

Published in final edited form as:

J Biogeogr. 2012 October 1; 39(10): 1891–1899. doi:10.1111/j.1365-2699.2012.02754.x.

Insular avian adaptations on two Neotropical continental islands

Natalie A. Wright^{1,2,*} and David W. Steadman²

¹Department of Biology, University of Florida, Gainesville, FL, USA

²Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

Abstract

Aim—Most studies of avian insular adaptations have focused on oceanic islands, which may not allow characters that are insular adaptations to be teased apart from those that benefit dispersal and colonization. Using birds on continental islands, we investigated characters that evolved *in situ* in response to insular environments created by late Pleistocene sea level rise.

Location—Trinidad and Tobago, nearby Caribbean islands and continental South America.

Methods—We weighed fresh flight muscles and measured museum skeletal specimens of seven species of birds common to the continental islands of Trinidad and Tobago.

Results—When corrected for body size, study species exhibited significantly smaller flight muscles, sterna and sternal keels on Tobago than on larger Trinidad and continental South America. Tobago populations were more ‘insular’ in their morphologies than conspecifics on Trinidad or the continent in other ways as well, including having longer bills, longer wings, longer tails and longer legs.

Main conclusions—We hypothesize that the longer bills enhance foraging diversity, the longer wings and tails compensate for the smaller pectoral assemblage (allowing for retention of volancy, but with a probable reduction in flight power and speed), and the longer legs expand perching ability. Each of these differences is likely to be related to the lower diversity and fewer potential predators and competitors on Tobago compared with Trinidad. These patterns of smaller flight muscles and larger bills, legs, wings and tails in island birds are not the results of selection for island dispersal and colonization, but probably arose from selection pressures acting on populations already inhabiting these islands.

Keywords

Birds; Caribbean; colonization; evolution; island adaptations; island biogeography; morphology; Trinidad and Tobago

INTRODUCTION

Island birds have long intrigued evolutionary biologists (e.g. Darwin, 1859; Wallace, 1881). Islands are often seen as microcosms where evolution occurs rapidly via small populations

*Correspondence and current address: Natalie A. Wright, Department of Biology & Museum of Southwestern Biology, 167 Castetter Hall, 1 University of New Mexico, Albuquerque, NM 87131-0001, USA. nawright@unm.edu.

Author contributions: N.A.W. and D.W.S. conceived the ideas and collected the data; N.A.W. analysed the data and led the writing.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

As a service to our authors and readers, this journal provides supporting information supplied by authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

experiencing strong selection pressures and therefore can be studied more easily than on continents (e.g. Grant & Grant, 2006). It is widely believed that insular organisms experience different selection pressures from those on continents, and that organisms on islands often differ from their continental relatives in predictable ways, presumably reflecting adaptations that arise from these insular selection pressures. For example, the 'island rule' states that vertebrates on islands tend to converge on a medium body size, with large organisms becoming smaller and small organisms becoming larger (Van Valen, 1973; Lomolino, 1985, 2005; Clegg & Owens, 2002; Boyer & Jetz, 2010), although the validity of this pattern has been debated (e.g. Meiri *et al.*, 2006, 2010). Island species also may exhibit taxon-specific adaptations, for example anoles (*Anolis* spp.), which tend to have smaller limbs and more well-developed toe pads on Caribbean islands than on continents (Pinto *et al.*, 2008).

The effects of insular selection pressures can be dramatic for birds especially, with hundreds if not thousands of species evolving flightlessness on oceanic islands (Steadman, 1995, 2006; Slikas *et al.*, 2002; Kirchman, 2009). Current island biogeography theory, via the idea of taxon cycling, suggests that most island birds (not just the flightless species) should exhibit reduced dispersal ability over time as they transition from widespread, generalist dispersers to sedentary specialists (e.g. Mayr & Diamond, 2001; Ricklefs & Bermingham, 2004). In addition to this loss of dispersal ability, insular birds often have larger bills and/or longer legs than their continental relatives; these morphological changes are generally thought to be the result of reduced interspecific competition on islands, with longer bills, or bills that are more variable in size, being advantageous in feeding on a wider range of food items, and longer legs allowing for a greater variety of perching and foraging capabilities (Grant, 1965, 1968; Schoener, 1965; Feinsinger & Swarm, 1982). We note, however, that direct evidence for this mechanism is lacking and that other factors are plausible, such as increased intraspecific competition or energetic constraints (Lomolino *et al.*, 2010).

Most of our understanding of intraspecific insular adaptations has been based on data collected during behavioural and ecological studies, where morphological information necessarily comes from measurements taken on live birds (e.g. Feinsinger & Swarm, 1982; Schlotfeldt & Kleindorfer, 2006). These characters have been limited to measurements such as bill proportions, tarsus length, body mass, tail length and wing chord: the latter two of which are subject to variation in feather wear and moult. Potentially important characters such as those related to the flight muscles and skeletal elements of the wing, leg and trunk have not been considered because they cannot be measured on live birds. Relative flight muscle mass, for example, appears to respond to insular selection pressures in flightless birds (McNab, 1994); if or how relative flight muscle size responds to insular selection pressures in volant species has not been examined.

