Journal of Caribbean Ornithology

RESEARCH ARTICLE

Vol. 34:41–52. 2021

Morphological traits of four land bird species in Grenada

Alexandra Heathcote Paulson Des Brisay Christopher De Ruyck Paula Grieef Nicola Koper

Photo: Paulson Des Brisay

BirdsCaribbean

Journal of Caribbean Ornithology
jco.birdscaribbean.org ISSN 1544-4953 https://doi.org/10.55431/ jco.2021.34.41-52
RESEARCH ARTICLE Vol. 34:41–52. 2021

BirdsCaribbean
birdscaribbean.org

Morphological traits of four land bird species in Grenada

Alexandra Heathcote[1,2], Paulson Des Brisay[1,3], Christopher De Ruyck[1,4], Paula Grieef[5], and Nicola Koper*[1,6]

Abstract Grenada is a Caribbean island with a volcanic origin and relatively low avian species diversity, which may result in location-specific evolutionary pressures and thus locally adapted populations. Despite this, the morphology of most of its avian species has not been described. The aim of this study was to identify differences in the morphology of resident land birds on Grenada compared with other island and mainland areas. We collected morphological measurements of Bananaquits (*Coereba flaveola*), Black-faced Grassquits (*Melanospiza bicolor*), Lesser Antillean Bullfinches (*Loxigilla noctis*), and Common Ground Doves (*Columbina passerina*) in the field between 2015 and 2017, which we compared with data available from other locations (Venezuela and 23 other Caribbean islands) collated from academic papers and researchers. The morphology of Grenadian populations of our focal species differed from other islands in numerous ways; for example, Common Ground Doves had shorter wings and longer tarsi, and Bananaquits had longer tarsi, than most other populations. These characteristics are consistent with adaptations for increased generalist foraging on Grenada. Grenadian birds are significantly different morphologically from the majority of both insular and mainland conspecifics, emphasizing the need for further research and for the conservation and management of Grenada's avian community.

Keywords ecological release, Grenada, island biogeography, land birds, morphology

Resumen Rasgos morfológicos de cuatro especies de aves terrestres en Granada • Granada es una isla del Caribe de origen volcánico y con una diversidad de especies de aves relativamente baja, lo que puede resultar en presiones evolutivas sitio-específicas y, por tanto, en poblaciones adaptadas localmente. A pesar de ello, no se ha descrito la morfología de la mayoría de sus especies de aves. El objetivo de este estudio fue identificar diferencias morfológicas en las aves terrestres residentes de Granada en comparación con otras áreas insulares y continentales. Recolectamos medidas morfológicas de *Coereba flaveola*, *Melanospiza bicolor*, *Loxigilla noctis* y *Columbina passerina* en el campo, entre 2015 y 2017; las cuales comparamos con los datos disponibles de otras localidades (Venezuela y otras 23 islas del Caribe), obtenidos a partir de artículos académicos e investigadores. La morfología de las poblaciones granadinas de las cuatro especies focales se diferenció de las de otras islas en numerosos aspectos; por ejemplo, individuos de *Columbina passerina* tuvieron alas más cortas y tarsos más largos y los de *Coereba flaveola* tarsos más largos, que la mayoría de las otras poblaciones. Estas características son consistentes con adaptaciones para un forrajeo más generalista en Granada. Las aves de esta isla difieren significativamente desde el punto de vista morfológico a de la mayoría de sus conespecíficos insulares y continentales, lo que subraya la necesidad de seguir investigando y de conservar y manejar la comunidad de aves de Granada.

Palabras clave aves terrestres, biogeografía de islas, Granada, liberación ecológica, morfología

Résumé Caractéristiques morphologiques de quatre espèces d'oiseaux terrestres à la Grenade • La Grenade est une île caribéenne d'origine volcanique dont l'avifaune présente une diversité relativement faible, ce qui peut entraîner des pressions évolutives spécifiques à cette île et donc des adaptations locales des populations. Malgré cela, la morphologie de la plupart de ses espèces d'oiseaux n'a jamais été décrite. Le but de la présente étude était d'identifier des différences morphologiques entre les oiseaux terrestres sédentaires de la Grenade et ceux d'autres zones insulaires ou continentales. De 2015 à 2017, nous avons collecté sur le terrain des mesures morphologiques sur le Sucrier à ventre jaune (*Coereba flaveola*), le Sporophile cici (*Melanospiza bicolor*), le Sporophile rouge-gorge (*Loxigilla noctis*), et la Colombe à queue noire (*Columbina passerina*), que nous avons ensuite comparées aux données pour d'autres lieux (Venezuela et 23 autres îles de la Caraïbe) disponibles dans des articles universitaires et des publications scientifiques. La morphologie des populations grenadiennes des espèces étudiées différait de celle des oiseaux des autres îles à de nombreux égards. Ainsi, comparativement à la plupart des autres populations, les Colombes à queue noire présentaient des ailes plus courtes et des tarses plus longs, et les Sucriers à ventre jaune des tarses plus longs. Ces caractéristiques sont cohérentes avec des adaptations pour une recherche de nourriture plus généraliste sur la Grenade. Les oiseaux de la Grenade sont significativement différents sur le plan morphologique de la plupart de leurs congénères

*Corresponding author: [1]Natural Resources Institute, University of Manitoba, Winnipeg, MB R3T 2M6, Canada; [6]e-mail: nicola.koper@umanitoba.ca. Full list of author information is available at the end of the article.

insulaires et continentaux, ce qui souligne la nécessité de poursuivre les recherches et d'assurer la conservation et la gestion de l'avifaune de l'île.

Mots clés biogéographie insulaire, Grenade, morphologie, oiseaux terrestres, relachement écologique

Morphology of species varies among populations relative to competition, predation risk, and environmental conditions that impose selective pressures on individuals. For example, populations in communities with relatively few species may develop characteristics that allow individuals or species to occupy a wide range of habitats, as interspecific competition and number of potential predator species are lower in communities with fewer species (a phenomenon hereafter called "ecological release"; Van Valen 1973, Scott *et al.* 2003, Hsu *et al.* 2014). As a result, species in low-diversity communities can make use of a broader range of habitat types. A well-documented pattern in the West Indies is that species tend to occupy a greater average number of habitats on species-poor islands than on species-rich islands (Cox and Ricklefs 1977, Terborgh and Faaborg 1980, Wunderle 1985). Among these are species termed "supertramps" (e.g., Diamond 1974), which have evolved varying combinations of behavioral, physiological, or morphological plasticity, which enable them to shift among habitats, diets, foraging behavior, or altitudinal ranges, and contribute to their ability to occupy a diversity of habitats (MacArthur 1968, Diamond 1974, Terborgh *et al.* 1978, Terborgh and Faaborg 1980, Arendt 2006).

Wunderle (1985) noted that the Caribbean island of Grenada has a relatively depauperate land bird community in comparison with Tobago (e.g., 34 land bird species on Grenada versus 68 on Tobago), and that as a result, many of the species found on both islands occupied more habitat types on Grenada than Tobago. This pattern leads to the prediction that bird populations on Grenada might also express morphological changes that typically result from ecological release. For example, this could result in longer tarsi, which allow for a greater range of perch use (e.g., diverse vegetation types) and facilitate walking or hopping on bare ground or tree limbs to enable more generalist foraging behavior (Scott *et al.* 2003). Ecological release could also result in shorter wings, as lower species diversity leads to fewer predator species (Terborgh and Faaborg 1980, Faaborg 1982, Wright *et al.* 2016) and thus less need for sudden or rapid flight. In combination, reduced competition and predation pressure on species-poor islands are predicted to lead to a decrease in wing length relative to the individual's size and a decrease in the wing chord-tarsus ratio.

