism among woodpeckers belonging to the *Centurus* clade of the currently recognized genus *Melanerpes*. The large number of subspecies and distinct populations that occur on islands and on the mainland render this group ideal for understanding how isolation could influence the evolution of morphological traits believed to be important for habitat use, foraging, and survival. Our statistical analyses supported only two of our six hypotheses. (1) Contrary to predictions of the island rule, smaller and larger mainland taxa did not converge on an intermediate body size. (2) Contrary to prior evidence from *Melanerpes* woodpeckers, island and mainland taxa and populations exhibited similar levels of male-biased SSD. (3) Contrary to Rensch's rule, no relationship existed between extent of SSD and body size. (4) Consistent with the broad trend among avian taxa globally, island forms consistently exhibited reduced wing length. (5) Contrary to prior evidence from *Melanerpes* woodpeckers, levels of male-biased SBCD in bill size were similar between island and mainland forms. And finally, (6) consistent with expectations hinted at by prior studies of *Melanerpes* woodpeckers, *Centurus* clade members consistently exhibited female-biased wing, tail, and tarsus SBCD, but the extent of dimorphism was similar among island and mainland forms. We detected female-biased SBCD—perhaps the most novel finding of the study—only because we used an unbiased measure of overall body size to assess these body components. Apart from these findings, there was also some tendency for island populations to be at the extremes of size (dwarfism or gigantism), shape, and dimorphism, suggesting that taxon- or region-specific island influences may exist. In the following sections, we relate our findings to what is generally known or might be expected of size, shape, and dimorphism in island versus mainland woodpeckers, and discuss potential sources of bias that could have influenced the analyses.

Body Size

At the interspecific level, body size varied dramatically among the 11 woodpecker species. The two island forms, *M. radiolatus* and *M. superciliaris,* comprise the largest species among the *Centurus* clade, but the sample here is too small to conclude these taxa represent island gigantism, as suggested by Selander & Giller (1963). The evolutionary history of the two sister species (Fig. 1) remains unclear. We don't know whether the common ancestor of both species had already evolved a large body size, or whether large size evolved separately in both species. However, both taxa evolved from a clade comprised of medium-sized mainland taxa (Fig. 1), from which it would be difficult to predict whether evolution, if influenced at all by island conditions, should lead to dwarfism or gigantism.

Intraspecific comparisons among the polytypic species more clearly failed to support the island rule, especially for the small and intermediate-sized species. The rule led us to predict that island forms of the two small species (*M. pygmaeus* and *M. rubricapillus*) would be larger than their mainland source populations, but two subspecies among the island forms were larger, one was similar in size, and one was smaller. We further predicted that island forms of the intermediate-sized species (*M. santacruzi* and *M. uropygialis*) would be similar in size to mainland source populations, but while two subspecies among the island forms were similar in size to mainland forms, two subspecies were larger.

Predictions for intraspecific variation within *M. superciliaris* at the large end of the size spectrum proved to be more complex. The substantial sample of large-bodied *superciliaris* from Cuba contributed to the large mean size for the species, offsetting the smaller size of subspecies on other islands that approximate the intermediate size of many mainland species. If Cuba is large enough to be treated as a mainland and as the potential source for all other populations, then all other forms occurring on smaller islands are smaller in body size (except for *florentinoi*), which would be consistent with the island rule of larger forms evolving toward dwarfism. The significant correlation between body size and island size suggests the presence of an isolation effect, which might be reinforced by distances from Cuba. However, without a detailed genetic analysis of all *M. superciliaris* populations, we do not yet understand how the species differentiated among the islands. The species might have evolved on Cuba first, and then colonized the smaller Bahamas islands and Grand Cayman while evolving toward dwarfism. Alternatively, the species might have evolved on one of the smaller islands first—or perhaps on the much larger Great Bahama Bank (ca. 103,000 km^2) and/or Little Bahama Bank (ca. 17,000 km^2) before submersion within the past 10,000 years resulting in the smaller islands in the Bahamas today (Steadman and Franklin, 2015)—and then evolved toward gigantism after colonizing Cuba. The fact that the Great Bahama Bank, like Cuba, may have been large enough to experience mainland-like effects (Lomolino, 2005) greatly complicates any evolutionary scenario.

We conclude that no clear effect of insularity on body size exists in this group of woodpeckers. We did not examine the potentially confounding abiotic and biotic factors that can also influence body size. Among the abiotic factors, for example, woodpeckers might be expected to be larger in colder environments (Bergmann's Rule), which has been documented for the mainland species *M. carolinus* (Kirchman & Schneider, 2014), and might well exist for other widely distributed species such as *M. aurifrons*, *M. rubricapillus*, *M. santacruzi*, and *M. uropygialis*. Among the biotic factors, competitors in the form of other woodpecker species, which varied in number from island to island and between islands and mainland, could influence body size through character displacement, thereby altering any effect that isolation might exert. Habitat structure, habitat quality, and population density might also exert unknown influences on body size.

Sexual Size Dimorphism

Ample data from woodpeckers of the genus *Melanerpes* and *C. striatus* led Selander & Giller (1963) to conclude that male-biased SSD is widespread, which our results support. Selander & Giller (1963) also concluded that island forms have larger SSD, which cannot be supported by our data. Male-biased SSD exists for many other woodpeckers (e.g., Hogstad, 1991; Osiejuk, 1994; Pasinelli, 2000; Pechacek, 2015; Peters & Grubb, 1983). At the interspecific level, SSD differed substantially among the 11 taxa we studied. However, none of the island (*M. radiolatus*, *M. superciliaris*) or predominantly island (*M. pygmaeus, M. rubricapillus*) species were at extreme ends of the SSD spectrum. Our results were largely consistent with those of Selander and Giller (1963); our larger samples, for example, confirmed the greatest level of SSD in *M.*

uropygialis and the least in *M. hypopolius*, which invites further study of behavioral differences between these taxa, including their mating systems. *Melanerpes hypopolius*, as the sole member of its own clade, *Zebrapicus*, differs markedly in this respect with its sister clades *Centurus*, *Melanerpes*, and *Tripsurus* in having reduced SSD (Selander and Giller, 1963). Both of our studies indicated relatively low levels of SSD in the island species *M. radiolatus*. At the intraspecific level, no consistent trend existed for island populations, but they tended to be at the high (*M. pygmaeus*, *M. rubricapillus*, *M. uropygialis*) or low (*M. santacruzi*) extreme of SSD. For *M. superciliaris*, there was no association of SSD with island size. In sum, we conclude that island conditions exert, at best, minimal effects on SSD in this woodpecker group.

The best-known trend in SSD for birds is Rensch's rule (Rensch, 1950), which states that the extent of SSD covaries allometrically with each species' mean body size such that male-biased SSD increases and female-biased SSD decreases with increasing body size. No such trend was exhibited by the 11 species, which comes as no surprise because many bird groups do not follow this rule. Székely et al. (2007) found allometry consistent with Rensch's rule in 125 (85.6%) of 146 avian families examined, whereas Dale et al. (2007) found evidence for the pattern in 110 (60.4%) of 182 avian subfamilies.

Climate factors might also contribute to SSD, which we did not control for. A phylogenetically-controlled study of 2,581 bird species revealed some associations of SSD with latitude and within-year variation in climate, but the direction and strength of the relationships varied regionally, and SSD appeared to be largely independent of the nine climate predictors examined (Friedman & Remeš, 2016). Further study is needed of mating systems within the group, as SSD is most strongly linked to sexual selection, especially the intensity of male mating competition (Székely et al., 2007). Polyandry has been documented in *M. s. blakei* (Willimont et al. 1991), and possible polygyny in *M. aurifrons* (Husak, 2005).

Body Shape

Given the strong tendency of island birds to evolve shorter wings (Wright et al., 2016), we had reason to expect this trend to appear within the woodpecker clade we examined. However, we found contrasting patterns between interspecific and intraspecific analyses. At the interspecific level, the two island species (*M. radiolatus*, *M. superciliaris*) exhibited relatively long tails and tarsi, with no apparent difference from mainland forms in wing length. The two smallest species (*M. pygmaeus*, *M. rubricapillus*), in contrast, possessed relatively short tails and tarsi. Considering the close phylogenetic affiliations of these two groups, we assume these body shape differences are taxon-specific rather than island attributes. At the intraspecific level, however, island forms almost always differed from mainland forms in having shorter wings, and relative wing length was associated with island size (isolation) in *M. superciliaris*. Relative bill size also trended larger in several island forms, with an association also existing between bill length and island size within *M. superciliaris*. The contrast in trends at different phylogenetic levels (among versus within subspecies) underscores the importance of identifying patterns, when possible, at the lowest taxonomic level.

The adaptive value of shape changes in island populations is best demonstrated for the trend of reduced wing length, which is associated with an evolutionary shift in investment from forelimbs to hindlimbs in response to smaller island size and reduced predation (Wright et al., 2016). Bill size differences relate to diet (Badyaev et al., 2008; Bowman, 1961; Herrel et al., 2010), song production (Fletcher, 1988; Giraudeau et al., 2014), and thermoregulation (Tattersall et al., 2017). We did not examine broader trends in body shape with other abiotic or biotic factors that may influence them. Endotherms, for example, often have longer extremities in warmer climates (Allen's rule), which appears to exist in the Red-cockaded Woodpecker (*Picoides borealis*; Mengel & Jackson, 1977), and may occur as well for other widely distributed species such as *M. aurifrons*, *M. rubricapillus*, *M. santacruzi*, and *M. uropygialis*. Vegetation structure may also influence the shape of these structures, but differences in bill and foot shape have received the most attention, with wing shape largely neglected (Cibois et al., 2007; Kaboli et al., 2007; Leisler & Winkler, 2015; Winkler & Leisler, 1985). Perhaps islands, and smaller islands in particular, have a denser forest structure that would select for shorter wings.