Some insular characteristics presumed to have evolved in response to ecological pressures unique to islands may instead be the result of non-random colonization of oceanic islands (Lomolino, 2005). For example, disproportionate numbers of birds may exhibit reduced dispersal abilities on islands because weak fliers such as rails (Rallidae) may be more likely to be blown off course and onto islands during stormy weather. Once on islands, weak dispersers may be more likely to evolve flightlessness than strong fliers (Roff, 1994; McCall *et al.*, 1998; McNab & Ellis, 2006). Similarly, organisms with generalist niches and associated morphological traits are more likely to find suitable food and habitat when colonizing an island than are organisms with more narrow requirements. The 'island rule' could also be the result of a colonization effect; larger individuals have more fuel reserves to keep them alive while rafting or flying to an island, but very large individuals may have reduced dispersal abilities. Most previous studies examining insular adaptations of birds have done so mostly on oceanic islands (e.g. Schoener, 1965; Grant, 1968; Clegg & Owens,

2002; McNab, 2003), and thus traits that may be related to dispersal and colonization may be difficult to distinguish from those due to *in situ* insular selection.

Having been connected to continental landmasses during periods of low sea level caused by Pleistocene glaciation, continental islands need not invoke dispersal to account for their biotas. What sort of adaptations might occur in volant species of birds on continental islands compared with those of conspecific continental populations?

MATERIALS AND METHODS

Study system

The continental islands of Trinidad and Tobago offer an excellent opportunity to study insular adaptations in birds. The two islands are not oceanic; they were connected to the South American continent during the late Pleistocene glacial interval from *c.* 30,000 until 11,000 and 14,000 years ago for Trinidad and Tobago, respectively (Comeau, 1991; Rohling *et al.*, 1998; Clark & Mix, 2000; Thomas *et al.*, 2009). Thus, the likely starting point for the accumulation of insular adaptations is known. Because of this former direct land connection, the avifaunas of Trinidad and Tobago are primarily subsets of that on nearby Venezuela (Graves & Gotelli, 1983; French, 1991; Hilty, 2003) rather than ones dominated by island colonists. As a result, potential confounding effects of selection for the ability to disperse and colonize are removed from the effects of insular selection pressures. The bananaquit, *Coereba flaveola* (Linnaeus, 1758) may be an exception; it is believed to have colonized Trinidad and South America from the Lesser Antilles (Bellemain *et al.*, 2008). Finally, the prehistoric record of birds on Trinidad and Tobago over the past several thousand years has disclosed no anthropogenic extirpation, unlike the nearby oceanic islands of the Lesser Antilles (Pregill *et al.*, 1994; Steadman & Stokes, 2002; Steadman & Jones, 2006). However, none of our study species in particular has been recovered in the prehistoric bone deposits on Trinidad and Tobago, probably due to their small sizes, which make them unlikely to be recovered. We note that few bird fossils have been found on these two islands. The much more extensive fossil-mammal record reveals the Holocene extirpation of a howler monkey (*Alouatta seniculus*), paca (*Agouti paca*) and peccary (*Tayassu pecari*).

Insular traits of species are thought to be more pronounced in smaller, more isolated islands with fewer species than on larger islands closer to a continent (Lomolino, 2005). Compared with Trinidad, Tobago is much smaller (298 vs. 4578 km²), lies farther from continental South America (115 vs. 11 km), has been isolated from the continent longer (14,000 vs. 11,000 years), and has far fewer species of resident landbirds (*c.* 99 vs. *c.* 251) (Comeau, 1991; French, 1991). Therefore, Tobago would be expected to sustain species with more pronounced insular traits than Trinidad. This has been noted already, from an ecological rather than morphological standpoint, in two species. The barred antshrike, *Thamnophilus doliatus* (Linnaeus, 1764), which has undergone a habitat niche expansion on Tobago, occurs at all heights in both closed-canopy forest and secondary growth on Tobago, but is restricted to the understory of secondary growth on Trinidad and the continent (Keeler-Wolf, 1986). Likewise, the copper-rumped hummingbird, *Amazilia tobaci* (Gmelin, 1788), uses a wider variety of flower nectar on Tobago than on Trinidad during the three driest and most resource-limited months of the year (Feinsinger & Swarm, 1982). Both of these niche expansions appear to be in response to the presence of fewer potential competitors on Tobago than on Trinidad or the South American continent.

Inspired by these two ecological studies, we investigated morphological insular adaptations in seven species of birds chosen because they occur commonly on Trinidad, Tobago and continental South America, and are fairly easy to capture in mist nets. The species consist of two hummingbirds [rufous-breasted hermit, *Glaucis hirsutus* (Gmelin, 1788), and copper-

rumped hummingbird, *Amazilia tobaci*], two suboscine passerines [barred antshrike, *Thamnophilus doliatus*, and ochre-bellied flycatcher, *Mionectes oleagineus* (Lichtenstein, 1823)], and three oscine passerines (white-necked thrush, *Turdus albicollis* Vieillot, 1818, bare-eyed thrush, *Turdus nudigenis* Lafresnaye, 1848, and bananaquit, *Coereba flaveola*). These species differ greatly in their inferred overwater dispersal abilities. No species of antbird (Thamnophilidae), including *Thamnophilus doliatus*, is found on oceanic islands, and even rivers can be barriers to dispersal in this group (Bates *et al.*, 2004; Hayes & Sewlal, 2004). While certain species of hummingbirds and tyrannid flycatchers can be excellent overwater dispersers, neither *Amazilia tobaci* nor *Mionectes oleagineus* occurs on any oceanic island, and *Glaucis hirsutus* is found on only one oceanic island: Grenada (Raffaele *et al.*, 1998). We also note that *Mionectes* has recently been classified outside the Tyrannidae *sensu stricto* (Ohlson *et al.*, 2008; Tello *et al.*, 2009). Thrushes in general are excellent overwater dispersers (Voelker *et al.*, 2007) and *Turdus nudigenis* occurs on four oceanic islands, but *Turdus albicollis* does not inhabit any. *Coereba flaveola* is widespread and common on nearly every island in the Caribbean (Raffaele *et al.*, 1998), and thus presumably is excellent at overwater colonization. Species that regularly disperse between Trinidad and Tobago would not be expected to exhibit as many (if any) morphological differences between populations, because regular gene flow may inhibit such differences from evolving.