Species richness on islands is a function of multiple processes, especially extinction and colonization rates (MacArthur and Wilson's 1967 equilibrium model). Larger islands support larger and thus less extinction-prone populations (MacArthur and Wilson 1967), and larger islands typically contain more habitat types, which provide more niche space and thus more species. At the same time, distance from source populations affects the rate at which new species colonize islands (MacArthur and Wilson 1967). However, species richness is also influenced by the geographic origins of islands. Oceanic islands typically have lower species richness, as these islands were never connected to a continent and thus all species found there colonized the islands via over-water dispersal. For example, bird species on the oceanic island of Grenada dispersed there either northward from the South American mainland or southward from the Greater Antilles, which is thought to have acted as a filter for strong, volant colonizers. More recent historical processes have interacted with these evolutionary ones to result in the animal communities found on islands today. Grenada's relatively low avian diversity may also be due, in part, to the widespread impacts of colonial plantation agriculture. An estimated 75% of the total land area of Grenada was used for agricultural production during the 1700s and 1800s, resulting in the near complete loss of dry-lowland and primary wet-tropical forest habitats and their potential accompanying habitat specialists (Groome 1970). Ultimately, biogeographic, ecological, and land management processes interact to explain species richness on islands today. In turn, species richness influences the morphological characteristics that are favored on each island.

In comparison with other Caribbean islands, Grenada has relatively few avian species; for example, of the 23 other islands for which we obtained data for the present study, only Montserrat had a smaller complete avian species count (122 species, including all guilds and both residents and migrants) than Grenada (177 species; Lepage 2018). This low species diversity may favor generalist foraging and use of a wide range of habitats by species on Grenada, as noted by Wunderle (1985). Grenada also has a larger proportion of South American species than the other Lesser Antillean islands (Ricklefs and Bermingham 2008), perhaps resulting in unique interspecific interactions, and thus morphological adaptations, compared with other islands. For example, it is likely that there is resource competition between Yellow-bellied Seedeaters (*Sporophila nigricollis*) and Lesser Antillean Bullfinches (*Loxigilla noctis*), but these species only co-exist on Grenada, the Grenadines, and St. Vincent. The Lesser Antillean Bullfinch may thus have different morphological adaptations in this portion of its range than on islands that lack Yellow-bellied Seedeaters.

A relatively low species diversity on Grenada may also mean that historically, land birds faced relatively few predator species. Although the island is now home to the invasive small Indian mongoose (*Herpestes auropunctatus*), which was introduced around the 1870s (Choudhary *et al.* 2013), historically, its predator diversity was likely low relative to other islands because the number of foraging guilds correlates strongly with total species diversity (Terborgh and Faaborg 1980, Faaborg 1982). This suggests that Grenadian bird populations may have experienced historical ecological release from predation as well as from interspecific competition. However, to the best of our knowledge, no previously published studies have compared the morphology of birds on Grenada to conspecifics elsewhere.

Our aim was to fill this knowledge gap by determining whether four focal species of resident land birds on Grenada are morphologically different from conspecifics elsewhere. We hypothesized that if birds on Grenada face relatively low interspecific competition and have historically faced low predation pressure, then birds on Grenada should show relatively short wings and long tarsi compared with species-rich island and mainland populations.

Table 1. Sample sizes of each of our four focal species measured at four sites on Grenada, 2015–2017. Site numbers correspond to those shown in Fig. 1.

Site	Black-faced Grassquit	Lesser Antillean Bullfinch	Bananaquit	Common Ground Dove
1 Almost Paradise	0	3	14	0
2 Bathway Gardens	26	13	51	0
3 Belmont Estates	20	49	115	12
4 Providence	10	31	92	6

Methods

We used passive mist-netting to capture, band, and measure birds across the island of Grenada. Data were collected during three banding trips to Grenada between November 2015 and February 2017. Of the 19 species caught, we had sufficient data from four species for this study: Black-faced Grassquit (*Melanospiza bicolor*), Lesser Antillean Bullfinch, Bananaquit (*Coereba flaveola*), and Common Ground Dove (*Columbina passerina*; Table 1).

Mist-netting occurred at four sites across the island of Grenada (Table 1, Fig. 1): (1) Almost Paradise (12°13'57.0"N, 61°39'57.5"W), (2) Bathway Gardens (12°12'31.3"N, 61°37'1.9"W), (3) Belmont Estates (12°10'35.7"N, 61°37'42.6"W), and (4) Providence (12°03'18.0"N, 61°40'45.5"W). Sites were representative of habitats typical of the island, and included mixed orchards (e.g., *Citrus* spp., *Persea americana*, *Musa* spp., *Mangifera* spp.), gardens, and cocoa (*Theobroma cacao*) plantations, often interspersed with or adjacent to forest patches (generally secondary forest including some introduced tree crops and bamboo [*Bambuseae* spp.]). The sites were spread out across the island and ranged in elevation from 30 m to 250 m. Birds were banded with a uniquely numbered aluminum band, sexed, and aged using a cycle-based aging system (Wolfe *et al.* 2010). For captured birds, we gathered a suite of standard morphological measurements, including mass and lengths of wing chord and tarsus. We measured