Sexual Body Component Dimorphism

Prior work on the *Melanerpes* species we studied demonstrated marked male-biased SSD and male-biased bill size SBCD (Selander, 1966; Selander & Giller, 1963). Other body components (wing, tail, legs) also averaged longer in males, but Short (1970) subsequently demonstrated the presence of female-biased tail length SBCD in several species. As these authors all conceded, lack of a suitable character for overall body size rendered their conclusions tenuous. We overcame this obstacle by using the geometric mean of the six characters we measured to correct for body size. The consistent trend at both interspecific and intraspecific levels was male-biased bill size (bill length being most dimorphic), as expected, and female-biased wing, tail, and tarsus lengths, which could be anticipated from prior studies (Selander, 1966; Selander et al., 1963; Short, 1970). Although the relative magnitude of SBCD for body components varied among taxa at both levels of analysis, as indicated by significant interactions, no consistent differences in SBCD existed between island and mainland groups. Given the pervasive nature of male-biased bill size and female-biased wing, tail, and leg lengths, many of the reversals (Table 3) were likely spurious, resulting from small sample sizes and/or seasonal artifacts (see Limitations below).

Our findings failed to support, but do not invalidate, the suggestion of Selander & Giller (1963) and Selander (1966) that island woodpeckers have greater male-biased SBCD in bill length compared to mainland forms. In light of the clades within *Melanerpes* elucidated by Navarro-Sigüenza et al. (2017), bill length dimorphism in the Puerto Rican Woodpecker (*C. portoricensis*) and Guadeloupe Woodpecker (*C. herminieri*) far exceeded that of a sister clade member, *C. erythrocephalus*, on the mainland. The remarkable bill length dimorphism in the enigmatic Hispaniolan Woodpecker (*C. striatus*), which is sister to the entire *Melanerpes* complex, far exceeded that of any of the 25+ North America woodpecker species included in Selander and Giller's study. Thus, a broader picture within *Melanerpes* gives a somewhat different picture than that within the *Centurus* clade.

Intersexual differences in bill size can evolve via at least four mechanisms (Selander, 1966; Selander & Giller, 1963; Wallace, 1974): (1) intraspecific competitive influences (the intersexual niche divergence hypothesis); (2) sexual selection (intrasexual competition or intersexual mate choice); (3) pressures for close association while foraging, promoting finer partitioning of food resources through sexual specialization; and (4) ecological differences, such as roost or nest construction. The first hypothesis, proposed to explain greater levels of bill size dimorphism in island populations of *Melanerpes* woodpeckers (Selander & Giller, 1963), invokes an expansion of the total feeding niche in response to fewer competitors present on islands, with males and females using different niches (or sub-niches) on the same territory to reduce intersexual competition. Selander (1966) supported the hypothesis by showing that the species with the greatest dimorphism in bill size, the Hispaniolan Woodpecker (*Chryserpes striatus,* an island species he considered a member of *Melanerpes*), exhibited greater intersexual divergence in foraging behavior than the moderately dimorphic Golden-fronted Woodpecker (*M. aurifrons*), a mainland species. Wallace (1974) provided additional support for the first hypothesis by similarly comparing *C. striatus* and the Puerto Rican Woodpecker (*M. portoricensis*) to the mainland forms *M. aurifrons* and the Red-bellied Woodpecker (*M. carolinus*). Wallace (1974) also found support for the third hypothesis, with the positive correlation among four woodpecker species between bill size dimorphism and sexual overlap in foraging height suggesting that dimorphism facilitates social behavior by allowing the sexes to forage in closer proximity.

Studies of the adaptive consequences of SBCD in woodpeckers have been limited to bill length dimorphism. Our findings suggest that additional studies would shed meaningful insight on the relative wing, tail, and leg lengths of these birds. We anticipate that SBCD of these characters may have arisen largely from either intrasexual or intersexual selection, but further study is needed.

Limitations

Several important factors undoubtedly limit the strength of our analyses. First, we obtained large sample sizes for many populations, but some populations were represented by small samples, which we have treated conservatively. Second, because bird feathers are prone to abrasion, specimens with worn feathers will yield shorter measurements for wing and tail length (e.g., Flinks & Salewski, 2012). One way to address this is to analyze birds collected only with fresh plumage, but doing so would have greatly restricted our sample size. Nevertheless, bias could arise if some taxa or populations were better represented for some seasons than others. Third, four investigators measured birds. We treated measurements by one individual (AK) separately from the others, but we identified minor bias in bill width, which averaged slightly narrower in LMS measurements compared to those of MA and WKH. For the most part, bill width differences were negligible at both the interspecific and intraspecific levels. However, the one comparison for which this bias could be a problem would be for separating the *M. rubricapillus* populations; MA measured *seductus*, which averaged thicker-billed than the two other taxa measured by LMS. Clearly, the difference should be disregarded, or at least further studied.

Conclusions

Based on extensive sampling of island and mainland taxa and populations, we conclude that islands have exerted limited influence on body size, shape, and sexual dimorphism of woodpeckers belonging to the *Centurus* clade. Substantial variation exists in body size, shape, and sexual dimorphism, but only wing length appears to be linked strongly to island conditions. Much of the variation can be attributed to other causes we did not measure, including phylogenetic relationships. Although insular effects of body size and shape have been widely studied in birds, island effects on sexual dimorphism have been largely ignored, for which use of an unbiased reference character is essential. We strongly recommend adoption of geometric mean as a measure of overall body size in future studies to better control for the confounding effect of body size when examining measurements of individual body components. Our findings revealed an unambiguous trend toward female-biased wing, tail, and tarsus length dimorphism within the clade, which merits further study, especially to understand evolutionary causes. Although we have not addressed species delimitation with our analyses, substantial intraspecific variation in a number of the polytypic taxa invites closer examination.

CHAPTER FIVE

CONCLUSIONS AND FUTURE DIRECTIONS

In this thesis, I summarize the size, shape, and sexual dimorphism of island and mainland *Melanerpes* woodpeckers of the *Centurus* clade. I present the results of this study to encourage the analysis of biodiversity at multiple levels.

My study revealed that body size varied dramatically within the 11 woodpecker species. However, the results supported only two of the six hypotheses that I tested, which can be summarized here. (1) Contrary to predictions of the island rule, smaller and larger mainland taxa do not converge on an intermediate body size. Mixed support exists for this rule (Grant, 1965; Leisler & Winkler, 2015; Ruiz Ramos, 2014; Wright et al., 2016), so it comes as no surprise that this particular clade fails to offer support. (2) Contrary to prior evidence from *Melanerpes* woodpeckers, island and mainland taxa and populations exhibit similar levels of male-biased SSD. The prior evidence was based on analyses primarily at the species level, and included a few additional *Melanerpes* species belonging to additional clades (Selander, 1966; Selander & Giller, 1963; Short, 1970; Wallace, 1974). The prior assertion could be an artifact of phylogenetic relationships. (3) Contrary to Rensch's rule, no relationship existed between extent of SSD and body size. Some but not all bird groups adhere to this rule (Dale et al., 2007; Nuñez-Rosas et al., 2017; Székely et al., 2007), so it comes as no surprise that this particular clade does not. (4) Consistent with the broad trend among avian taxa globally (Wright et al., 2016) island forms consistently exhibited reduced wing length. This trend reflects an evolutionary allocation of energy from the wings to the legs, leading ultimately to the flightless condition sometimes seen on islands. (5) Contrary to prior evidence from *Melanerpes* woodpeckers (Selander, 1966; Selander & Giller, 1963), levels of male-biased SBCD in bill size were similar between island and mainland forms. Similar to SSD, prior evidence for bill size differences was based on analyses primarily at the species level, and included a few additional *Melanerpes* species belonging to additional clades (Selander, 1966; Selander & Giller, 1963; Short, 1970; Wallace, 1974). The prior assertion could be an artifact of phylogenetic relationships. Finally, (6) consistent with expectations hinted at by prior studies of *Melanerpes* woodpeckers, *Centurus* clade members usually exhibited female-biased wing, tail, and tarsus SBCD, but the extent of dimorphism was similar among island and mainland forms. Studies of the adaptive consequences of SBCD in woodpeckers have been limited to bill length dimorphism, so future studies could shed meaningful insight on the relative wing, tail, and leg lengths of these birds.

My findings bring to mind a number of directions that future research could address within this clade. First, some of the relationships identified here are based on relatively small samples, and warrant reexamination. Second, there are additional island populations we were unable to sample, in particular *M. rubricapillus* in northern South America. It would be interesting to see whether island differences exist in those populations. Third, additional studies examining the functional basis for island/mainland differences and sexual differences would help us better understand the evolution of these traits. Fourth, abiotic and biotic factors should be explored to learn how size, shape, and dimorphism within the clade are influenced by factors like temperature, vegetation structure, and potential competition from other woodpecker species. Finally, the data and results presented here can be used for phylogenetic inferences. Some of the polytypic species demonstrated substantial differentiation, especially among the island forms, and may represent unrecognized species.