Data collection

We utilized specimens in the collections of the Florida Museum of Natural History, University of Florida (UF), Smithsonian National Museum of Natural History (USNM) and American Museum of Natural History (AMNH) from Trinidad, Tobago and continental South America. We took the following measurements on prepared skeletal material: rostrum (bill) length, coracoid length, total sternum length, sternum keel length, sternum keel depth, humerus length, ulna length, carpometacarpus length, femur length, tibiotarsus length and tarsometatarsus length (Appendix S1 in Supporting Information describes these measurements in detail). Associated data taken by the specimen collector or preparator were recorded, including mass, wing chord length, tail length, flight muscle mass, age and body condition.

While preparing the UF specimens, we extracted the pectoralis major and supracoracoideus muscles (commonly referred to as the pectoral flight muscles) from one side of the body and weighed these fresh. As right and left pectoral muscles are symmetrical within an individual (A.W. Kratter, D.W. Steadman & N.A. Wright, unpublished data), the combined masses of each pectoralis major and supracoracoideus were multiplied by two to obtain a total mass of the pectoral flight muscles. We define ‘flight apparatus’ as the suite of pectoral bone (sternum, including keel) and muscle (pectoralis major and supracoracoideus) that provides the main power during flight. Pectoral flight muscle mass is strongly correlated with keel length (e.g. *Amazilia tobaci*, linear regression: $R^2 = 0.802$, $P < 0.001$). Given that all skeletal element measurements were conducted by one person (N.A.W.) in controlled settings, but many different preparators measured flight muscle masses in non-ideal field conditions, skeletal element measurements are more precise and accurate than flight muscle masses. Some of the variation in flight muscle mass left unexplained by keel length is probably due to measurement error of flight muscle masses in the field. Additionally, flight muscle mass data were not available for any individuals from continental South America, so using keel length and depth measurements allowed us to incorporate a continental perspective.

Data analysis

We performed a principal components analysis (PCA) for each species to correct for body size. We were unable to include all elements that were measured in the PCA due to a high

incidence of missing data for certain variables. Additionally, different taxa were missing data for different morphological characters. Coracoid, sternum, keel, humerus, ulna and femur length measurements and keel depth measurements were included in the PCA for all species. Tarsometatarsus lengths were also included in the PCA for *Thamnophilus doliatus*, *Coereba flaveola*, *Turdus albicollis* and *Turdus nudigenis*. For *Glaucis hirsutus*, carpometacarpus, tibiotarsus and tarsometatarsus lengths were also included in the PCA. For *Mionectes oleagineus*, carpometacarpus and tarsometatarsus lengths were also included in the PCA. Principal component one (PC1) tracked body size in all cases, with all variables loading positively. We then used PC1 to correct for body size to further analyse sternal keel lengths. For each species, we performed a linear regression for each morphological character of interest (e.g. keel length, bill length, etc.) by PC1. The residuals from these analyses were used as body size-corrected estimates of the morphological characters. To compare species trends on the same scale, we scaled these body size-corrected morphological characters for each species to have means of 0 and standard deviations of 1. We conducted a MANOVA on these scaled morphological characters to test for overall effect of location (continental South America, Trinidad or Tobago) on morphology across all species and Tukey's honestly significant difference (HSD) tests on differences in morphology across species between location pairs. We also performed ANOVAs to test for differences in body size-corrected morphological characters (un-scaled) among different locations within each species. For each morphological character examined via ANOVA, we controlled for false discovery rate (Benjamini & Hochberg, 1995). Due to potential problems with residual analysis (e.g. Darlington & Smulders, 2001; Garcia-Berthou, 2001; Freckleton, 2002), we also performed ANCOVAs of each morphological trait with both PC1 and location as factors. As the results from the ANCOVAs did not differ qualitatively from the other analyses, results from residual analysis are presented. All analyses were performed in the statistical package R 2.12.1 (R Development Core Team, 2010).

RESULTS

Results are given for body size-corrected morphological characters; the results of analyses on measurements uncorrected for body size are similar, but not identical, and are presented in Appendices S2 and S3. There was a strong overall effect of location on morphology (MANOVA, $P < 0.0001$; Table 1). Study species had smaller flight apparatuses on Tobago than on Trinidad, and smaller on Trinidad than on continental South America (MANOVA, $P < 0.001$; Table 1; Fig. 1). The species examined also had significantly longer wings, longer legs and longer tails on Tobago than on Trinidad or South America (Table 1; Fig. 1). There was no overall effect of location on bill length, coracoid length or body mass, but individual species did show differences (Table 1; Fig. 1). The results of the ANOVAs for each species and morphological character are as follows.

Flight apparatus

Data for sternum length, keel length, keel depth and flight muscle size all exhibited similar trends; consequently, we will discuss the results for keel length and depth, for which sample sizes were larger. Individuals of *Glaucis hirsutus*, *Amazilia tobaci*, *Thamnophilus doliatus*, *Mionectes oleagineus*, *Coereba flaveola* and *Turdus albicollis* from Tobago had smaller body size-corrected flight apparatuses than those from Trinidad and continental South America (Fig. 1, Table 2, Appendices S2 & S3.1). *Turdus nudigenis* did not exhibit significant differences in keel length in individuals from Trinidad, Tobago and continental South America (Fig. 1, Table 2, Appendices S2 & S3.1).