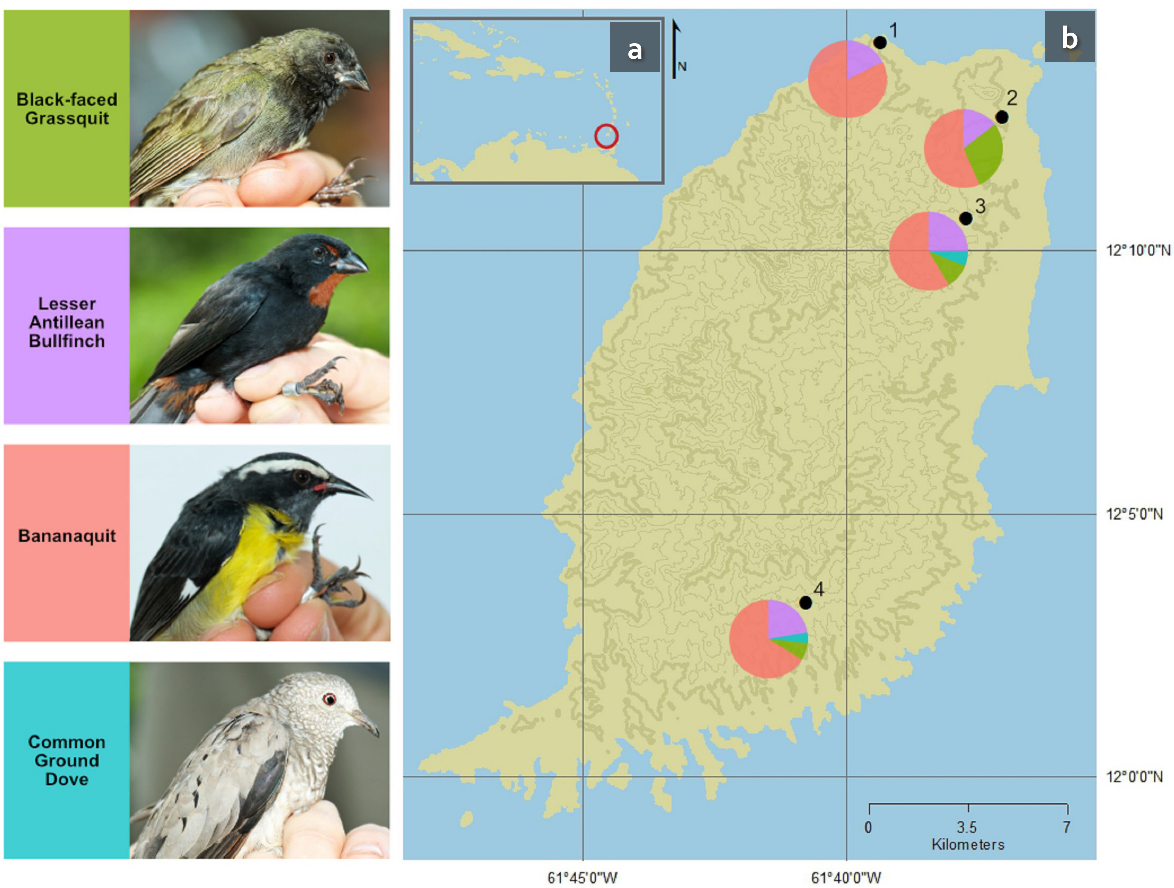

Fig. 1. (a) Island of Grenada situated within the Caribbean. (b) Study sites on Grenada, where we collected data on the morphology of Black-faced Grassquits (green), Lesser Antillean Bullfinch (purple), Bananaquit (pink), and Common Ground Dove (blue), from 2015 to 2017. The proportion of individuals caught at each site is depicted for each site. Site numbers correspond to those described in Table 1.

mass using a digital scale with a precision of 0.1 g while birds were immobile in cloth bags, wing chord length using a wing rule to the nearest millimeter, and minimum tarsus length (interstitial notch of intertarsal joint to the first complete scute of the middle phalange with toes folded down) using a caliper accurate to 0.1 mm.

We used wing chord-mass ratios to assess whether wings were relatively short once we controlled for individual size, and wing chord-tarsus ratios to determine whether wings were relatively short in comparison with tarsus length, as specifically predicted by the ecological release hypothesis. However, it can be challenging to interpret the meaning of ratios in ecology, as the value of ratios may increase either because the numerator increases or the denominator decreases. To account for this and ensure we interpreted ratios correctly, we assessed variation in wing chord and tarsus length separately, as well as within the wing chord-mass ratio (i.e., wing chord relative to individual's size) and wing chord-tarsus ratios. This allowed us to understand whether wing chord-tarsus ratios were relatively low on Grenada in comparison with other islands because the tarsi were longer, wings were shorter, or both, and vice versa. We also explored whether using the cube root of mass as a volumetric ratio in this analysis would produce different results, but statistical results were the same other than the change in scale. Therefore, we only present results based on the mass ratio.

To determine whether resident land birds on Grenada were morphologically different from conspecifics located elsewhere, we collated morphological data for our focal species from across the Caribbean (up to 25 populations including Grenada; Table 2, Appendices 1–4). We gathered data from 23 other islands and Venezuela (Arendt *et al.* 2004, Hayes *et al.* 2004, Lloyd *et al.* 2015, Lentino 2016), which we used as an index of characteristics of mainland populations as it represents the closest continental land mass to these islands. We included both male and female birds, with sex (or "unknown") included as a variable in our models. Where information on age was provided, we used data exclusively from adults (defined as any birds determined to be in a definitive cycle). Sample sizes for each analysis differed, as not all species are found on all islands. Data were available for some species on some islands but not on others, and not all sites collected the same morphological data (see Appendix for model-specific sample sizes).

Numerous observers collected data from Grenada and other islands used in this study, which could lead to variation among islands as a result of different field methods rather than different morphology among populations. However, we suggest that this methodological variation is insufficient to explain the patterns we observed because it is unlikely that differences in research methods varied systematically among all 25 study populations, and because protocols for measuring tarsus, mass, and unflattened wing chord have been well described, precisely to allow for comparisons among different studies (e.g., Pyle 1997, North American Banding Council 2001). Thus, we follow Arendt and Faaborg (1989) and assume that observer bias should not significantly affect our results and conclusions.

We used analysis of variance (ANOVA) to determine if Grenadian avifauna differed morphologically from conspecifics on other Caribbean islands and Venezuela, and present parameter estimates (treatment effects) of the differences between species morphology on Grenada and each comparison population for each morphological variable (Table 3, Appendices 1–4). Response variables included mass, wing chord, tarsus length, wing chord-mass ratio, and wing chord-tarsus length ratio. We used diagnostic plots to ensure assumptions were met. The Pearson correlation between island area and avian species richness of all birds found in each population (estimated using Lepage 2018) was very high ($r = 0.94$), so we assumed risk of interspecific competition was correlated with island size. We could not include elevation as a covariate in our models as elevation varied relatively little among our sites on Grenada (< 300 m) and because we lacked elevation information for other island sample sites, but we note that environmental pressures and thus morphology might also vary with elevation. We conducted all statistical analyses using R 1.1.442 (R Core Team 2008).

Results

Mass

Bananaquits on Grenada were significantly heavier than conspecifics in Venezuela and on large islands, but were generally lighter than individuals on moderately sized islands (Table 3). Black-faced Grassquits were lighter on Grenada than most other islands, and Lesser Antillean Bullfinches were lighter on Grenada than any other island for which we had data (Table 3). Common Ground Doves varied in size among islands, but showed no clear pattern relative to island size (Table 3).

Wing Chord

Bananaquits on Grenada tended to have significantly longer wings than continental or large-island conspecifics, but shorter wings than those on moderately sized islands (Table 3). Wing chords of Black-faced Grassquits and Lesser Antillean Bullfinches on Grenada differed from those on other islands but did not follow a clear pattern relative to island size (Table 3). Common Ground

Table 2. Mean and standard deviation of body mass, wing chord, and tarsus length of Black-faced Grassquit, Lesser Antillean Bullfinch, Bananaquit, and Common Ground Dove on Grenada, 2015–2017.

	Body Mass (g)			Wing Chord (mm)			Tarsus (mm)		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Black-faced Grassquit	56	8.97	1.01	56	49.37	1.50	54	16.02	0.70
Lesser Antillean Bullfinch	95	15.00	1.46	96	64.63	3.08	93	19.11	0.90
Bananaquit	257	9.59	0.84	272	55.26	2.81	261	18.23	0.74
Common Ground Dove	15	35.82	1.93	17	78.85	1.66	18	17.57	0.53

Table 3. Parameter (effect size) estimates for difference between morphological variables on Grenada relative to those from populations on other Caribbean islands and Venezuela for four resident land bird species, ordered by location size (largest to smallest). Parameter estimates are highlighted to aid in identification of patterns: bold italics indicate significant negative parameter estimates (parameter is lower in that population than on Grenada), bold indicates significant positive parameter estimates (parameter is higher in that population than on Grenada), normal type indicates an insignificant parameter estimate ($p > 0.05$). Vertical dotted line indicates size of Grenada relative to other islands (349 km²). M = mass (g), W = wing chord (mm), T = tarsus length (mm). Confidence intervals for parameter estimates, R^2 values for models, and sample sizes can be found in Appendices 1–4; they are not shown here to facilitate comparison. Areas in the first row are areas of Venezuela and of each island.