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Table 1. Named taxa and populations (with abbreviations) of *Melanerpes* woodpeckers analyzed in this study (except for *M. santacruzi hughlandi*). Clade and species delineation based on Navarro-Sigüenza et al., 2017. Geography is indicated as mainland or island, with island size indicated in square kilometers.

Clade	**Species**	**Subspecies**	**Location (and island area)**	**Geography**	**Taxonomy and Location**
Centurus	*aurifrons*	Monotypic	South-central U.S. to northeast Mexico	Mainland	Husak and Maxwell, 1998
Centurus	*carolinus*	*carolinus* (ca)	East of Appalachian Mts., U.S.	Mainland	Shackelford et al., 2000
		harpaceus (ha)	Central and east Texas, U.S.	Mainland	
		perplexus (pe)	Southern Florida and Florida Keys, U.S.	Mainland/island	
		zebra (ze)	Central U.S. west of Appalachian Mts., U.S.	Mainland	
Centurus	*chrysogenys*	*chrysogenys* (ch)	Pacific slope of central Mexico (north portion)	Mainland	Winkler and Christie, 2019; Sieburth et al., 2018 (intergrades)
		intergrades (in)	Nayarit, Mexico	Mainland	
		flavinuchus (fl)	Pacific slope of central Mexico (south portion)	Mainland	
Centurus	*hoffmannii*	Monotypic	Pacific slope from south Honduras to Costa Rica	Mainland	Winkler and Christie, 2019
Centurus	*pygmaeus*	*pygmaeus* (py)	Cozumel, Mexico (647 km^2)	Island	Winkler and Christie, 2019
		rubricomus (ru)	Yucatan Peninsula of Mexico to Belize	Mainland	
		tysoni (ty)	Guanaja Island, Honduras (50 km^2)	Island	
Centurus	*radiolatus*	Monotypic	Jamaica (10,991 km^2)	Island	Winkler and Christie, 2019
Centurus	*rubricapillus*	*paraguanae* (pa)	Paraguaná Peninsula of northwest Venezuela	Mainland	Short, 1982; Winkler and Christie, 2019
		rubricapillus (ru)	Southwest Costa Rica to northern South America	Mainland	
		seductus (se)	Isla del Rey, Panama (234 km^2)	Island	
		subfusculus (su)	Coiba Island, Panama (503 km^2)	Island	
		terricolor (te)	Northeast Venezuela, Margarita Is., Tobago, Guyana	Mainland/island	
Centurus	*santacruzi*	*canescens* (ca)	Roatán and Isla Barbareta, Honduras (89 km^2)	Island	Husak and Maxwell, 1998
		dubius (du)	Yucatán Peninsula, Belize, and n.e. Guatemala	Mainland	
		grateloupensis (gr)	Central San Luis Potosí and east coast of Mexico	Mainland	
		hughlandi	Upper Rio Negro and Motagua Valleys, Guatemala	Mainland	
		insulanus (in)	Utila, Honduras (45 km^2)	Island	
		leei (le)	Cozumel, Mexico (647 km^2)	Island	
		pauper (pa)	Lowlands of northern Honduras	Mainland	
		polygrammus (po)	Pacific slope of extreme southwest Mexico	Mainland	
		santacruzi (sa)	Pacific slope extreme s.w. Mexico to Honduras	Mainland	
		turneffensis (tu)	Turneffe Island, Belize (400 km^2)	Island	
		veraecrucis (ve)	Atlantic slope s. Veracruz MX to n.e. Guatemala	Mainland	

Centurus	*superciliaris*	*bahamensis* (ba)	Grand Bahama, The Bahamas (1,373 km^2)	Island	Bond, 1980; Buden and Storrs, 1989
		blakei (bl)	Abaco, The Bahamas (2,009 km^2)	Island	
		caymanensis (ca)	Grand Cayman (196 km^2)	Island	
		florentinoi (fl)	Cayo Largo, Cuba (33 km^2)	Island	
		murceus (mu)	Isla de la Juventud, Cuba (2,419 km^2)	Island	
		murceus (mu-CA)	Cayo Avalos, Cuba (2 km^2)	Island	
		murceus (mu-LI)	Cayos Los Indios, Cuba (5 km^2)	Island	
		nyeanus (ny)	San Salvador Island, The Bahamas (163 km^2)	Island	
		sanfelipensis (sa)	Cayos de San Felipe, Cuba (20 km^2)	Island	
		superciliaris (su)	Cuba - main island (105,007 km^2)	Island	
Centurus	*uropygialis*	*albescens* (al)	Lower Colorado and Imperial Valleys, U.S./MX	Mainland	Edwards and Schnell, 2000
		brewsteri (br)	Baja California Sur south of San Ignacio, Mexico	Mainland	
		cardonensis (ca)	Central, n. Baja California e. side of peninsula, MX	Mainland	
		fuscescens (fu)	S.w. Sonora, s.w. Chihuahua, n. Sinaloa, Mexico	Mainland	
		sulfuriventer (su)	Sinaloa to Aguascalientes, Mexico	Mainland	
		tiburonensis (ti)	Tiburon Island, Gulf of California, MX (1201 km^2)	Island	
		uropygialis (ur)	S. Arizona, U.S. to n.w. Mexico	Mainland	
Zebrapicus	*hypopolius*	Monotypic	Southwestern Mexico	Mainland	García-Trejo et al., 2009

Table 2. Summary of ANOVAs for overall body size (based on geometric mean of six body components) of *Melanerpes* woodpeckers belonging to the *Centurus* clade, including models for all species (plus *M. hypopolius* of the *Zebrapicus* clade), all polytypic species, and a second *M. superciliaris* data set from Cuba (C) only. Number of taxa/populations is indicated parenthetically.[a]

Model	***N***		**Taxon**		**Sex**		**Interaction**	
	♂	♀	***P***	**Partial η^2**	***P***	**Partial η^2**	***P***	**Partial η^2**
All species (11)	787	569	<0.001	0.760	<0.001	0.117	<0.001	0.028
carolinus (4 ssp.)	70	49	<0.001	0.199	<0.001	0.129	0.644	0.015
chrysogenys (3 pops.)	19	18	0.247	0.040	<0.001	0.485	0.833	0.001
pygmaeus (3 ssp.)[b]	44	27	<0.001	0.484	<0.001	0.375	0.002	0.142
rubricapillus (3 ssp.)	33	19	0.217	0.064	<0.001	0.423	0.008	0.187
santacruzi (9 ssp.)	136	115	<0.001	0.346	<0.001	0.305	0.895	0.015
superciliaris (6 ssp.)[b]	121	62	<0.001	0.648	<0.001	0.300	0.040	0.052
superciliaris-C (4 pops.)	87	78	<0.001	0.290	<0.001	0.161	0.128	0.035
uropygialis (7 ssp.)	194	132	<0.001	0.137	<0.001	0.533	0.352	0.021

[a] Only those taxa or populations with at least one male and one female included in ANOVAs.

[b] Adjusted partial **η^2** effect size (see Methods)

Table 3. Lovich-Gibbons (1992) index values for sexual size dimorphism (SSD) and sexual body component dimorphism (SBCD: bill length = BL, bill width = BW, bill depth = BD, wing length = WL, tail length = TL, tarsus length = TaL) in *Melanerpes* woodpeckers. Values >0 indicate females larger; values <0 indicate males larger. Significant effects for each two-way ANOVA model examining individual body measurements are shown in parentheses (T = taxon, S = sex, I = interaction). Color indicates moderate or larger effect sizes (Cohen's *d* ≥ 0.5) for SSD or SBCD of each taxon (males larger, blue; females larger, yellow). Asterisks indicate island populations. Index values for Cuban populations of *M. superciliaris* (*florentinoi*-C, *murceus*-C, *murceus*-CLI, *superciliaris*-C) were analyzed from a separate data set and excluded from ANOVAs.