Wing elements

We define the ‘wing elements’ as the humerus, ulna and carpometacarpus (which sequentially provide most of bony length of the wing), and wing chord (which measures the length of the wing bones from the carpometacarpus distally and the longest primary feathers). Body size-corrected wing elements of *Amazilia tobaci*, *Thamnophilus doliatus*, *Mionectes oleagineus*, *Coereba flaveola* and *Turdus nudigenis* were longer on Tobago than on Trinidad and continental South America (Fig. 1, Table 2, Appendices S2 & S3.2). *Glaucis hirsutus* and *Turdus albicollis* exhibited no significant differences in body size-corrected wing element lengths (Fig. 1, Table 2, Appendix S2).

Leg elements

Birds from Tobago had longer legs than conspecifics from Trinidad, which had longer legs than those on continental South America (Fig. 1, Table 2, Appendices S2 & S3.3). *Glaucis hirsutus*, *Thamnophilus doliatus*, *Mionectes oleagineus* and *Coereba flaveola* had longer femora, tibiotarsi and tarsometatarsi, corrected for body size, on Tobago than on Trinidad or continental South America. Additionally, the tarsometatarsi of *Turdus albicollis* and the tibiotarsi of *Amazilia tobaci* were longer on Tobago than on Trinidad or continental South America. *Turdus nudigenis* did not exhibit significant differences in lengths of leg elements.

Bill size

The bills of *Glaucis hirsutus*, *Thamnophilus doliatus* and *Mionectes oleagineus* were longer on Tobago than on Trinidad and continental South America (Fig. 1, Table 2, Appendices S2 & S3.4). The other four species did not exhibit significant differences in body size-corrected bill length.

Tail length

Amazilia tobaci, *Coereba flaveola* and *Turdus nudigenis* had longer tails, corrected for body size, on Tobago than on Trinidad (Fig. 1, Table 2, Appendices S2 & S3.5). The other four study species exhibited no significant inter-island differences in body size-corrected tail length.

Body mass

Coereba flaveola had greater body mass on both Trinidad and Tobago than on continental South America (Table 2). None of the other study species differed significantly in body mass among locations. Many species have longer wings and legs on Tobago than on Trinidad or continental South America, but the same species had smaller sternal keels (Appendices S2 & S3) and flight muscles (data not shown) on Tobago than on Trinidad, so this may account for the overall similarity in body mass among populations.

DISCUSSION

In general, birds on Tobago are characterized by having smaller flight apparatuses (sternum and associated muscles) yet longer wings, legs, tails and bills than conspecifics on Trinidad or continental South America. While not all study species follow each of these trends, all species with significant differences among populations in any of these characters do follow this pattern. None of the seven species has significantly larger flight apparatuses or shorter wings, legs or tails on Tobago than on Trinidad or South America.

Glaucis hirsutus, *Amazilia tobaci*, *Thamnophilus doliatus*, *Mionectes oleagineus*, *Coereba flaveola* and *Turdus albicollis* have smaller flight muscles and associated sterna and sternal keels on Tobago than Trinidad and continental South America. Larger flight muscles

provide greater power, which is most important for birds during periods of take-off or short bursts of speed during sustained flight (Gill, 2007). Quick take-offs are important in avoiding predation, and bursts of speed during flight may be used in territorial battles, reaching food resources before competitors (e.g. trapline foraging hummingbirds; Gill, 1985), and courtship displays. No literature exists on inter-island differences in territory size or courtship habits on Trinidad versus Tobago. Feinsinger & Swarm (1982) observed that *Amazilia tobaci* on Trinidad and Tobago spends similar amounts of time in aggressive encounters, implying that this species does not exhibit inter-island differences in territoriality. While reduced interspecific competition on Tobago relative to Trinidad has been documented for two of the study species, *Amazilia tobaci* (Feinsinger & Swarm, 1982) and *Thamnophilus doliatus* (Keeler-Wolf, 1986), there is no evidence to suggest that intraspecific competition or total competition for resources is reduced on Tobago relative to Trinidad.

There are, however, important differences in real or potential predation pressures between Trinidad and Tobago. Fifteen species of diurnal or crepuscular forest raptors occur regularly on Trinidad, including species that specialize in predating small birds (e.g. short-tailed hawk, *Buteo brachyurus*, and ferruginous pygmy-owl, *Glaucidium brasilianum*; ffrench, 1991). Only two species of diurnal forest raptors are found on Tobago: broad-winged hawk, *Buteo platypterus*, and great black hawk, *Buteogallus urubitinga*, neither of which regularly eats small birds (ffrench, 1991). The lack of a specialized avian predator on Tobago implies lower predation pressure for its small birds. *Amazilia tobaci* tends to perch in more exposed areas and vocalize more often on Tobago than Trinidad (Feinsinger & Swarm, 1982), as would be expected on an island with lower predation pressure. Reduced predation on Tobago birds may have allowed them to lessen energy expenditure by decreasing the size of metabolically expensive flight muscles (McNab, 1994). These differences in flight muscle size among conspecific populations of volant birds are previously undocumented in birds.