Site[a]	VE	H	PR	T	GP	DM	LC	C	VC	BQ	AN	NP	AW	KN	MG	BU	S	MS	M	B	LD	BU	I	G
km²	716,445	76,192	9,102	4,768	1,624	750	617	374	344	281	207	179	174	102	171	161	110	102	57	27	21	18	13	4
Black-faced Grassquit																								
M	***−2.23***	**1.84**	**0.65**		**0.68**		−0.09					**1.38**				**1.16**		**1.46**			**1.00**		0.11	0.67
W		**3.47**	−0.36		0.30		***−1.82***					**1.16**				**1.28**		−0.45			**0.67**		−0.84	0.49
W/M		***−0.67***	***−0.45***		***−0.41***		−0.20					***−0.66***				***−0.56***		***−0.82***			***−0.54***		***−0.27***	***−0.40***
T		**2.32**	−0.17		**1.56**		−0.14											0.27			0.81		−0.14	
W/T		***−0.19***	0.00		***−0.30***		−0.12											−0.09			−0.11		−0.08	
Lesser Antillean Bullfinch																								
M					**2.42**	**3.39**	**1.13**		**2.28**		**1.10**			**1.73**		**0.55**		**1.95**			**1.18**		**1.85**	
W					**2.66**	**6.01**	**1.43**		**2.49**		***−0.92***			0.18		***−1.76***		0.45			0.22		**4.25**	
W/M					***−0.46***	***−0.49***	***−0.24***		***−0.46***		***−0.38***			***−0.46***		***−0.30***		***−0.50***			***−0.33***		***−0.23***	
T					**0.71**		−0.32		0.48		−0.21							0.26					***0.50***	
W/T					0.06		**0.11**		0.01		***−0.10***							−0.09					***0.14***	
Bananaquit																								
M	***−0.95***	***−0.69***	**0.26**	**0.7**	**1.12**	**1.33**	**0.36**		**2.13**	−0.40	**0.49**	**1.93**		0.31	**1.74**	**0.19**	−0.13	**0.75**		***−1.35***	***−0.32***	**1.17**	***−0.32***	1.33
W	***−1.43***	−0.51	0.04	**1.89**	**0.78**	**5.41**	**1.74**		**3.82**	1.52	**2.37**	1.34		0.80	**1.07**	**2.05**	−0.76	**1.90**		***−2.95***	0.42	**1.21**	**1.35**	−0.45
W/M	**0.45**	**0.46**	***−0.09***	***−0.21***	***−0.47***	***−0.16***	0.04		***−0.67***	**0.55**	0.02	***−0.8***		−0.05	***−0.73***	**0.14**	0.05	***−0.18***		**0.64**	**0.3**	***−0.47***	**0.4**	***−0.73***
T	***−2.30***	***−0.91***	***−1.16***	***−1.82***	***−0.54***		***−0.42***		**0.82**	**0.79**		**1.48**			−0.32	0.12		−0.08					−0.56	−0.58
W/T	**0.34**	**0.17**	**0.19**	**0.47**	**0.14**		**0.15**		0.09	−0.04		−0.l7			**0.12**	−0.03		**0.10**					**0.18**	0.07
Common Ground Dove																								
M	−0.66	1.40	−0.04		−0.22		**4.83**	**3.87**		***−4.55***			−0.88			***−4.12***			***−6.07***	1.88	−0.70		−1.32	
W		**1.64**	0.83		0.51		**4.31**	**3.52**		***−1.48***			***−2.39***			***−1.71***			***−2.39***	**2.31**	0.65		−0.36	
W/M		−0.04	0.04		−0.01		−0.15	−0.03		**0.28**			0.01			**0.24**			**0.39**	−0.05	0.04		0.06	
T		***−2.52***	***−0.89***		***−2.38***		***−1.00***	***−1.67***		***−1.27***			***−1.20***						***−1.42***				***−2.59***	
W/T		**0.87**	**0.31**		**0.69**		**0.45**	**0.92**		0.24			0.20						**0.16**					

[a]VE = Venezuela, H = Hispaniola, PR = Puerto Rico, T = Trinidad, GP = Guadeloupe, DM = Dominica, LC = St. Lucia, C = Cayo Coco, Cuba, VC = St. Vincent, BQ = Bonaire, AN = Antigua, NP = New Providence, AW = Aruba, KN = St. Kitts, MG = Marie Galante, BU = Barbuda, S = Soana, MS = Montserrat, M = Mona, B = Beata, LD = La Desirade, BU = Bequia, I = Isles des Saintes, G = Guana

Doves on Grenada tended to have shorter wings than ground doves on large islands, but longer wings than those on small islands (Table 3).

Wing Chord-Mass Ratio

Wing chord-mass ratios of Grenadian Bananaquits differed from those on other islands, but not in a predictable pattern (Table 3). Black-faced Grassquits and Lesser Antillean Bullfinches on Grenada had longer wings relative to their mass compared to conspecifics on other islands (Table 3). Conversely, Common Ground Doves on Grenada tended to have shorter wings relative to their mass compared to ground doves on other islands. (Table 3).

Tarsus

Bananaquits had longer tarsi on Grenada than in Venezuela and on islands larger than Grenada, but not relative to Bananaquits on smaller islands (Table 3). Common Ground Doves had longer tarsi on Grenada than on any other island (Table 3). Black-faced Grassquits and Lesser Antillean Bullfinches showed little variation in tarsus length on Grenada compared with conspecifics on other islands (Table 3).

Wing Chord-Tarsus Ratio

Bananaquits and Common Ground Doves had a shorter wing chord relative to tarsus length on Grenada than on most other islands (Table 3). There was little trend in this ratio for Black-faced Grassquits and Lesser Antillean Bullfinches (Table 3).

Discussion

Our study confirms that the morphologies of our four focal species on Grenada differ significantly from other insular and continental conspecifics, likely due to a combination of mechanisms, including evolutionary and geospatial isolation, natural selection pressures unique to this community, and founder effects that continue to shape the island's unique avifauna (Lomolino 2005, McClain *et al.* 2013). The habitat and island distributions of Bananaquits and Common Ground Doves are also characteristic of "supertramp" or "near supertramp" species, suggesting that morphological plasticity may be a key factor enabling them to inhabit multiple habitat types and islands throughout the West Indies (MacArthur 1968, Diamond 1974, Terborgh *et al.* 1978, Terborgh and Faaborg 1980, Arendt 2006). It seems likely that other species that are widespread on Grenada may also exhibit unique morphological characteristics if compared with populations elsewhere.