Taxon (*N* ♂,♀)	SSD	BL	BW	BD	WL	TL	TaL
SPECIES	(T,S,I)	(T,S,I)	(T,S)	(T,S)	(T,S,I)	(T,S,I)	(T,S,I)
aurifrons (63,45)	-5.87	-5.28	2.37	-0.98	2.38	-0.35	2.01
carolinus (73,51)	-4.74	-3.24	-1.56	-1.99	2.22	2.33	2.50
chysogenys (23,21)	-5.66	-4.13	-0.81	-2.09	2.86	3.29	1.22
hoffmannii (11,6)	-5.24	-3.50	-6.81	-1.86	3.80	6.65	1.91
hypopolius (20,20)	-1.73	-0.81	-2.00	-3.33	3.05	4.02	-0.79
pygmaeus (45,28)	-4.90	-3.67	-1.10	-0.29	0.96	2.15	2.95
radiolatus (21,25)*	-2.69	-0.59	-1.60	-0.96	0.81	3.25	-0.76
rubricapillus (35,20)	-5.42	-7.36	-0.20	1.01	2.10	2.68	1.46
santacruzi (163,142)	-5.75	-3.85	-1.07	-2.09	2.85	2.59	1.54
superciliaris (122,62)*	-5.38	-4.73	-3.60	-0.88	3.15	4.47	1.63
uropygialis (212,150)	-8.38	-8.66	-2.33	-1.37	4.96	4.34	3.09
CAROLINUS	(T,S)	(T,S)	(T)	(T)	(T)	(T)	(-)
carolinus (23,17)	-5.28	-4.16	-4.45	0.11	3.60	3.76	1.25
harpaceus (6,2)	-0.98	-5.30	1.92	-0.51	0.58	2.32	0.56
perplexus (11,7)	-4.75	-1.19	-0.96	-3.55	0.46	1.92	3.41
zebra (30,23)	-5.09	-2.91	0.00	-2.82	1.99	0.84	3.17
CHRYSOGENYS	(S)	(T,S)	(-)	(-)	(T,S)	(T)	(-)
chrysogenys (15,14)	-5.76	-3.31	-2.82	-1.30	2.35	4.17	1.19
intergrades (4,3)	-4.64	-5.58	4.30	-7.08	3.46	3.42	1.32
flavinuchus (4,4)	-6.15	-5.46	2.10	-0.31	3.25	-0.28	1.12
PYGMAEUS	(T,S,I)	(T,S)	(T)	(-)	(T,S)	(T)	(T,S)
pygmaeus (18,16)*	-5.55	-5.00	-3.60	-0.33	2.96	5.12	2.94
rubricomus (18,5)	-1.54	-2.99	0.78	2.31	0.40	-1.60	0.89
tysoni (8,7)*	-8.18	-5.05	-3.47	-1.38	3.31	3.60	3.03
RUBRICAPILLUS	(S,I)	(T,S)	(T)	(T)	(T,S)	(T)	(-)
rubricapillus (9,4)	-0.72	-2.03	4.48	-2.45	0.63	-0.64	-0.07
seductus (9,5)*	-6.97	-6.17	-2.27	4.86	4.00	0.21	-0.69
subfusculus (15,10)*	-6.63	-10.05	-1.68	-0.24	2.58	6.15	2.86

Taxon (*N* ♂,♀)	SSD	BL	BW	BD	WL	TL	TaL
SANTACRUZI	(T,S)	(T,S)	(T,I)	(T,S)	(T,S)	(T,S)	(T,S,I)
canescens (10,7)*	-4.74	-2.67	-3.14	-2.46	4.80	3.85	-0.33
dubius (13,9)	-5.13	-3.72	2.33	-0.99	2.71	3.48	-3.77
grateloupensis (30,26)	-6.01	-2.69	-1.24	-2.17	2.52	3.18	0.60
insulanus (8,2)*	-4.10	1.02	-2.74	-5.12	0.55	1.93	3.98
leei (12,16)*	-4.54	-7.90	5.36	-5.26	1.01	3.77	2.74
pauper (8,9)	-7.34	-1.93	-1.08	-2.12	4.01	-1.47	2.70
polygrammus (24,22)	-5.84	-5.58	-2.25	-0.20	3.33	2.86	1.83
santacruzi (27,20)	-6.62	-2.71	-7.53	-2.28	4.38	4.46	3.52
veraecrucis (4,4)	-9.06	-9.68	8.73	-2.02	1.95	-6.46	8.31
SUPERCILIARIS	(T,S,I)	(T,S)	(T,S)	(T)	(T,S,I)	(T,S,I)	(T)
bahamensis (9,6)*	-4.40	-4.94	-4.39	-0.90	5.34	3.74	0.72
blakei (20,11)*	-6.74	-4.65	-7.97	-0.18	4.11	6.53	1.98
caymanensis (26,12)*	-3.36	-1.78	-0.27	-0.61	-0.04	2.13	0.62
murceus (22,8)*	-2.85	-3.57	-3.80	-0.71	2.64	5.80	-0.29
nyeanus (14,8)*	-7.97	-7.49	-5.75	0.04	6.26	7.85	-0.57
superciliaris (30,17)*	-5.73	-5.77	-1.45	-0.55	2.04	1.47	4.21
florentinoi-C (4,3)*	-6.36	-6.24	5.50	-7.17	5.02	-5.28	8.16
murceus-C (25,15)*	-3.48	-3.26	-4.07	-4.07	2.25	4.55	4.51
murceus-CLI (2,1)*	-11.02	-0.54	-3.71	-9.44	11.38	0.22	2.18
superciliaris-C (56,59)*	-5.66	-4.97	-2.76	-3.10	3.05	2.93	4.84
UROPYGIALIS	(T,S)	(T,I)	(T,S,I)	(T)	(T,S,I)	(T,S,I)	(S)
albescens (38,27)	-7.92	-8.43	0.36	-0.52	4.65	1.68	2.09
brewsteri (20,13)	-8.46	-10.47	-0.51	-0.66	4.73	4.55	2.01
cardonensis (21,18)	-6.99	-9.75	1.37	-0.81	3.59	3.57	1.63
fuscescens (32,20)	-10.86	-6.91	-8.94	-4.94	7.83	8.54	5.27
sulfuriventer (28,18)	-8.32	-9.08	-3.19	0.29	4.61	4.98	2.31
tiburonensis (8,4)*	-9.42	-10.38	-3.20	1.72	3.53	7.19	0.61
uropygialis (47,32)	-8.56	-9.05	-1.28	-1.67	4.28	3.54	4.03

Table 4. Summary of eight discriminant function models for *Melanerpes* woodpeckers of the *Centurus* clade, including models for males of all species (plus *M. hypopolius* of the *Zebrapicus* clade) and subspecies of all polytypic species (both sexes and intergrades for *M. chrysogenys*), and both sexes pooled for a second *M. superciliaris* data set from Cuba (C) only. Values for the six body components (bill length, width, and depth; wing, tail, and tarsus length) are standardized canonical discriminant function coefficients, with the largest (most discriminating) coefficients for each function shown in bold.

Model	Function	Bill length	Bill width	Bill depth	Wing length	Tail length	Tarsus length	% variance	Wilks' Λ	*P*	η^2	% discrim. (cross-valid.)
All species (11) (*N* = 787 ♂)	F1	0.235	0.171	-0.310	0.025	**0.638**	**0.494**	62.5	0.020	<0.001	0.980	76.5 (74.6)
	F2	-0.009	0.220	0.403	**0.869**	**-0.914**	-0.004	17.5				
carolinus (4 ssp.) (*N* = 70 ♂)	F1	**0.682**	**-0.566**	0.203	**0.599**	-0.121	0.055	63.9	0.437	<0.001	0.563	61.4 (47.1)
	F2	0.344	0.277	**0.758**	**-0.760**	-0.038	-0.054	24.9				
chrysogenys (3 pop.) (N = 23 ♂ 21 ♀)	F1	**-1.052**	-0.018	0.280	-0.170	**1.084**	0.104	65.7	0.237	<0.001	0.763	93.2 (86.4)
	F2	-0.622	-0.011	-0.146	**1.177**	-0.034	-0.089	34.3				
pygmaeus (3 ssp.) (*N* = 44 ♂)	F1	**0.812**	0.319	0.236	-0.206	0.331	0.370	60.3	0.126	<0.001	0.874	93.2 (90.9)
	F2	-0.146	0.279	-0.105	**1.057**	0.105	-0.444	39.7				
rubricapillus (5 ssp.) (*N* = 35 ♂)	F1	-0.233	**0.934**	-0.133	**-0.514**	0.103	0.193	86.1	0.108	<0.001	0.892	91.4 (71.4)
	F2	**0.589**	0.176	-0.242	-0.332	**0.947**	**0.577**	9.2				
santacruzi (10 ssp.) (*N* = 136 ♂)	F1	**0.634**	-0.132	0.156	**-0.987**	**0.862**	-0.003	44.4	0.128	<0.001	0.872	55.1 (37.5)
	F2	0.211	0.411	**0.868**	0.096	-0.389	-0.442	23.8				
superciliaris (7 ssp.) (*N* = 122 ♂)	F1	**0.470**	0.075	0.043	**0.590**	0.103	0.296	88.9	0.058	<0.001	0.942	76.2 (66.4)
	F2	-0.038	0.234	**0.794**	-0.365	-0.410	0.263	5.6				
superciliaris-C (6 pop.) (*N* = 87 ♂ 79 ♀ 2 unk)	F1	-0.344	0.144	-0.194	**0.947**	0.330	0.015	87.5	0.344	<0.001	0.656	73.2 (66.7)
	F2	**-0.830**	0.109	**1.006**	0.087	0.008	0.471	6.7				
uropygialis (7 ssp.) (*N* = 194 ♂)	F1	-0.059	-0.248	0.076	**1.114**	-0.205	-0.116	73.1	0.488	<0.001	0.512	40.2 (33.5)
	F2	-0.245	0.392	**0.759**	-0.117	0.229	0.266	13.2				

Model parameters include Wilks' lambda (Λ); effect size as eta-squared (η^2 = 1 – Wilks' Λ), corresponding to percent variance explained by the model; and percent discrimination for original (and cross-validated) cases.