Longer legs and bills (*Glaucis hirsutus*, *Amazilia tobaci*, *Thamnophilus doliatus*, *Mionectes oleagineus* and *Coereba flaveola*) on Tobago than on Trinidad and continental South America are possibly related to habitat and foraging niche expansions on Tobago relative to Trinidad and the continent. Longer legs are thought to allow use of a greater variety of perches (Grant, 1965) and foraging methods. Longer bills allow birds to eat larger food items (Grant, 1965) or, in nectarivores, drink from larger flowers (Feinsinger & Swarm, 1982) and may be related to an increase in either the mean food size or in the range of sizes of food consumed. Such habitat and foraging niche expansions have been documented for *Amazilia tobaci* and *Thamnophilus doliatus* and are most likely to be the result of the presence on Tobago of fewer species of hummingbird and forest insectivore competitors, respectively (Feinsinger & Swarm, 1982; Keeler-Wolf, 1986). Whether *Glaucis hirsutus*, *Mionectes oleagineus* or *Coereba flaveola* have expanded their habitat or foraging niches on Tobago relative to Trinidad and the continent has not been studied, but such a situation seems probable, given that far fewer species of hummingbirds, flycatchers and nectarivorous passerines occur on Tobago than on Trinidad or northern South America (ffrench, 1991; Restall *et al.*, 2006). Selection for longer legs on Tobago could be related to take-off mechanics rather than perch and foraging niche expansion. It is well known that birds use a leg thrust to produce initial velocity during take-off (e.g. Tobalske *et al.*, 2004). Longer legs could provide a longer lever during the initial thrust, helping to compensate for smaller flight muscles during take-off.

Longer wings on Tobago than Trinidad or continental South America (*Amazilia tobaci*, *Mionectes oleagineus*, *Thamnophilus doliatus*, *Coereba flaveola* and *Turdus nudigenis*) and longer tails on Tobago than Trinidad (*Amazilia tobaci*, *Coereba flaveola* and *Turdus nudigenis*) could be related to a variety of factors. Longer wings and tails could compensate

for these birds' smaller flight muscles by providing more lift, but at the expense of fast take-offs and rapid manoeuvres (Gill, 2007). Longer wings in hummingbirds are associated with a reduction in territoriality and increase in generalist foraging (Feinsinger & Colwell, 1978), and in *Amazilia tobaci* could be an indication of reduced need for territorial defence against other species on Tobago, in association with its wider foraging niche. Alternatively, longer wings and tails on Tobago could be the result of inter-island differences in sexual selection pressures, although such differences have not been noted or studied for any of the species.

Wing lengths have been used regularly as proxies for overall body size (e.g. Grant, 1965, 1968), but our study species do not differ significantly in body mass between Trinidad and Tobago. When these species differ in the size of trunk skeletal elements (sternum, keel and coracoid lengths) or flight muscle mass, the Trinidad and South America populations have larger trunk elements. The distinct morphology of birds on Tobago seems to be the result of an ontogenic trade-off, with conditions on Tobago (hypothesized to be reduced predation and competition) allowing for the reduction of flight muscles, thereby freeing resources to be devoted to the development of longer wings, tails, legs and bills. Total body mass, however, remains essentially the same.

This is, to our knowledge, the first study to show that volant birds on small islands have smaller flight muscles. Studies in other island systems need to be conducted to understand whether the differences seen here are characteristic of islands in general or are unique to Trinidad and Tobago, and to better understand the selection pressures driving this pattern. Our study species range in size from about 4–60 g. Whether larger birds would exhibit similar patterns is unclear. It seems unlikely that large raptors would have smaller flight muscles on islands if this trait were indeed related to reduced predation. On the other hand, we expect larger birds lower on the food chain [e.g. large pigeons and doves (Columbidae)] to follow this pattern. Two other morphological differences that we found among birds of the continent, Trinidad, Tobago and oceanic Caribbean islands, i.e. longer legs and bills in the more insular populations, have both been previously suggested as possible adaptations to island life (Mayr & Vaurie, 1948; Grant, 1965; Clegg & Owens, 2002), although the studies cited did not find evidence that longer wings and tails are characteristic of island birds per se. Our study highlights the value of examining a greater number of morphological characters.

Species impoverishment is probably a key driving force behind the observed morphological differences among birds of continental South America, Trinidad and Tobago. The richness and diversity of both potential predators and competitors decrease from continental South America to Trinidad and from Trinidad to Tobago (French, 1991; Raffaele *et al.*, 1998). These patterns, in turn, may be related to island size and temporal and geographical isolation. Similar morphological trends are probably present in other avian species on Trinidad and Tobago, or among oceanic Caribbean islands that vary dramatically in size and isolation. Studies on other island systems will help us to understand how widespread these morphological patterns are, and what their underlying causes might be. Regardless of the specific selective pressures, these patterns of smaller flight muscles and larger bills, legs, wings and tails in island birds are not the result of selection for island colonization, and are most likely to have arisen from selection acting on populations that became insular without dispersing across the ocean.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

The Ornithology Endowment at Florida Museum of Natural History funded much of this project. We thank all collectors and preparators of the museum specimens used, especially Andrew Kratter, Erica Rose Egan, Jessica Oswald and Amy Schwarzer. We also thank James Dean of the Smithsonian National Museum of Natural History and Paul Sweet of the American Museum of Natural History for access to specimens. We gratefully acknowledge the agencies and persons who granted permission to conduct field research on Trinidad (David Buccoo, Nadra Nathai-Gyan, Floyd Hayes, Howard Nelson) and Tobago (Ashton James, Angela Ramsey, Raye Sandy). Jeffrey Long and John Hammond helped to improve the statistical analyses. Two anonymous referees, Shai Meiri, and the lab groups of Edward Braun, Rebecca Kimball and Christopher Witt provided much appreciated and insightful comments on earlier versions of this manuscript. N.A.W. is supported by the Program in Interdisciplinary Biomedical and Biological Sciences funded through the University of New Mexico award number T32EB009414 from the National Institute of Biomedical Imaging and Bioengineering. The content is the sole responsibility of the authors and does not necessarily represent the official views of the National Institute of Biomedical Imaging and Bioengineering or the National Institutes of Health.