Some of the species we studied are quite different from other populations. For example, Grenadian Common Ground Doves have the longest tarsi and Lesser Antillean Bullfinches have the smallest mass of any of the populations we compared. Lesser Antillean Bullfinches and Black-faced Grassquits on Grenada were morphologically different from conspecifics on all other islands in the context of at least one parameter, and Bananaquit and Common Ground Dove populations differed from most other populations we studied. Despite Grenada's proximity and similar geologic history and environment to St. Vincent, Lesser Antillean Bullfinches and Bananaquits—the two species for which we had data from both islands—were significantly smaller and lighter on Grenada.

The degree to which geographic variation has been studied varies among our focal species, but based on the available literature and our analyses, Grenada's land birds clearly contribute significantly to the range-wide phenotypic diversity of these species. Bananaquits on Grenada and across the Grenadines (*C. f. aterrima*) constitute one of 41 recognized subspecies, and together with populations on St. Vincent, form a genetically distinct group (Bellemain *et al.* 2008). *C. f. aterrima* represent an atypical phenotype based on the high proportion of melanistic individuals, as well as some superficial differences noted in bill morphology (Hilty and Christie 2020). Given the considerable variability throughout its range, it is unsurprising that we found Bananaquits on Grenada to be morphologically distinct; however, it is noteworthy that some morphological differences we document here may represent a response to ecological release on Grenada.

Lesser Antillean Bullfinches on Grenada (*L. n. grenadensis*) similarly constitute one of eight subspecies distributed through the Lesser Antilles (Rising and Jaramillo 2020). The genetic diversity among the subspecies has not been documented, but it is worth noting that the recently split Barbados Bullfinch (*Loxigilla barbadensis*) was classified as a distinct species primarily due to geographic separation and the absence of the definitive male plumage seen on other islands (Buckley and Buckley 2004). Grenada is the southernmost island inhabited by the Lesser Antillean Bullfinch within the archipelago and is also relatively isolated, although the Grenadines may facilitate movement between St. Vincent and Grenada. The morphological dissimilarities and lighter mass we observed in Grenada suggests that *L. n. grenadensis* is relatively distinct compared with the other subspecies.

Grenada's Black-faced Grassquits (*M. b. omissa*) are part of a subspecies (one of eight recognized subspecies) ranging from Puerto Rico, through the Lesser Antilles, to Venezuela and Columbia (Rising 2020). *M. b. omissa* is a relatively small subspecies, yet individuals from Grenada were even smaller than individuals of other populations of this subspecies. We recommend genetic analyses of this species across its range to evaluate whether further delineations among subspecies might be appropriate.

The subspecies of Common Ground Dove on Grenada (*C. p. antillarum*), which is distributed from St. Lucia to Barbados to Grenada, is one of up to 19 subspecies currently recognized (Bowman 2020). Patterns driving the variations in morphology and plumage among these subspecies are not well understood, but Caribbean populations are generally described as smaller than continental populations in the USA and Mexico (Bowman 2020). While these North American continental populations were outside the scope of our analyses, our results indicate that within the Caribbean, *C. p. antillarum* may be one of the larger subspecies.

Our results suggest that ecological release from competition and predation pressure may have contributed to some unique morphological characteristics of Bananaquits and Common Ground Doves on Grenada. Ecological release from interspecific competition may result in numerous morphological changes, including longer tarsi, which are better adapted for using a variety of perching sites, thus enabling more generalist foraging strategies (Grant 1971). Decreased competition and predation pressure can also favor energy savings through decreased wing or pectoral muscle size (Wright and Steadman 2012, Wright *et al.* 2016). Bananaquits tended to show these patterns regarding their tarsus length, relative to Venezuela and islands larger than Grenada, whereas Common Ground Doves on Grenada showed the predicted longitudinal patterns in wing and tarsus length. The morphological characteristics expressed are consistent with more generalized foraging and habitat use, consistent with Wunderle's (1985) observation that in comparison with Tobago, Grenadian avifauna used a wider variety of habitats.

Other understudied and unknown mechanisms likely also contribute to the observed variation in morphology. The R^2 values for our models ranged from 0.12 to 0.63 (Appendices 1–4), leaving significant explanatory space for the selective impacts of variables we did not include, such as abundance and diversity of non-avian competitors, parasites, food resources, seasonality, disturbance rates, founder effects, elevation, and other factors. We also note that variation in mass among locations may reflect phenotypic plasticity, dietary differences, effects of parasites or pathogens, or size of food items rather than heritable morphological changes. Rainfall and temperature gradients are among the primary determinants of tropical forest structure and diversity (Medina and Klinge 1983, Givnish 1999). If Grenada has fewer food resources than other islands due to temperature and rainfall patterns, this could also contribute to smaller body sizes in some species.

It is clear that our four focal species are morphologically distinct from conspecifics found on other island and mainland populations. Relatively low avian species diversity and a unique community composition that includes species from both South American and Greater Antillean origins (Ricklefs and Bermingham 2008) may have led to selection pressures that contributed to these distinct characteristics. The Grenadian populations of our four focal species therefore contribute to morphological, and perhaps, genetic diversity of these species. Further research on Grenada's unique avian community may demonstrate other characteristics that distinguish its bird populations from other island or continental populations. Worldwide conservation and management efforts should consider not just species endemism but also the evolutionarily significant contributions of distinct populations among the numerous and diverse avian communities spread across the Caribbean region, including the island of Grenada.

Acknowledgments

We thank the following researchers for generously sharing their morphological data with us: Floyd Hayes, Miguel Lentino, Chris Rimmer, Kent MacFarlane, John D. Lloyd, Stewart White, Bob Wilkerson, and The Institute for Bird Populations. We would like to thank George Wallace for directing us to a publicly accessible database compiled from years of research, which was invaluable. We thank all volunteer banders and assistants, including Chelsea Enslow, Christoph Ng, Laura Burns, Ezra Campbell, Nicholas Bergen, Marie-Ève Cyr, Hannah Carey, and Alice Davey. We thank BirdsCaribbean for their advice and input, and the Grenada Forestry Department and Mr. Anthony Jeremiah for facilitating our research. We thank Belmont Estate, St. George's University, St. Patrick's Environmental and Community Tourism Organization, and Almost Paradise cottages for in-kind support and collaboration. We also sincerely thank David Steadman, Wayne Arendt, and an anonymous reviewer for their thoughtful comments, which significantly improved the quality of our paper. Funding statement: Funding was provided by the Natural Sciences and Engineering Research Council of Canada Discovery Grant to NK (RGPIN 4038/2017) and the Clayton H. Riddell Endowment Fund of the University of Manitoba. No funders had input into the content of the manuscript, and no funders required input into the manuscript prior to its submission or publication. Ethics statement: This research was conducted in compliance with the Forestry Department, Government of Grenada regulations, and with the approval of the University of Manitoba Animal Care Committee (AC11116). Author contributions: AH conducted field work, analyzed data, prepared tables and figures, and wrote text; PDB and PG conducted field work, formulated questions, interpreted results, collected data, and developed local banding protocols; CDR interpreted results and wrote text; NK conducted field work, formulated questions, interpreted results, collected data, wrote text, prepared tables, and supervised the research. Data Availability: Upon publication, data will be made publicly available through the University of Manitoba's data repository, mspace.lib.umanitoba.ca.

Title Page Illustration

Pair of Common Ground Doves (*Columbina passerina*) at Belmont Estate, Grenada, in 2015. Photograph by Paulson Des Brisay.