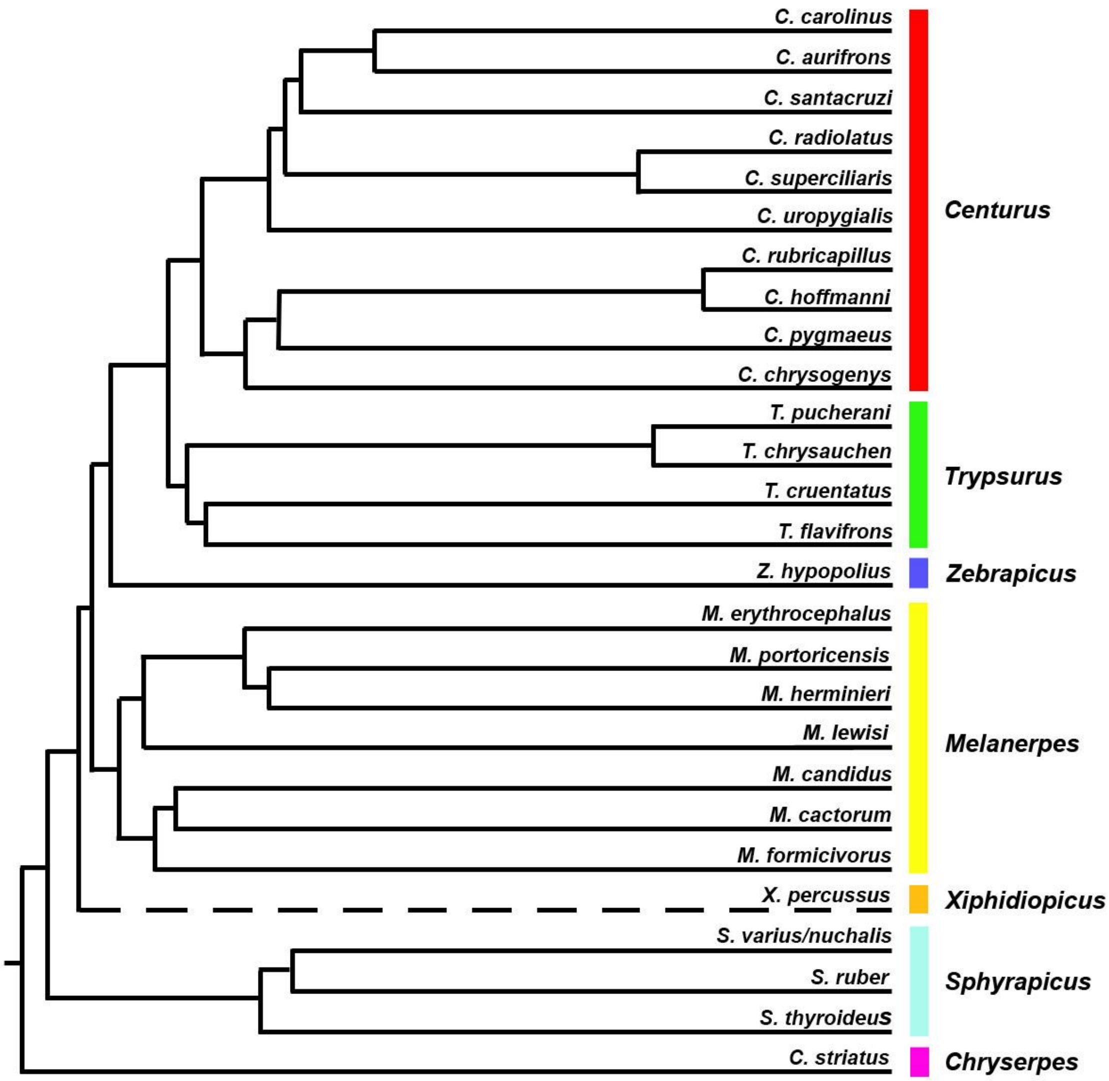

Fig. 1. Proposed phylogeny and taxonomy of Navarro-Sigüenza et al. (2017: Fig. 6) for the woodpecker genera *Melanerpes*, *Sphyrapicus*, and *Xiphidiopicus* based on 5073 base pairs from two mitochondrial and four nuclear genes. Five *Melanerpes* clades are recognized: *Centurus*, *Chryserpes*, *Melanerpes*, *Trypsurus*, and *Zebrapicus*. The putative position of *Xiphidiopicus percussus* is indicated by dashed line.

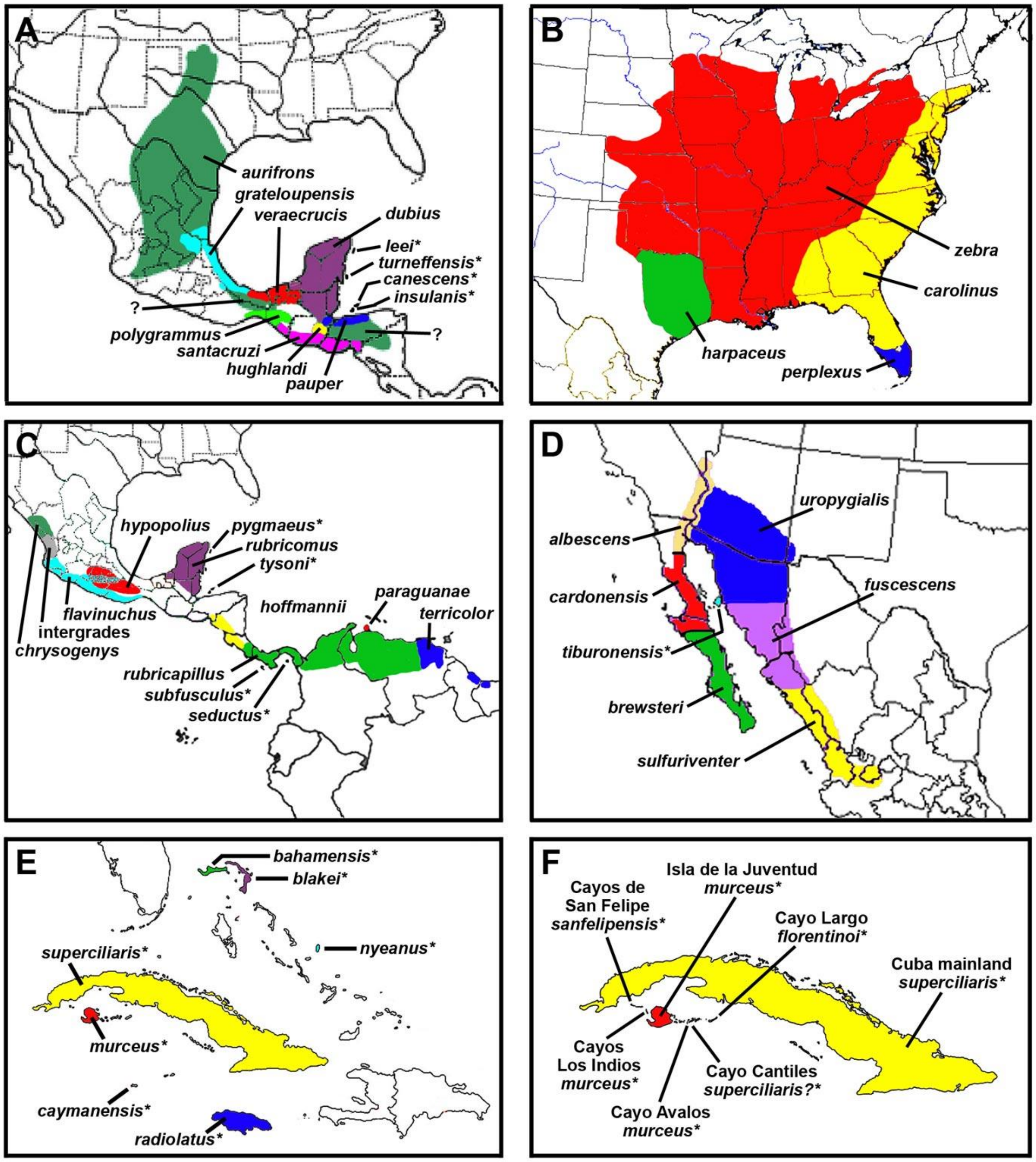

Fig. 2. Approximate distributions of species, subspecies, and populations of *Melanerpes* woodpeckers within the *Centurus* clade. (A) *M. aurifrons* and subspecies of *M. santacruzi* (*canescens*, *dubius*, *grateloupensis*, *hughlandi*, *insulanis*, *leei*, *pauper*, *polygrammus*, *santacruzi*, *turneffensis*, *veraecrucis*; subspecies uncertain for some areas). (B) *M. carolinus* subspecies. (C) *M. chrysogenys* (subspecies *chrysogenys*, *flavinuchus*, and intergrades), *M. hoffmannii*, *M. hypopolius* (belongs to *Zebrapicus* clade) *M. pygmaeus* (subspecies *pygmaeus*, *rubricomus*, *tysoni*), and *M. rubricapillus* (subspecies *paraguanae*, *rubricapillus*, *sedutus*, *subfusculus*, *terricolor*). (D) *M. uropygialis* subspecies. (E) *M. radiolatus* and *M. superciliaris* (subspecies *bahamensis*, *blakei*, *caymanensis*, *murceus*, *nyeanus*, *superciliaris*). (F) *M. superciliaris* subspecies and populations in Cuba. Asterisks indicate island taxa and populations. Sources in Table 1.