References

- Bates JM, Haffer J, Grismer E. Avian mitochondrial DNA sequence across a headwater stream of the Rio Tapajós, a major Amazonian river. *Journal of Ornithology*. 2004; 145:199–205.
- Bellemain E, Bermingham E, Ricklefs RE. The dynamic evolutionary history of the bananaquit (*Coereba flaveola*) in the Caribbean revealed by a multigene analysis. *BMC Evolutionary Biology*. 2008; 8:240. [PubMed: 18718030]
- Benjamini Y, Hochberg Y. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)*. 1995; 57:289–300.
- Boyer AG, Jetz W. Biogeography of body size in Pacific island birds. *Ecography*. 2010; 33:369–379.
- Clark PU, Mix AC. Ice sheets by the volume. *Nature*. 2000; 406:689–690. [PubMed: 10963583]
- Clegg SM, Owens IPF. The ‘island rule’ in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B: Biological Sciences*. 2002; 269:1359–1365.
- Comeau PL. Geological events influencing natural vegetation in Trinidad. *Living World (Journal of the Trinidad and Tobago Field Naturalists Club)*. 1991; 1991–1992:29–38.
- Darlington RB, Smulders TV. Problems with residual analysis. *Animal Behaviour*. 2001; 62:599–602.
- Darwin, C. *The origin of species*. Murray; London: 1859.
- Feinsinger P, Colwell RK. Community organization among Neotropical nectar-feeding birds. *American Zoologist*. 1978; 18:779–795.
- Feinsinger P, Swarn LA. Ecological release, seasonal variation in food supply and the hummingbird *Amazilia tobaci* on Trinidad and Tobago. *Ecology*. 1982; 63:1574–1587.
- French R. *A guide to the birds of Trinidad and Tobago*. Cornell University Press; Ithaca, NY: 1991.
- Freckleton R. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology*. 2002; 71:542–545.
- García-Berthou E. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology*. 2001; 70:708–711.
- Gaston KJ, Blackburn TM. Birds, body size, and the threat of extinction. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 1995; 347:205–212.
- Gill FB. Hummingbird flight speeds. *The Auk*. 1985; 102:97–101.
- Gill, FB. *Ornithology*. 3. W. H. Freeman and Company; New York: 2007.
- Grant PR. The adaptive significance of some size trends in island birds. *Evolution*. 1965; 19:355–367.
- Grant PR. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Systematic Zoology*. 1968; 17:319–333. [PubMed: 5751172]
- Grant PR, Grant BR. Evolution of character displacement in Darwin’s finches. *Science*. 2006; 313:224–226. [PubMed: 16840700]
- Graves GR, Gotelli NJ. Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. *Oikos*. 1983; 41:322–333.

- Hayes FE, Sewlal J-AN. The Amazonian River as a dispersal barrier to passerine birds: effects of river width, habitat, and taxonomy. *Journal of Biogeography*. 2004; 31:1809–1818.
- Hilty, SL. *Birds of Venezuela*. Princeton University Press; Princeton, NJ: 2003.
- Keeler-Wolf T. The Barred Antshrike (*Thamnophilus doliatus*) on Trinidad and Tobago: habitat niche expansion of a generalist forager. *Oecologia*. 1986; 70:309–317.
- Kirchman JJ. Genetic tests of rapid parallel speciation of flightless birds from an extant volant ancestor. *Biological Journal of the Linnean Society*. 2009; 96:601–616.
- Lomolino MV. Body size of mammals on islands: the island rule re-examined. *The American Naturalist*. 1985; 125:310–316.
- Lomolino MV. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*. 2005; 32:1683–1699.
- Lomolino, MV.; Riddle, BR.; Whittaker, RJ.; Brown, JH. *Biogeography*. 4. Sinauer Associates; Sunderland, MA: 2010.
- Mayr, E.; Diamond, JM. *The birds of northern Melanesia*. Oxford University Press; New York: 2001.
- Mayr E, Vaurie C. Evolution in the family Dicuridae (birds). *Evolution*. 1948; 2:238–265. [PubMed: 18884665]
- McCall RA, Nee S, Harvey PH. The role of wing length in the evolution of avian flightlessness. *Evolutionary Ecology*. 1998; 12:569–580.
- McNab BK. Energy conservation and the evolution of flightlessness in birds. *The American Naturalist*. 1994; 144:628–642.
- McNab BK. The energetics of New Zealand's ducks. *Comparative Biochemistry and Physiology*. 2003; Part A 135:229–247. [PubMed: 12781824]
- McNab BK, Ellis HI. Flightless rails endemic to islands have lower energy expenditures and clutch sizes than flighted rails on islands and continents. *Comparative Biochemistry and Physiology*. 2006; A 145:295–311. [PubMed: 16632395]
- Meiri S, Dayan T, Simberloff D. The generality of the island rule re-examined. *Journal of Biogeography*. 2006; 33:1571–1577.
- Meiri S, Raia P, Phillimore AB. Slaying dragons: limited evidence for unusual body size evolution on islands. *Journal of Biogeography*. 2010; 38:89–100.
- Ohlson J, Fjeldsa J, Ericson PGP. Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). *Zoologica Scripta*. 2008; 37:315–335.
- Pinto G, Mahler DL, Harmon LJ, Losos JB. Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland Anolis lizards. *Proceedings of the Royal Society B: Biological Sciences*. 2008; 275:2749–2757.
- Pregill GK, Steadman DW, Watters DR. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bulletin of the Carnegie Museum of Natural History*. 1994; 30:1–51.
- R Development Core Team. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing; Vienna, Austria: 2010. Available at: <http://www.R-project.org/>
- Raffaele, H.; Wiley, J.; Garrido, O.; Keith, A.; Raffaele, J. *A guide to the birds of the West Indies*. Princeton University Press; Princeton, NJ: 1998.
- Restall, R.; Rodner, C.; Lentino, M. *Birds of northern South America: an identification guide*. Yale University Press; New Haven, CT: 2006.
- Ricklefs RE, Bermingham E. History and the species-area relationship in Lesser Antillean birds. *The American Naturalist*. 2004; 163:227–239.
- Roff DA. The evolution of flightlessness: is history important? *Evolutionary Ecology*. 1994; 8:639–657.
- Rohling EJ, Fenton M, Jorissen FJ, Bertrand P, Ganssen G, Caulet JP. Magnitudes of sea-level lowstands of the past 500,000 years. *Nature*. 1998; 394:162–165.
- Schlotfeldt BE, Kleindorfer S. Adaptive divergence in the Superb Fairy-wren (*Malurus cyaneus*): a mainland versus island comparison of morphology and foraging behaviour. *Emu*. 2006; 106:309–319.