Author Information

[1]Natural Resources Institute, University of Manitoba, Winnipeg, MB R3T 2M6, Canada; [2]e-mail: alheathcote@outlook.com; [3]e-mail: pauldesbrisay@gmail.com; [4]e-mail:ccdr_sc@hotmail.com; [5]Oak Hammock Marsh Interpretive Centre, Ducks Unlimited Canada, Stonewall, MB R0C 2Z0, Canada; e-mail: p_grieef@ducks.ca; [6]e-mail: nicola.koper@umanitoba.ca

Literature Cited

Arendt, W.J. 2006. Adaptations of an avian supertramp: distribution, ecology, and life history of the Pearly-Eyed Thrasher *Margarops fuscatus*. USDA Forest Service General Technical Report no. IITF-GTR-27. International Institute of Tropical Forestry, San Juan, PR.

Arendt, W.J., and J. Faaborg. 1989. Sources of variation in measurements of birds in Puerto Rican dry forest. Journal of Field Ornithology 60:1–11.

Arendt, W.J., J. Faaborg, G.E. Wallace, and O.H. Garrido. 2004. Biometrics of birds throughout the greater Caribbean Basin. Proceedings of the Western Foundation of Vertebrate Zoology 8:1–33.

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

Bowman, R. 2020. Common Ground Dove (*Columbina passerina*), version 1.0. *In* Birds of the World (A.F. Poole and F.B. Gill, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.cogdov.01.

Buckley, P.A., and F.G. Buckley. 2004. Rapid speciation by a Lesser Antillean endemic, Barbados Bullfinch *Loxigilla barbadensis*.

Bulletin of the British Ornithologists' Club 124:108–123.

Choudhary, S., U. Zieger, R.N. Sharma, A. Chikweto, K.P. Tiwari, L.R. Ferreira, S. Oliveira, L.J. Barkley, S.K. Verma, O.C.H. Kwok, C. Su, and J.P. Dubey. 2013. Isolation and RFLP genotyping of *Toxoplasma gondii* from the mongoose (*Herpestes auropunctatus*) in Grenada, West Indies. Journal of Zoo and Wildlife Medicine 44:1127–1130.

Cox, G.W., and R.E. Ricklefs. 1977. Species diversity and ecological release in Caribbean land bird faunas. Oikos 28:113–122.

Diamond, J.M. 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. Science 184:803–806.

Faaborg, J. 1982. Trophic and size structure of West Indian bird communities. Proceedings of the National Academy of Sciences 79:1563–1567.

Givnish, T.J. 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology 87:193–210.

Grant, P.R. 1971. Variation in the tarsus length of birds in island and mainland regions. Evolution 25:599–614.

Groome, J.R. 1970. A Natural History of the Island of Grenada, West Indies. Caribbean Printers, San Juan, Trinidad.

Hayes, F.E., S.A. White, R.P. ffrench, and S. Bondar. 2004. Geographic variation in body mass of the Bananaquit (*Coereba flaveola*) in the Trinidad and Tobago archipelago. Journal of Caribbean Ornithology 17:18–22.

Hilty, S., and D.A. Christie. 2020. Bananaquit (*Coereba flaveola*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.banana.01.

Hsu, Y.C., P.J. Shaner, C.I. Chang, L. Ke, and S.J. Kao. 2014. Trophic niche width increases with bill-size variation in a generalist passerine: a test of the niche variation hypothesis. Journal of Animal Ecology 83:450–459.

Lentino, M. 2016. Manual de Anillado e Identificación de las aves del Paso Portachuelo, Parque Nacional Henri Pittier, Venezuela (Sociedad Conservacionista Audubon de Venezuela, ed.). 2nd edn. Sociedad Conservacionista Audubon de Venezuela, Caracas, Venezuela.

Lepage, D. 2018. Avibase: the world bird database. avibase.bsc-eoc.org.

Lloyd, J., K. McFarland, C. Rimmer, and Vermont Center for Ecostudies. 2015. Sierra de Bahoruco Constant-effort Mist Netting. Knowledge Network for Biocomplexity Data Repository. doi:10.5063/f1m906k7.

Lomolino, M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

MacArthur, R.H. 1968. The theory of the niche. Pp. 159–176 *in* Population Biology and Evolution (R.C. Lewontin, ed.). Syracuse University Press, Syracuse, NY.

MacArthur, R.H., and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

McClain, C.R., P.A.P. Durst, A.G. Boyer, and C.D. Francis. 2013. Unravelling the determinants of insular body size shifts. Biology Letters 9:20120989.

Medina, E., and H. Klinge. 1983. Productivity of tropical forests and tropical woodlands. Pp. 281–303 *in* Physiological Plant Ecology IV (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.). Springer, Berlin, Heidelberg, Germany.

North American Banding Council. 2001. North American banders' study guide. Technical report. North American Banding Council, Point Reyes Station, CA.

Pyle, P. 1997. Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

R Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Ricklefs, R., and E. Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. Philosophical Transactions: Biological Sciences 363:2393–2413.

Rising, J.D. 2020. Black-faced Grassquit (*Melanospiza bicolor*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.bkfgra.01.

Rising, J.D., and A. Jaramillo. 2020. Lesser Antillean Bullfinch (*Loxigilla noctis*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.leabul1.01.

Scott, S.N., S.M. Clegg, S.P. Blomberg, J. Kikkawa, and I.P.F. Owens. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. Evolution 57:2147–2156.

Terborgh, J.W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. American Naturalist 116:178–195.

Terborgh, J.W., J. Faaborg, and H.J. Brockmann. 1978. Island colonization by Lesser Antillean birds. Auk 95:59–72.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1:1–30.

Wolfe, J.D., T.B. Ryder, and P. Pyle. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. Journal of Field Ornithology 81:186–194.

Wright, N.A., and D.W. Steadman. 2012. Insular avian adaptations on two Neotropical continental islands. Journal of Biogeography 39:1891–1899.

Wright, N.A., D.W. Steadman, and C.C. Witt. 2016. Predictable evolution toward flightlessness in volant island birds. Proceedings of the National Academy of Sciences 113:4765–4770.

Wunderle, J.M. 1985. An ecological comparison of the avifaunas of Grenada and Tobago, West Indies. Wilson Bulletin 97:356–365.

Cite this article as:

Heathcote, A., P. Des Brisay, C. De Ruyck, P. Grieef, and N. Koper. 2021. Morphological traits of four land bird species in Grenada. Journal of Caribbean Ornithology 34:41–52. https://doi.org/10.55431/ jco.2021.34.41-52

Appendix 1. Parameter estimates (Estimates), confidence intervals (CI), and sample sizes (*n*) for comparison between Black-faced Grassquit morphology on Grenada with populations in Venezuela and on other Caribbean islands. Sex (male, female or unknown) was included as a variable in each model.