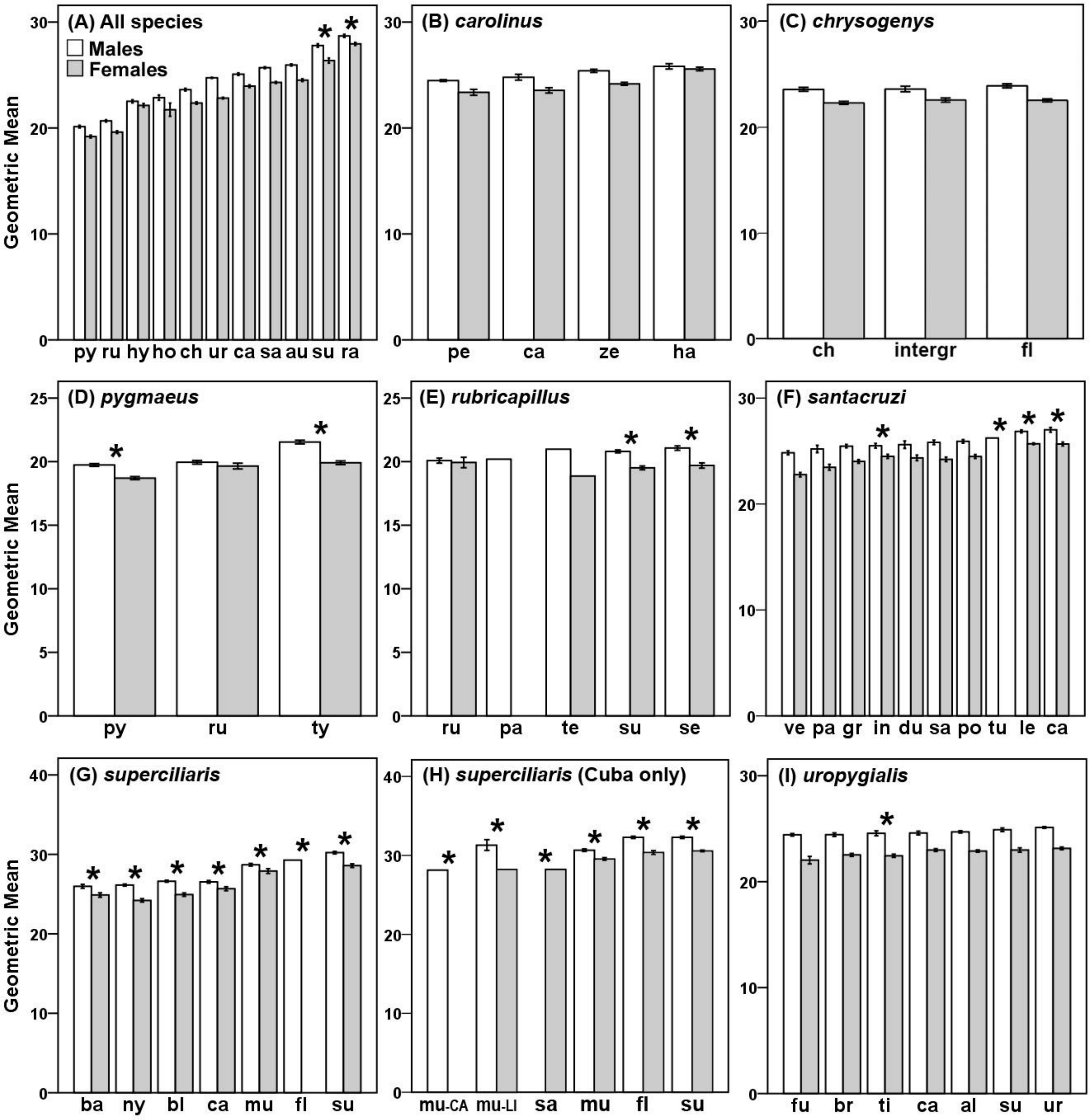

Fig. 3. Overall body size (geometric mean, mean ± 1 S.E.) of *Melanerpes* woodpeckers belonging to the *Centurus* clade, including (A) comparisons for all species (plus *M. hypopolius* of the *Zebrapicus* clade), (B-I) all polytypic species, and a second *M. superciliaris* data set from Cuba only (H). Differences between males (white bars) and females (gray bars) indicate relative degree of sexual size dimorphism (SSD). Island groups are indicated by asterisks. Scale for geometric mean (ordinate) varies. Subspecies/population abbreviations are provided in Table 1; sample sizes are provided in Table 3.

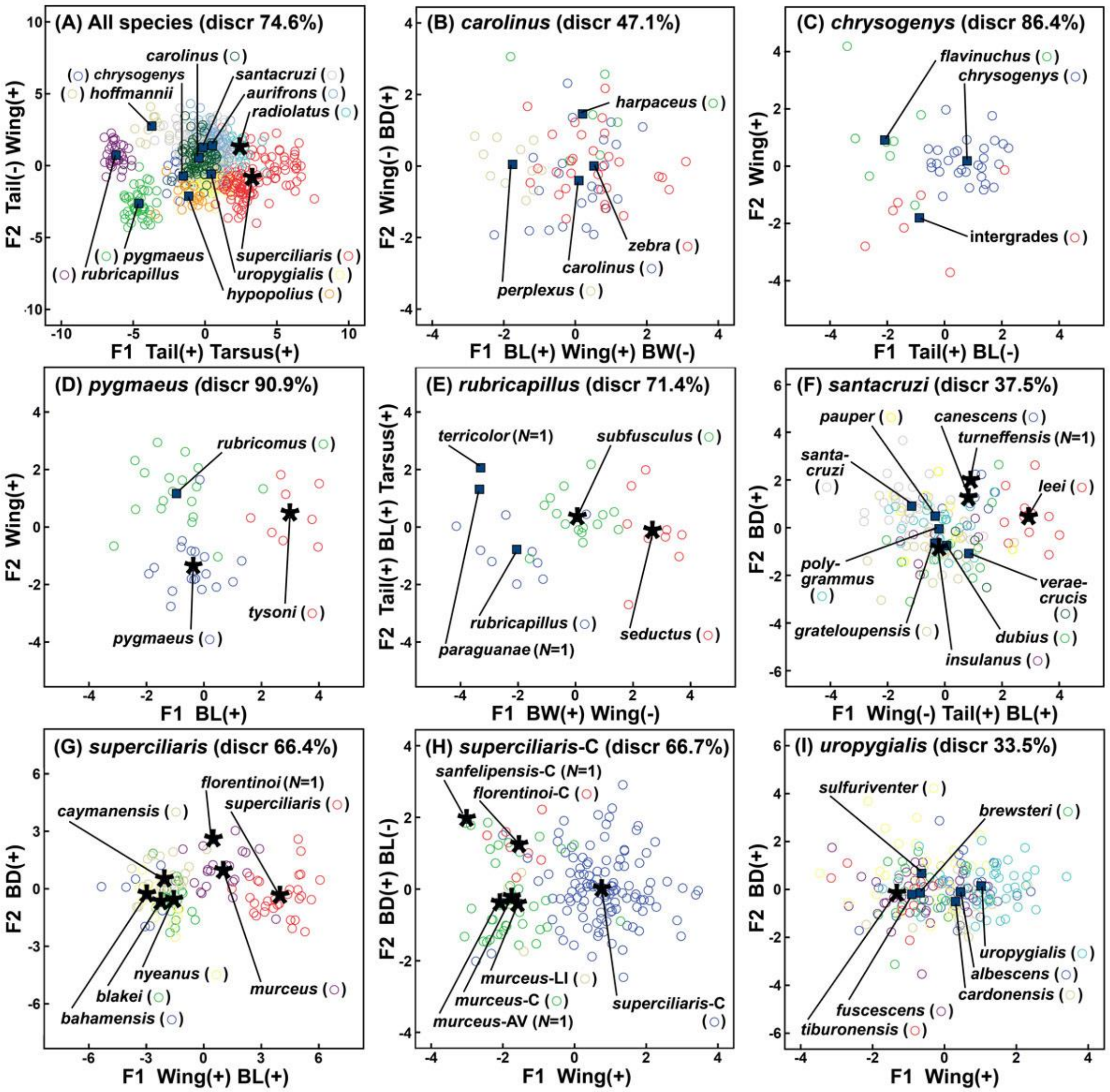

Fig. 4. Canonical plots for discriminant function analyses (DFAs) of *Melanerpes* woodpeckers of the *Centurus* clade, including models for (A) males of all species (plus *M. hypopolius* of the *Zebrapicus* clade) and (B–I) males of all polytypic species, except that, to increase sample size, both sexes and intergrades were included for *M. chrysogenys* (C), and both sexes were pooled for a second *M. superciliaris* data set from Cuba only (H). Axis labels indicate direction of correlation (positive or negative) between the most discriminating body measurements (coefficients with highest absolute values in Table 4) and discriminant functions 1 (F1) and 2 (F2). Cross-validated discrimination success of each model is indicated parenthetically. Taxa represented by a single specimen and omitted from ANOVAs (Tables 2 and 3) were included in DFAs. Island taxa are indicated with asterisks. Sample sizes are provided in Table 3, except that subspecies/populations with *N* = 1 are indicated here.