- Schoener TW. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution*. 1965; 19:189–213.
- Slikas B, Olson SL, Fleisher RC. Rapid, independent evolution of flightlessness in four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence data. *Journal of Avian Biology*. 2002; 33:5–14.
- Steadman DW. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science*. 1995; 267:1123–1131. [PubMed: 17789194]
- Steadman, DW. *Extinction and biogeography of tropical Pacific birds*. University of Chicago Press; Chicago, IL: 2006.
- Steadman DW, Jones S. Long-term trends in prehistoric fishing and hunting on Tobago, West Indies. *Latin American Antiquity*. 2006; 17:316–334.
- Steadman DW, Stokes AV. Changing exploitation of terrestrial vertebrates during the past 3000 years on Tobago, West Indies. *Human Ecology*. 2002; 30:339–367.
- Tello JG, Moyle RG, Marchese DJ, Cracraft J. Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannides). *Cladistics*. 2009; 25:429–467.
- Thomas AL, Henderson GM, Deschamps P, Yokoyama Y, Mason AJ, Bard E, Hamelin B, Durand N, Camoin G. Penultimate deglacial sea-level timing from uranium-thorium dating of Tahitian corals. *Science*. 2009; 324:1186–1189. [PubMed: 19390000]
- Tobalske BW, Altshuler DL, Powers DR. Take-off mechanics in hummingbirds (Trochilidae). *The Journal of Experimental Biology*. 2004; 207:1345–1352. [PubMed: 15010485]
- Van Valen L. A new evolutionary law. *Evolutionary Theory*. 1973; 1:1–33.
- Voelker G, Rohwer S, Bowie RCK, Outlaw DC. Molecular systematics of a speciose, cosmopolitan songbird genus: defining the limits of, and relationships among, the *Turdus* thrushes. *Molecular Phylogenetics and Evolution*. 2007; 42:422–434. [PubMed: 16971142]
- Wallace, AR. *Island life*. Macmillan; London: 1881.

Biographies

Natalie Wright is a graduate student in the Department of Biology and Museum of Southwestern Biology at the University of New Mexico. She is interested in the morphological evolution, biogeography, ecology and systematics of birds.

David Steadman is curator of birds at the Florida Museum of Natural History, University of Florida. He is interested in avian biogeography, systematics and palaeoecology.