	Mass (g)			Wing Chord (mm)			Wing Chord-Mass Ratio			Tarsus (mm)			Wing Chord-Tarsus Ratio		
	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*
Barbuda	1.16	0.82 – 1.50	29	1.28	0.68 – 1.88	29	−0.56	−0.74 – −0.39	29						
Guadeloupe	0.68	0.22 – 1.13	13	0.30	0.50 – 1.11	13	−0.41	−0.65 – −0.18	13	1.56	0.69 – 2.43	6	−0.30	−0.47– −0.13	6
Guana	0.67	−0.02 – 1.36	5	0.49	−0.72 – 1.70	5	−0.40	−0.75 – −0.04	5						
Hispaniola	1.84	1.57 – 2.11	65	3.47	3.00 – 3.94	69	−0.67	−0.81 – −0.53	65	2.32	1.89 – 2.75	31	−0.19	−0.27 – −0.10	31
Isles des Saintes	0.11	−0.17 – 0.40	55	−0.84	−1.35 – −0.33	53	−0.27	−0.42 – −0.12	53	−0.13	−0.60 – 0.30	38	−0.08	−0.18 – 0.01	36
La Desirade	1.00	0.70 – 1.30	43	0.67	0.14 – 1.21	43	−0.54	−0.70 – −0.39	43						
Montserrat	1.46	0.83 – 2.10	6	−0.45	−1.56 – 0.67	6	−0.82	−1.14 – −0.49	6	0.27	−0.59 – 1.12	6	−0.09	−0.25 – 0.08	6
New Providence	1.38	0.82 – 1.94	8	1.16	0.17 – 2.15	8	−0.66	−0.95 – −0.38	8						
Puerto Rico	0.65	0.42 – 0.88	153	−0.36	−0.76 – 0.05	153	−0.45	−0.57 – −0.33	152	−0.17	−0.52 – 0.17	88	0.00	−0.07 – 0.07	88
St. Lucia	−0.09	−0.58 – 0.40	11	−1.82	−2.68 – −0.96	11	−0.20	−0.45 – 0.05	11	−0.14	−0.90 – 0.62	8	−0.12	−0.27 – 0.02	8
Venezuela	2.23	1.56 – 2.89	6												
Sex– Male	0.51	0.36 – 0.66		1.69	1.42 – 1.96		−0.10	−0.17 – −0.02		0.26	−0.05 – 0.56		0.02	−0.04 – 0.08	
Sex–Unknown	−0.05	−0.32 – 0.21		0.16	−0.29 – 0.62		0.06	−0.08 – 0.19		−0.27	−0.83 – 0.30		0.04	−0.07 – 0.15	
Total *n*			450			446			438			237			233
Grenada *n*			56			56			53			53			52
R^2 / adjusted R^2	0.445 / 0.429			0.621 / 0.610			0.243 / 0.221			0.437 / 0.415			0.158 / 0.124		

Appendix 2. Parameter estimates (Estimates), confidence intervals (CI), and sample sizes (*n*) for comparison between Lesser Antillean Bullfinch morphology on Grenada with populations in Venezuela and on other Caribbean islands. Sex (male, female or unknown) was included as a variable in each model.

	Mass (g)			Wing Chord (mm)			Wing Chord-Mass Ratio			Tarsus (mm)			Wing Chord-Tarsus Ratio		
	Estimates	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***
Antigua	1.10	0.69 – 1.52	61	−0.92	−1.69 – −0.15	61	−0.38	−0.49 – −0.28	61	−0.21	−0.69 – 0.27	22	−0.10	−0.19 – −0.00	22
Barbuda	0.55	0.15 – 0.95	69	−1.76	−2.50 – −1.03	71	−0.30	−0.40 – −0.19	69						
Dominica	3.39	3.07 – 3.71	237	6.01	5.42 – 6.60	242	−0.49	−0.58 – −0.41	235						
Guadeloupe	2.42	1.88 – 2.96	27	2.66	1.66 – 3.66	27	−0.46	−0.60 – −0.33	27	0.71	0.01 – 1.40	9	0.06	−0.08 – 0.19	9
Isles des Saintes	1.85	1.37 – 2.34	36	4.25	3.39 – 5.11	43	−0.23	−0.36 – −0.11	36	0.50	0.02 – 0.97	23	0.14	0.05 – 0.24	23
La Desirade	1.18	0.43 – 1.92	12	0.22	−1.17 – 1.61	12	−0.33	−0.52 – −0.14	12						
Montserrat	1.95	1.45 – 2.46	32	0.45	−0.48 – 1.38	33	−0.50	−0.63 – −0.37	32	0.26	−0.26 – 0.78	18	−0.09	−0.19 – 0.01	18
St. Kitts	1.73	1.19 – 2.27	27	0.18	−0.81 – 1.17	28	−0.46	−0.60 – −0.32	27						
St. Lucia	1.13	0.82 – 1.45	284	1.43	0.85 – 2.01	285	−0.24	−0.32 – −0.16	283	−0.32	−0.67 – 0.03	57	0.11	0.04 – 0.18	56
St. Vincent	2.28	1.65 – 2.91	18	2.49	1.32 – 3.66	18	−0.46	−0.62 – −0.30	18	0.48	−0.07 – 1.04	15	0.01	−0.10 – 0.12	15
Sex–Male	0.78	0.61 – 0.94		3.61	3.30 – 3.91		0.03	−0.01 – 0.08		0.49	0.21 – 0.77		0.10	0.04 – 0.15	
Sex–Unknown	−0.01	−0.61 – 0.59		−0.80	−1.92 – 0.31		−0.02	−0.18 – 0.13		−0.07	−0.17 – 0.04		−0.07	−0.17 – 0.04	
Total *n*			898			916			893			237			235
Grenada *n*			95			96			93			93			92
R^2 / adjusted R^2	0.507 / 0.500			0.679 / 0.674			0.197 / 0.186			0.116 / 0.085			0.200 / 0.172		

Appendix 3. Parameter estimates (Estimates), confidence intervals (CI), and sample sizes (*n*) for comparison between Bananaquit morphology on Grenada with populations in Venezuela and on other Caribbean islands. Sex (male, female or unknown) was included as a variable in each model.