Appendix 1. List of specimens examined from the following museums; The Academy of Natural Sciences of Drexel University (ANSP); American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CMNH); Donald R. Dickey Bird and Mammal Collection, University of California, Los Angeles (UCLA); Florida Museum of Natural History (FMNH); Louisiana State University Museum of Natural Science (LSUMZ); LSA Museum of Zoology, University of Michigan (UMich); Moore Lab of Zoology, Occidental College (OXY); Museum of Comparative Zoology, Harvard University (MCZ); Natural History Museum of Los Angeles (NHM); San Diego Natural History Museum (SDNHM); United States National Museum of Natural History, Smithsonian Institution (USNM).

Melanerpes aurifrons: UCLA 11872, 11988, 23468, 23495, 23508, 23530, 23539, 23618, 23626, 23647, 27262, FMNH 9273, 118792, 121039, 139199, UMich 164945, 164965, 164968, OXY 17104, 18387, 18389, 18390, 21933, 22294, 22618, 22619, 22621, 22840, 24872, 24873, 24874, 24875, 27895, 27898, 28522, 30742, 32460, 32461, 33604, 34203, 34226, 34229, 34246, 34251, 38780, 38797, 39390, 39393, 40287, 40298, 40314, 40565, 40599, 40623, 40624, 40628, 40876, 41762, 41834, 42037, 42076, 42142, 42254, 42258, 42806, 42930, 46634, 46721, 49078, 49079, 49080, 49100, 49101, 49102, 49103, 50157, 50158, 50159, 51597, 51598, 53947, 55455, 55456, 55457, 55458, 55459, 55460, 55461, 55463, 55464, 55465, 55466, 55467, 55468, 55469, 55470, 55817, 57201, 57213, 57232, 57362, 57440, 57684, 57685, 57748, 58185, NHM 6388, 6389, 22048, 22049, 77867. SDNHM 22613, 22614, 22615, 22616, 22617, 22618, 22619.

Melanerpes carolinus, ***carolinus***: UCLA 7951, 34328, 34329, FMNH 39361, 48473, 139149, 139188, 303137, 303143, 303144, UMich 112973, 112974, 113690, 126830, 126831, 137857, 240140, OXY 2 unknown numbers, MCZ 253171, 291064, 334769, 363216, 364259, NHM 4348, 6383, 6384, 6385, 6386, 6387, 22050, 22052, 85115, SDNHM 11755, 22606, 22607, 22608, 22609, 22610, 22611, 22612, 31562. ***harpaceus***: UCLA 9927, FMNH 94621, 139191, UMich 126859, 164987, 164988, 164989, 164990, 227419. ***perplexus***: FMNH 325747, 372801, 372810, 372815, 372818, 372820, 372822, UMich 47955, 62649, 126850, 126851, 126852, 126853, 126854, 126855, 126856, 126857, 126858, 1 unknown number. ***zebra***: UCLA 9248, 9926, 27263, 34326, 34327, 40392, FMNH 5818, 21353, 39363, 39884, 70265, 94625, 159948, 159950, 161114, 231983, 231990, 231991, 303136, 349050, 437259, 442562, 466367, 466655, 472882, 496584, 498308, 498309, 1 unknown number, UMich 68686, 68687, 113452, 126820, 126821, 126822, 126824, 126825, 126826, 211662, 211664, 241202, 241203, 241875, 242008, MCZ 337151, NHM 22051, 22053, 22054, 22055, 22056, 22057, SDNHM 534, 535, 536, 537, 538, 31563. **unassigned subspecies**: UCLA 32581, FMNH 303135, UMich 211665, 227400, NHM 16143.

Melanerpes chrysogenys, ***chrysogenys***: UCLA 34482, 37763, 37764, 37765, 37766, 51767, OXY 5910, 5911, 5912, 5913, 5914, 5915, 5916, 5917, 11887, 11888, 11889, 11900, 12689, 12690, 12765, 12766, 16229, 16230, 16231, 17996, 17997, 20907, 20908, 20909, 28042, 28043, 28044, 28045, 41948, 41957, 41978. ***flavinuchus***: OXY 44561, 54815, 54819, 54820, 54821, 55790, 56446, 59116.

Melanerpes hoffmannii: UCLA 13992, 13993, 14401, 1440, 14403, 35325, 35326, 35327, 35328, 35329, 35330, 35331, 35332, 35333, 35334, 35335, 35336, 35337, 35338.

Melanerpes hypopolius: OXY 38040, 38043, 38051, 38064, 38068, 38079, 38082, 38157, 38207, 38242, 38253, 38295, 44643, 44649, 44671, 44714, 45843, 45848, 45854, 45887, 47463, 47699, 47719, 53946, 54479, 54480, 59095, 59096, 59097, 59098, 59099, 59100, 59101, 59102, 59103, 59104, 59105, 59106, 59107, 59108, 59109, 59110, 59111, 59112, 59113.

Melanerpes pygmaeus, ***pygmaeus***: CMNH 131420, 131426, 142063, 142068, 143023, 143039, 143054, 143074, 143102, 143103, 143104, 143117, 144749, 144779, FMNH 39500, 42134, USNM 102785, 102788, 102789, 102790, 129592, 129593, 129594, 129595, 129596, 129597, 167444, 167446, 167447, 167448, 167449, 167450, 167451, 167455. ***rubricomus***: CMNH 141527, 142270, 166064, 166065, UCLA 33503, FMNH 1 unknown number, UMich 70588, 103675, 155725, USNM 106302, 106303, 130134, 130135, 130136, 130137, 130138, 130139, 145598, 167452, 167453, 167454, 167455, 167456, 167457, 167458, 167698, 167699. ***tysoni***: CMNH 131596, 131601, 131602, 131603, 131609, 132457, 132463, 132464, 132465, 132466, 132491, 132492, 132493, MCZ 179912, 179913. **unassigned subspecies**: USNM 36803

Melanerpes radiolatus: FMNH 6398, 9392, 18445, 18446, 18447, 33420, MCZ 30813, 37531, 37532, 37533, 37534, 37535, 37536, 37537, 37539, 37540, 37541, 37542, 37543, 37544, 37546, 37547, 37548, 37549, 37550, 37551, 37552, 37553, 37554, 37555, 46673, 46674, 46675, 46676, 47764, 71771, 71772, 103741, 103742, 103743, 122905, 141486, 150796, 230477, 237910, 237911, 279876.

Melanerpes rubricapillus, ***paraguanae***: NHM 73203. ***rubricapillus***: NHM 36351, 36352, 37394, 37395, 37396, 37643, 37644, 37645, 39487, 39488, 40627, 41935, 59068, 59069. ***seductus***: MCZ 40411, 40412, 40413, 40414, 104889, 104890, 104891, 104892, 104893, 104894, 104895, 104896, 104897, 104898, 104899, 104900, 114347. ***subfusculus***: NHM 30357, USNM 173342, 173343, 460776, 460777, 460778, 460779, 460780, 460781, 460782, 460783, 460785, 460786, 460787, 471283, 471284, 471285, 471286, 471287, 471288, 471289, 471290, 471291, 471292, 47129. ***terricolor***: NHM 36009, 36010.

Melanerpes santacruzi, ***canescens***: CMNH 131504, 131509, 131510, 131511, 131512, 131521, 131523, 131566, 132700, 132701, FMNH 39494, 42141, 111933, 111934, 111935, 111936, 111938. ***dubius***: UCLA 33502, FMNH 13243, 39495, 39496, 39497, 42137, 42138, 110252, 110253, 121036, 121037, UMich 70582, 70587, 137877, 137878, 137880, 137881, 137882, 137884, 137886, 137887, OXY 41627. ***grateloupensis***: UCLA 33501, FMNH 12272, 12273, 12279, 12280, 13447, 122798, 124521, 124522, 124523, 124525, 124526, 187183, 187184, 187185, 208840, OXY 31613, 32972, 33099, 33735, 33736, 33737, 34808, 35783, 35786, 35787, 35788, 35789, 39520, 39522, 39947, 39991, 40177, 40329, 41513, 43126, 43155, 43156, 43191, 45578, 45579, 46822, 46824, 46899, 46905, 46908, 46923, 46924, 46925, 48130, 48131, 48132, 48143, 48161, 53544, 53545, 53546, 53547, 53548, 53549, 53550, 53551, 53552, 53553, 53948, 57409. ***insulanus***:

CMNH 132729, 132758, 132759, 132760, FMNH 119022, 119023, 119024, 119025, 119026, MCZ 179911. ***leei***: CMNH 131406, 142057, 143052, 143053, 143105, 143128, 143161, NHM 85334, USNM 102772, 102773, 102774, 102775, 102778, 102779, 102780, 102781, 102782, 102783, 129599, 129600, 129602, 129604, 129606, 129607, 129608, 129609, 130144, 167433, 167434, 167435, 167436, 167437. ***pauper***: FMNH 25555, 42122, 88418, 93734, 93735, 93763, 95201, UMich 155272, 155273, 199591, OXY 13955, 13956, 13957, NHM 41157, 41158, 41159, 41160. ***polygrammus***: FMNH 208834, 208836, 208837, 208838, 208841, 208842, UMich 109169, 109170, 109171, 109172, 109173, 109174, 109175, 110175, OXY 27143, 45486, 45487, 45488, 45489, 45490, 45496, 47407, 47704, 47724, 49090, 49098, 50160, 50300, 50301, 50302, 51590, 51591, 51593, 51595, 54470, 54471, 54473, 54475, 54476, 54477, 56750, 56929, 57056, 57149, 57192, 57193, 57194, 57195, 59825, NHM 24260, 24261, 24407. ***santacruzi***: UCLA 7419, 8134, 15453, 15480, 15532, 15912, 16108, 16546, 16563, 16593, 16594, 17024, 17182, 17434, 17675, 18973, 19246, 19451, 19453, FMNH 42121, UMich 94182, 94183, 94186, 94187, 94189, 102380, 102381, 102382, 102383, 102384, 102385, 107699, OXY 15397, 15398, 15399, 37446, NHM 17792, 17793, 17794, 17795, 17796, 17797, 17798, 17799, 17800, 17801, 17802, 17803, 17804, 17805, 41161, 41162, 41163. ***turneffensis***: FMNH 111932. ***veraecrucis***: FMNH 470466, 470467, 470468, OXY 59222, 59223, 59224, 59225, 59226, 59227, 59228, 65368. **unassigned subspecies**: FMNH 59167, 59168 UMich 199590, OXY 26342, 31493, 34811, 34821, 34822, 38771, 43053, 43079, 43166, 43818, 44254, 44300, 44305, 44749, 45485, 45491, 45492, 45493, 45494, 45495, 47214, 47330, 47350, 47684, 47725, 48807, 48906, 48918, 50173, 51584, 51585, 51586, 51587, 51588, 51589, 51592, 51594, 51596, 52821, 52822, 52823, 53554, 54472, 54474, 54478, 55823, 55835, 55851, 57391, 57394, 59495, 59590, 59592, 59821, 59823, 59824.

Melanerpes superciliaris, ***bahamensis***: ANSP 111850, AMNH 174702, FMNH 39416, 39418, 41922, MCZ 141481, 166715, 166716, 166717, 171677, 171678, 171679, 171682, 171683, 171684, Cuba specimens: 111850, 174702. ***blakei***: ANSP 111851, 111852, AMNH 44183, 808811, 808812, CMNH 19794, 31051, 31066, 31101, 31102, 31125, 130966, 130967, 2 unknown numbers, FMNH 39419, 39420, 41925, 41926, LSUMZ 143719, 143720, 143721, 143722, 143723, MCZ 40209, 56797, USNM 108618, 108619, 108620, 108623, 108626, 108627, 108631, 108632, Cuba specimens: 808811, 808812, 108618, 108619, 108620, 108623, 108626, 108627, 108631, 108632, 111851. ***caymanensis***: ANSP 48069, 191124, 191125, FMNH 39369, 39372, 41964, 41965, 41970, 42161, 42164, 42167, 42170, 42178, 42180, 42184, 42189, 42191, 42194, 42202, 42203, 42205, 42209, LSUMZ 68339, 68341, 68342, 68344, 68345, 68346, 68347, 143744, 143745, 143746, 143747, 143748, USNM 109924, 111188, 111189, 111192, 111193, 114984, 316761, 316762, 323543, Cuba specimens: 48069, 109924, 111188, 111192, 316761, 316762, 323543. ***florentino***: ANSP 169869. ***murceus***: ANSP 111920, AMNH 64914, 64915, 399445, 399447, 487743, 487745, 487746, 487747, 487748, FMNH 72061, 72062, 72063, 72064, LSUMZ 23673, 143741, MCZ 67491, 67492, 80791, 80792, 113261, 113262, USNM 172780, 172781, 323540, 395698, 395700, 395706, 453875, 453877, 453878, Cuba specimens: 13261, 13266, 67491, 67492, 80791 80792, 111920, 172780, 172781, 172782, 323540, 395698, 399445, 399447, 453875, 453877, 453878, 487743, 487745, 487746, 487747, 487748. ***nyeanus***: ANSP 111853, 111854, 111855, AMNH 175015, 808813, CMNH 19643, 19656, 19688, 30900, 30907, 30913, 30914, 30926, 30945, LSUMZ 143724, 143725, 143726, MCZ 56798, 157736, 157738, 157740, 1 unknown number, USNM 107996, 189685, 559666, Cuba specimens: 107996, 111853, 111854, 111855, 175015, 189685, 808813. ***superciliaris***: ANSP 19119, 19120, 19121, 19122, 19123, 25206, 25207, 25639, 25640, 35034,FMNH 39423, 39424, 41942, 72021, 372837, 372838, 372839, 372840, LSUMZ 23672, 23674, 143728, 143729, 143732, 143734, 143735, 143738, 143739, 1 unknown number, MCZ 46662, 46664, 65508, 67250, 67251, 71773 111969, 235118, 235119, 235120, 235121, 235122, 235123, 235124, 235125, USNM 29583, 80877, 80878, 171388, 171389, 171390, 171391, 200370, 200371, 200372, 239846, 316239, 316240, 316242, 358616, 395702, 395703, 395883, 396672, 453880, 453881, 453883, 453884, 453885, 453887, Cuba specimens: 19119, 19120, 19121, 19122, 19123, 25206, 25207, 25639, 29583, 35034, 46662, 46664, 65508, 67250, 67251, 71773, 80877, 80878, 171388, 171389, 171390, 171391, 172583, 200370, 200372, 235118, 235119, 235121, 235122, 235123, 235124, 235125, 239846, 316239, 316240, 395702, 395883, 453880, 453881, 453882, 453883, 453884, 453885, 453887.

Melanerpes uropygialis, ***albescens***: UCLA 8607, 8616, 8617, 8618, 8626, 8731, 8732, 14706, 14707, 14714, 14727, 14728, 14744, 14745, 14747, 14748, 24345, 24364, 24365, 24381, 24389, 24413, 24419, 32343, 32344, 32347, 32348, 32349, 32350, 32351, 33005, 33008, 33016, 33017, 33018, 33026, 33027, 33028, 33199, 33342, 33342, 33346, 33347, 33357, 33358, 33359, 33360, 33361, 33362, 33363, 33364, 33375, 33382, 40379, 40380, 40381, 40382, 40383, 40384, 40389, 40390, 3 unknown numbers, NHM 3665, 51732, 51779, 51780. ***brewsteri***; UCLA 29847, 29848, 29864, 29900, 29901, 29904, 29914, 29915, 29922, 29993, 29994, 29995, 30061, 30120, 30148, 30149, 31070, NHM 14182, 19162, 19163, 19164, 19165, 19166, 19167, 19168, 19169, 35024, 50534, 50535, 60508, 60509, 60510, 74173, 74174, 84428. ***cardonensis***: NHM 78193, 78194, SDNHM 8658, 10475, 11770, 13513, 13668, 13669, 13670, 13680, 13686, 13701, 13850, 13851, 13853, 13958, 13959, 13961, 13962, 13964, 13984, 13985, 14043, 14044, 14064, 14065, 14066, 14099, 17361, 17370, 19219, 19242, 19247, 30212, 31582, 31583, 31584, 31585, 35279. ***fuscescens***: UCLA 27856, 27866, 27872, 27880, 27956, 28034, 28072, 28103, 28158, 28176, 28228, 29376, 29377, 29382, 29575, 29780, 29781, 30201, 30223, 30338, 30441, 30529, 30559, 30591, 30815, 30865, 30866, 30906, 31984, 33244, 33249, 33874, 33891, 34210, 34238, 34239, 34245, 34480, 34481, 40391, 50931, 51125, OXY 5901, 5903, 5909, 11085, 11102, 11103, 11104, 11105, 11342, 11483, 11903, 11904, 12763, 17321, NHM 30020. ***sulfuriventer***: UCLA 50295, OXY 5902, 5904, 5905, 5906, 5907, 5908, 8698, 8699, 11313, 11314, 11315, 11479, 11481, 12764, 15329, 15330, 15331, 15332, 17320, 17402, 17998, 17999, 18000, 18001, 18002, 19672, 19673, 19674, 19675, 19676, 20153, 20154, 21273, 21448, 21449, 21450, 21907, 21908, 21921, 28530, 28531, 41334, 41342, 41473, NHM 23970, 83627, 83628, 83629, 83630. ***tiburonensis***: UCLA 33296, 33297, 50219, 50264, 50265, NHM 50536, 50537, 50538, SDNHM 15368, 15369, 30332, 35971, 35972. ***uropygialis***: UCLA 11458, 11477, 11478, 11544, 22506, 22507, 23046, 23050, 23084, 23105, 27260, 27261, 28337, 28338, 28353, 28373, 28441, 28655, 29147, 29162, 29263, 29286, 29304, 29305, 29306, 29307, 31429, 31490, 32257, 32259, 32704, 32705, 32707, 32727, 32728, 32769, 32786, 33049, 33050, 33059, 33181, 33195, 33674, 33675, 33678, 33679, 33684, 33687, 33688, 33689, 33690, 33703, 33735, 33736, 33739, 33740, 33743, 33744, 33748, 33773, 33774, 33775, 33814, 33832, 33895, 34000, 34001, 34002, 40385, 40386, 50286, 50287, 51126, 5 unknown numbers, OXY 11404, 11405, NHM 6390, 6392, 6393, 6394, 22045, 22046, 22047, 50941. **unassigned subspecies**: UCLA 27799, 32269, 33156, 33158, 33164, 33165, 33211, 33212, 33221, 33230, 33314, 33672, 33915, 33916, 33982, 40387, 40388, 50182, 50191, 50198, 50199, 50888, 50932, 50946, 51762, 51766, OXY 5900, 9249, 10770, 10771, 10772, 16232, 16233, 17319, 17401, 17496, NHM 18686.