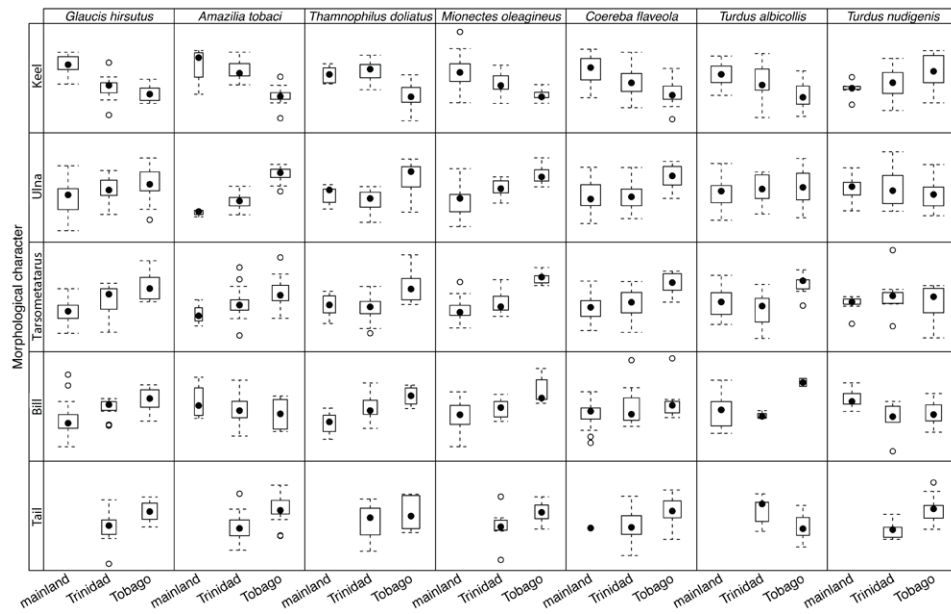


Figure 1. Body size-corrected length measurements of five representative morphological characters for all seven avian study species on South America, Trinidad and Tobago. Values for each character and species are scaled to have mean = 0 and standard deviation = 1 to allow for comparisons on the same scale. Box lengths encompass the first and third quartiles, the filled circles are at the median, and whiskers extend from the first and third quartiles to 1.5 times the inner quartile range or the outermost data point within that range. Box widths reflect relative sample size (wider being a larger sample).

Table 1

P-values from the MANOVA on the effect of location on body size-corrected, scaled morphological characters of all species and *P*-values from Tukey's HSD tests on differences between locations for the seven Neotropical avian species studied. Response variables and *P*-values that are statistically significant at $\alpha = 0.05$ are in bold.

Response variable	Location	S. America–Trinidad	Trinidad–Tobago	S. America–Tobago
Multivariate response	< 0.0001	-	-	-
Keel length	< 0.001	0.002	< 0.0001	< 0.0001
Keel depth	< 0.001	0.11	< 0.0001	< 0.0001
Coracoid	0.40	0.13	0.003	< 0.0001
Humerus	0.007	0.97	< 0.0001	< 0.0001
Ulna	< 0.0001	0.76	< 0.0001	< 0.0001
Carpometacarpus	0.44	0.96	0.07	0.032
Wing chord	< 0.0001	-	-	-
Femur	0.28	0.004	0.004	< 0.0001
Tibiotarsus	0.022	< 0.001	< 0.0001	< 0.0001
Tarsometatarsus	0.002	0.09	< 0.0001	< 0.0001
Bill length	0.23	0.15	0.049	< 0.0001
Tail length	< 0.001	-	-	-
Body mass (not size-corrected)	0.051	0.009	0.05	0.42

Table 2

Sample sizes for South America, Trinidad and Tobago, and *P*-values for the effect of location on the morphological character (ANOVA), respectively, for each body size-corrected character and avian species examined. *P*-values that are statistically significant after false discovery rate controlling procedure at $q^* = 0.05$ are in bold.

Morphological character	<i>Glaucis hirsutus</i>	<i>Amazilia tobaci</i>	<i>Thaenophilus dolius</i>	<i>Miomeetes oleagineus</i>	<i>Coereba flaveola</i>	<i>Turdus albicollis</i>	<i>Turdus nudigenis</i>
Keel length	20,13,18; <0.001	4,23,21; <0.001	7,19,16; <0.001	18,10,9; <0.001	19,20,16; <0.001	17,8,7; 0.02	7,10,10; 0.09
Keel depth	20,13,18; <0.001	4,23,21; <0.001	7,19,16; <0.001	18,10,9; <0.001	19,20,16; 0.07	17,8,7; 0.03	7,10,10; 0.28
Coracoid	20,13,18; 0.029	4,23,21; 0.27	7,19,16; <0.001	18,10,9; 0.26	19,20,16; <0.001	17,8,7; 0.86	7,10,10; 0.06
Humerus	20,13,18; 0.024	4,23,21; <0.001	7,19,16; 0.12	18,10,9; 0.003	19,20,16; 0.70	17,8,7; 0.15	7,10,10; 0.86
Ulna	20,13,18; 0.09	4,23,21; <0.001	7,19,16; <0.001	18,10,9; <0.001	19,20,16; <0.001	17,8,7; 0.66	7,10,10; 0.68
Carpometacarpus	20,13,18; 0.72	4,15,14; <0.001	5,13,11; 0.23	18,9,10; 0.004	19,17,13; 0.14	17,5,5; 0.42	7,7,8; 0.47
Wing chord	0,10,11; 0.19	0,21,18; <0.001	0,18,15; 0.087	0,7,8; 0.029	1,19,15; 0.23	0,8,7; 0.18	0,9,9; <0.001
Femur	20,13,18; <0.001	4,23,21; 0.52	7,19,16; 0.006	18,10,9; <0.001	19,20,16; 0.002	17,8,7; 0.47	7,10,10; 0.89
Tibiotarsus	20,13,18; <0.001	4,18,15; 0.02	6,16,16; <0.001	17,8,9; <0.001	19,19,15; <0.001	17,7,7; 0.05	7,10,10; 0.14
Tarsometatarsus	20,13,18; <0.001	3,18,15; 0.063	7,19,16; <0.001	18,10,9; <0.001	19,20,16; <0.001	17,8,7; 0.003	7,10,10; 0.47
Bill length	18,11,16; <0.001	4,13,11; 0.47	7,9,6; 0.004	17,8,5; 0.001	18,12,10; 0.18	17,3,2; 0.049	7,5,6; 0.03
Tail	0,10,11; 0.03	0,21,18; <0.001	0,18,14; 0.16	0,7,8; 0.10	1,19,15; 0.02	0,7,7; 0.06	0,8,9; 0.003
Body mass (not size-corrected)	9,25,24; 0.87	1,24,23; 0.025	0,19,16; 0.098	8,12,9; 0.52	7,24,21; <0.001	10,9,8; 0.13	0,11,11; 0.90