	Mass (g)			Wing Chord (mm)			Wing Chord-Mass Ratio			Tarsus (mm)			Wing Chord-Tarsus Ratio		
	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*	Estimates	CI	*n*
Antigua	0.49	0.09 – 0.88	19	2.37	1.22 – 3.53	19	0.02	−0.21 – 0.24	19						
Barbuda	0.19	0.01 – 0.38	129	2.05	1.52 – 2.59	129	0.14	0.03 – 0.24	129	0.12	−0.86 – 1.11	5	−0.03	−0.26 – 0.20	5
Beata	−1.35	−1.69 – −1.02	27	−2.95	−3.93 – −1.96	27	0.64	0.45 – 0.83	27						
Bequia	1.17	0.87 – 1.47	35	1.22	0.35 – 2.08	35	−0.47	−0.64 – −0.30	35						
Bonaire	−0.40	−0.96 – 0.16	9	1.52	−0.11 – 3.16	9	0.55	0.24 – 0.87	9	0.79	0.05 – 1.53	9	−0.04	−0.22 – 0.13	9
Dominica	1.33	1.09 – 1.57	62	5.41	4.72 – 6.11	62	−0.16	−0.29 – −0.02	62						
Guadeloupe	1.12	0.92 – 1.33	90	0.78	0.17 – 1.39	89	−0.47	−0.59 – −0.35	89	−0.54	−1.05 – −0.03	20	0.14	0.02 – 0.26	20
Guana	1.33	0.84 – 1.81	12	−0.45	−1.88 – 0.98	12	−0.72	−0.99 – −0.44	12	−0.58	−1.23 – 0.07	12	0.07	−0.08 – 0.22	12
Hispaniola	−0.69	−0.87 – −0.50	110	−0.51	−1.01 – 0.04	110	0.46	0.35 – 0.57	110	−0.91	−1.23 – −0.60	58	0.17	0.10 – 0.25	58
Isles des Saintes	−0.24	−0.46 – −0.02	75	1.35	0.72 – 2.00	75	0.40	0.27 – 0.52	75	−0.56	−1.18 – 0.07	13	0.18	0.04 – 0.33	13
La Desirade	−0.32	−0.52 – −0.11	98	0.42	−0.17 – 1.01	98	0.30	0.19 – 0.42	98						
Marie Galante	1.74	1.52 – 1.97	72	1.07	0.41 – 1.73	72	−0.73	−0.86 – −0.61	72	−0.32	−0.76 – 0.12	28	0.12	0.01 – 0.22	28
Montserrat	0.75	0.55 – 0.95	106	1.90	1.32 – 2.48	103	−0.18	−0.29 – −0.07	103	−0.08	−0.42 – 0.25	54	0.10	0.02 – 0.18	54
New Providence	1.93	1.37 – 2.49	9	1.34	−0.39 – 3.07	8	−0.09	−1.13 – −0.46	8	1.48	0.70 – 2.27	8	−0.17	−0.35 – 0.02	8
Puerto Rico	0.26	0.14 – 0.37	1,386	0.04	−0.30 – 0.39	1,205	−0.09	−0.15 – −0.02	1,198	−1.16	−1.32 – −1.00	860	0.19	0.16 – 0.23	857
Saona	−0.13	−0.69 – 0.43	9	−0.76	−2.40 – 0.87	9	0.04	−0.27 – 0.36	9						
St. Kitts	0.31	−0.03 – 0.64	27	0.80	−0.17 – 1.77	28	−0.05	−0.24 – 0.14	27						
St. Lucia	0.36	0.14 – 0.59	74	1.74	1.11 – 2.37	81	0.04	−0.08 – 0.17	74	−0.42	−0.81 – −0.02	36	0.15	0.06 – 0.25	36
St. Vincent	2.13	1.90 – 2.36	65	3.87	3.18 – 4.55	65	−0.67	−0.80 – −0.53	65	0.82	0.41 – 1.23	33	0.09	−0.01 – 0.18	33
Trinidad	0.70	0.58 – 0.82	982	1.89	1.55 – 2.22	1,017	−0.21	−0.28 – −0.15	978	−1.82	−1.97 – −1.67	1,025	0.47	0.43 – 0.50	1,011
Venezuela	−0.95	−1.12 – −0.79	171	−1.43	−1.90 – −0.96	183	0.45	0.36 – 0.55	170	−2.30	−2.55 – −2.04	110	0.34	0.29 – 0.40	110
Sex–Male	0.89	0.82 – 0.95		3.82	3.62 – 4.03		−0.12	−0.16 – −0.08		0.57	0.44 – 0.70		0.11	0.08 – 0.14	
Sex–Unknown	0.61	0.52 – 0.70		1.77	1.49 – 2.05		−0.10	−0.16 – −0.05		0.46	0.31 – 0.61		0.02	−0.02 – 0.05	
Total *n*			3,824			3,729			3,621			2,532			2,512
Grenada *n*			257			272			252			261			258
R^2 / adjusted R^2	0.399 / 0.395			0.402 / 0.398			0.238 / 0.233			0.283 / 0.278			0.291 / 0.287		

Appendix 4. Parameter estimates (Estimates), confidence intervals (CI), and sample sizes (*n*) for comparison between Common Ground Dove morphology on Grenada with populations in Venezuela and on other Caribbean islands. Sex (male, female or unknown) was included as a variable in each model.

	Mass (g)			Wing Chord (mm)			Wing Chord-Mass Ratio			Tarsus (mm)			Wing Chord-Tarsus Ratio		
	Estimates	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***	**Estimates**	**CI**	***n***
Aruba	−0.88	−3.34 – 1.56	12	−2.38	−3.95 – −0.82	11	0.01	−0.15 – 0.18	11	−1.20	−1.89 – −0.51	11	0.2	−0.01 – 0.41	11
Barbuda	−4.12	−5.96 – −2.29	58	−1.71	−2.82 – −0.60	61	0.24	0.12 – 0.36	58						
Beata	1.88	−0.52 – 4.28	13	2.31	0.82 – 3.81	13	−0.05	−0.21 – 0.11	13						
Bonaire	−4.55	−6.92 – −2.19	14	−1.48	−2.94 – −0.01	14	0.28	0.13 – 0.44	14	−1.27	−1.92 – −0.62	14	0.24	0.04 – 0.43	14
Cuba	3.87	2.02 – 5.73	52	3.52	2.52 – 4.52	500	−0.03	−0.15 – 0.09	50	−1.67	−2.38 – −0.96	10	0.92	0.70 – 1.13	10
Hispaniola	1.40	−0.45 – 3.24	91	1.64	0.53 – 2.74	91	−0.04	−0.16 – 0.08	90	−2.52	−3.26 – −1.79	9	0.87	0.64 – 1.10	8
Guadeloupe	−0.22	−2.58 – 2.14	16	0.51	−0.91 – 1.94	17	−0.01	−0.17 – 0.15	15	−2.38	−3.15 – −1.60	9	0.69	0.45 – 0.92	9
Isles des Saintes	−1.32	−3.37 – 0.74	34	−0.36	−1.59 – 0.87	37	0.06	−0.07 – 0.20	34	−2.59	−3.43 – −1.74	7	0.58	0.33 – 0.84	7
La Desirade	−0.70	−3.54 – 2.14	8	0.65	−1.05 – 2.34	9	0.04	−0.14 – 0.23	8						
Mona	−6.07	−7.84 – −4.31	301	−2.39	−3.44 – −1.34	307	0.39	0.27 – 0.50	296	−1.42	−1.91 – −0.92	190	0.16	0.01 – 0.32	190
Puerto Rico	−0.04	−1.74 – 1.66	186	0.83	−0.20 – 1.86	169	0.04	−0.07 – 0.15	166	−0.89	−1.35 – −0.44	127	0.31	0.17 – 0.44	126
St. Lucia	4.83	2.05 – 7.61	8	4.31	3.13 – 5.50	46				−1.00	−1.56 – −0.45	43	0.45	0.28 – 0.62	43
Venezuela	−0.66	−3.19 – 1.86	12												
Sex–Male	1.51	0.82 – 2.20		1.28	0.98 – 1.58		−0.05	−0.09 – −0.00	0.04	0.04	−0.23 – 0.30		0.11	0.03 – 0.19	
Sex–Unknown	−0.09	−0.89 – 0.71		0.37	−0.04 – 0.77		0.05	−0.00 – 0.11	0.71	0.71	0.39 – 1.02		−0.05	−0.14 – 0.05	
Total *n*			820			1290			778			438			435
Grenada *n*			15			17			15			18			17
R^2 / adjusted R^2	0.566 / 0.558			0.621 / 0.617			0.484 / 0.474			0.202 / 0.181			0.350 / 0.333		